The Families and Genera of Vascular Plants

Edited by K. Kubitzki

Volume VIII
Flowering Plants
Eudicots
Asterales

J.W. Kadereit and C. Jeffrey (Eds.)

Springer

THE FAMILIES AND GENERA OF VASCULAR PLANTS

Edited by K. Kubitzki

Volumes published in this series

Volume I Pteridophytes and Gymnosperms
Edited by K.U. Kramer and P.S. Green (1990)
Date of publication: 28.9.1990

Volume II Flowering Plants. Dicotyledons. Magnoliid, Hamamelid and Caryophyllid Families
Edited by K. Kubitzki, J.G. Rohwer, and V. Bittrich (1993)
Date of publication: 28.7.1993

Volume III Flowering Plants. Monocotyledons: Lilianae (except Orchidaceae)
Edited by K. Kubitzki (1998)
Date of publication: 27.8.1998

Volume IV Flowering Plants. Monocotyledons: Alismatanae and Commelinanae (except Gramineae)
Edited by K. Kubitzki (1998)
Date of publication: 27.8.1998

Volume V Flowering Plants. Dicotyledons: Malvales, Capparales and Non-betalain Caryophyllales
Edited by K. Kubitzki and C. Bayer (2003)
Date of publication: 12.9.2002

Volume VI Flowering Plants. Dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales
Edited by K. Kubitzki (2004)
Date of publication: 21.1.2004

Volume VII Flowering Plants. Dicotyledons: Lamiales (except Acanthaceae including Avicenniaceae)
Edited by J.W. Kadereit (2004)
Date of publication: 13.4.2004

Volume VIII Flowering Plants. Eudicots: Asterales
Edited by J.W. Kadereit and C. Jeffrey (2007)

The Families and Genera of Vascular Plants

Edited by K. Kubitzki

VIII *Flowering Plants · Eudicots*

Asterales

Volume Editors:
J.W. Kadereit and C. Jeffrey

With 131 Figures

Springer

Professor Dr. Klaus Kubitzki
Universität Hamburg
Biozentrum Klein-Flottbek und Botanischer Garten
Ohnhorststraße 18
22609 Hamburg
Germany

Professor Dr. Joachim W. Kadereit
Johannes Gutenberg-Universität Mainz
Institut für Spezielle Botanik und Botanischer Garten
55099 Mainz
Germany

Charles Jeffrey
flat 91, block 5, pr. Morisa Toreza 102
194017 St. Petersburg
Russia

Library of Congress Control Number: 2006924681

ISBN-10 3-540-31050-9 Springer Berlin Heidelberg New York
ISBN-13 978-3-540-31050-1 Springer Berlin Heidelberg New York

This work is subject to copyright. All rights are reserved, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilm or in any other way, and storage in data banks. Duplication of this publication or parts thereof is permitted only under the provisions of the German Copyright Law of September 9, 1965, in its current version, and permissions for use must always be obtained from Springer-Verlag. Violations are liable for prosecution under the German Copyright Law.

Springer is a part of Springer Science+Business Media
springer.com

© Springer-Verlag Berlin Heidelberg 2007

The use of general descriptive names, registered names, trademarks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

Cover design: WMXDesign, Heidelberg, Germany
Typesetting and production: LE-TEX Jelonek, Schmidt & Vöckler GbR, Leipzig, Germany

Printed on acid-free paper 31/3150/YL – 5 4 3 2 1 0

Preface

It is a great pleasure to introduce this volume of the "Families and Genera of Vascular Plants", containing the treatments of Compositae and all other families of the Asterales. In these treatments, the immense amount of evidence recently accrued has been taken into account to present an up-to-date picture of the systematics of these groups. This fully meets the aim of this series to distil and organise knowledge.

Compositae have always been in the focus of plant systematists, and here more than elsewhere it is obvious how much we owe to our predecessors, of which Cassini and Bentham may be singled out. Note, for instance, that as early as 1816 Calyceraceae and Campanulaceae were suggested to be the closest relatives of Compositae, a concept very similar to our present understanding. Although most of what is known about interrelationships among organisms is based on comparative morphology, we have also learned that morphology alone is unable to resolve all problems in systematics; for example, the placement of *Roussea* or the recognition of the sister-group relationship between Barnadesioideae and the other Compositae would never have been possible without molecular data.

I am highly indebted to the editors of this volume, Joachim W. Kadereit and Charles Jeffrey, for their Herculean effort in bringing the book to a successful end, and this despite several obstacles. Moreover, deep appreciation is due to those who have provided the scholarly and meticulous treatments assembled in this volume. Kåre Bremer is acknowledged for invaluable advice on the selection of potential authors given during early stages of this work. We are grateful to Linda Klöckner for the editing of the figures, and to Sabine von Mering, Miriam Repplinger and Christian Uhink for their assistance in the assembly of the final manuscript of Compositae. Our thanks also go to Monique Delafontaine who so ably copy-edited the book. Special thanks are due to the copyright holders of published illustrations who so generously permitted the inclusion of their valuable material in the present volume.

Finally, it is a pleasure to acknowledge the agreeable collaboration with the staff of Springer-Verlag who so willingly responded to all requests raised in connection with planning and production.

Hamburg, August 2006 K. Kubitzki

Contents

Asterales: Introduction and Conspectus

J.W. Kadereit 1

Alseuosmiaceae J. Kårehed 7

Argophyllaceae J. Kårehed 13

Calyceraceae F.H. Hellwig 19

Campanulaceae T.G. Lammers 26

Carpodetaceae M.H.G. Gustafsson 57

Compositae A.A. Anderberg, B.G. Baldwin, R.G. Bayer, J. Breitwieser, C. Jeffrey, M.O. Dillon, P. Eldenäs, V. Funk, N. Garcia-Jacas, D.J.N. Hind, P.O. Karis, H.W. Lack, G. Nesom, B. Nordenstam, Ch. Oberprieler, J.L. Panero, C. Puttock, H. Robinson, T.F. Stuessy, A. Susanna, E. Urtubey, R. Vogt, J. Ward and L.E. Watson 61

- **Introduction with Key to Tribes** C. Jeffrey 61
- **I. Tribe Barnadesieae** T.F. Stuessy and E. Urtubey 87
- **II. Tribe Mutisieae** D.J.N. Hind 90
- **III. Tribe Cardueae** A. Susanna and N. Garcia-Jacas 123
- **Carduoid Genera of Uncertain Placement** C. Jeffrey 146
- **IV. Tribe Gymnarrheneae** C. Jeffrey 147
- **V. Tribe Moquinieae** H. Robinson 148
- **VI. Tribe Vernonieae** H. Robinson 149
- **VII. Tribe Liabeae** V.A. Funk, H. Robinson and M.O. Dillon 175
- **VIII. Tribe Cichorieae** H.W. Lack 180
- **IX. Tribe Gundelieae** C. Jeffrey 199
- **X. Tribe Arctotideae** P.O. Karis 200
- **XI. Tribe Corymbieae** B. Nordenstam 207
- **XII. Tribe Senecioneae** B. Nordenstam 208
- **XIII. Tribe Calenduleae** B. Nordenstam 241

XIV. Tribe Gnaphalieae	R.J. Bayer, I. Breitwieser, J. Ward and C. Puttock	246
XV. Tribe Astereae	G. Nesom and H. Robinson	284
XVI. Tribe Anthemideae	Ch. Oberprieler, R. Vogt and L.E. Watson	342
XVII. Tribe Inuleae	A.A. Anderberg and P. Eldenäs	374
Key to the Tribes of the Heliantheae Alliance	J.L. Panero	391
XVIII. Tribe Athroismeae	J.L. Panero	395
XIX. Tribe Helenieae	J.L. Panero	400
XX. Tribe Coreopsideae	J.L. Panero	406
XXI. Tribe Neurolaeneae	J.L. Panero	417
XXII. Tribe Tageteae	J.L. Panero	420
XXIII. Tribe Chaenactideae	J.L. Panero	431
XXIV. Tribe Bahieae	J.L. Panero	433
XXV. Tribe Polymnieae	J.L. Panero	439
XXVI. Tribe Heliantheae	J.L. Panero	440
XXVII. Tribe Millerieae	J.L. Panero	477
XXVIII. Tribe Madieae	B.G. Baldwin and J.L. Panero	492
XXIX. Tribe Perityleae	J.L. Panero	507
XXX. Tribe Eupatorieae	D.J.N. Hind and H. Robinson	510
Asteroid Genus of Uncertain Placement	C. Jeffrey	574
Selected Bibliography to Compositae		576
Goodeniaceae	R.C. Carolin	589
Menyanthaceae	G. Kadereit	599
Pentaphragmataceae	T.G. Lammers	605
Phellinaceae	G. Barriera, V. Savolainen and R. Spichiger	608
Rousseaceae	J.A. Koontz, J. Lundberg and D.E. Soltis	611
Stylidiaceae	R.C. Carolin	614
Index to Scientific Names		621

List of Contributors

Anderberg, A.A.	Department of Phanerogamic Botany, Swedish Museum of Natural History, P.O. Box 50007, 10405 Stockholm, Sweden
Baldwin, B.G.	Jepson Herbarium & Dept. of Integrative Biology, 1001 Valley Life Sciences Bldg. #2465, University of California, Berkeley, CA 94720-2465, USA
Barriera, G.	Conservatoire et Jardin botaniques de la Ville de Genève, 1 ch. de l'Impératrice, Case postale 60, 1292 Chambésy, Switzerland
Bayer, R.J.	CSIRO – Plant Industry, Australian National Herbarium, GPO Box 1600, Canberra, ACT 2601, Australia
Breitwieser, I.	Biosystematics of New Zealand Plants, Manaaki Whenua – Landcare Research, P.O. Box 69, Lincoln 8152, New Zealand
Carolin, R.C.	Pulman's Cottage, 30 Pulman Street, Berry, N.S.W. 2535, Australia
Dillon, M.O.	Department of Botany, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605-2496, USA
Eldenäs, P.	Molecular Systematics Laboratory, Swedish Museum of Natural History, P.O. Box 50007, 10405 Stockholm, Sweden
Funk, V.A.	US National Herbarium, Department of Botany, Smithsonian Institution, MRC 166, Washington, DC 20560, USA
Garcia-Jacas, N.	Botanic Institute of Barcelona, Passeig del Migdia s.n., Parc de Montjuic, 08038 Barcelona, Spain
Gustafsson, M.H.G.	Institute of Biological Sciences, University of Aarhus, Ny Munkegade, Building 540, 8000 Århus C, Denmark
Hellwig, F.H.	Institut für Spezielle Botanik mit Botanischem Garten und Herbarium Haussknecht, Friedrich-Schiller-Universität Jena, Philosophenweg 16, 07743 Jena, Germany
Hind, D.J.N.	The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK
Jeffrey, C.	Flat 91, Block 5, pr. Morisa Toreza 102, 194017 St. Petersburg, Russia
Kadereit, G.	Institut für Spezielle Botanik und Botanischer Garten, Johannes Gutenberg-Universität, 55099 Mainz, Germany
Kadereit, J.W.	Institut für Spezielle Botanik und Botanischer Garten, Johannes Gutenberg-Universität, 55099 Mainz, Germany

Kårehed, J.	Department of Systematic Botany, Evolutionary Biology Centre, Norbyvägen 18D, Uppsala University, 75236 Uppsala, Sweden
Karis, P.O.	Department of Botany, Stockholm University, 10691 Stockholm, Sweden
Koontz, J.A.	Department of Biology, Augustana College, 639 38th Street, Rock Island, IL 61201, USA
Lack, H.W.	Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin, Königin-Luise-Str. 6–8, 14195 Berlin, Germany
Lammers, T.G.	Department of Biology and Microbiology, University of Wisconsin Oshkosh, Oshkosh, WI 54901, USA
Lundberg, J.	Department of Systematic Botany, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, 75236 Uppsala, Sweden
Nesom, G.	Botanical Research Institute of Texas, 509 Pecan Street, Fort Worth, TX 76102-4060, USA
Nordenstam, B.	Department of Phanerogamic Botany, Swedish Museum of Natural History, P.O. Box 50007, 10405 Stockholm, Sweden
Oberprieler, Ch.	Institute of Botany, University of Regensburg, Universitätsstr. 31, 93040 Regensburg, Germany
Panero, J.L.	Section of Integrative Biology, 1 University Station C0930, The University of Texas, Austin, TX 78712, USA
Puttock, C.	Bishop Museum, Department of Botany, 1525 Bernice Street, Honolulu, HI 96817-2704, USA
Robinson, H.	US National Herbarium, Department of Botany, Smithsonian Institution, MRC 166, Washington, DC 20560, USA
Savolainen, V.	Molecular Systematics Section, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, London, UK
Soltis, D.E.	Department of Botany, University of Florida, Gainesville, FL 32611, USA
Spichiger, R.	Conservatoire et Jardin botaniques de la Ville de Genève, 1 ch. de l'Impératrice, Case postale 60, 1292 Chambésy, Switzerland
Stuessy, T.F.	Department of Systematic and Evolutionary Botany, Institute of Botany, University of Vienna, Rennweg 14, 1030 Vienna, Austria
Susanna, A.	Botanic Institute of Barcelona, Passeig del Migdia s.n., Parc de Montjuic, 08038 Barcelona, Spain
Urtubey, E.	Division Plantas Vasculares, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s.n., La Plata, Argentina
Vogt, R.	Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin, Königin-Luise-Str. 6–8, 14191 Berlin, Germany

Ward, J.	School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand
Watson, L.E.	Department of Botany, Miami University, Oxford, OH 45056, USA

Asterales: Introduction and Conspectus

J.W. Kadereit

Asterales (incl. Campanulales of many authors), with Alseuosmiaceae, Argophyllaceae, Compositae (= Asteraceae), Calyceraceae, Campanulaceae (incl. Cyphiaceae, Lobeliaceae, Nemacladaceae), Carpodetaceae (included in Rousseaceae by APG II 2003), Goodeniaceae, Menyanthaceae, Pentaphragmataceae, Phellinaceae, Rousseaceae and Stylidiaceae (incl. Donatiaceae), contain about 26,300 species in c. 1,720 genera. The large majority of species and genera belong to Compositae and Campanulaceae. The order is well supported in all major molecular phylogenetic analyses (APG II 2003), and is part of the Euasterids II or Campanulids sensu Bremer et al. (2002).

Phylogenetic structure within Campanulids (also containing Apiales, Aquifoliales, Dipsacales and several families of uncertain ordinal placement; APG II 2003) is not sufficiently well resolved to identify the sister group of Asterales. It appears to be evident, however, that of all representatives of the Campanulids, Aquifoliales are least closely related to Asterales (Savolainen et al. 2000a, b; Soltis et al. 2000; Albach et al. 2001; Bremer et al. 2001, 2002).

Although several of the constituent families of the order had been recognized to be closely related to one another long ago (for discussion, see Lammers 1992), the recognition of the relationship of others to Asterales (Lundberg and Bremer 2003) is the result mainly (but not only) of recent molecular phylogenetic work. This applies particularly to Alseuosmiaceae (Backlund and Bremer 1997; Gustafsson and Bremer 1997; Kårehed et al. 1999; Cronquist 1981: Rosales; Thorne 1992: Saxifragales; Takhtajan 1997: Hydrangeales), Argophyllaceae (Kapil and Bhatnagar 1992; Gustafsson et al. 1996; Kårehed et al. 1999; Olmstead et al. 2000; Cronquist 1981: Rosales; Takhtajan 1997: Hydrangeales), Carpodetaceae (Gustafsson and Bremer 1997; Lundberg 2001; Takhtajan 1997: Hydrangeales), Phellinaceae (Backlund and Bremer 1997; Gustafsson and Bremer 1997; Kårehed et al. 1999; Cronquist 1981: Celastrales; Thorne 1992: Theales; Takhtajan 1997: Icacinales) and Rousseaceae (Lundberg 2001; Takhtajan 1997: Brexiales), and partly also to Menyanthaceae (Downie and Palmer 1992; Olmstead et al. 1992; Cronquist 1981: Solanales; Thorne 1992: Campanulales; Takhtajan 1997: Menyanthales) and Stylidiaceae (Cronquist 1981: Campanulales; Thorne 1992: Saxifragales; Takhtajan 1997: Stylidiales). Further sampling may identify other taxa from distant corners of the traditional angiosperm system which should be included in the order. On the other hand, Sphenocleaceae, as a family often associated with Asterales/Campanulales (e.g. Lammers 1992), do not belong here but rather in Solanales (APG II 2003).

Members of Asterales are mostly herbaceous and in most cases have alternate leaves without stipules. Flowers are very rarely solitary but mostly aggregated in sometimes axillary but more commonly terminal inflorescences which are capitulate and involucrate in most of the closely related Goodeniaceae, Calyceraceae and Compositae, and also in some Campanulaceae. The mostly zoophilous flowers typically are tetracyclic and pentamerous but variation of organ number per whorl is known from several families. Flower symmetry is actinomorphic or zygomorphic with bilabiate or unilabiate flowers – actinomorphic and zygomorphic flowers are both found in the capitula of many Compositae – and resupination of flowers is known from Campanulaceae-Lobelioideae and some Stylidiaceae. The sepals are commonly fused (not in Alseuosmiaceae and some Menyanthaceae), and in Compositae the calyx commonly is replaced by a pappus of variable structure assisting in fruit dispersal. Petals are free only in Carpodetaceae, Phellinaceae and some Argophyllaceae, Pentaphragmataceae and Stylidiaceae (*Donatia*). The androecium normally is isomerous with calyx and corolla, and the stamens alternate with the petals. Reduction of stamen number is largely limited to Stylidiaceae. Stamens can be inserted on the corolla or not, and

anthers are mostly tetrasporangiate, basifixed and commonly introrse. Pollen grains are mostly tricolporate, but both colpate or porate pollen grains with an increased number of apertures are known. *Carpodetus* (Carpodetaceae) and *Lechenaultia* (Goodeniaceae) are unusual in having pollen tetrads. The pluri- to unilocular ovary is commonly inferior (or semi-inferior) but superior ovaries are found in some Carpodetaceae, some Goodeniaceae, some Campanulaceae, and in Menyanthaceae, Phellinaceae and Rousseaceae. Ovules usually are anatropous (hemi- to campylotropous in Phellinaceae), unitegmic and tenuinucellate and, where known, endosperm formation is mostly cellular, but nuclear in some Compositae. Fruits are commonly capsules or achenes (= cypselae), rarely berries or drupes. Inulin is found in several families (Calyceraceae, Campanulaceae, Compositae, Goodeniaceae, Menyanthaceae and Stylidiaceae), and iridoids or seco-iridoids are common, but absent from Campanulaceae and Compositae, and apparently also from Alseuosmiaceae, Phellinaceae and Rousseaceae.

A tight integration of stamens and style is found in several families. In most Stylidiaceae, the two stamens are fused with the style to form a pressure-sensitive gynostemium. In Calyceraceae, Campanulaceae, Compositae and Goodeniaceae, the interaction of style and either fused or free anthers results in various forms of secondary pollen presentation (Carolin 1960; Leins and Erbar 1990, 2003; Erbar and Leins 1995). Erbar and Leins (1995) classified these as (1) brushing or pump mechanism in Compositae and Campanulaceae-Lobelioideae (pollen is removed from an anther tube by the elongating style which is hairy or not), (2) deposition (or rarely brushing) mechanism in Campanulaceae-Campanuloideae (pollen from free anthers is deposited on hairs on the outside of the style, these hairs can invaginate or not), (3) cup and cup/brushing mechanism in Goodeniaceae (pollen is deposited in a cup-like outgrowth below the stigma, the indusium; in addition to this cup, hairs can be present on the style) and (4) deposition mechanism of Goodeniaceae (deposition of pollen grains on top of the style). Detailed summaries of character distribution in Asterales have been provided by Lammers (1992; excl. Alseuosmiaceae, Argophyllaceae, Carpodetaceae, Phellinaceae, Rousseaceae) and, covering the entire order, particularly by Lundberg and Bremer (2003).

In spite of the very high molecular support for the order, it is difficult to identify synapomorphies. Following Lundberg and Bremer (2003), valvate corolla aestivation and the absence of apotracheal wood parenchyma can be identified as synapomorphic. Both these characters, however, are not unique for the order and are variable within it. Previously identified synapomorphies, such as secondary pollen presentation (which is present in the form of different mechanisms and is likely to have arisen more than once; see above) and the presence of inulin, are characteristic only of subgroups of Asterales.

Relationships within the order are clear and well supported in some parts but not in others (Lundberg and Bremer 2003). One well-supported clade identified in several analyses (Chase et al. 1993; Morgan and Soltis 1993; Cosner et al. 1994; Gustafsson and Bremer 1995; Olmstead et al. 2000; Soltis et al. 2000; Bremer et al. 2001; Lundberg and Bremer 2003) consists of Menyanthaceae, Goodeniaceae, Calyceraceae and Compositae (MGCA clade; Fig. 1). This clade is characterized by the presence of petal lateral veins (Gustafsson 1995), the loss of micropylar endosperm haustoria (Cosner et al. 1994), and a thick and multilayered (> 10 cells) integument (Inoue and Tobe 1999). Within this clade, the sister-group relationship between Calyceraceae and Compositae is supported by several potential synapomorphies in wood anatomical (Carlquist and De Vore 1998), inflorescence, flower and fruit morphological and anatomical (Hansen 1992; Gustafsson 1995), and pollen (Hansen 1992) characters. Goodeniaceae are sister to these two families, and the clade consisting of Goodeniaceae/Calyceraceae/Compositae may be supported by pollen grains with a prominent layer with branched columellae and secondary pollen presentation involving fused anthers (Lundberg and Bremer 2003). Lundberg and Bremer (2003) suggested that Stylidiaceae incl. Donatiaceae, a strongly supported clade in their study, are sister to the MGCA clade. A close relationship between Donatiaceae and Stylidiaceae, however, was not found in other analyses (Albach et al. 2001; Bremer et al. 2002), and neither Donatiaceae nor Stylidiaceae were sister to the MGCA clade in these two analyses. Instead, Stylidiaceae were sister to Campanulaceae (Albach et al. 2001; Bremer et al. 2002), and Donatiaceae sister to Alseuosmiaceae/Argophyllaceae/Phellinaceae (Bremer et al. 2002) or to all families except Stylidiaceae/Campanulaceae (Albach et al. 2001). A second possible clade of the order consists of Alseuosmiaceae, Phellinaceae and Argophyllaceae (APA clade; Fig. 1), where

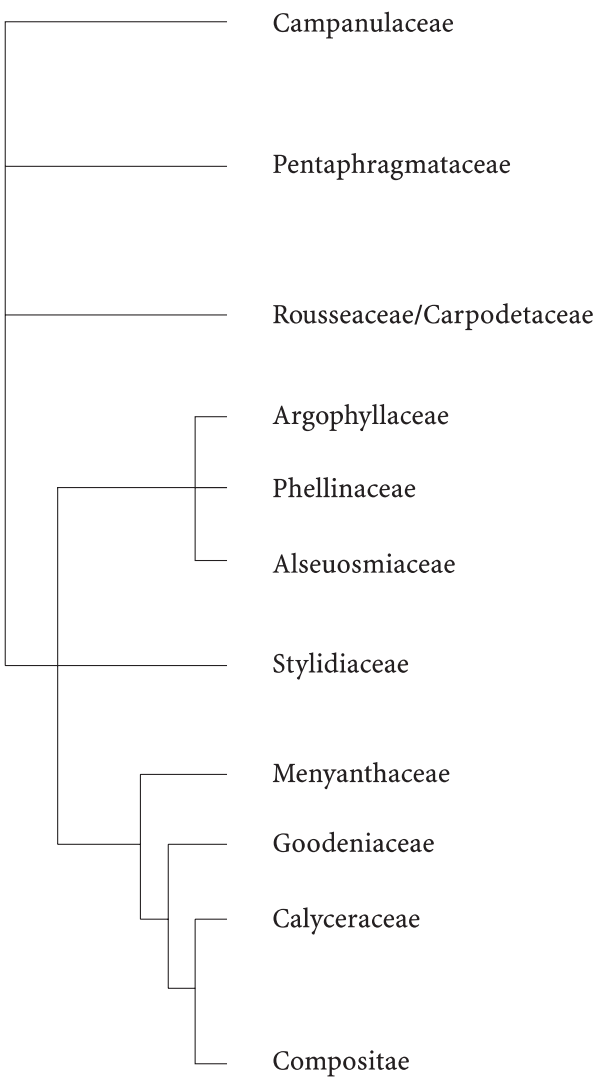

Fig. 1. A phylogenetic hypothesis for the families of Asterales. (Modified from Lundberg and Bremer 2003)

the latter two families probably are sister to each other (Lundberg and Bremer 2003). This clade had already been identified in earlier analyses (Gustafsson et al. 1996; Backlund and Bremer 1997; Gustafsson and Bremer 1997; Källersjö et al. 1998; Kårehed et al. 1999; Savolainen et al. 2000b; Lundberg 2001) and may be supported by pollen being 3-celled at anthesis and the presence of ellagic acid (not known in all groups; Lundberg and Bremer 2003). Stevens (2001 onwards) further records the presence of subepidermal cork as well as serrate and gland-toothed leaf blades as possible synapomorphies. In the analysis of Lundberg and Bremer (2003), the APA clade is sister to the Stylidiaceae/MGCA clade. All three groups together constitute the "Core Asterales" of these authors and are characterized by having a non-intrusive placenta (Lundberg and Bremer 2003). Sister to this in the analysis by Lundberg and Bremer (2003) is a clade consisting of Rousseaceae (incl. Carpodetaceae), Pentaphragmataceae and Campanulaceae. This clade was resolved as a basal grade (incl. Stylidiaceae as sister to Campanulaceae) by Bremer et al. (2002). The close relationship between *Roussea* and Carpodetaceae is well supported (Savolainen et al. 2000b; Lundberg 2001; Bremer et al. 2002). The possible sister-group relationship between Pentaphragmataceae and Campanulaceae found by Lundberg and Bremer (2003) but not in several other analyses (Cosner et al. 1994; Jansen and Kim 1996; Backlund and Bremer 1997; Olmstead et al. 2000; Savolainen et al. 2000b) may be supported (Lundberg and Bremer 2003) by the presence of a free hypanthium and petal veins which form a dense reticulum (Gustafsson 1995).

In summary, relationships within the order should be viewed (Fig. 1), as by Stevens (2001 onwards), as a polytomy consisting of four lineages. These are (1) Campanulaceae, (2) Pentaphragmataceae, (3) Rousseaceae/Carpodetaceae and (4) a trichotomy of the APA clade, Stylidiaceae (incl. Donatiaceae), and the MGCA clade.

Although the earliest fossils of the order are of Oligocene (c. 29 Ma B.P.) age (Magallón et al. 1999), consideration of phylogenetic relationships and molecular evidence led to the conclusion that the order must have originated c. 100 Ma B.P. in the Cretaceous (Bremer and Gustafsson 1997; Wikström et al. 2001). Stem node and crown node ages of 112 and 93 Ma B.P. respectively were recently estimated by Bremer et al. (2004). The notion of a Cretaceous origin of Asterales certainly requires revision of the observation by Magallón and Sanderson (2001) that Asterales have the highest diversification rate of all angiosperm orders. This inference was based on the assumption of an Oligocene age of Asterales.

Apart from the cosmopolitan Campanulaceae, Compositae and Menyanthaceae, of which Compositae have been postulated to have originated in South America (Bremer 1994) and Campanulaceae which have centres of diversity in southern Africa and Andean South America but also in Eurasia between the Mediterranean region and the Himalayas, all other families of the order have an almost exclusively southern hemispherical distribution, mostly in Australasia and partly in South America. Based on an analysis of ancestral

areas, Bremer and Gustafsson (1997) concluded that the order originated in Australasia. Although this interpretation was based on a rather terminal position of the cosmopolitan Campanulaceae in the phylogeny of the order these authors used, the placement of this family in a basal polytomy (see above) probably will not change the outcome of an ancestral area analysis. Many species of the small families of the order are found in either temperate forest or more open, often humid to wet habitats.

By far the largest amount of generic and species diversity is found in Campanulaceae and Compositae. Interestingly, these are the two major families of the order lacking iridoids or secoiridoids. In Compositae, the biosynthetic pathway producing iridoids has been blocked and diverted to the production of sesquiterpene lactones (Zdero and Bohlmann 1990), and the diversification of secondary compounds in the family has been held responsible for its great success in terms of species diversity (Cronquist 1977; Lammers 1992). In Campanulaceae, iridoids are replaced by polysterols (particularly Campanuloideae), acetylenes and/or alkaloids (particularly Lobelioideae) which, however, have a biosynthetic origin unrelated to the iridoid pathway (Lammers 1992). It has not been claimed that the success of Campanulaceae is related to their biochemical diversification.

Conspectus of families as treated in this volume

1. Stamens as many as corolla lobes
   2. Corolla lobes with distinct wings or appendages
      3. Corolla zygomorphic; herbs, shrubs or scramblers with zygomorphic flowers, fruit a drupe, nut or capsule; 11/400, southern hemisphere, mainly Australia **Goodeniaceae**
      3. Corolla actinomorphic
         4. Plants herbaceous, from wet habitats; flowers actinomorphic, petal lobes often fimbriate or crested; fruit a capsule or rarely a berry; 5/c. 60, subcosmopolitan **Menyanthaceae**
         4. Plants woody
            5. Sepals free, fruit a berry; shrubs or subshrubs, leaf axils with tufts of hairs; flowers actinomorphic; 4/9, Australia, New Zealand, New Guinea and New Caledonia **Alseuosmiaceae**
            5. Sepals fused, fruit a capsule or drupe; shrubs or small trees with actinomorphic flowers; 2/c. 20, Australia, New Zealand, Lord Howe and Rapa Islands, New Caledonia **Argophyllaceae**
   2. Corolla lobes without distinct wings or appendages
      6. Petals free
         7. Fruit a drupe; shrubs or small trees with actinomorphic flowers; 1/11, New Caledonia **Phellinaceae**
         7. Fruit a berry or capsule; shrubs or trees with actinomorphic flowers; 3/5, Australia, New Zealand, New Guinea and Solomon Islands **Carpodetaceae**
      6. Petals fused, sometimes corolla tube short
         8. Ovary unilocular with one ovule, inflorescence capitulate
            9. Calyx mostly modified, anthers connate, ovule insertion apical; 1,621/c. 23,300, cosmopolitan **Compositae**
            9. Calyx not modified, anthers free, ovule insertion basal; annual or perennial herbs with actinomorphic flowers in involucrate head, fruit an achene; 4/c. 60, South America and Falkland Islands **Calyceraceae**
         8. Ovary two- to multilocular, rarely unilocular with only one ovule, then inflorescence not capitulate
            10. Climbing shrub with opposite or verticillate leaves; flowers actinomorphic, fruit a berry; 1 sp., Mauritius **Rousseaceae**
            10. Not as above
               11. Shrub, flowers inclined, corolla tube short, stamens sessile, fruit a 2-locular capsule; 1 sp., New Caledonia ***Platyspermation*** **(Alseuosmiaceae)**
               11. Not as above
                  12. Leaf bases asymmetrical, plants without milky latex; mostly fleshy perennial herbs with asymmetrical leaf blades and actinomorphic flowers, fruit a berry; 1/c. 30, SE Asia **Pentaphragmataceae**
                  12. Leaf bases not asymmetrical, plants with milky latex; herbs, lianas, rosette plants, subshrubs, shrubs, treelets or trees with actinomorphic or zygomorphic flowers, fruit a capsule or berry; 84/c. 2,400, cosmopolitan **Campanulaceae**

1. Stamens fewer than corolla lobes
   13. Corolla lobes free, gynoecium with separate stylodia; perennial herbs with solitary, actinomorphic flowers and capsular fruits; 1/2, South America, Tasmania and New Zealand ***Donatia*** **(Stylidiaceae)**
   13. Corolla lobes fused, gynoecium with one style; herbs or subshrubs with mostly zygomorphic flowers, filaments and style fused into a column in most genera, fruits capsular; 6/c. 160, southern hemisphere, mainly Australia **Stylidiaceae**

References

Albach, D.C., Soltis, P.S., Soltis, D.E., Olmstead, R.G. 2001. Phylogenetic analysis of Asterids based on sequences of four genes. Ann. Missouri Bot. Gard. 88: 163–212.

APG II 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436.

Backlund, A., Bremer, B. 1997. Phylogeny of the Asteridae s.str. based on *rbc*L sequences, with particular reference to the Dipsacales. Pl. Syst. Evol. 207: 225–254.

Bremer, K. 1994. Asteraceae. Cladistics and classification. Portland, OR: Timber Press.

Bremer, K., Gustafsson, M.H.G. 1997. East Gondwanan ancestry of the sunflower alliance of families. Proc. Natl Acad. Sci. U.S.A. 94: 9188–9190.

Bremer, K., Backlund, A., Sennblad, B., Swenson, U., Andreasen, K., Hjertson, M., Lundberg, J., Backlund, M., Bremer, B. 2001. A phylogenetic analysis of 100+ genera and 50+ families of euasterids based on morphological and molecular data with notes on possible higher level morphological synapomorphies. Pl. Syst. Evol. 229: 137–169.

Bremer, B., Bremer, K., Heidari, N., Olmstead, R.G., Anderberg, A.A., Källersjö, M., Barkhordarian, E. 2002. Phylogenetics of asterids based on 3 coding and 3 noncoding chloroplast DNA markers and the utility of noncoding DNA at higher taxonomic levels. Mol. Phylog. Evol. 24: 274–301.

Bremer, K., Friis, E.-M., Bremer, B. 2004. Molecular phylogenetic dating of Asterid flowering plants shows early Cretaceous diversification. Syst. Biol. 53: 496–505.

Carlquist, S., De Vore, M.L. 1998. Wood anatomy of Calyceraceae with reference to ecology, habit, and systematic relationships. Aliso 17: 63–76.

Carolin, R.C. 1960. The structures involved in the presentation of pollen to visiting insects in the order Campanulales. Proc. Linn. Soc. New South Wales 85: 197–207.

Chase, M.W. et al. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rcb*L. Ann. Missouri Bot. Gard. 80: 528–580.

Cosner, M.E., Jansen, R.K., Lammers, T.G. 1994. Phylogenetic relationships in the Campanulales based on *rbc*L sequences. Pl. Syst. Evol. 190: 79–95.

Cronquist, A. 1977. The Compositae revisited. Brittonia 29: 137–153.

Cronquist, A. 1981. An integrated system of classification of flowering plants. New York: Columbia University Press.

Downie, S.R., Palmer, J.D. 1992. Restriction site mapping of the chloroplast DNA inverted repeat: a molecular phylogeny of the Asteridae. Ann. Missouri Bot. Gard. 79: 266–283.

Erbar, C., Leins, P. 1995. Portioned pollen release and the syndromes of secondary pollen presentation in the Campanulales-Asterales-complex. Flora 190: 323–338.

Gustafsson, M.H.G. 1995. Petal venation in Asterales and related orders. Bot. J. Linn. Soc. 118: 1–18.

Gustafsson, M.H.G., Bremer, K. 1995. Morphology and phylogenetic interrelationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and related families (Asterales). Amer. J. Bot. 82: 250–265.

Gustafsson, M.H.G., Bremer, K. 1997. The circumscription and systematic position of Carpodetaceae. Austral. J. Bot. 10: 855–862.

Gustafsson, M.H.G., Backlund, A., Bremer, B. 1996. Phylogeny of the Asterales sensu lato based on *rbc*L sequences with particular reference to the Goodeniaceae. Pl. Syst. Evol. 199: 217–242.

Hansen, H.V. 1992. Studies in the Calyceraceae with a discussion of its relationships to Compositae. Nordic J. Bot. 12: 63–75.

Inoue, N., Tobe, H. 1999. Integumentary studies in Menyanthaceae (Campanulales sensu lato). Acta Phytotax. Geobot. 50: 75–79.

Jansen, R.K., Kim, K.-J. 1996. Implications of chloroplast DNA data for the classification and phylogeny of the Asteraceae. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994, vol. 1. Royal Botanic Gardens, Kew, pp. 317–339.

Källersjö, M., Farris, J.S., Chase, M.W., Bremer, B., Fay, M.F., Humphries, C.J., Petersen, G., Seberg, O., Bremer, K. 1998. Simultaneous parsimony jackknife analysis of 2538 *rbc*L DNA sequences reveals support for major clades of green plants, land plants, seed plants and flowering plants. Pl. Syst. Evol. 213: 259–287.

Kapil, R.N., Bhatnagar, A.K. 1992. Embryology and systematic position of *Corokia* A. Cunn. In: Proceedings of the 11th International Symposium on Embryology and Seed Reproduction, Leningrad, 1990. St. Petersburg: Nauka, pp. 246–247.

Kårehed, J., Lundberg, J., Bremer, B., Bremer, K. 1999. Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae. Syst. Bot. 24: 660–682.

Lammers, T.G. 1992. Circumscription and phylogeny of the Campanulales. Ann. Missouri Bot. Gard. 79: 388–413.

Leins, P., Erbar, C. 1990. On the mechanisms of secondary pollen presentation in the Campanulales-Asterales-complex. Bot. Acta 103: 87–92.

Leins, P., Erbar, C. 2003. The pollen box in Cyphiaceae (Campanulales). Intl J. Pl. Sci. 164 suppl. 5: S321–S328.

Lundberg, J. 2001. The asteralean affinity of the Mauritian *Roussea* (Roussaceae). Bot. J. Linn. Soc. 137: 267–276.

Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–578.

Magallón, S., Sanderson, M.J. 2001. Absolute diversification rates in angiosperm clades. Evolution 55: 1762–1780.

Magallón, S., Crane, P.R., Herendeen, P.S. 1999. Phylogenetic pattern, diversity and diversification of eudicots. Ann. Missouri Bot. Gard. 86: 297–372.

Morgan, D.R., Soltis, D.E. 1993. Phylogenetic relationships among members of Saxifragaceae *sensu lato* based on *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 631–660.

Olmstead, R.G., Michaels, H.J., Scott, K.M., Palmer, J.D. 1992. Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbc*L. Ann. Missouri Bot. Gard. 79: 249–265.

Olmstead, R.G., Kim, K.-J., Jansen, R.K., Wagstaff, S.J. 2000. The phylogeny of the Asteridae sensu lato based on chloroplast *ndh*F gene sequences. Mol. Phylog. Evol. 16: 96–112.

Savolainen, V., Chase, M.W., Hoot, S.B., Morton, C.M., Soltis, D.E., Bayer, C., Fay, M.F., De Bruijn, A.Y., Sullivan, S., Qiu, Y.-L. 2000a. Phylogenetics of flowering plants based on combined analysis of plastid *atp*B and *rbc*L gene sequences. Syst. Biol. 49: 306–362.

Savolainen, V., Fay, M.F., Albach, D.C., Backlund, A., van der Bank, M., Cameron, K.M., Johnson, S.A., Lledo, M.D., Pintaud, J.-C., Powell, M., Sheahan, M.C., Soltis, D.E., Soltis, P.S., Weston, P., Whitten, W.M., Wurdack, K.J., Chase, M.W. 2000b. Phylogeny of the eudicots: a nearly complete familial analysis based on *rbc*L gene sequences. Kew Bull. 55: 357–309.

Soltis, D.E., Soltis, P.S., Chase, M.W., Mort, M.E., Albach, D.C., Zanis, M., Savolainen, V., Hahn, W.H., Hoot, S.B., Fay, M.F., Axtell, M., Swensen, S.M., Prince, L.M., Kress, W.J., Nixon, K.C., Farris, J.S. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbc*L and *atp*B sequences. Bot. J. Linn. Soc. 133: 381–461.

Stevens, P.F. 2001 onwards. Angiosperm Phylogeny website, version 5, May 2004 (and more or less continuously updated since). http://www.mobot.org/MOBOT/research/APweb/

Takhtajan, A. 1997. Diversity and classification of flowering plants. New York: Columbia University Press.

Thorne, R.F. 1992. An updated phylogenetic classification of flowering plants. Aliso 13: 365–389.

Wikström, N., Savolainen, V., Chase, M.W. 2001. Evolution of the angiosperms: calibrating the family tree. Proc. Roy. Soc. London ser. B 268: 2211–2220.

Zdero, C., Bohlmann, F. 1990. Systematics and evolution within the Compositae, seen with the eyes of a chemist. Pl. Syst. Evol. 171: 1–14.

Alseuosmiaceae

Alseuosmiaceae Airy Shaw, Kew Bull. 18: 249 (1965).

Platyspermatiaceae Doweld (2001).

J. Kårehed

Shrubs, sometimes creeping or epiphytic subshrubs. Leaves alternate, sub-opposite or in pseudo-whorls, simple, entire or serrate, estipulate. Multicellular, uniseriate hairs present in leaf axils, rarely also on leaves and stems, and erect unicellular hairs sometimes present on both leaves and stems. Flowers regular, hermaphroditic or functionally unisexual, tetra- or pentamerous, rarely up to hexamerous, fascicled in the leaf axils or terminally, sometimes solitary, rarely racemose. Calyx with free lobes. Corolla funnel-shaped or campanulate to urn-shaped, sympetalous, sometimes only shortly tubular (*Platyspermation*), with more or less lobed petal wings (not *Platyspermation*), sometimes carunculate inside the lobes. Aestivation valvate. Stamens isomerous, attached to the corolla, sometimes inserted at the very base of the corolla tube, alternating with the corolla lobes, sometimes sessile (*Platyspermation*). Anthers introrse, longitudinally dehiscent. Disc present or absent. Style single with capitate or discoid stigma, often more or less bi- or trilobed. Ovary inferior or sometimes semi-inferior, with two to three locules, each containing two to many anatropous ovules. Placentation axile. Fruits berries or (*Platyspermation*) capsules with one to several seeds with minute embryo and copious endosperm.

Ten species classified into five genera in eastern Australia, New Zealand, New Caledonia and New Guinea.

Vegetative Morphology. Alseuosmiaceae are shrubs, ranging from the creeping or epiphytic subshrubs of *Wittsteinia* to the sometimes 6-m-tall *Periomphale*. The simple leaves are either entire or serrate, lack stipules, and are alternate, subopposite, or in pseudo-whorls. Venation is pinnate, very faint in *Crispiloba*. Leaves size varies between 3 and 20 cm.

Vegetative Anatomy (Gardner 1976; Dickison 1986, 1989; *Platyspermation* not investigated). Rusty brown, multicellular uniseriate hairs are present in the leaf axils. In *Platyspermation* uniseriate hairs with persistent reddish bases are found also on other parts of the plant (Stevens 2001). Erect unicellular hairs may be present on both leaves and stems. The latter type is especially abundant in *Wittsteinia vacciniacea*, forming an indumentum on stems, petioles and basal portions of the leaves. In contrast, *Crispiloba* and *Periomphale* are (almost) completely devoid of this hair type.

The leaf epidermis is thin and consists of one cell layer. In transectional view, the epidermal cells are square or rectangular. Their anticlinal walls are usually undulate and deeply lobed in surface view. The anomocytic stomata are level with the epidermis and have prominent outer cuticular ledges. The one-layered palisade cells are poorly differentiated from the lacunose spongy mesophyll. In *Crispiloba*, numerous long sclereids with thick lignified walls form an "interwoven mass . . . that permeates the mesophyll" (Dickison 1989). More or less rod-shaped sclereids may be found around the midvein in *Periomphale*. The latter are lobed or armed, have thinner walls, and are not as elongate as the sclereids of *Crispiloba*. Sclerenchyma is present either as bundle sheaths or as idioblastic sclereids in the leaves of all taxa except *Wittsteinia vacciniacea*, which completely lacks foliar sclerenchyma.

The nodes are trilacunar with three traces. In *Alseuosmia* the traces fuse about halfway up the petiole, in *Wittsteinia papuana* and *Periomphale* they fuse at the base of the lamina, and in *Crispiloba* and *W. vacciniacea* they remain separated throughout the petiole and into the lamina. Fibrous bundle caps develop distally in the petiole, except in *W. vacciniacea*.

All genera have an endodermis with prominent Casparian banding present in young stems and surrounding the petiolar vascular bundles in all genera but *Periomphale*. Calcium oxalate crystals have not been detected.

The wood has very faint or no growth rings. The narrow vessels are mostly solitary, sometimes in radial multiples, or rarely clustered. The mean number of bars of the scalariform perforation plates ranges from 20 (*Crispiloba*) to 43 (*Periomphale*). Intervessel pits commonly have circular borders and are opposite and transitional to alternate, or sometimes scalariform. In *Alseuosmia* and *Crispiloba* the vessel elements have fine helical thickenings. The imperforate elements are living, store starch at maturity, and have indistinctly bordered or simple pits. Both septate and non-septate fibres are present in all genera. *Periomphale* has tall (> 1.5 cm) and wide, multiseriate rays, whereas the rays of *Crispiloba* are heterocellular, shorter and narrower. No rays are present in the other genera. Axial parenchyma is very sparse or absent.

Inflorescences. *Alseuosmia* and *Wittsteinia* have few-flowered fascicles or solitary flowers in the leaf axils. In *Periomphale* the inflorescences are predominantly terminal. Commonly, they consist of fascicled flowers but racemes are sometimes found. Terminal, umbel-like, mostly pedunculate inflorescences of one to five flowers are found in *Crispiloba*. *Platyspermation* has few-flowered inflorescences with inclined flowers. Pedicels have few bracts which are very early caducous in *Periomphale*.

Flower Morphology. The flowers are regular with whorls of normally four or five flower parts; hexamerous flowers are sometimes encountered (septamerous flowers in *Periomphale* were reported by Baillon 1888). According to Tirel and Jérémie (1996), *Periomphale* has both hermaphroditic (perhaps functionally male) and functionally female flowers. In the other genera, the flowers are hermaphroditic. The calyx lobes are valvate, free, more or less triangular, and persistent or circumscissile-caducous (*Alseuosmia*). The corolla tube of *Platyspermation* is short whereas in the other genera the clearly sympetalous corolla is funnel-shaped or campanulate to urn-shaped. The colour of the corolla ranges from dull red in *Alseuosmia macrophylla* over various pale shades of pink, yellow and green, with or without red markings, to pure white in *Crispiloba*. The valvate corolla lobes have appendages, so-called petal wings, which are more or less lobed (Fig. 2A–E). In *Crispiloba* they are conspicuously fringed whereas in *Platyspermation* the corolla lobes lack evident petal wings but are papillate. Petal wings reminiscent of those in Alseuosmiaceae are also found in Goodeniaceae and Menyanthaceae (Gustafsson 1995). In *Crispiloba*, the base of the midrib on the inside of the lobes is fringed in a similar way. Also, there are irregular appendages at the throat of the corolla tube. In *Wittsteinia* and *Periomphale*, a caruncle at the base of the lobes forms a 'corona' which may cover the tube (Fig. 2D). The length of the tube varies from c. 0.5 cm (*Wittsteinia papuana* and small-flowered *Periomphale*) to 4.5 cm (*Alseuosmia macrophylla* and *Crispiloba*). The stamens alternate with the corolla lobes, and are inserted either in the throat of the corolla tube (*Alseuosmia* and *Crispiloba*) or at the very base of the tube. The introrse anthers open by longitudinal slits. In *Platyspermation* the anthers are sessile and extrorse (?), brown hairy below, and with a large flat connective appendage at the apex (van Steenis 1982). A disc is mostly present. It is very reduced or missing in *Wittsteinia*, and inhabited by parasitic insects in flowers of *Periomphale* (see below). The single style has a capitate or discoid, often bilobed stigma, sometimes trilobed in *Wittsteinia vacciniacea*. The ovary is inferior or sometimes initially semi-inferior in *Periomphale* and two-locular; *Wittsteinia vacciniacea* commonly has three locules. Each locule contains two to many anatropous ovules with axile placentation, in *Platyspermation* the placenta is brown and very thick (van Steenis 1982). Besides the normal type of flowers, Tirel (1996) and Tirel and Jérémie (1996) described flowers inhabited by parasitic insects in *Periomphale*. These are globose or obconical, do not open, and are often borne on elongated pedicels (up to 6 cm long). The stamens and the style are frequently only weakly developed, as is the corolla, which is shed prematurely or withers. A disc is usually lacking and the ovules, if present, do not develop into seeds. Similar flowers are reportedly present also in *Wittsteinia* and *Platyspermation* (van Steenis 1984; Stevens 2001).

Floral Anatomy. The floral anatomy of *Alseuosmia* and *Periomphale* was investigated by Gardner (1976). According to him, the anatomical features are uniform within *Alseuosmia*, and essentially agree with those in *Periomphale*. Notably, at the top of the ovary the locules interconnect above the placental region for about 50–100 µm, due to the septum being transversely divided (in one examined flower of *Periomphale*, this resulted in parietal placentation of the uppermost ovule).

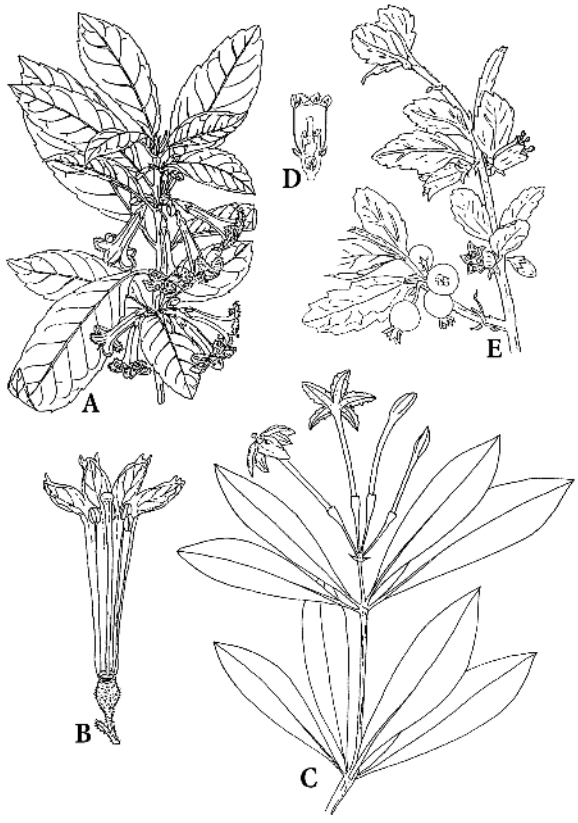

Fig. 2. Alseuosmiaceae. **A** *Alseuosmia macrophylla*, habit. **B** *A. banksii*, flower with opened corolla. **C** *Crispiloba disperma*, habit. **D** *Periomphale balansae*, female flower; longitudinal section of ovary. **E** *Wittsteinia vacciniacea*, habit. (Redrawn after **A** Hooker 1887, **B** Hooker 1853–1855, **C** van Steenis 1984, **D** Tirel and Jérémie 1996, **E** Mueller 1885)

Embryology. In *Alseuosmia* the anther wall consists of an epidermis, an endothecium with fibrous thickenings when mature, two middle layers and a one-layered tapetum. The tapetum cells are binucleate before meiosis in the pollen mother cells, remain in place during pollen development, and subsequently undergo nuclear fusion. The pollen is shed in the trinucleate condition. The ovules of *Alseuosmia* are unitegmic and tenuinucellate, and the embryo sac is eight-nucleate at maturity (Gardner 1976).

Karyology. The diploid chromosome number of *Alseuosmia* is $2n = 18$ (Gardner 1976).

Pollen. The 3-colporate pollen of *Alseuosmia* was studied by Erdtman (1952) who described the pollen grains as often angulaperturate, oblate spheroidal-prolate (longest axis 45–50 µm). Sexine tegillate, slightly undulating, thicker than the nexine, sometimes with small fissures; ectosexine thicker than endosexine, the latter only faintly baculate. According to Hufford (1992) and Kårehed et al. (1999), *Alseuosmia* pollen has well-developed columellae. The pollen of *Periomphale* is similar in appearance to that of *Alseuosmia* (Bortenschlager et al. 1966), as is that of *Platyspermation* (3-colpor(oid)ate, oblate, spheroidal, c. 31×36 µm and with the sexine thicker than the nexine; Erdtman 1952).

Fruit and Seed. The fruits of Alseuosmiaceae are two-locular berries, two- to three-locular in *Wittsteinia*, or two-locular capsules (*Platyspermation*). Their shape varies from globose (*W. vacciniacea*) to narrowly ellipsoid. Each fruit contains one to many ellipsoid or ovoid, more or less compressed seeds with a brown to black testa. In *Platyspermation*, seeds are sculptured and have fine, inflated hairs on the margin (van Steenis 1982). The seed coat structure and the lignified exotesta cells of *Alseuosmia* have been described by Nemirovich-Danchenko and Lobova (1998).

Reproductive Biology. According to Gardner (1976), *Alseuosmia pusilla* is self-compatible, whereas *A. macrophylla* is an obligate outbreeder with an incompatibility mechanism operating at the stylar level.

Phytochemistry. In the leaves of *Alseuosmia*, Cambie and Parnell (1969) detected lupeol, lupenyl acetate, stigmasterol, stearic acid, and triterpene acetates. Also from *Alseuosmia*, Gardner (1976) reported the presence of a condensed tannin (leucocyanidin) and ellagitannin, together with simple phenols (quercetin, caffeic acid, kaempferol, and p-coumaric acid) and triterpenoid saponins. He could not detect either alkaloids or iridoids.

Affinities. Alseuosmiaceae form a monophyletic group in Asterales, together with Argophyllaceae and Phellinaceae (Gustafsson et al. 1996; Backlund and Bremer 1997; Gustafsson and Bremer 1997; Källersjö et al. 1998; Kårehed et al. 1999; Lundberg and Bremer 2003).

Before the recent addition of *Platyspermation* (see below), several studies supported Alseuosmiaceae as a well-defined family (e.g. van Steenis 1984; Dickison 1986, 1989; Kårehed et al. 1999). Already when Cunningham (1839) described *Alseuosmia*, he suggested it to be a distinct family,

related to Cornaceae, Caprifoliaceae and Loranthaceae. *Alseuosmia* was, however, mostly treated as a more or less aberrant member of Caprifoliaceae (e.g. Hooker 1873; Fritsch 1891), as were the two New Caledonian genera *Memecylanthus* and *Pachydiscus* (Schlechter 1906; Guillaumin 1948) now included in *Periomphale* (van Steenis 1978). Initially, Baillon (1888) placed *Periomphale* in Gesneriaceae and, due to lack of detailed knowledge, the genus was mostly kept in that family until Airy Shaw (1965) realized its correct affinities. Airy Shaw (1965) also gave the first formal description of Alseuosmiaceae, indicating affinities with Escalloniaceae. Gardner (1976, 1978a) suggested Alseuosmiaceae to be most closely related to Argophyllaceae, then included in Escalloniaceae but now considered a separate family of Asterales (e.g. Källersjö et al. 1998; Kårehed et al. 1999). van Steenis (1978, 1984) added to the family the newly discovered *Wittsteinia papuana* and *W. vacciniacea*, formerly thought to belong in Ericaceae (von Mueller 1861; Bentham 1869; Drude 1889; Stevens 1971) or Epacridaceae (Burtt 1949), and *Crispiloba*, earlier misplaced in Rubiaceae (Moore 1917). van Steenis (1984) included *Periomphale* in *Wittsteinia* but Tirel (1996) and Tirel and Jérémie (1996) argued that it should be regarded as a distinct genus. Alseuosmiaceae obtained their present circumscription when molecular studies showed the little known genus *Platyspermation* to be the sister to Alseuosmiaceae (Lundberg and Bremer 2003). Here, *Platyspermation* is included in the family, rather than recognising a monotypic Platyspermataceae (Doweld 2001). *Platyspermation* was originally described as a member of Myrtaceae (Guillaumin 1950). Airy Shaw (in Willis 1973) placed it in Rutaceae, while a relationship to Escalloniaceae was suggested by Erdtman (1952), Schmid (1980) and van Steenis (1982).

Distribution and Habitats. *Alseuosmia* is found in lowland to montane forests in New Zealand (Gardner 1976). *Crispiloba* is endemic to rain forests of Queensland, Australia. On New Caledonia, *Periomphale* inhabits humid forests (Tirel and Jérémie 1996), as does *Platyspermation* which is also found in the maquis vegetation. *Wittsteinia* is a mountainous genus; the Australian *W. vacciniacea* grows in crevices of rocks and on rocky summits of Victorian mountains (Bentham 1869), and the Papua New Guinean *W. papuana* has been collected in woodland at 3,000 m (van Steenis 1978).

Key to the Genera

1. Corolla tube short; stamens sessile; fruit a capsule **5. *Platyspermation***
– Corolla tube well developed; stamens inserted in the corolla tube; fruit a berry 2
2. Corolla funnel-shaped or narrowly cylindrical; stamens inserted at the apex of the corolla tube 3
– Corolla campanulate to urn-shaped or narrowly barrel-shaped; stamens inserted at the base of the corolla tube 4
3. Leaves alternate, (sub)serrate; flowers fascicled or solitary in the leaf axils; calyx circumscissile-caducous; corolla funnel-shaped with ± lobed petal wings **1. *Alseuosmia***
– Leaves in pseudo-whorls, entire; flowers terminal; calyx persistent; corolla narrowly cylindrical with strongly fringed petal wings **2. *Crispiloba***
4. Shrubs; leaves entire; inflorescences terminal; corolla with entire petal wings **3. *Periomphale***
– Subshrubs; leaves serrate; inflorescences axile; corolla with lobed petal wings **4. *Wittsteinia***

Genera of Alseuosmiaceae

1. *Alseuosmia* A. Cunn. Fig. 2A, B

Alseuosmia A. Cunn., Ann. Nat. Hist. 2: 209 (1839); Merrett & Clarkson, N. Z. J. Bot. 38: 153–164 (2000), rev.

Shrubs. Leaves alternate, simple, serrate, sometimes subentire. Flowers fascicled in the leaf axils or solitary, regular, hermaphroditic, tetra- or pentamerous, rarely up to hexamerous. Corolla with a funnel-shaped tube and valvate lobes with more or less fringed petal wings. Stamens inserted at apex of corolla tube. Disc present. Stigma capitate or bilobed on elongate style. Ovary inferior, two-locular with two to many ovules in each locule. Fruit a two-locular berry. $n = 9$. Five species in New Zealand.

2. *Crispiloba* Steen. Fig. 2C

Crispiloba Steen., Blumea 29: 391 (1984).

Shrub. Leaves in pseudo-whorls of 3–6, entire. Inflorescences terminal, predominantly pedunculate, umbel-like with (one) up to five flowers. Flowers (tetra-) pentamerous, with a salver-shaped corolla and a long, narrow, cylindrical tube. Corolla lobes fringed inside and with strongly fringed petal wings. Stamens inserted at the throat of the corolla tube. Ovary inferior with two locules, each containing 2–3 ovules. Fruit a berry with black, more or less planoconvex seeds. One species, *C. disperma* (S. Moore) Steen., Queensland, Australia.

3. *Periomphale* Baill. Fig. 2D

Periomphale Baill., Bull. Mens. Soc. Linn. Paris 1: 731 (1888); Tirel & Jérémie, Fl. Nouvelle-Calédonie 20: 100–106 (1996), rev.
Memecylanthus Gilg & Schltr. (1906).
Pachydiscus Gilg & Schltr. (1906).

Shrubs with flexuose branches. Leaves alternate, often sub-opposite or in pseudo-whorls at the tip of the branches, entire. Inflorescences predominantly terminal, rarely racemose or more commonly of (1)2–8(15)-fascicled flowers. Flowers tetra- or pentamerous (rarely hexamerous), hermaphroditic or functionally unisexual. Corolla urn-shaped to campanulate; corolla lobes carunculate inside. Stamens inserted at the very base of the corolla tube. Disc present, rarely only weakly developed. Ovary inferior, sometimes initially semi-inferior, with two locules, each containing 4–6 ovules. Fruit a subcylindric to ovoid-fusiform berry with more or less compressed, ellipsoid seeds. One species, *P. balansae* Baill., endemic to New Caledonia.

4. *Wittsteinia* F. Muell. Fig. 2E

Wittsteinia F. Muell., Fragm. 2: 136 (1861).

Subshrubs, creeping with ascending branches, *W. papuana* (Steen.) Steen. epiphytic. Leaves alternate or in pseudo-whorls, serrate. Inflorescences of one or two axillary flowers. Corolla more or less campanulate or narrowly barrel-shaped (*W. papuana* (Steen.) Steen.); corolla lobes carunculate inside (inconspicuously so in *W. vacciniacea* F. Muell.) and with lobed petal wings. Stamens inserted on the corolla tube at the very base. Ovary inferior, two- to three-locular, few ovules in each locule. Fruit a globose berry with ovoid seeds. Two species; one endemic to Victoria, Australia, and one to Papua New Guinea.

5. *Platyspermation* Guillaumin

Platyspermation Guillaumin, Acta Horti Gotob. 18: 253 (1950).

Shrub up to 5 m high. Leaves alternate, pseudo-whorled at the end of branches, with small dentations on the recurved margins, sclerophyllous. Inflorescences few-flowered with inclined flowers. Corolla with short tube. Stamens sessile. Anthers with brown hairs below. Ovary inferior, two-locular, with few ovules on thick, brown placenta. Fruit a two-locular capsule with few, flat seeds. One species, *P. crassifolium* Guillaumin, endemic to New Caledonia.

Selected Bibliography

Airy Shaw, H.K. 1965. Diagnoses of new families, new names, etc., for the seventh edition of Willis' 'Dictionary'. Kew Bull. 18: 249–273.

Backlund, A., Bremer, B. 1997. Phylogeny of the Asteridae s. str. based on *rbc*L sequences, with particular reference to the Dipsacales. Pl. Syst. Evol. 207: 225–254.

Baillon, H.E. 1888. Observations sur les Gesnériacées. Bull. Mens. Soc. Linn. Paris 1: 731–732.

Bentham, G. 1869. Flora Australiensis, vol. IV. London: Lovell Reeve.

Bortenschlager, S., Erdtman, G., Praglowski, J. 1966. Pollenmorphologische Notizen über einige Blütenpflanzen incertae sedis. Bot. Notiser 119: 160–168.

Burtt, B.L. 1949. Studies in the Ericales, IX. The taxonomic position of *Wittsteinia*. Kew Bull. 3: 493–495.

Cambie, R.C., Parnell, J.C. 1969. A New Zealand phytochemical survey, part 7. Constituents of some dicotyledons. N. Z. J. Sci. 12: 453–466.

Cunningham, A. 1839. Florae Insularum Novae Zelandiae Precursor; or a specimen of the botany of the islands of New Zealand. Genus *Corneis affine*. Ann. Nat. Hist. 2: 209–210.

Dickison, W.C. 1986. Wood anatomy and affinities of the Alseuosmiaceae. Syst. Bot. 11: 214–221.

Dickison, W.C. 1989. Stem and leaf anatomy of the Alseuosmiaceae. Aliso 12: 567–578.

Doweld, A.B. 2001. Prosyllabus Tracheophytorum. Tentamen Systematis Plantarum Vascularium (Tracheophytorum). Moscow: GEOS.

Drude, O. 1889. Ericaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, IV, 1. Leipzig: W. Engelmann, pp. 15–65.

Erdtman, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. Stockholm: Almqvist & Wiksell.

Fritsch, K. 1891. Caprifoliaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, IV, 4. Leipzig: W. Engelmann, pp. 156–169.

Gardner, R.O. 1976. Studies in the Alseuosmiaceae. Ph.D. Thesis, University of Auckland, Auckland, New Zealand.

Gardner, R.O. 1978a. Systematic notes on the Alseuosmiaceae. Blumea 24: 138–142.

Gardner, R.O. 1978b. The species of *Alseuosmia* (Alseuosmiaceae). N. Z. J. Bot. 16: 271–277.

Guillaumin, A. 1948. Flore (analytique et synoptique) de la Nouvelle Calédonie, Phanérogams. Paris: Office de la Recherche Scientifique Coloniale.

Guillaumin, A. 1950. Plantae Neocaledonicae a C. Skottsberg a. 1949 lectae (96ème contribution à la flore de la Nouvelle-Calédonie). Acta Horti Gotob. 18: 247–265

Gustafsson, M.H.G. 1995. Petal venation in Asterales and related orders. Bot. J. Linn. Soc. 118: 1–18.

Gustafsson, M.H.G., Bremer, K. 1997. The circumscription and systematic position of Carpodetaceae. Austral. Syst. Bot. 10: 855–862.

Gustafsson, M.H.G., Backlund, A., Bremer, B. 1996. Phylogeny of the Asterales sensu lato based on *rbc*L sequences with particular reference to the Goodeniaceae. Pl. Syst. Evol. 199: 217–242.

Hooker, J.D. 1853–1855. The botany of the Antarctic voyage of H.M. Discovery ships Erebus and Terror in

the years 1839–43. II. Flora Novae-Zelandiae. London: Lovell Reeve.
Hooker, J.D. 1873. Caprifoliaceae. In: Bentham, G., Hooker, J.D., Genera Plantarum, vol. II, part 1. London: Lovell Reeve, pp. 1–7.
Hooker, J.D. 1887. Curtis's Botanical Magazine, vol. CXIII. London: Lovell Reeve.
Hufford, L. 1992. Rosidae and their relationships to other nonmagnoliid dicotyledons: a phylogenetic analysis using morphological and chemical data. Ann. Missouri Bot. Gard. 79: 218–248.
Källersjö, M., Farris, J.S., Chase, M.W., Bremer, B., Fay, M.F., Humphries, C.J., Petersen, G., Seberg, O., Bremer, K. 1998. Simultaneous parsimony jackknife analysis of 2538 *rbc*L DNA sequences reveals support for major clades of green plants, land plants, seed plants and flowering plants. Pl. Syst. Evol. 213: 259–287.
Kårehed, J., Lundberg, J., Bremer, B., Bremer, K. 1999. Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae. Syst. Bot. 24: 660–682.
Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–578.
Moore, S. 1917. A contribution to the phyto-geography of Bellenden-Ker. II. Systematic account. Phanerogams. J. Bot. 55: 302–309.
Mueller, F. von 1861. Fragmenta Phytographiae Australiae, vol. II. Melbourne: Auctoritate Gubern. Coloniae Victoriae.
Mueller, F. von 1885. Key to the system of Victorian plants. Melbourne: Government Printer.
Nemirovich-Danchenko, E.N., Lobova, T.A. 1998. The seed coat structure in some representatives of the order Hydrangeales. Bot. Zhurn. (Moscow & Leningrad) 83: 1–9.
Schlechter, R. 1906. Beiträge zur Kenntnis der Flora von Neu-Kaledonien. Bot. Jahrb. Syst. 39: 1–274.
Schmid, R. 1980. Comparative anatomy and morphology of *Psiloxylon* and *Heteropyxis*, and the subfamilial and tribal classification of Myrtaceae. Taxon 29: 559–595.
Stevens, P.F. 1971. A classification of the Ericales: subfamilies and tribes. Bot. J. Linn. Soc. 64: 1–53.
Stevens, P.F. 2001 (onwards). Angiosperm Phylogeny website, version 4, May 2003. http://www.mobot.org/MOBOT/research/APweb/
Tirel, C. 1996. Rétablissement de *Periomphale* Baill. (Alseuosmiaceae), genre endémique de Nouvelle-Calédonie. Bull. Mus. Natl Hist. Nat. B, Adansonia 18: 155–160.
Tirel, C., Jérémie, J. 1996. Alseuosmiaceae. In: Morat, P. (ed.) Flore de la Nouvelle-Calédonie, vol. 20. Paris: Muséum National d'Histoire Naturelle, pp. 100–106.
van Steenis, C.G.G.J. 1978. The genus *Periomphale* in New Guinea (Caprifoliaceae). Blumea 24: 480–481.
van Steenis, C.G.G.J. 1982. 157. Preliminary note on the taxonomic disposition of *Platyspermation* Guillaumin (Myrtaceae) from New Caledonia. In: van Steenis, C.G.G.J., Veldkamp, J.F., Miscellaneous botanical notes XXVI. Reinwardtia 10: 21–26.
van Steenis, C.G.G.J. 1984. A synopsis of Alseuosmiaceae in New Zealand, New Caledonia, Australia, and New Guinea. Blumea 29: 387–394.
Willis, J.C. 1973. A dictionary of the flowering plants and ferns, ed. 8, revised by H.K. Airy Shaw. Cambridge: University Press.

Argophyllaceae

Argophyllaceae (Engl.) Takht., Systema Magnoliophytorum: 208 (1987).
Corokiaceae Kapil ex Takht. (1997).

J. Kårehed

Shrubs or small trees. T-shaped trichomes present on stems, leaves, inflorescences, and flowers. Leaves alternate (or in 3–4-leaved fascicles on brachyblasts), simple, estipulate with entire or serrate margins. Flowers borne in axile or sometimes terminal panicles or racemes, sometimes in few-flowered fascicles or solitary, regular, hermaphroditic, mostly pentamerous. Aestivation valvate. Sepals 5(8), connate at base, persistent. Petals 5(8), white or yellow, joined at their very base or free, alternating with the sepals, with fringed appendages (corolline ligules) on the adaxial side. Stamens isomerous, alternipetalous, anthers elongate-ovate or elongate. Ovary semi-inferior or inferior, 1–3(6)-locular, with one to many anatropous ovules in each locule. Placentation axile. Style with more or less capitate, 2–5-lobed stigma. Fruits loculicidal capsules or drupes. Seeds obovate or linear-elongate with minute or elongate embryo in fleshy endosperm.

Two genera comprising c. 20 species distributed in eastern Australia, Lord Howe Island, New Caledonia, New Zealand, and Rapa Island.

Vegetative Morphology. Argophyllaceae are a family of shrubs or small trees up to 7 m tall. *Argophyllum* has branches with brown or blackish (*A. ellipticum*) bark and yellow or reddish (*A. ellipticum*) wood. In *Corokia* the branches are dark brown to almost black. Zigzagging, interlacing branches are characteristic for *C. cotoneaster*. The leaves are alternate or arranged in fascicles of three to four on brachyblasts (*C. cotoneaster*), simple, entire or serrate, and exstipulate. *Argophyllum* has ovate, obovate, or linear-elliptic leaves, whereas the lamina in *Corokia* is elliptic or lanceolate to obovate or oblanceolate. The leaf shape is variable in *C. cotoneaster*; adult leaves are obovate to orbicular, sometimes emarginate, and leaves on seedlings are obovate-spathulate, often three-lobed.

Vegetative Anatomy. T-shaped hairs are present on (young) stems, leaves (depending on species in various degrees on petioles, upper and lower side, as well as on the margin), inflorescences, sepals, and on the abaxial side and the margin of the petals. Especially on the lower side of the leaves, they may give the impression of a whitish, silvery, or rusty indumentum. They consist of a multicellular, uniseriate stalk (in *Corokia cotoneaster* the stalk sometimes consists of only one cell) and a very elongated, T-shaped terminal cell (see, e.g. Al-Shammary and Gornall 1994). There are small slits at the junction of this T-cell with the stalk. In some *Argophyllum* species, these are oriented parallel to the long axis of the T-cell, whereas in other species and in *Corokia* the slits cross the long axis obliquely or at right angles. Carbonate deposits are present on the cuticle of the T-hairs in some *Corokia* species but not in *Argophyllum*.

The leaves have a poorly differentiated, uni- or biseriate palisade layer and a compact or lacunose (*Corokia*) spongy mesophyll. The uppermost palisade cells, as seen in cross-section, are columnar-elongate or short and square (some *Argophyllum* species). A one- to three-layered hypodermis is present in *Argophyllum ellipticum* and *A. nitidum*. The stomata are of the haplocheilic type and are anomocytic. The nodes are trilacunar (pentalacunar in *A. laxum* and unilacunar in *C.* x *virgata*), with three traces which either fuse halfway up the petiole into a shallow arc or split into more traces (*A. ellipticum* and *A. laxum*).

The following description of wood anatomy is based mainly on the studies of Patel (1973a, b), Hils (1985), and Noshiro and Baas (1998). The wood is dense, diffuse-porous or semi-ring-porous, whitish to yellow, pinkish to reddish, or very pale brown. The vessels are mostly solitary, occasionally in pairs or small groups, round-angular to angular in outline. Perforation plates are scalariform with rather numerous bars (6–32+). Intervessel pits and vessel-ray pits are transitional, opposite or, more

commonly, alternate. Fine helical thickenings are present in the vessel elements. The vascular tracheids (not present in *Argophyllum* and *Corokia collenettei*) have distinct helical thickenings. Both genera have septate fibres with minutely, non-bordered, distinctly or indistinctly bordered pits on the tangential and radial walls. Very fine helical thickenings have been recorded in the fibres of *Corokia*. Axial parenchyma is absent or very sparse, scanty paratracheal and diffuse. Rays are heterocellular, one to six cells broad. Crystals are not present.

Inflorescences. The inflorescences are axile or sometimes terminal panicles, racemes, corymbs (in some *Argophyllum*), or few-flowered fascicles (*Corokia cotoneaster*; along with solitary flowers). The bracts and prophylls are mostly small and linear.

Flower Structure. The flowers are regular, hermaphroditic, and predominantly pentamerous. In *Corokia collenettei*, hexamerous flowers are the normal condition. Higher merism occurs occasionally; eight-merous flowers have been reported for *C. collenettei* (Brown 1928). Aestivation is valvate. The calyx is turbinate and the calyx tube is adnate to the ovary. The sepals are 0.5–3 mm long. The petals, which alternate with the sepals, are 2–6 mm long, white or yellow, and have fringed appendages adaxially. These appendages (Fig. 3C, D, F), called corolline ligules by Eyde (1966), are only a few cells thick and almost as long as to a little longer than half the length of the petals. They are divided for two-thirds of their length into about 10–20 fringes, and are found in all species except *Corokia macrocarpa*. The alternipetalous, free stamens have elongate-ovate or elongate (*Corokia*), longitudinally dehiscent, introrse anthers. The short style has a capitate or inconspicuously 2–3(5)-lobed stigma. In *Argophyllum* the ovary is semi-inferior at anthesis but inferior early in development (Tobe and Raven 1999). It has predominantly two or three locules (occasionally four; in *A. verae* this number is normal (Forster 1990); Eichler (1878) reported of an ovary with five locules in *A. nitidum*). In *Corokia* there is one pendulous ovule in each locule of the inferior ovary. The number of locules is mostly one or two, sometimes up to four in *C. buddleioides* (Kapil and Bhatnagar 1992). Ovaries of *C. collenettei* have regularly up to four locules, and Eyde (1966) reported a five-locular ovary in this species. The placentation in both genera is axile and the ovules are anatropous, unitegmic, and tenuinucellate (e.g. Mauritzon 1933; Kapil and Bhatnagar 1992). Numerous ovules are present in each locule in *Argophyllum*, whereas in *Corokia* there is a single, pendulous, apically attached ovule in each locule. *Corokia* has a usually bright orange, epigynous, pulvinate nectariferous disk.

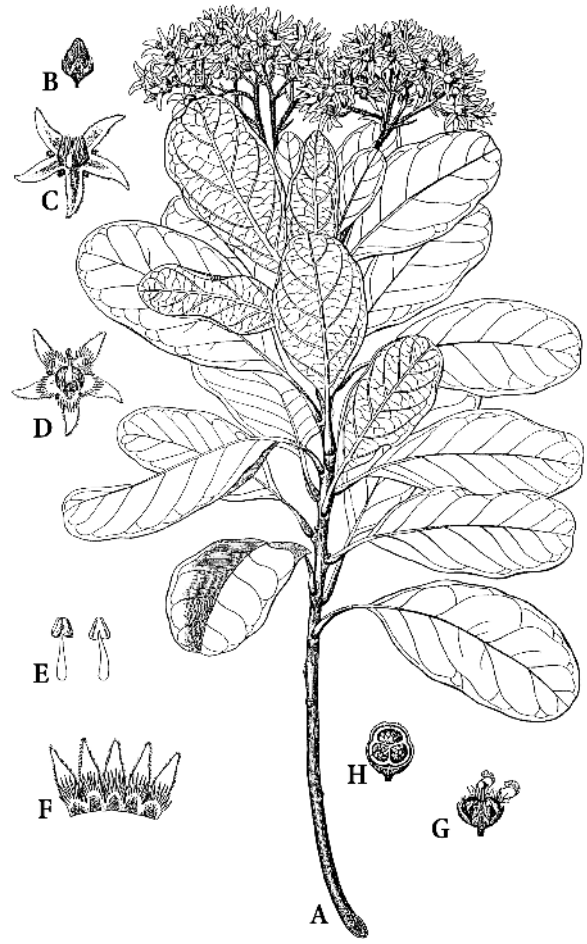

Fig. 3. Argophyllaceae. *Argophyllum ellipticum*. **A** Habit. **B** Bud. **C** Flower. **D** Flower opened out. **E** Stamens, adaxial and abaxial view. **F** Corolla, laid open. **G** Flower with corolla partly removed. **H** Transverse section of capsule. (From Labillardière 1824)

Floral Anatomy. The vascular pattern of *Corokia* flowers was thoroughly described by Eyde (1966). He noted anatomical similarities with *Argophyllum* and that *Corokia* differs from Cornaceae in having vascular bundles running longitudinally through the centre of the inferior gynoecium (Eyde 1966).

Embryology. The anthers of *Corokia* are tetrasporangiate, have a four-layered wall, a secre-

tory tapetum, and endothecial cells which develop fibrous thickenings prior to dehiscence (Kapil and Bhatnagar 1992).

The embryo of *Argophyllum* is minute and surrounded by fleshy endosperm. The following information on *Corokia* is extracted mainly from the works of Mauritzon (1933), Kapil and Bhatnagar (1992), and Lobova (1997). The layer of integument cells which border the embryo sac is uniform and the cells are radially elongated. The embryo sac is of the Polygonum type. The synergids are very long and have a small vacuole below their nuclei. The egg cell is small and the polar nuclei are positioned just below it. The antipodal cells are persistent. The pollen tube traverses through a wide stylar canal to reach the ovule and the embryo sac. Endosperm is cellular with aggressive micropylar and chalazal haustoria (Kapil and Bhatnagar 1992). Embryogeny is of the Chenopodiad type. When mature, the cylindrical embryo has a long radicle-hypocotyl axis and short cotyledons, compared to the embryo of *Argophyllum*.

Karyology. The diploid chromosome number for *Corokia* is $2n = 18$ (Wanscher 1933; Hamel 1953; Hair and Beuzenberg 1959).

Pollen Morphology. Hideux and Ferguson (1976) and Ferguson and Hideux (1978) have studied the pollen of Argophyllaceae. The pollen is tricolporate with colpi longer than two-thirds of the polar axis. It has a prominent, complex H-shaped endo-aperture with thinning of the endexine and association of the lamellation in the apertural region (Ferguson and Hideux 1978). The pollen grains are spheroidal; 15–20 × 15–20 µm (polar axis × equatorial diameter) in *Argophyllum*, and 25–33 × 24–30 µm in *Corokia*. The exine is 1–1.5 µm thick in both genera. The tectum is complete perforate and *Corokia* has supratectal spines. The tectum:columellae ratio is less than 1, and the solea (foot-layer):endexine ratio is equal to or larger than 1.

Pollination. Webb (1994) studied the pollination system of *Corokia cotoneaster*. The flowers seem to be functional for 5–6 days and are self-incompatible. They are not dichogamous, but are slightly herkogamous when fully open. Twelve insect species, mostly bees and flies, have been recorded to visit the flowers, some of which, especially the bee *Lasioglossum sordidum*, seem to be legitimate pollinators.

Fruit and Seed. The fruit of *Argophyllum* is a loculicidal capsule opening with as many teeth as locules. The teeth split, however, along their midrib, so that in the open fruit their number is twice the number of locules. The ripe seeds are obovate, weakly triangular, and the shiny brown surface is large-celled. The proximal and radial walls of the almost hexagonal exotestal cells have very strong thickenings. *Corokia* has yellow, orange, bright red to purplish red, or blackish drupes, c. 2–12 mm long, crowned by the persistent calyx. The spherical to obovoid endocarp is thick and woody. At the apical end of the endocarp, there are woody germination plugs formed by the lignification of cells of the placentae. The seed surface is small-celled compared to that of *Argophyllum*, the exotestal layer is thinner, and the cells are smaller and have thinner walls. More elaborate descriptions of the fruits and seeds of Argophyllaceae are found in, for example, Eyde (1966) and Lobova (1997).

Phytochemistry. Two species of *Argophyllum* are able to hyperaccumulate nickel (Jaffré et al. 1979). Triterpenes have been reported from both *Argophyllum* and *Corokia* (Briggs et al. 1967; Cambie and Parnell 1969). Flowers, fruits, and leaves of *Corokia* have darkly stained cells, which Eyde (1966) called tannin-containing cells. Similar cells from *Argophyllum* have been mentioned by Zemann (1907) and Kårehed et al. (1999), and tannin-like substances in the testa of both genera were noticed by Lobova (1997). Leucoanthocyanins are present in both genera (Cambie et al. 1961; Gibbs 1974). In addition, gallotannin (Hegnauer 1969) and a number of additional phenolic constituents have been detected in *Corokia* (cyanidin, quercetin, caffeic acid, kaempferol: Gardner 1976; gallic acid, quinic acid: Hegnauer 1969), as well as iridoids (Wieffering 1966; Jensen et al. 1975). Attempts to detect HCN in *Corokia* have given negative results (Gibbs 1974).

Affinities. Argophyllaceae belong in Asterales (Gustafsson et al. 1996; Backlund and Bremer 1997; Gustafsson and Bremer 1997; Källersjö et al. 1998; Kårehed et al. 1999). According to morphological and DNA sequence data (*rbc*L and *ndh*F), Argophyllaceae and their sister group Phellinaceae form a monophyletic group with Alseuosmiaceae (Kårehed et al. 1999). Hallier (1908) was the first to suggest that the two genera of Argophyllaceae are related to each other, emphasizing the presence of corolline ligules and T-hairs in both *Ar-*

gophyllum and *Corokia*. The family was erected by Takhtajan (1987) to acknowledge the increased evidence for a close relationship between the two genera from, e.g. floral anatomy (Eyde 1966), pollen morphology (Hideux and Ferguson 1976; Ferguson and Hideux 1978), and wood anatomy (e.g. Hils 1985). Previously, *Argophyllum* had been regarded as a member of either Saxifragaceae (e.g. Engler 1890, 1928; Schlechter 1906; Thorne 1992) or Escalloniaceae (Willis 1966; Takhtajan 1983). *Corokia* had mostly been placed either in Cornaceae (Hooker 1867; Harms 1897; Wangerin 1909; Melchior 1964; Hutchinson 1967; Cronquist 1981) or together with *Argophyllum* in the aforementioned families (e.g. Engler 1928; Takhtajan 1983; Thorne 1983, 1992).

Takhtajan (1997) elevated *Corokia* to family level, noting that it differs from *Argophyllum* in the structure of fruit and seed, placentation and the number of locules (1–2-locular ovaries). The latter, however, is not correct (see above). The two genera are closely related to each other and share the presence of, for example, the easily recognized corolline ligules and the T-shaped hairs.

Distribution and Habitats. The Australian *Argophyllum* species, one in New South Wales and about four in Queensland, inhabit more or less mountainous rainforests, except *A. verae* which grows on sandstone ledges far north on the Cape York Peninsula (Forster 1990). The ten New Caledonian species are more frequent in open, sunny places (Schlechter 1906; Guillaumin and Virot 1953).

Corokia species are found in diverse habitats, ranging from lowland shrubland, river flats, and rocky places (*C. cotoneaster*) to rainforests (*C. whiteana*). The distribution of the genus is intriguing. *Corokia whiteana* is known only from one mountain range in New South Wales, on Lord Howe Island there is another species (*C. carpodetoides*), three species inhabit New Zealand (*C. cotoneaster* on both the North and South Island, *C. buddleioides* restricted to the North Island, and *C. macrocarpa* on the Chatham Islands), and yet another species is found on the isolated, volcanic Rapa Island (*C. collenettei*), more than 6,000 km from Australia.

Economic Importance and Conservation. The New Zealand species of *Corokia* and the hybrid *C.* x *virgata* are cultivated as ornamentals. *Argophyllum nullumense* is cultivated in some plant nurseries in Australia for its beautiful foliage. An increased interest in cultivating this and the other Australian *Argophyllum* species would facilitate the conservation of these rare rainforest plants. One *Argophyllum* species, *A. verae*, is known only from the type locality (Forster 1990), as is the vulnerable *C. whiteana* (Smith 1958).

Key to the Genera

1. Ovary semi-inferior with many ovules in each locule; loculicidal capsules **1. *Argophyllum***
– Ovary inferior with one apically attached ovule in each locule; drupes **2. *Corokia***

1. *Argophyllum* J.R. Forst. & G. Forst. Fig. 3

Argophyllum J.R. Forst. & G. Forst., Char. Gen. 29, t. 15 (1776); Zemann, Ann. K.K. Naturhist. Hofmus. 22: 270–292 (1907), rev.

Shrubs or small trees with alternate, simple leaves, either entire or serrate. Inflorescence a panicle or raceme with regular pentamerous or rarely hexamerous flowers. Stigma capitate, two- to five-lobed, on short style. Semi-inferior ovary with many ovules in each locule. Locules mostly two or three, rarely four or five. Fruit a loculicidal capsule with obovate seeds. About 15 species from eastern Australia (five, including one undescribed) and New Caledonia (ten).

2. *Corokia* A. Cunn.

Corokia A. Cunn., Ann. Nat. Hist. 3: 249 (1839).

Shrubs or small trees with alternate, simple leaves, either entire or with a few teeth (*C. carpodetoides* (F. Muell.) L.S. Sm. and *C. collenettei* L. Riley). Inflorescence mostly a panicle or raceme, sometimes a few-flowered fascicle or flowers solitary. Flowers yellow, pentamerous or rarely with higher merism. Stigma capitate, shallowly bilobed or rarely up to five-lobed. Inferior ovary with mostly one to three, rarely up to five, uni-ovulate locules. Drupes containing elongated, spindle-shaped seeds. $n = 9$. Six species from eastern Australia, Lord Howe Island, New Zealand, and Rapa Island.

Selected Bibliography

Al-Shammary, K.I., Gornall, R.J. 1994. Trichome anatomy of the Saxifragaceae s.l. from the southern hemisphere. Bot. J. Linn. Soc. 114: 99–131.

Backlund, A., Bremer, B. 1997. Phylogeny of the Asteridae s. str. based on *rbc*L sequences, with particular reference to the Dipsacales. Pl. Syst. Evol. 207: 225–254.

Briggs, L.H., Cambie, R.C., Couch, R.A.F. 1967. Triterpenes from some New Zealand dicotyledons. N. Z. J. Sci. 10: 1076–1082.

Brown, F.B.H. 1928. Cornaceae and allies in the Marqesas and neighboring islands. Bernice P. Bishop Mus. Bull. 52: 1–22.

Cambie, R.C., Parnell, J.C. 1969. A New Zealand phytochemical survey. Part 7. Constituents of some dicotyledons. N. Z. J. Sci. 12: 453–466.

Cambie, R.C., Cain, B.F., Laroche, S. 1961. A New Zealand phytochemical survey. Part 2. The dicotyledons. N. Z. J. Sci. Technol. 4: 604–663.

Cronquist, A. 1981. An integrated system of classification of flowering plants. New York: Columbia University Press.

Eichler, A.W. 1878. Blütendiagramme, II. Leipzig: W. Engelmann.

Engler, A. 1890. Saxifragaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, III, 2a. Leipzig: W. Engelmann, pp. 41–93.

Engler, A. 1928. Saxifragaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, ed. 2, 18a. Leipzig: W. Engelmann, pp. 74–226.

Eyde, R.H. 1966. Systematic evolution of the flower and fruit of *Corokia*. Amer. J. Bot. 53: 833–847.

Ferguson, I.K., Hideux, M.J. 1978. Some aspects of the pollen morphology and its taxonomic significance in Cornaceae sens. lat. In: Proceedings IV International Palynological Conference, Lucknow, 1976–1977, vol. 1, pp. 240–249.

Forster, P.I. 1990. *Argophyllum verae* (Saxifragaceae), a new species from northern Queensland. Austrobaileya 3: 173–176.

Gardner, R.O. 1976. Studies in the Alseuosmiaceae. Ph.D. Thesis, University of Auckland, Auckland, New Zealand.

Gibbs, D.R. 1974. Chemotaxonomy of flowering plants, vol. III. Montreal: McGill-Queen's University Press.

Guillaumin, A., Virot, R. 1953. Contributions à la Flore de la Nouvelle Calédonie, CII. Plantes récoltées par M.R. Virot. Mém. Mus. Natl Hist. Nat. B, Bot. 4: 1–82.

Gustafsson, M.H.G., Bremer, K. 1997. The circumscription and systematic position of Carpodetaceae. Austral. Syst. Bot. 10: 855–862.

Gustafsson, M.H.G., Backlund, A., Bremer, B. 1996. Phylogeny of the Asterales sensu lato based on *rbc*L sequences with particular reference to the Goodeniaceae. Pl. Syst. Evol. 199: 217–242.

Hair, J.B., Beuzenberg, E.J. 1959. Contributions to a chromosome atlas of the New Zealand Flora, 2. N. Z. J. Sci. 2: 148–156.

Hallier, H. 1908. Über *Juliana*, eine Terebinthaceen-Gattung mit Cupula, und die wahren Stammeltern der Kätzchenblütler. Beih. Bot. Centralbl. 13: 81–265.

Hamel, J.L. 1953. Contribution à l'étude cyto-taxonomique des Saxifragacées. Rev. Cytol. Biol. Vég. 14: 9–313.

Harms, H. 1897. Cornaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, III, 8. Leipzig: W. Engelmann, pp. 250–270.

Hegnauer, R. 1969. Chemical evidence for the classification of some plant taxa. In: Harborne, J.B., Swain, T. (eds.) Perspectives in phytochemistry. Proceedings Phytochemical Society Symposium, Cambridge, April 1968. London: Academic Press, pp. 121–138.

Hideux, M.J., Ferguson, I.K. 1976. The stereo-structure of the exine and its evolutionary significance in Saxifragaceae s.l. In: Ferguson, I.K., Muller, J. (eds) The evolutionary significance of the exine. London: Academic Press, pp. 327–377.

Hils, M.H. 1985. Comparative anatomy and systematics of twelve woody Australian genera of the Saxifragaceae. Ph.D. Thesis, The University of Florida.

Hooker, J.D. 1867. Cornaceae. In: Bentham, G., Hooker, J.D., Genera Plantarum, vol. I, part 3. London: Lovell Reeve, pp. 947–952.

Hutchinson, J. 1967. The genera of flowering plants. Dicotyledons, vol. 2. Oxford: Clarendon Press.

Jaffré, T., Brooks, R.R., Trow, J.M. 1979. Hyperaccumulation of nickel by *Geissois* species. Pl. Soil 51: 157–162.

Jensen, S.R., Nielsen, B.J., Dahlgren, R. 1975. Iridoid compounds, their occurrence and systematic importance in the Angiosperms. Bot. Notiser 128: 148–180.

Källersjö, M., Farris, J.S., Chase, M.W., Bremer, B., Fay, M.F., Humphries, C.J., Petersen, G., Seberg, O., Bremer, K. 1998. Simultaneous parsimony jackknife analysis of 2538 *rbc*L DNA sequences reveals support for major clades of green plants, land plants, seed plants and flowering plants. Pl. Syst. Evol. 213: 259–287.

Kapil, R.N., Bhatnagar, A.K. 1992. Embryology and systematic position of *Corokia* Cunn. In: Proceedings XI International Symposium on Embryology and Seed Reproduction, Leningrad, 1990. St. Petersburg: Nauka.

Kårehed, J., Lundberg, J., Bremer, B., Bremer, K. 1999. Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae. Syst. Bot. 24: 660–682.

Labillardière, J.J.H. de 1824. Sertum Austro-Caledonicum. Paris: Huzard.

Lobova, T.A. 1997. Seed morphology and anatomy in the genera *Argophyllum* and *Corokia* (Argophyllaceae). Bot. Zhurn. (Moscow & Leningrad) 82: 68–78.

Mauritzon, J. 1933. Studien über die Embryologie der Familien Crassulaceae und Saxifragaceae. Lund: Gleerupska Univ.-Bokhandeln.

Melchior, H. 1964. A. Engler's Syllabus der Pflanzenfamilien, Angiospermen, ed. 12, vol. 2. Berlin: Gebrüder Borntträger.

Noshiro, S., Baas, P. 1998. Systematic wood anatomy of Cornaceae and allies. IAWA J. 19: 43–97.

Patel, R.N. 1973a. Wood anatomy of the dicotyledons indigenous to New Zealand. 1. Cornaceae. N. Z. J. Bot. 11: 3–22.

Patel, R.N. 1973b. Wood anatomy of the dicotyledons indigenous to New Zealand. 2. Escalloniaceae. N. Z. J. Bot. 11: 421–434.

Schlechter, R. 1906. Beiträge zur Kenntnis der Flora von Neu-Kaledonien. Bot. Jahrb. Syst. 39: 1–274.

Smith, L.S. 1958. *Corokia* A. Cunn. An addition to the Australian genera of Saxifragaceae. Proc. Roy. Soc. Queensland 69: 53–55.

Takhtajan, A. 1983. The systematic arrangement of dicotyledonous families. In: Metcalfe, C.R., Chalk, L. (eds.) Anatomy of the dicotyledons, 2nd edn, vol. 2. Oxford: Clarendon Press, pp. 180–201.

Takhtajan, A. 1987. Systema Magnoliophytorum. Leningrad: Nauka.

Takhtajan, A. 1997. Diversity and classification of flowering plants. New York: Columbia University Press.
Thorne, R.T. 1983. Proposed new realignments in angiosperms. Nordic J. Bot. 3: 85–117.
Thorne, R.T. 1992. Classification and geography of the flowering plants. Bot. Rev. 58: 225–348.
Tobe, H., Raven, P.H. 1999. Floral structures of Alseuosmiaceae, Argophyllaceae, Carpodetaceae, Phellinaceae and Rousseaceae: additional members in Asterales. In: Abstract Volume XVI International Botanical Congress, St. Louis, MO, 1999.
Wangerin, W. 1909. Cornaceae. In: Engler, A., Das Pflanzenreich, IV, 229. Leipzig: W. Engelmann, pp. 1–110.
Wanscher, J.H. 1933. Studies on the chromosome numbers of the Umbelliferae, III. Bot. Tidsskr. 42: 384–399.
Webb, C.J. 1994. Pollination, self-incompatibility, and fruit production in *Corokia cotoneaster* (Escalloniaceae). N. Z. J. Bot. 32: 385–392.
Wieffering, J.H. 1966. Aucubinartige Glucoside (Pseudoindikane) und verwandte Heteroside als systematische Merkmale. Phytochemistry 5: 1053–1064.
Willis, J.C. 1966. A dictionary of the flowering plants and ferns, 7th edn. Revised by Airy Shaw. H.K. Cambridge: University Press.
Zemann, M. 1907. Studien zu einer Monographie der Gattung *Argophyllum* Forst. Ann. K.K. Naturhist. Hofmus. 22: 270–292.

Calyceraceae

Calyceraceae R. Br. ex Rich., Mém. Mus. Hist. Nat. 6: 74 (1820), nom. cons.

F.H. Hellwig

Perennial or rarely annual herbs, occasionally subligneous, often stemless or with scapiform flowering shoots. Leaves alternate, often forming a basal rosette, somewhat fleshy, without stipules, sessile or narrowed into a distinct petiole, undivided to dissected, margin entire, sinuate, dentate or serrate, sometimes revolute. Flowers in capitula, surrounded by triangular to lanceolate involucral bracts which are more or less united. Receptacle flat to conical, often with herbaceous to membranous, subulate to obovate or lanceolate receptacular bracts, usually free but rarely fused. Flowers perfect or rarely functionally male (and then plants andromonoecious), epigynous, actinomorphic, calyx adnate to the ovary, with (4)5(6) small, hyaline to membranous lobes or teeth, these rounded-orbicular or flat, linear-lanceolate and tapering. Corolla sympetalous, pentamerous or sometimes tetramerous, only occasionally hexamerous in individual flowers, cylindrical to narrowly infundibuliform with (4)5 short corolla lobes or with a slender basal tube and a widened limb, uppermost part campanulate with (4)5 valvate lobes, white or greenish. Stamens enclosed in corolla or subexserted, (4)5(6), as many as and alternating with the corolla lobes, inserted at various levels in the corolla. Filaments united into a tube over most of their length, sometimes distally free; anthers connate, at least at their bases, tetrasporangiate, dithecal, introrse, opening by longitudinal slits, mostly without appendages, sometimes with subsagittate bases and inconspicuous apical appendages. Nectary glands at base of filament tube alternating with the vascular bundles of the filaments. Gynoecium of two carpels, unilocular, inferior. Ovule solitary, pendulous, anatropous, tenuinucellate. Style strongly exserted, slender, cylindrical, stigma capitate, dry, papillose, with two (three) vascular bundles. Fruit an achene, often crowned by the calyx lobes which sometimes become lignified and spiny, often calyx also accrescent; achene cylindrical or prismatic, more or less distinctly ribbed. Seed with well-developed endosperm, embryo straight.

The family comprises four genera and about 60 species and is endemic to southern South America. One species occurs in the Falkland Islands (Islas Malvinas).

Vegetative Morphology. Besides inconspicuous annual herbs, the family contains many species which form vegetative rosettes until the inflorescences are formed. Growth is then continued by stolons, rhizomes or by lateral shoots arising from lower parts of the plant. Branching of Calyceraceae is sympodial, and in some genera monochasia are formed (in *Acicarpha* the capitula are terminal and the shoot system is continued by secondary axes overtopping the preceding ones). Metatopies with re- and concaulescence can be observed in some species (e.g. *Calycera sessiliflora*, *C. eryngioides*).

Vegetative Anatomy. Plants usually are glabrous but sometimes uniseriate filiform hairs are present, especially on the stems (*Calycera*). No external glands or secretory cavities have been observed (Hansen 1992), nor are resin-like droplets present in the wood (Carlquist and DeVore 1998). However, droplets of a resin-like substance seem to be present on and in stems and involucral bracts of *Boopis gracilis* (pers. obs.). Stem vascular bundles are arranged in a circle and are separated from each other by broad rays. The bundles are embedded in a ring of mechanical tissue in some species (*Boopis* spp.). Phloem strands of *Acicarpha* are accompanied externally by sclerenchyma, xylem includes moderately wide vessels with simple perforation plates, with bordered pits between vessels and ray parenchyma. Secondary medullary rays are wanting (Cronquist 1981). Two types of imperforate tracheary elements occur in the family, i.e. vasicentric tracheids and libriform fibres, the latter with small simple pits. Pits

between vessels and libriform fibres are alternate and circular to oval (Carlquist and DeVore 1998). Laterally elongated pits, called pseudoscalariform pits, are present in several species of Calyceraceae (Carlquist and DeVore 1998). The amount of wood is always very limited, with a maximum at stem bases and adjacent parts of the roots (Carlquist and DeVore 1998). The wood has strong indications of paedomorphosis with varying degrees in different species. This is supported by the presence of pseudoscalariform pitting and predominantly upright ray cells (Carlquist and DeVore 1998). Secondary xylem vessels with pseudoscalariform pitting transitional to helical-banded patterns support the ability of the roots to be bent or to expand and contract in reaction to changing water content (*Boopis graminea*, *Nastanthus* spp.). Seasonality is mirrored in the formation of growth rings observed in *Boopis anthemoides* (Carlquist and DeVore 1998).

The family exhibits an unusually wide range of mesomorphy values. This may be explicable by the very different habitats the plants live in. Wood anatomy is not yet sufficiently known to be used systematically. It is believed to largely reflect autapomorphic ecological adaptations (Carlquist and DeVore 1998). The primary cortex and the central pith are rich in clustered Ca-oxalate crystals. There are no specialized bast strands in the cortical parenchyma (Reiche 1901). The fleshy stems found in various species of *Boopis* result from the presence of massive medullary and cortical parenchyma (Reiche 1901). Tuberous roots of the fleshy species of *Boopis* have a strongly transversely rugose cortex which is a feature connected to the ability of many alpine plants to translocate themselves into deeper strata of the soil by root contraction (Reiche 1901).

Inflorescence and Flower Structure. The most striking feature of many species is the condensed, often many-flowered inflorescence. This condensation reaches several levels in the family. While *Acicarpha* has simple capitula with centripetal anthesis, the other genera have more complicated capitula of higher orders. It has been hypothesized that these consist of cymose units (Baillon 1880; Reiche 1901; DeVore 1994) but this has not been confirmed by detailed analyses. Some species of *Calycera* and *Boopis* tend to aggregate few to many capitula.

Flowers usually are hermaphrodite but functionally male flowers occur regularly in the centre of the capitula of *Acicarpha* (Miers 1870). The flowers are characterized by the transformed calyx and a close association of corolla, androecium and the style. The free part of the calyx is reduced to five small lobes above the edges of the gynoecium, the lower part being fused and closely attached to the inferior ovary. It does not protect the flower bud (Erbar 1993).

The filaments form a tube which consists of their fused lower parts. In *Acicarpha tribuloides*, this tube overtops the corolla tube in mature flowers. Below the separation of the filaments from the corolla tube, there is a corolla stamen tube. Five nectaries are present in the flower. The glandular tissue extends from the base of the filament tube to the top of the stamen corolla tube (Erbar 1993). Nectar is secreted through nectar slits outside of the filament tube into five small pockets. Form and alternate position with the filaments of the nectaries are very distinctive for the family (Brown 1817; Reiche 1901). The style is cylindrical with a club-like papillose head. Intercalary growth of the receptacle results in a carpel stamen corolla tube between the ovary and the other parts of the flower, except the sepals. This feature seems to be unique among the families of Asteridae (Erbar 1993). The unilocular gynoecium usually is interpreted to consist of two carpels (Cronquist 1981). Investigations by Erbar (1993) and Hansen (1992), however, revealed the existence of five ledges in the ovary which can be interpreted as rudimentary septa. Following this interpretation, the family has five carpels (Erbar 1993).

Floral Anatomy. The free corolla contains 10 parallel longitudinal vascular bundles. The commissural bundles are bifurcated below the corolla lobes and anastomose with the median bundles of the corolla lobes just below their apex (Gustafsson 1995; Gustafsson and Bremer 1995). Micromorphological characters of the corolla (petal epidermis patterns) are rather uniform in the Calyceraceae, the cells always being Senecioid. Cells are often long (more than 200 µm) and confluent. A transversely striate pattern prevails on the adaxial surface, while the abaxial pattern is mostly longitudinally striate although rugose, reticulate-rugose or glabrous cells also occur. The cells are generally distinctly sculptured on both surfaces (Hansen 1992).

Embryology. An integumentary tapetum is formed by the innermost layers of the one massive integument (Dahlgren 1915). The mature embryo

sac has eight nuclei; the polar nuclei fuse before fertilization. The seed, which is suspended from the top of the locule and fixed by a short funiculus near the upper end of the seed, contains a straight, terete embryo and abundant endosperm (Cronquist 1981). Endosperm development is cellular, and no haustoria are formed. The endosperm contains protein grains, rather than starch. The outer cells of the testa contain chloroplasts before the seed is mature. The radicula points towards the micropyle, i.e. the apex of the seed (Miers 1870). The pollen grains are binucleate when released. No periplasmodial tapetum is formed in the pollen sacs (Dahlgren 1915).

Pollen Morphology. Pollen grains of Calyceraceae are tricolporate. The colpi are very long, rendering the grains of some species sub-syncolporate. The colpus membrane is more or less granular. The pores are lalongate, the ends overlapping or joined, forming a colpus transversalis of irregular width in some species (Heusser 1971; Markgraf and D'Antoni 1978). Minute spinules are usually present on the pollen surface but rarely they are almost lacking. The exine has thickened ridges above the pores and rounded depressions in the mesocolpi. A granulate colpus margin (Skvarla et al. 1977) is prominent in many species. The pollen grains rarely exceed 30 µm in length and 20 µm in width, and are often rather irregularly shaped. The majority of pollen grains are at first glance spheroidal but, seen in equatorial view, they are irregularly rhomboidal (Hansen 1992). Prolate (elliptic, ellipsoidal) grains occur in a few species. Dimorphic grains are rare (*Boopis gracilis*) but shape can vary within species. Avetisjan (1980) distinguishes two pollen types in the family, the *Moschopsis*-type and the *Calycera*-type. They differ by the shape of pollen grains (polar view rounded, three-lobed, elliptical in equatorial view, pores elliptical in the *Moschopsis*-type, polar view irregularly hexagonal, equatorial view transversely elliptical, pores broad-elliptical (lalongate) in the *Calycera*-type) and by the shape of the colpi, especially by the ridges above the apertures, which are weakly to moderately thickened in the *Moschopsis*-type and strongly developed in the *Calycera*-type. The *Moschopsis*-type is regarded as primitive, and the *Calycera*-type as derived by the author. The pollen grains have TEM-patterns approaching the plesiomorphic Anthemoid pattern of Compositae, i.e. with distinct infratectal bacula and an infratectum. The tectum is massive and a cavus is lacking (Hansen 1992).

Karyology. Several chromosome numbers are known in the family. Stebbins (1977) suggested $x = 7$, 8 and 9 as base numbers. The only known diploid species of the family is an *Acicarpha* (DeVore 1994). All other species investigated are interpreted as being polyploid. Accepting this, species of *Calycera* and the species of *Boopis* based on $x = 7$ are mostly hexaploid or hexaploid-derived, or derived from tetraploids, and species of *Boopis* with the base number $x = 9$ are tetraploid or tetraploid-derived. In *Calycera*, $n = 21$ or 22, 17 and 13 are found in the Chilean species, while Argentinean species are all polyploids with $n = 21$. DeVore (1994) interprets the base number $x = 8$ as ancestral; $x = 7$ would then have originated by descending aneuploidy, and the counts in *Boopis* point to the other derived base number $x = 9$. However, the interpretation of karyotype evolution in Calyceraceae is inconclusive, due to lack of data and a well-supported phylogenetic hypothesis.

Pollination. Calyceraceae show secondary pollen presentation. The mechanism corresponds to the pump mechanism (Leins and Erbar 1990) as known from *Acicarpha*. This mechanism seems to prevail in some basal lineages of Asteraceae (Bremer 1994). Initially, the pollen grains are released into the cavity of the anther tube which is basally sealed by the tip of the style. The pollen is then extruded apically by the growing style. One major difference to the pump mechanism of Asteraceae is that the anthers are not fused over their entire length in many species, and are bent outwards at least in *Acicarpha tribuloides*.

Fruit, Seed and Seed Dispersal. The gynoecium consists basically of two carpels forming a compound, inferior, unilocular, pseudomonomerous ovary (Cronquist 1981). The fruit is an achene, crowned by the persistent lobes of the calyx. In some species, all lobes or some of them are enlarged and become indurated to spine-like structures. In *Calycera*, capitula are distinctly heterocarpic. In *Calycera eryngioides*, the smaller achenes are dispersed individually whereas those with elongated calyx lobes remain attached to the receptacle and are dispersed with the whole capitulum (DeVore 1994). *Acicarpha* is characterized by partly fused achenes which remain attached to the receptacle. The spine-like elongated calyx lobes point to epizoochorous dispersal. A spongy tissue in the pericarp may facilitate hydrochory or even anemochory.

Phytochemistry. Calyceraceae commonly produce iridoid compounds, e.g. seco-loganin (Jensen et al. 1975), but are not tanniferous. They lack proanthocyanins and presumably also ellagic acid. No latex or secretory cavities are known (Cronquist 1981). The seeds store inulin (Cronquist 1981; Bohm et al. 1995). Acetylenes (Mabry and Bohlmann 1977), sedoheptulose, aluminium accumulation, raphides, leucoanthocyanins, cyanogenic glycosides, saponins and l-inositol are absent (Gibbs 1974). For flavonoids, refer to Bohm et al. (1995).

Distribution and Habitats. The family is endemic to southern South America. Its range extends from the extreme south of the continent to southern Peru and Bolivia in the west and as far north as Bahia (Brazil) in the east. One species occurs in the Falkland Islands (Islas Malvinas). Most species grow in high-altitude arid habitats, e.g. open grassland and meadows, in the Andes of Chile and Argentina. A few species grow in coastal sand dunes. *Acicarpha tribuloides* grew in the south-western United States for some decades in the 19th century after it was introduced by man, but did not become naturalized there (DeVore 1991).

Subdivisions and Relationships in the Family. The generic classification of the family is unsatisfactory. Currently, six genera are widely accepted (Reiche 1901; Pontiroli 1963; Marticorena and Quezada 1985; Chiapella 1999). Possibly apomorphic characters have been identified for *Acicarpha*, *Calycera* and *Gamocarpha* but not for *Nastanthus*, *Boopis* and *Moschopsis* (Hansen 1992), and the diagnostic characters reported for these latter three genera proved to be unsuitable because of erroneous observations and misinterpretations of morphology. In the present treatment, *Boopis*, *Moschopsis* and *Nastanthus* are united under the oldest generic name, *Boopis*, in order to obtain recognizable genera. The relationships among the genera of the family are discussed in several papers without satisfactory result. The only unanimously accepted fact is that *Acicarpha* is distinct from the other genera by centripetal anthesis within the capitula and the presence of functionally male flowers in the centre of the receptacle. It is further believed (DeVore 1994) that *Calycera* and *Nastanthus* are closely related to each other (chromosome numbers), while the relationships of *Boopis*, *Gamocarpha* and *Moschopsis* remain uncertain (Hansen 1992). No formal phylogeny has been published for the family.

Phylogeny and Systematic Position of the Family. *Calycera herbacea*, the first species of Calyceraceae described (Cavanilles 1797), was placed in Dipsacaceae by Ruiz and Pavón in 1798, and the family was kept in Dipsacales by several taxonomists throughout the last two centuries. On the other hand, *Acicarpha tribuloides*, described by Jussieu in 1803, was included, although with doubts, in Asteraceae by the author. In 1816, Brown and Cassini independently recognized Calyceraceae as a separate family in oral presentations before the Linnaean Society and the French Académie des Sciences respectively, and placed it between Dipsacaceae and Asteraceae (see also Cassini 1817). The nomenclaturally valid publication of Calyceraceae was provided by Richard (1820). Miers (1870) underlined the close affinity between Asteraceae and Calyceraceae. Cladistic studies in Asteridae supported such relationship (Gustafsson 1996). The family is very likely to be the closest living relative of Compositae (Lundberg and Bremer 2003). This position is indicated not only by evidence from DNA sequence variation but also by characters such as pollen morphology, petal venation, morphology of the receptacle and receptacular bracts, and wood anatomy (DeVore and Stuessy 1995; Carlquist and DeVore 1998). Similarities with Dipsacales include the pendulous ovule, copious endosperm, morphology of capitula in the majority of Calyceraceae, and phytochemical features such as the absence of iridoid compounds from Asteraceae. This may have caused Dahlgren (1989) to place Calyceraceae in Dipsales. However, iridoids are found also in Goodeniaceae, a family closely related to Calyceraceae plus Asteraceae and Menyanthaceae. Lack of iridoids in Asteraceae may therefore be apomorphic for this family. Hansen (1992) and Erbar (1993) provide a summary of differences and similarities of Calyceraceae with various possibly related groups (see also Moore 1993). The molecular phylogenetic studies of Gustafsson and Bremer (1995) and Albach et al. (2001) showed Calyceraceae as sister to Asteraceae, while Calyceraceae are sister to Goodeniaceae in the combined 18S/*rbc*L analysis of Bremer et al. (2001), as they were in previous *rbc*L analyses (Cosner et al. 1994; Gustafsson et al. 1996). This latter position is supported by chemical features: both contain bis-secoiridoids of the sylvestroside type (Jensen et al. 1979; Capasso et al. 1996). The

combined analysis of morphology, *rbc*L and *ndh*F sequences confirmed the sister-group relationship between Calyceraceae and Asteraceae, while Goodeniaceae were placed as sister to these two (Bremer et al. 2001). Takhtajan (1997) established the order Calycerales, which is not recognized in systems which reflect the results of cladistic studies.

Economic Importance. Some species are weeds in South America (*Boopis gracilis*, *Boopis anthemoides*, *Acicarpha tribuloides*). Medicinal use of *Acicarpha tribuloides* has been reported (Capasso et al. 1996).

Key to the Genera

1. Capitula with dimorphic flowers, upper/central flowers functionally male, lower/outer flowers hermaphrodite; all achenes with spiny calyx lobes, outer achenes with united bases and also fused to the receptacle **1. *Acicarpha***
– Capitula with isomorphic flowers, all flowers hermaphrodite and fertile; achenes not united 2
2. Achenes dimorphic, some with spiny calyx lobes, some without **2. *Calycera***
– Achenes monomorphic, without spiny calyx lobes 3
3. Receptacular bracts fused into groups, these and involucral bracts around groups of flowers **3. *Gamocarpha***
– Receptacular bracts free or absent **4. *Boopis***

Genera of Calyceraceae

1. *Acicarpha* Juss.

Acicarpha Juss., Ann. Mus. Paris 2: 347 (1803).

Annual or perennial herbs; stems more or less branched, erect or procumbent, terminating in an inflorescence overtopped by lateral branches. Leaves petiolate or sessile, subamplexicaulous, undivided to pinnatifid, margin entire to dentate, leaf bases attenuate to auriculate. Capitula solitary, sessile or pedunculate; involucral bracts about five in one series, linear-oblong, unequal, similar to the uppermost cauline leaves, fused in their lower part; receptacle convex to conical; receptacular bracts free, linear to lanceolate. Flowers pentamerous, dimorphic, the outer (or lower) hermaphrodite, the upper (or central) functionally male; corolla with a long slender tube and an infundibuliform to campanulate limb deeply divided into five corolla lobes; stamens 5, enclosed, fused to the lower 2/3 of the corolla; anthers connate from base to middle, free in distal part and bent outwards at anthesis; achenes cylindrical to obconical, pentasulcate to prismatic, crowned by variously elongated spiny calyx lobes. Marginal achenes fused to the receptacle and united with each other. $2n = 16$. Three species in Brazil, Peru, Bolivia, Paraguay, Uruguay and Argentina.

2. *Calycera* Cav.

Calycera Cav., Icon. Pl. 4: 14 (1797).

Annual or perennial herbs, glabrous or weekly lanuginose; stems erect or decumbent. Leaves alternate or in rosettes, undivided to pinnatifid, spathulate to elliptical; margin entire to dentate-mucronate. Involucral bracts 4–7 in one series, sometimes with additional bracts, broadly triangular to linear-lanceolate, united to various degrees, entire or dentate; receptacle convex or subglobose; receptacular bracts lanceolate to linear or absent. Flowers hermaphrodite, tetramerous or pentamerous; corolla with a long tubular part and an infundibuliform to campanulate limb, or limb more or less truncate at base, abruptly narrowed into a short slender tube, upper part of limb divided to various degrees into four or five lobes; stamens 4 or 5, not exserted, inserted at the base or higher up in the corolla tube; anthers connate, bases rounded or sagittate, connectives sometimes with apical appendages; achenes cylindrical to obconical or prismatic, dimorphic, some crowned by short or long spiny calyx lobes, some with only very short calyx lobes, not spiny. $2n = 26, 24, 42, 44$. About 20 species, Andes of Bolivia, Chile and Argentina. Two subgenera, subg. *Calycera* and subg. *Leucocera* (Turcz.) Reiche, have been distinguished (Miers 1870; DeVore 1994).

3. *Gamocarpha* DC.

Gamocarpha DC., Prodr. 5: 2 (1836).

Perennial herbs, glabrous, some species stoloniferous. Leaves generally forming a rosette, entire or divided. Capitula surrounded by 6–12 involucral bracts, these and receptacular bracts more or less fused, forming chambers which contain several flowers. Bracts with triangular distal parts, fused in the lower part, entire or weakly lobed. Flowers pentamerous (occasionally tetramerous); corolla tube long, slender, with an infundibuliform to campanulate limb, corolla lobes long, or corolla cylindrical to infundibuliform, base sometimes abruptly narrowed into a short filiform tube, corolla lobes short; anthers subsagittate at base, connate in the lower part; achenes cylindrical to prismatic, ribs weak,

crowned by ovate to triangular non-spinescent calyx lobes. Six or seven species in Chile and Argentina.

4. *Boopis* Juss. Fig. 4

Boopis Juss., Ann. Mus. Natl. Hist. Nat. 2: 350 (1803).

Perennial or rarely annual herbs, glabrous; stems erect or decumbent, scapose or ramified. Leaves alternate or clustered in a rosette, entire to pinnatisect, linear-lanceolate, laciniate, dentate or pectinate, or spathulate with dentate or crenate lamina. Capitula terminal, solitary or in groups of few, then shortly pedunculate to almost sessile, sometimes densely surrounded by foliar leaves, rarely scapose. Terminal capitula sometimes overtopped by axillary shoots, in some species terminal and lateral scapes forming a disk-like to hemispherical syncephalium; involucral bracts 5–10, united from basis to middle or beyond, exceptionally free, triangular to lanceolate, sometimes laciniate; receptacle flat to convex or conical, inflated in some species; receptacular bracts free, linear to lanceolate, or absent. Flowers pentamerous or tetramerous, hermaphrodite, uniform within species; corolla with short or moderately long tube and cylindrical to infundibuliform or slightly campanulate limb, or with slender tube and limb consisting of lower infundibuliform part and distal, more or less campanulate part; corolla lobes mostly short, long in flowers with long tube; stamens five or four, anthers connate at their base, free in the upper half; achenes prismatic, 5- or 4-ribbed, ribs crowned by ovate or broadly lanceolate, acute, more or less rigid but not spiny calyx lobes. $2n$ = 36, 40, 42. About 30 species, some of them polymorphic, in Chile, Argentina incl. Islas Malvinas (Falkland Islands), very few in Brazil, Peru, Bolivia.

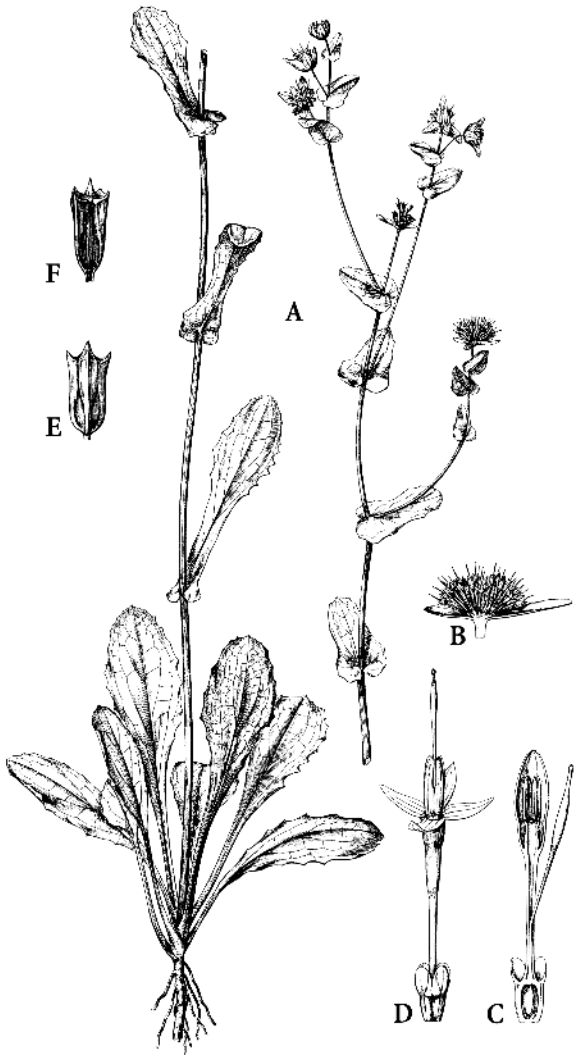

Fig. 4. Calyceraceae. *Boopis bupleuroides*. **A** Habit. **B** Inflorescence. **C** Flower bud, longitudinal section. **D** Open flower. **E** Fruit. **F** Fruit, longitudinal section. (Martius 1878)

Selected Bibliography

Albach, D.C., Soltis, P.S., Soltis, D.E., Olmstead, R.G. 2001. Phylogenetic analysis of Asterids based on sequences of four genes. Ann. Missouri Bot. Gard. 88: 163–212.

Avetisjan, E.M. 1980. Pollen morphology of the family Calyceraceae (in Russian). In: Sistematika i Évolyutsiya Vysshikh Rastenii. Leningrad: Nauka, pp. 57–64.

Baillon, H. 1880. Histoire des plantes, VII. Paris: Hachette.

Bohm, B.A., Reid, A., DeVore, M., Stuessy, T.F. 1995. Flavonoid chemistry of Calyceraceae. Canad. J. Bot. 73: 1962–1965.

Bremer, K. 1994. Asteraceae. Cladistics and classification. Portland, OR: Timber Press.

Bremer, K., Backlund, A., Sennblad, B., Swenson, U., Andreasen, K., Hjertson, M., Lundberg, J., Backlund, M., Bremer, B. 2001. A phylogenetic analysis of 100+ genera and 50+ families of euasterids based on morphological and molecular data with notes on possible higher level morphological synapomorphies. Pl. Syst. Evol. 229: 137–169.

Brown, R. 1817. Observations on the natural family of plants called Compositae. Trans. Linn. Soc. 12: 76–142.

Capasso, A., Urruñaga, R., Garofala, L. et al. 1996. Phytochemical and pharmacological studies on the medical herb *Acicarpha tribuloides*. Intl J. Pharmacog. 34. 255–261.

Carlquist, S., DeVore, M.L. 1998. Wood anatomy of Calyceraceae with reference to ecology, habit, and systematic relationships. Aliso 17: 63–76.

Cassini, H. 1817. Boopidées (Bot.). Dict. Sci. Nat. suppl. 5: 26–28.

Cavanilles, A.J. 1797. Icones et descriptiones plantarum, IV. Matriti: Regia Typographia.
Chiapella, J. 1999. Calyceraceae. In: Correa, M.N. (ed.) Flora Patagonica, VI. Buenos Aires: Colección científica del INTA, pp. 492–517.
Cosner, M.E., Jansen, R.K., Lammers, T.G. 1994. Phylogenetic relationships in the Campanulales based on *rbc*L sequences. Pl. Syst. Evol. 190: 79–95.
Cronquist, A. 1981. An integrated system of classification of flowering plants. New York: Columbia University Press.
Dahlgren, O. 1915. Über die Embryologie von *Acicarpha tribuloides* Juss. Svensk Bot. Tidskr. 9: 184–191.
Dahlgren, G. 1989. The last Dahlgrenogram. System of classification of dicotyledons. In: Tan, K. (ed.) The Davis and Hedge Festschrift. Edinburgh: University Press, pp. 249–260.
DeVore, M. 1991. The occurrence of *Acicarpha tribuloides* (Calyceraceae) in eastern North America. Rhodora 93: 26–35.
DeVore, M. 1994. Systematic studies of Calyceraceae. Ph.D. Thesis, Ohio State University, Columbus, OH.
DeVore, M., Stuessy, T.F. 1995. The place and time of origin of the Asteraceae, with additional comments on the Calyceraceae and Goodeniaceae. In: Hind, D.J.N., Jeffrey, C., Pope, G.V. (eds) Advances in Compositae systematics. Royal Botanic Gardens, Kew, pp. 23–40.
Erbar, C. 1993. Studies on the floral development and pollen presentation in *Acicarpha tribuloides* with a discussion of the systematic position of the family Calyceraceae. Bot. Jahrb. Syst. 115: 325–350.
Gibbs, R.D. 1974. Chemotaxonomy of flowering plants, vol. 2. Montreal: McGill-Queen's University Press.
Gustafsson, M.H.G. 1995. Petal venation in the Asterales and related orders. Bot. J. Linn. Soc. 118: 1–18.
Gustafsson, M.H.G. 1996. Phylogenetic hypotheses for Asteraceae relationships. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994, vol. 1. Royal Botanic Gardens, Kew, pp. 9–19.
Gustafsson, M.H.G., Bremer, K. 1995. Morphology and phylogenetic interrelationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae and related families (Asterales). Amer. J. Bot. 82: 250–265.
Gustafsson, M.H.G., Backlund, A., Bremer, B. 1996. Phylogeny of the Asterales sesu lato based on *rbc*L sequences with particular reference to the Goodeniaceae. Pl. Syst. Evol. 199: 217–242.
Hansen, H.V. 1992. Studies in the Calyceraceae with a discussion of its relationship to Compositae. Nordic J. Bot. 12: 63–75.
Heusser, C.J. 1971. Pollen and spores of Chile. Tucson, AR: University of Arizona Press.
Jensen, S.R., Nielsen, B.J., Dahlgren, R. 1975. Iridoid compounds, their occurrence and systematic importance in angiosperms. Bot. Notiser 128: 148–180.
Jensen, S.R., Lyse-Pedersen, S.E., Nielsen, B.J. 1979. Novel bis-iridoid glucosides from *Dipsacus sylvestris*. Phytochemistry 18: 273–277.
Jussieu, A.L. 1803. Mémoire sur l'*Acicarpha* et le *Boopis*, deux genres nouveaux de plantes de la famille des Cinarocéphales. Ann. Mus. Natl Hist. Nat. 2: 345–350.
Leins, P., Erbar, C. 1990. On the mechanisms of secondary pollen presentation in the Campanulales-Asterales-complex. Bot. Acta 103: 87–92.
Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–578.
Mabry, T.J., Bohlmann, F. 1977. Summary of the chemistry of the Compositae. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, I. London: Academic Press, pp. 1097–1104.
Markgraf, V., D'Antoni, H.L. 1978. Pollen flora of Argentina. Tucson, AR: University of Arizona Press.
Marticorena, C., Quezada, M. 1985. Catálogo de la flora vascular de Chile. Gayana (Bot.) 42: 5–157.
Martius, C.F.P. 1878. Flora Brasiliensis, vol. 6. London: Lovell Reeve.
Miers, J. 1870. Contributions to Botany, II. London: Williams and Norgate.
Moore, D.M. 1993. Calyceraceae. In: Heywood, V.H. (ed.) Flowering plants of the world. London: B.T. Bastford.
Pontiroli, A. 1963. Flora Argentina, Calyceraceae. Revista Mus. La Plata 9, Bot. 41: 175–214.
Reiche, K. 1901. Beiträge zur Systematik der Calyceraceen. Bot. Jahrb. Syst. 29: 107–119.
Richard, L.C. 1820. Mémoire sur une famille de plantes, dites les Calycérées. Mém. Hist. Nat. 6: 28–82.
Ruiz, H., Pavón, J. 1798. Systema vegetabilium florae peruvianae et chiliensis. Madrid: Gabrielis de Sancha.
Skvarla, J.J., Turner, B.L., Patel, V.C., Tomb, A.S. 1977. Pollen morphology in the Compositae and in morphologically related families. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, I. London: Academic Press, pp. 141–248.
Stebbins, L. 1977. Development and comparative anatomy of the Compositae. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, I. London: Academic Press, pp. 91–109.
Takhtajan, A. 1997. Diversity and classification of flowering plants. New York: Columbia University Press.

Campanulaceae

Campanulaceae Jussieu, Gen. Pl. 163 (1789), nom. cons.

T.G. Lammers

Herbaceous perennials, less often annuals or biennials, herbaceous or woody lianas (sometimes twining), pachycaul rosette plants, subshrubs, shrubs, treelets, or trees to 15 m tall, typically terrestrial, rarely aquatic or epiphytic, with milky (sometimes coloured) latex; stems simple to much branched, sometimes rhizomatous or acaulescent. Leaves estipulate, alternate, rarely opposite or whorled, commonly simple (pinnate when compound), entire, variously toothed, or sometimes dissected, petiolate or sessile, sometimes sheathing. Inflorescences monotelic or polytelic, commonly appearing racemose, paniculate, spicate, umbellate or capitate, the last sometimes involucrate, typically terminal or sometimes axillary, or the flowers solitary in an axillary or rarely terminal position; bracts foliose or reduced, rarely absent; pedicels often bracteolate. Flowers tetracyclic, commonly perfect, rarely imperfect and the plants dioecious or gynodioecious, with a specialized method of proterandrous secondary pollen presentation, rarely with extrafloral nectaries, sometimes resupinate. Calyx synsepalous, adnate to the ovary, forming a hypanthium, rarely free; lobes (3–)5(–10), valvate, sometimes with a reflexed appendage in each sinus. Corolla sympetalous, radially or bilaterally symmetric, most often some shade of blue or violet; lobes (4–)5(–10), valvate or rarely induplicate. Stamens equalling the number of corolla lobes, antesepalous, inserted at base of corolla tube, on rim of hypanthium or atop the inferior ovary, rarely epipetalous; filaments distinct or connate; anthers tetrasporangiate, dithecal, introrsely dehiscent by longitudinal slits, basifixed, rarely dorsifixed, distinct, connivent, or connate. Gynoecium syncarpous, 2–5(–10)-locular with axile placentation, rarely 1-locular with parietal, basal, or apical placentation; ovary inferior, rarely superior or nearly so, often crowned by an annular nectary; style solitary, pubescent below apex; stigma typically with as many lobes as ovary locules. Fruit a capsule, commonly apically loculicidal or laterally poricidal, or a berry. Seeds usually small, numerous; embryo small, straight; endosperm copious, cellular, oily or rarely starchy.

As circumscribed here, Campanulaceae comprise 84 genera and almost 2,400 species. The family is cosmopolitan, with representatives on six continents and several of the world's archipelagos.

Vegetative Morphology. Most Campanulaceae are polycarpic perennial herbs; in seasonally cold or dry climates, they overwinter as hemicryptophytes by means of basal rosettes or basal portions of the axis, or as geophytes by means of the stem base, rhizomes or tuberous roots. Among taxa which are monocarpic, an annual habit is commonest; relatively few are biennial (e.g. *Campanula medium*) or long-lived (e.g. *Lobelia wollastonii*).

Though Campanulaceae are primarily an herbaceous family, a significant number of taxa are woody to some degree (e.g. *Azorina*, *Centropogon*, *Cyanea*, *Heterochaenia*). Woody species are typically evergreen, branched or unbranched, and range in stature from subshrubs a decimetre or so tall (e.g. *Merciera*), to treelets and shrubs a meter or two tall (e.g. *Delissea rhytidosperma*), up to trees of 15 m (e.g. *Cyanea leptostegia*). Of special interest are the so-called giant rosette plants found in certain insular and montane habitats. These are pachycaul plants, often long-lived and pliestesial, of large stature and bulk, with dense apical rosettes of typically sessile leaves, large racemose inflorescences, and a hollow pith which narrows basipetally (e.g. *Lobelia rhynchopetalum*).

A number of species are lianas, either herbaceous or woody. Many simply sprawl over surrounding vegetation. Those which climb typically do so with twining stems (e.g. *Cyphia lasiandra*, *Siphocampylus convolvulaceus*). In *Canarina*, however, support is provided by the twining petioles and pedicels, while *Cyanea copelandii* climbs by adventitious roots produced at the nodes.

Roots typically are coarse, fibrous, and of adventitious origin, though in some genera (e.g. *Canarina*, *Codonopsis*, *Cyphia*, *Platycodon*) the primary root becomes fleshy, greatly enlarged and tuberous. Stem branching may be monopodial or sympodial. Mature herbs may have elongate multinodal shoots, or form basal rosettes; in seedlings of the former, the epicotyl is well developed whereas in the latter, it is distinctly shortened or lacking (Shulkina 1980). Many of the woody taxa form dense apical rosettes of leaves.

Leaves are generally dorsiventral (rarely centric) and conform to a dillenid pattern (Hickey and Wolfe 1975), with pinnate (craspedodromous or camptodromous) venation (rarely parallellodromous, e.g. *Siphocampylus smilax*). They lack stipules and may be petiolate or sessile. Phyllotaxy typically is alternate, with a 2/5 sequence, though in a few taxa the leaves are opposite (e.g. *Cyclocodon*) or whorled (e.g. *Ostrowskia*, *Siphocampylus orbignianus*).

Vegetative Anatomy and Ultrastructure. A major anatomical characteristic of the family is the anastomosing network of articulated lactifers associated with the phloem of leaves, stems, and floral organs. The viscous latex produced typically is copious and white but in some species it is coloured, e.g. tan (*Lobelia excelsa*), bright orange (*L. cordifolia*) or canary yellow (*Cyanea leptostegia*).

In the stem, xylem and phloem typically form a continuous cylinder, rather than discrete bundles; medullary bundles are commonly present, cortical bundles rarely. The xylem lacks tracheids and fibre-tracheids but libriform fibres are common. Vessels typically have simple perforation plates (less often scalariform) and simple pits; helical thickenings are absent (Carlquist 1969, 1992). Internal phloem is lacking, as are phloem transfer cells. Plastids found in the sieve-elements lack proteinaceous inclusions, i.e. they are S-type. Axial parenchyma is scanty vasicentric, and sclerenchyma is generally lacking from the pericycle. Nodes are unilacunar.

Stomates are anomocytic and usually found on both surfaces of the leaf, though sometimes they are solely abaxial. Hydathodes are common, often associated with marginal teeth of leaves. Xerophytic species often have a fibrous hypoderm. The mesophyll typically comprises one or two palisade layers. Mesophyll cells of certain Campanuloideae (*Campanula*, *Edraianthus*, *Jasione*, *Phyteuma*, *Trachelium*) contain protein intranuclear inclusions of a unique fibrillar structure (Bigazzi 1986), though these are absent from other genera of Campanuloideae (*Asyneuma*, *Canarina*, *Legousia*, *Petromarula*, *Platycodon*, *Wahlenbergia*) as well as from Lobelioideae (*Downingia*, *Isotoma*, *Lobelia*, *Solenopsis*). Cystoliths occur occasionally.

Trichomes typically are unicellular or sometimes uniseriate. Arbusculiform (dendritic) trichomes (Batterman and Lammers 2004) characterize many species of *Centropogon* (e.g. sect. *Siphocampyloides*) and a few in other genera (e.g. *Siphocampylus furax*, *Cyanea calycina*). Some *Cyanea* (e.g. *C. tritomantha*) have prickles on the vegetative and floral organs which represent a unicellular trichome with a thick secondary wall, atop an enlarged multicellular mass of epidermal cells (Carlquist 1962). Glandular trichomes are unknown.

Inflorescence Structure. Flowers of Campanulaceae may occur singly (commonly in leaf axils, rarely at the stem apex) or may be aggregated into diverse types of monotelic or polytelic inflorescences, commonly in a terminal position (Philipson 1948; Carolin 1967). Most have a racemose, paniculate or spicate appearance but are actually more complex and often composed of essentially cymose subunits. Corymbose, umbellate and capitate inflorescences are not uncommon and, in *Cryptocodon*, *Jasione*, *Treichelia* and some species of *Campanula* (e.g. *C. glomerata*), the capitate inflorescence may be subtended by an involucre. In *Ruthiella*, flowers are epiphyllous.

Flowers of Lobelioideae, with few exceptions (e.g. *Downingia laeta*, *Monopsis stellarioides*), are resupinate through torsion of the pedicel; in genera with sessile flowers (e.g. *Downingia*, *Grammatotheca*), it is the hypanthium which undergoes torsion. As a result, the visually dorsal components of the flower arise from the ventral portion of the floral primordium. Throughout this treatment, the terms "dorsal" and "ventral" refer to the apparent orientation of fully formed structures, irrespective of resupination.

Floral Structure and Anatomy. Flowers are commonly complete (tetracyclic) and perfect (bisexual), though a few species are dioecious (e.g. *Lobelia dioica*) or gynodioecious (e.g. some *L. siphilitica*). Proterandry characterizes the family and is correlated with specialized mechanisms for secondary presentation of pollen to floral visitors (see below). Cleistogamy occurs in some genera of Campanuloideae (*Githopsis*, *Heterocodon*, *Trioda-*

nis, and a few *Campanula*, e.g. *C. dimorphantha*) and Lobelioideae (*Howellia*, *Legenere*).

Typically, the calyx, corolla and androecium are isomerous and pentamerous. Certain Campanuloideae have more than 5 units in a whorl: 6 (*Canarina*, *Cyclocodon lancifolius*), 7 (*Ostrowskia*) or 8–10 (*Michauxia*). A few taxa are tetramerous (e.g. *Cyananthus hookeri*, *Cyclocodon parviflorus*, *Echinocodon*, *Phyteuma tetramerium*). In cleistogamous flowers, sepals are often as few as 3 and the corolla is typically absent.

In Campanuloideae, the odd (unpaired) sepal originates in a dorsal (posterior) position on the primordium, while in the remainder of the family, it arises in a ventral (anterior) position; in Lobelioideae, however, floral resupination brings it into a visually dorsal position at anthesis. The sepals are connate for a portion of their length and (except in *Cyananthus*) this connate basal portion is adnate to the basal portions of the corolla and androecium, forming a hypanthium of appendicular origin (Kaplan 1967). This hypanthium is adnate to the ovary, typically for its entire length, thus placing the ovary in an inferior position relative to the other whorls. In some taxa, however, the adnate hypanthium is shorter than the ovary, i.e. a portion of the ovary extends above the rim of the point of insertion of the calyx lobes. In *Diastatea*, *Unigenes*, and occasional species of *Siphocampylus* (e.g. *S. reflexus*), *Lobelia* (e.g. *L. xalapensis*) and *Wahlenbergia* (e.g. *W. welwitschii*), the hypanthium is reduced to such a degree that the ovary appears nearly superior. *Cyclocodon* is unique in having the calyx lobes inserted at the base of the hypanthium; in some species of *Codonopsis* (e.g. *C. javanica*), they are inserted at its middle. The anatomy of this bizarre situation has not been studied in detail. In some taxa (e.g. *Campanula alliariifolia*, *Lobelia appendiculata*, *Zeugandra*), the calyx bears a reflexed appendage or auricle in each sinus.

The epigynous portions of the petals are likewise connate for some part of their length, typically half or more. This fusion is the result of early sympetaly: the petals arise on a ring primordium or are already connected at initiation. In some genera (e.g. *Asyneuma*, *Dialypetalum*, *Jasione*, *Michauxia*), the corolla tube may be so short that the flower appears choripetalous. The corollas of *Physoplexis* and *Phyteuma* are also of this sort but the tips of the lobes are connate or coherent apically, forming a tube; the medial portion of the corolla is bowed out between this apical tube and the base of the corolla, forming five prominent fenestrations. In some species of Lobelioideae (e.g. *Lobelia fenestralis*), the corolla tube bears a single lateral fenestration on each side. Venation of the petals consists of a prominent midvein (marginal veins may also be present) which anastomoses into a dense reticulum distally (Gustafsson 1995). Radial symmetry (actinomorphy) characterizes the corolla in Campanuloideae, and is expressed in a broad diversity of corolla shapes, including campanulate, infundibular, urceolate, tubular, salverform, and rotate. Bilateral symmetry (zygomorphy) characterizes the remaining subfamilies; the degree of zygomorphy varies from scarcely perceptible (e.g. *Dialypetalum*, some Cyphioideae) to pronounced (e.g. Cyphocarpoideae, most *Lobelia*). Most are bilabiate, with 3 ventral and 2 dorsal corolla lobes (3 dorsal and 2 ventral in non-resupinate taxa); some may form a definite palate on the ventral lip (e.g. *Lobelia coronopfolia*). Unilabiate corollas also occur, with all 5 lobes in a ventral position (e.g. *Clermontia peleana*); in such flowers, the five lobes are sometimes coherent at their apices (e.g. *Lobelia tupa*). Cyphocarpoideae are characterized by a unique bilabiate pattern, with 1 cucullate dorsal lobe and 4 ventral lobes. Nectar spurs are found in *Heterotoma* and some *Lobelia* (e.g. *L. goldmannii*). The commonest colours are various shades of blue and violet, often with undertones of rose or mauve. Other colours include pink (e.g. *Lobelia bridgesii*), red (e.g. *L. cardinalis*), orange (e.g. *Canarina canariensis*), yellow (e.g. *Musschia aurea*), green (e.g. *Clermontia kakeana*) and white (e.g. *Hippobroma longiflora*). Bicoloured flowers are not uncommon, particularly among Lobelioideae (e.g. *Centropogon granulosus*, *Lobelia laxiflora*).

Stamens are antesepalous (i.e. alternating with the corolla lobes) and inserted at the very base of the corolla tube, on the rim of the hypanthium or atop the inferior ovary. In a few genera (*Cyphocarpus*, *Rhigiophyllum*, *Siphocodon*), the filaments are inserted higher on the corolla tube, apparently through adnation of the basal portions of the filaments. Among Campanuloideae, the bases of the filaments often are expanded and elaborated in diverse ways; though not connate, they may cohere in such a way that a chamber is formed over the nectary atop the ovary. In *Nemacladus* and *Parishella* the filaments have unique multicellular appendages. Anthers are tetrasporangiate, basifixed (dorsifixed in *Berenice*), and commonly dehisce introrsely by longitudinal slits. In Lobelioideae, the anthers (and distal portions of their filaments) are connate, forming a ventrally

oblique tube around the style into which the pollen is shed. The two ventral (sometimes all five) anthers typically bear a tuft of stiff trichomes at the mouth of this tube. In Nemacladoideae and most Cyphioideae, the filaments are connate for part of their length but the anthers are distinct. In many Campanuloideae, the anthers cohere around the style but separate following pollen discharge. In the few Campanuloideae with connate anthers (e.g. *Campanula cretica*), the tube formed is symmetrical, not oblique.

Carpels are fully connate, forming an ovary which is characteristically inferior. Among Campanuloideae, a 3-locular ovary is most common; some taxa have 5 locules, others have only 2 (sometimes reduced to 1); some genera (e.g. *Michauxia*, *Ostrowskia*) appear to have more than 5 (up to 10) due to intrusive partitions from the carpellary midribs. Among the other subfamilies, a 2-locular ovary is the general rule, though in some taxa this is reduced to a single locule. Each locule typically contains several to many ovules; in 2–5(–10)-locular ovaries, placentation is axile whereas in 1-locular ovaries (e.g. *Legenere*) it is parietal. In some genera, the number of ovules per locule is reduced to a few or even 1, in which case placentation may be basal (e.g. *Unigenes*) or apical (e.g. *Rhigiophyllum*). In most of the subfamilies, the single style is topped by stigmatic branches equal to the number of carpels in the gynoecium. The exception is Cyphioideae, which feature a unique stigmatic cavity which is fluid-filled and communicates with the outer air by means of a lateral aperture (Leins and Erbar 2003).

Embryology. Anther wall development follows the Dicotyledonous pattern, forming a single middle layer (Rosén 1932). Microsporogenesis is simultaneous, the tetrads tetrahedral or isobilateral. Fibrous thickenings are found in the endothecium. The tapetum is of the glandular (secretory) type, and the tapetal cells are binucleate. Pollen grains may be either binucleate or trinucleate when shed.

Ovules are anatropous, unitegmic, and tenuinucellar. Embryo sac formation is monosporic and of the Polygonum type (Tobe and Morin 1996). Upon coming in contact with the embryo sac, the inner layer of the integument develops as an endothelium (integumentary tapetum). Embryogenesis follows the Solanad pattern. Endosperm formation is cellular ab initio (Rosén 1949); the endosperm typically is copious and oily (starchy in some Campanuloideae). Haustoria form at both the chalazal and micropylar ends, and are equally aggressive. No hypostase forms.

Pollen Morphology. Pollen grains are spheroidal or variously compressed (oblate or prolate). Tricolporate pollen characterizes Cyphioideae, Cyphocarpoideae, Lobelioideae and Nemacladoideae (6-colpate in *Parishella*), though the pores may be lacking (i.e. the grain is 3-colpate) in some Lobelioideae (Chapman 1966; Dunbar 1984). Campanuloideae show greater diversity. In most genera, grains are 3–4(–5)-porate (6-porate in *Githopsis*). Pantoporate grains with 8, 12 or 14–20 pores characterize a few North American species of *Campanula* (e.g. *C. americana*, *C. exigua*). Other genera are 3–6-colporate (*Canarina*, *Platycodon*) or 6–10-colpate (*Cyananthus*, *Ostrowskia*). Surface ornamentation is variable (Dunbar 1975). Spinules are all but ubiquitous on porate grains but reduced to verrucae in the colpate and colporate Campanuloideae. Spinules also characterize Cyphioideae and Cyphocarpoideae but are lacking in Lobelioideae and Nemacladoideae. Pollen grains are dispersed as monads (tetrads in *Namacodon*).

Karyology. Chromosome numbers have been counted in 415 species of Campanuloideae. The commonest by far is $2n = 2x = 34$, accounting for about 42% of the published counts; another 13% are presumed polyploid derivatives: $2n = 4x = 68$ and $2n = 6x = 102$. A base number as large as $x = 17$ may well have been derived from some smaller number by aneuploidy following polyploidization, or by allopolyploidy. Other numbers which have been reported are $2n = 12$, 14, 16, 18, 20, 22, 24, 26, 28, 30, 32, 36, 38, 40, 42, 46, 48, 50, 52, 54, 56, 58, 60, 68, 70, 72, 80, 84 and 90 (Gadella 1966). Of particular significance is the occurrence of $2n = 2x = 14$ in *Cyananthus*, the only genus of the subfamily characterized by a truly superior ovary, which suggests $x = 7$ for the family. *Codonopsis* and *Echinocodon* with $2n = 2x = 16$, and *Platycodon* with $2n = 2x = 18$ may represent lineages with $x = 8$ and $x = 9$ respectively. Ancient hybridization of such plants could have yielded the $x = 17$ found in much of the rest of the subfamily.

About 170 species of Lobelioideae have been counted (Lammers 1993). Over three-fourths have $2n = 2x = 14$ or its presumed polyploid derivatives, $2n = 4x = 28$, $2n = 6x = 42$, $2n = 10x = 70$ and $2n = 20x = 140$. The base number of the subfamily thus appears to be $x = 7$. Other numbers reported are $2n = 12$, 16, 18, 20, 22, 24, 26 and 38. Diversifica-

tion in some taxa has been accompanied by significant aneuploidy, e.g. *Downingia* with $2n = 2x = 12$, 16, 18, 20, 22 and 24, and *Lobelia* sect. *Delostemon* with $2n = 2x = 12$, 14, 16, 18, 20 and 22.

Cyphioideae and Nemacladoideae have $2n = 2x = 18$ in the two species of each which have been examined, suggesting a base number of $x = 9$. No chromosome numbers are known for Cyphocarpoideae.

Pollination and Reproductive Systems. A major characteristic of the flowers of Campanulaceae is their specialized mechanism for secondary pollen presentation, i.e. presentation of pollen to potential pollinators on the style or other floral structures, rather than directly from the anther (Carolin 1960; Erbar and Leins 1989, 1996; Leins and Erbar 1990). Key aspects of this phenomenon in Campanulaceae are the proterandry of the flowers, the introrse discharge of pollen from the anthers, and the gathering of the stamens around the style by coherence or connation. The combination of these features results in deposition of pollen onto the style prior to its elongation and the maturation of the stigma. Here, the pollen is typically held by some sort of hairs. Those found in subfamilies with merely coherent stamens are dispersed along a significant portion of the length of the style. In such plants, pollinators pick up pollen from the style. The hairs of at least some Campanuloideae are able to invaginate as a means of dislodging adherent pollen grains (Shetler 1979). In the syngenesious Lobelioideae, however, the stylar hairs are concentrated into a ring just below the unreceptive stigmatic lobes. As the style lengthens through the anther tube, these hairs sweep the accumulated pollen load ahead of it towards the tube's orifice. In most lobelioid genera, the dorsal anthers are longer than the ventral, occluding the orifice, and the ventral anthers are tipped by tufts of stiff trichomes. Pressure builds up on the pollen load within the anther tube as the expanding style pushes it forwards. When a pollinator searching for nectar inadvertently depresses the stiff trichomes at the orifice of the anther tube, the orifice is levered open and a load of pollen discharged onto the foraging animal. A somewhat similar mechanism characterizes the campanuloid genera *Phyteuma* and *Physoplexis*, with the coherent or connate tips of the corolla lobes replacing the anther tube.

Most species are zoophilous. Those with actinomorphic corollas may be visited by a broad suite of generalized insects, including bees, flies, wasps, butterflies and settling moths. Species with zygomorphic corollas have a more restricted range of specialized, not infrequently vertebrate vectors. Ornithophily is well documented among Lobelioideae, involving both nectarivorous passerines (e.g. *Clermontia*, *Lobelia* sect. *Rhynchopetalum*) and hummingbirds (e.g. *Centropogon*, *Siphocampylus*). Chiropterophily has been reported in *Burmeistera* and *Siphocampylus*, while the long slender corollas of *Brighamia*, *Hippobroma* and two species of *Burmeistera* (Lammers 2002) appear adapted to sphingophily.

Autogamy is also an option for some taxa. Some Campanuloideae (e.g. *Githopsis*, *Triodanis*) and Lobelioideae (e.g. *Howellia*, *Legenere*) bear reduced cleistogamous flowers in addition to normal chasmogamous ones. Certain, otherwise zoophilous lobelioid flowers will self-pollinate if the pollen load is not removed by the time the carpellate phase of the proterandrous flower begins. As the stigmatic lobes spread and recurve, they eventually come into contact with the pollen-bearing ring of hairs on the style just below.

Fruit and Seed. Most Campanulaceae form capsular fruits, which typically open by valves, slits or pores, located either at the apex of the ovary (i.e. above the calyx lobes) or on the lateral walls of the hypanthium (i.e. below the calyx lobes). Capsules in a few genera (e.g. *Craterocapsa*, *Lysipomia*, *Parishella*) open by an operculum.

In some genera, dehiscence is arrested. The pericarp may become papery, forming a capsule which releases its seeds only by irregular rupture or decomposition (e.g. *Cyphocarpus*, *Legenere*, *Peracarpa*), or it may become fleshy, forming a variously coloured berry (e.g. *Canarina*, *Clermontia*), which sometimes may be quite inflated (e.g. *Burmeistera glabrata*). The fruit is a schizocarp in *Theodoravia*. Winged seeds are of sporadic occurrence in the family (e.g. *Ostrowskia*, *Trematolobelia*, some *Cyphia*). Seed germination is phanerocotylar.

Dispersal. The genera with fleshy fruits are obviously adapted to endozoochory, but seeds from dry fruits have no apparent adaptation for dispersal, aside from their small size. The few species with winged seeds may be presumed to be anemochorous to some degree.

Phytochemistry. In Campanulaceae, starch is replaced as a storage carbohydrate by inulin. Pyri-

dine alkaloids such as lobeline commonly accumulate in the latex of Lobelioideae but appear to be all but absent from the other subfamilies. Among Campanuloideae, polysterols apparently take their place. Some species produce polyacetylenes. Those isolated from Campanulaceae are aliphatic with 14 carbon atoms; the tetrahydropyranes are unique to the family. Campanulaceae do not produce iridoids nor sesquiterpene lactones.

Caffeic acid is a common phenolic constituent of Campanuloideae, primarily as esters with quinic acid, but is lacking from Lobelioideae where it is seemingly replaced by chelidonic acid; *p*-coumaric acid is likewise common in Campanuloideae but absent from Lobelioideae. Other phenolics reported from various Campanulaceae include quercetin, kaempferol, ferulic acid, cyanidin, sinapic acid and anthocyanins. Ellagic acid, myricetin, leucodelphinidin and leucoanthocyanins are absent from the family as a whole. A few species are cyanogenic, due to the presence of tyrosine-derived triglochin (Tjon Sie Fat 1978). Saponins are scarce and known primarily from *Platycodon*.

Subdivision of and Relationships Within the Family. In its broadest circumscription (e.g. Schönland 1889; Takhtajan 1980), the family includes not only the genera treated here but also *Pentaphragma* Wallich ex G. Don (see Pentaphragmataceae) and *Sphenoclea* Gaertn. (see Sphenocleaceae). In its narrowest circumscription (e.g. Shetler and Morin 1986; Kolakovskii 1994; Takhtajan 1997), it includes only those genera treated here as Campanuloideae. The intermediate circumscription adopted here (following Wagenitz 1964, and Cronquist 1981) is supported by phylogenetic analyses of both morphological and molecular data (Cosner et al. 1994; Gustafsson and Bremer 1995; Gustafsson et al. 1996; Bremer and Gustafsson 1997; Kårehed et al. 1999; Lundberg and Bremer 2003). In all these analyses, the taxa included here as Campanulaceae form a monophyletic group, whereas *Sphenoclea* and *Pentaphragma* consistently fall outside this clade, sometimes at a considerable distance.

The genera of Campanulaceae typically have been divided among three subordinate groups, ranked as tribes (Bentham 1876) or more commonly subfamilies (Schönland 1889; Wagenitz 1964; Wimmer 1968): Campanuloideae, Cyphioideae and Lobelioideae. However, Cyphioideae as traditionally circumscribed (i.e. to include *Cyphia*, *Cyphocarpus*, *Nemacladus*, *Parishella* and *Pseudonemacladus*) are almost certainly not monophyletic. Though exact relationships remain uncertain, it is clear that the traditional Cyphioideae comprise three disparate evolutionary lineages, based on morphological (Bentham 1875; Lammers 1992; Gustafsson and Bremer 1995), palynological (Dunbar 1975, 1984) and molecular data (Cosner et al. 1994; Lundberg and Bremer 2003). To remedy this situation, these five genera have been divided among three subfamilies (Lammers 1998a): Cyphioideae (*Cyphia*), Cyphocarpoideae (*Cyphocarpus*) and Nemacladoideae (*Nemacladus*, *Parishella* and *Pseudonemacladus*).

Several divergent classifications have been proposed for the genera within Campanuloideae. Schönland (1889) divided them among three subtribes, based on features of the ovary and mature fruit; Yeo (1993) accepted this classification but employed tribal rank. In Platycodoneae Yeo, the five carpels alternate with the calyx lobes. In the other two tribes, the carpels are fewer than the calyx lobes or, if isomerous, are positioned opposite the calyx lobes. In Campanuleae Dumort., dehiscence is lateral, i.e. the capsule opens below the calyx lobes, whereas in Wahlenbergieae Endl., dehiscence is apical, i.e. the capsule opens above the calyx lobes.

Fedorov (1957) proposed a new system which accounted only for genera in the Soviet Union. It was "based primarily on the different modes of dehiscence of the capsule, the shape of the corolla and aggregate characters, determining general similarity." In it, four tribes (Michauxieae Fed., Ostrowskieae Fed., Peracarpeae Fed., and Phyteumeae Dumort.) were segregated from Campanuleae, and two more (Edraiantheae Fed., Jasioneae Dumort.) from Wahlenbergieae; in addition, Platycodoneae were subsumed into Wahlenbergieae. This system was applied to the species of China by Hong et al. (1983), with the addition of one tribe, Cyanantheae Meisn.

More recently, three additional classifications have been proposed. Kolakovskii (1987, 1994) recognized four subfamilies within Campanulaceae s. str.: Prismatocarpoideae Kolak., Canarinoideae Kolak. (two tribes), Wahlenbergioideae (Endl.) Kolak. (10 tribes) and Campanuloideae (nine tribes); only Old World genera were covered, leaving unknown the disposition of the North American endemics *Githopsis*, *Heterocodon* and *Triodanis*. Takhtajan (1997) likewise divided Campanulaceae s. str. into four subfamilies: "Cyananthoideae",

nom. invalid. sub Art. 36.1 (three tribes); Ostrowskioideae (Fed.) Takht.; Canarinoideae Kolak.; and Campanuloideae (13 tribes). Hong (1995) tentatively divided the family into six unnamed groups: the *Cyananthus* group (two subgroups), *Platycodon* group (two subgroups), *Ostrowskia* group, *Wahlenbergia* group (four subgroups), *Jasione* group and *Campanula* group (three subgroups).

Lobelioideae have not received as much classificatory attention. Presl (1836) recognized three tribes, based largely on fruit characteristics. Delisseeae C. Presl comprised genera with baccate fruit, versus the dehiscent fruits of the other two. Those of Clintonieae C. Presl (nom. illegit. sub Art. 19.5) had a single locule, those of Lobelieae Rchb., two locules. De Candolle (1839) modified this system by dividing the 1-locular genera between those with an elongate laterally dehiscent capsule (Clintonieae) and those with a more isodiametric pyxicidal capsule (Lysipomieae A. DC.). In his monograph of the subfamily, Wimmer (1943, 1953, 1968) merged Clintonieae, Lysipomieae and Lobelieae. As such, he recognized only two tribes: Delisseeae with baccate, and Lobelieae with dehiscent fruits. The former was divided into two subtribes, the latter into nine. In as much as *Lobelia* and *Isotoma* as here circumscribed include both baccate and capsular species, this classification is scarcely tenable.

In summary, there is a lack of consensus among authors who have proposed classifications of Campanuloideae, compounded by a lack of attention to this topic in Lobelioideae. None of the existing classifications has been expounded in great detail, nor has any been tested through phylogenetic analysis and/or the addition of molecular data. For these reasons, no formal classification below the rank of subfamily is employed here.

Affinities. Campanulaceae traditionally have been assigned to Campanulales. The varying circumscriptions and taxonomic history of this order have been discussed in detail by Lammers (1992). In that summary, other families assigned to the order were Asteraceae, Brunoniaceae, Calyceraceae, Goodeniaceae, Menyanthaceae, Pentaphragmataceae and Sphenocleaceae. Since that time, phylogenetic analyses of DNA sequences (Olmstead et al. 1992, 1993; Chase et al. 1993; Michaels et al. 1993; Cosner et al. 1994; Gustafsson et al. 1996; Bremer and Gustafsson 1997; Kårehed et al. 1999; Lundberg and Bremer 2003) have consistently shown that (1) these families, with the exception of Sphenocleaceae, do indeed form a monophyletic group; (2) Stylidiaceae and Donatiaceae, excluded to Ericales or Stylidiales by Lammers (1992), belong to this lineage; and (3) additional families traditionally assigned to Saxifragales or Cornales also belong to this lineage (here called Asterales, despite Rec. 16B.1). Although a complete evaluation of this expanded circumscription in light of non-molecular data has not been completed, preliminary studies (Gustafsson and Bremer 1995; Lundberg and Bremer 2003) suggest that it could be supported by morphology.

Within Asterales, relationships are not yet fully resolved. In some studies (Cosner et al. 1994), Stylidiaceae were shown to be the sister group of Campanulaceae whereas in others (Kårehed et al. 1999; Lundberg and Bremer 2003), Pentaphragmataceae were sister to Campanulaceae. However, each of these studies utilized slightly different sets of taxa.

Distribution and Habitats. Campanulaceae taken as a whole are cosmopolitan in distribution, with representatives on all six continents and many oceanic islands, from the tropics to the frigid zones. However, the subfamilies are not evenly distributed. The three smaller subfamilies are endemic to rather restricted areas: Cyphioideae to southern Africa, Cyphocarpoideae to central Chile, and Nemacladoideae to south-western North America. The two major subfamilies, Campanuloideae and Lobelioideae, have much wider distributions but are largely non-overlapping. In general, Campanuloideae are found primarily in the temperate zones of the Old World, whereas Lobelioideae are distributed predominantly in the world's tropical and subtropical zones. For example, South America is home to approximately 575 species of Lobelioideae but only 10 Campanuloideae, while Europe harbours 275 Campanuloideae but only 8 Lobelioideae.

For the family as a whole, Africa and South America each has about one-fourth of the species; 18% are Asian, 11% European, 11% North American, 6% Polynesian and 4% Australasian. Specifically, the greatest concentration of diversity occurs in southern Africa, where 18 genera and nearly 400 species occur. This large total is due to the fact that this is the only region to have significant numbers of both Campanuloideae and Lobelioideae, as well as all Cyphioideae. Other major centres of diversity are the Andes of South America, with over 500 species of Lobelioideae, and Eurasia between the Mediterranean and the Himalayas, where the Campanuloideae are similarly diverse. Particularly

notable is the presence of over 130 endemic species of Lobelioideae (almost 6% of the family) on the small but highly isolated Hawaiian islands.

Ecologically, the family is extremely diverse. The majority of species are mesophytes, many occurring in montane habitats. Though exceptions are numerous, there is a discernible trend among Campanuloideae for more open habitats, especially meadows, while many Lobelioideae tend to be associated with forested areas, particularly rainforests and cloud forests. Some of the latter are facultative epiphytes (e.g. *Clermontia*). The species of *Lobelia* which have adapted to the alpine conditions in the mountains of East Africa (e.g. *L. rhynchopetalum*, *L. telekii*) are particularly noteworthy.

A significant number of taxa grow under xeric conditions, either as sclerophyllous shrubs and subshrubs (e.g. *Roella*, *Merciera*), by developing underground storage organs (e.g. *Cyphia*) or by adopting an annual habit (e.g. *Cyphocarpus*, *Nemacladus*). A few species are rooted freshwater hydrophytes, growing submersed in shallow water. *Howellia* is cabomboid in habit, with flimsy stems and leaves, while *Lobelia dortmanna* is isoetid, with a basal rosette of stiff linear aerenchymatous leaves and emergent scapose inflorescences. *Downingia* and its allies *Legenere* and *Porterella* have exploited seasonally dry, vernal pool habitats. A number of species (e.g. *Lobelia boykinii*, *Siphocampylus verticillatus*) grow in saturated soil of marshes, bogs, and other wetland habitats.

Palaeobotany. The sole fossil remains ascribed to Campanulaceae are seeds from the Miocene of Poland, described by Lancucka-Srodoniowa (1977, 1979) as *Campanula palaeopyramidalis* and "*Campanula* sp.".

Economic Importance. The primary economic value of the Campanulaceae is in horticulture. Many species are cultivated as ornamentals and commonly available in the home gardening trade. Those best known to the average grower are the large perennial species of *Campanula* planted in beds and borders (e.g. *C. persicifolia*, *C. carpatica*, *C. glomerata*); *Lobelia cardinalis*, *Platycodon grandiflorus* and *Trachelium caeruleum* are used similarly. *Lobelia erinus* is a standard annual for bedding, window boxes and hanging baskets, while biennial *Campanula medium* is a staple of old-fashioned cottage gardens. Other genera (e.g. *Adenophora*, *Azorina*, *Brighamia*, *Canarina*, *Codonopsis*, *Isotoma*, *Jasione*, *Michauxia*, *Phyteuma*, *Wahlenbergia*) are cultivated to a lesser extent, primarily by those who fancy the rare and unusual. *Favratia zoysii* and the many dwarf species of *Campanula* (e.g. *C. alpestris*, *C. arvatica*, *C. waldsteiniana*) are quite popular with rock garden and alpine enthusiasts. Compared to many horticultural groups (e.g. *Rosa*, *Tulipa*), Campanulaceae have been only moderately affected by selective breeding and cultivar development, and even less by hybridization. Most of the family's garden representatives are not far removed from their wild relatives, and are readily referred to naturally occurring species.

In addition to ornament, a few species are cultivated as comestibles. *Campanula rapunculus*, the rampion or rapunzel, has been grown as a vegetable in Europe, for both its young leaves and its roots, but the cultivars with sweet, well-developed taproots have largely been lost. *Platycodon grandiflorus* has been used similarly in eastern Asia.

The family also produces several pharmaceuticals. *Lobelia inflata* is the commercial source of lobeline, a pyridine alkaloid used in anti-smoking therapy and formerly in the treatment of bronchial asthma and as a respiratory stimulant. The roots of *Codonopsis*, primarily *C. pilosula*, are the source of *dang-shen*, a mainstay of traditional Chinese medicine. A popular substitute for the more costly ginseng, like that drug it is employed as a tonic for fatigue, loss of appetite, and weakness. Research has demonstrated that the raw extract promotes digestion, strengthens the immune system, dilates peripheral blood vessels and inhibits adrenal cortex activity, but the active principle has to date not been isolated. The root of *Platycodon grandiflorus* yields another important Asian drug, *jie-geng* or *kikyo*, much used as an expectorant and antitussitive; recent studies have shown it to also have analgesic, antipyretic, anti-inflammatory and antibacterial properties. The active principle appears to be a saponin (platycodin or kikyosaponin). Various other species of the family have been reported to have local usages in folk medicine, particularly among non-industrialized populations, but have not been researched in detail nor exploited commercially.

Classification of Campanulaceae

I. Subfamily Campanuloideae Burnett (1835). Genera 1–50
II. Subfamily Nemacladoideae Lammers (1998). Genera 51–53

III. Subfamily Lobelioideae Burnett (1835). Genera 54–82
IV. Subfamily Cyphocarpoideae Miers (1848). Genus 83
V. Subfamily Cyphioideae (A. DC.) Walp. (1852). Genus 84

Key to the Genera

1. Corolla actinomorphic; odd (unpaired) sepal in a dorsal (posterior) position; locules and stigmas (1–)3–5(–10) 2
– Corolla zygomorphic (sometimes only slightly so); odd (unpaired) sepal in a ventral (anterior) position prior to any floral resupination; locules and stigmas (1–)2 51
2. Fruit dehiscing apically (i.e. above the calyx lobes), if indehiscent, pericarp fleshy 3
– Fruit dehiscing laterally (i.e. below the calyx lobes), if indehiscent, then pericarp dry, membranous or papery 22
3. Ovary wholly superior, completely free from calyx **1. *Cyananthus***
– Ovary inferior or semi-superior, at least its base adnate to the calyx, forming a hypanthium 4
4. Ovary 5-locular, locules alternating with the sepals 5
– Ovary 2–6-locular, if 5-locular, then locules opposite the sepals 6
5. Perennial with tuberous roots; flowers solitary; corolla large, bowl-shaped; pollen 5–7-colpate **2. *Platycodon***
– Annual; flowers in corymbs or heads; corolla small, cylindric; pollen 3-porate **19. *Microcodon***
6. Calyx lobes inserted at base of hypanthium **4. *Cyclocodon***
– Calyx lobes inserted at summit (rarely middle) of hypanthium 7
7. Roots greatly enlarged, tuberous; stems typically scandent or climbing, rarely erect or ascending 8
– Roots fibrous; stems erect or ascending 9
8. Plant often malodorous; leaves entire or toothed; petioles and pedicels not twining; corolla lobes and stamens 5; fruit a capsule, rarely a berry partially subtended by the calyx lobes **3. *Codonopsis***
– Plant not malodorous; leaves hastate or sagittate; petioles and pedicels twining; corolla lobes and stamens 6; fruit a berry crowned by the calyx lobes **7. *Canarina***
9. Leaves pinnately lobed or parted; corolla lobes and stamens typically 4; pollen 4–5-colpate **5. *Echinocodon***
– Leaves typically entire or toothed; corolla lobes and stamens typically 5; pollen 3-porate 10
10. Capsule dehiscent by pores, an operculum, or irregularly, never by valves 11
– Capsule dehiscent by valves, rarely also by pores 16
11. Annuals; capsule dehiscent by 1 apical pore **41. *Githopsis***
– Perennial herbs and subshrubs; capsule dehiscent by an operculum or irregularly (rarely by 1 apical pore) 12
12. Capsule irregularly dehiscent **23. *Edraianthus***
– Capsule dehiscent by an operculum (rarely by 1 apical pore) 13
13. Corolla cylindrical; filaments adnate to corolla 14
– Corolla campanulate or funnelform; filaments free from corolla 15
14. Leaves dense; flowers in a head; ovules several to numerous in each locule **22. *Rhigiophyllum***
– Leaves sparse; flowers in a raceme or panicle; ovules 2–6 per locule **21. *Siphocodon***
15. Ovary and capsule 2-locular **15. *Roella***
– Ovary (2–)3-locular, capsule 1 locular at maturity **14. *Craterocapsa***
16. Anthers dorsifixed **11. *Berenice***
– Anthers basifixed 17
17. Shrubs; flowers with conspicuous nectaries 18
– Herbs or subshrubs (rarely shrubs); flowers lacking nectaries, or nectaries inconspicuous 19
18. Flowers in racemes or panicles; ovary topped by a 5-notched nectar disc; each valve of capsule with a pair of pores and three more pairs of pores at base of capsule **10. *Heterochaenia***
– Flowers solitary; ovary topped by 5 ellipsoid nectaries; capsule lacking pores **9. *Nesocodon***
19. Inflorescence involucrate; anthers connate at base **25. *Jasione***
– Inflorescence not involucrate; anthers distinct or coherent 20
20. Flowers in flat-topped corymbs; anthers apiculate, inner pollen sacs shorter than outer **24. *Feeria***
– Flowers solitary or in various racemose or paniculate inflorescences; anthers not apiculate, thecae equal 21
21. Corolla cylindric; filaments filiform; placentation basal **12. *Theilera***
– Corolla campanulate, funnelform, rotate, or rarely urceolate; filaments basally dilated; placentation axile **8. *Wahlenbergia***
22. Calyx lobes, corolla lobes, stamens and locules (6–)7–10 23
– Calyx lobes, corolla lobes and stamens 3–5 (corolla rarely lacking); locules 1–5 24
23. Biennial; leaves alternate; corolla rotate, lobes much longer than tube; pollen 3-porate; capsule dehiscent by 8–10 basal valves **49. *Michauxia***
– Perennial; leaves whorled; corolla funnelform, lobes shorter than tube; pollen 6–7-colpate; capsule dehiscent by (10–)14(–18) median longitudinal slits **6. *Ostrowskia***
24. Fruit indehiscent, or dehiscing only tardily and irregularly 25
– Fruit dehiscent by definite valves, pores, fissures or slits, or breaking into 3 mericarps joined by the persistent style bases 27
25. Suffruticose perennial or subshrub; corolla tubular or cylindric, lobes shorter than tube; ovary 1- or imperfectly 2-locular, containing only 4 ovules on basal placentae; mature seeds 1–2 **20. *Merciera***
– Annual or herbaceous perennial; corolla funnelform or campanulate, lobes equalling or longer than tube; ovary 2–3-locular, containing 10 to many ovules on axile placentae; mature seeds 10 to many 26
26. Annual; locules 2; ovules and seeds numerous **16. *Gunillaea***
– Perennial; locules (2–)3; ovules 8–10 per locule; seeds 10–16 per capsule **36. *Peracarpa***
27. Fruit a schizocarp, the 3 locules indehiscent but separating from the ovary and held together by the persistent style **33. *Theodorovia***
– Fruit a capsule, locules opening with valves, pores, fissures or slits 28

28. Corolla bright yellow or reddish brown; capsule dehiscent by numerous transverse slits **26. *Musschia***
– Corolla various shades of violet, lilac, blue or white, only rarely yellowish or pinkish; capsule dehiscent by valves, pores, or longitudinal fissures or slits 29
29. Capsule split for almost its entire length by 3–5 longitudinal fissures 30
– Capsule opening by relatively short valves, pores or slits 33
30. Biennial; capsule splitting from base to apex; seeds large, few **35. *Sachokiella***
– Suffruticose perennials and subshrubs; capsule splitting from apex to base; seeds small, many 31
31. Capsule splitting into 3 fragments; pollen shed in tetrads **13. *Namacodon***
– Capsule splitting into 5 fragments; pollen in monads 32
32. Locules 2 **17. *Prismatocarpus***
– Locules 3 **34. *Muehlbergella***
33. Corolla cleft nearly to base, appearing choripetalous 34
– Corolla cleft for 1/10–3/4 of its length, clearly sympetalous 40
34. Corolla lobes coherent or connate apically, creating an apical tube separated from the basal tube by the bowed-out lobes 35
– Corolla lobes distinct apically 36
35. Flowers distinctly pedicellate; corolla lobes connate throughout anthesis; filaments filiform **48. *Physoplexis***
– Flowers sessile or nearly so; corolla lobes merely coherent, separating after fertilization; filaments dilated basally **47. *Phyteuma***
36. Capsule dehiscent by basal valves **46. *Sergia***
– Capsule dehiscent by subapical or medial pores or slits 37
37. Flowers solitary; hypanthium several times longer than broad; capsule dehiscent by slits **45. *Cylindrocarpa***
– Flowers in racemes, panicles, spikes or heads; hypanthium slightly longer than broad; capsule dehiscent by pores 38
38. Leaves pinnatifid; stigmatic lobes minute, stigma capitate **44. *Petromarula***
– Leaves entire or toothed; stigmatic lobes filiform, obvious 39
39. Inflorescence involucrate; sinuses of calyx appendaged; corolla tubular **43. *Cryptocodon***
– Inflorescence lacking an involucre; sinuses of calyx unappendaged; corolla rotate or funnelform **42. *Asyneuma***
40. Rosette shrub; herbage viscid **27. *Azorina***
– Herbs; herbage not viscid 41
41. Flowers with a large, conspicuous, cylindrical or tubular nectary 42
– Flowers with no obvious nectary, or nectary inconspicuous, disciform 43
42. Anthers connate throughout anthesis **32. *Hanabusaya***
– Anthers distinct, or coherent in bud but distinct in anthesis or after fertilization **31. *Adenophora***
43. Filaments connate; anthers apically apiculate; seeds large, c. 15 per locule **30. *Zeugandra***
– Filaments distinct; anthers not apiculate apically; seeds small, numerous 44
44. Corolla urceolate, each sinus with a large saccate appendage **29. *Favratia***
– Corolla campanulate, funnelform, tubular, or rotate, lacking saccate appendages 45
45. Flowers in an involucrate head; corolla narrowly cylindric above a globose base; base of style conspicuously swollen, globose; locules 2; capsule dehiscent with longitudinal slits, covered by the solid, conic style base **18. *Treichelia***
– Flowers solitary or in various inflorescences, only rarely in an involucrate head; corolla rotate, bowl-shaped, funnelform, or campanulate; base of style filiform, confluent with ovary; locules typically 3–5, sometimes 1 by abortion of septa, only rarely 2; capsule dehiscent with valves or pores, style deciduous 46
46. Flowers in elongate spike-like inflorescence; hypanthium elongate, 3–8 times longer than broad; corolla rotate 47
– Flowers solitary or in various racemose, paniculate, or corymbiform inflorescences, seldom spike-like; hypanthium compact, twice as long as broad or less; corolla campanulate, funnelform, or tubular, rarely rotate 48
47. All flowers chasmogamous, with 5 calyx lobes and well-developed corolla; filaments filiform or nearly so **38. *Legousia***
– Most flowers in inflorescence cleistogamous, calyx lobes reduced to 3 and corolla rudimentary or lacking; filaments basally dilated **39. *Triodanis***
48. Leaves all sessile; flowers sessile, solitary opposite a leaf, many cleistogamous **40. *Heterocodon***
– Some leaves on plant petiolate; flowers sessile or pedicellate, in various inflorescences, if solitary, then either terminal or in leaf axil, any cleistogamous flowers pedicellate 49
49. Stems distinctly triquetrous; flowers sessile or nearly so, 1–3 in leaf axils **37. *Homocodon***
– Stems terete or shallowly winged; flowers pedicellate, in various racemose, paniculate or corymbiform inflorescences, if solitary, then terminal 50
50. Perennial lacking basal rosette; flowers very small, narrowly tubular, in a pedunculate flat-topped corymb; filaments filiform; style greatly exserted **50. *Trachelium***
– Annuals, biennials, or perennials with basal rosette; flowers small to more commonly medium-sized or large, campanulate, funnelform, bowl-shaped, tubular, or rotate, solitary or in various racemose or paniculate inflorescences; filaments basally dilated; style included or only slightly exserted **28. *Campanula***
51. Flowers oriented normally, the odd (unpaired) sepal in a ventral (anterior) position at anthesis; anthers distinct, all alike 52
– Flowers typically resupinate, the odd (unpaired) sepal in a dorsal (posterior) position at anthesis; anthers connate, the dorsal 3 longer than the ventral 2 56
52. Flowers sessile; corolla of a single cucullate dorsal lobe bearing an apical appendage plus 4 ventral lobes; stamens all epipetalous **83. *Cyphocarpus***
– Flowers pedicellate; corolla composed of 2 more or less flat, unappendaged ventral lobes plus 3 dorsal lobes; stamens inserted at base of corolla tube, on the rim of the hypanthium or atop the inferior ovary, rarely the dorsal two epipetalous 53

53. Perennials with tuberous roots; style tipped by a fluid-filled stigmatic cavity with a lateral pore **84. *Cyphia***
– Annuals (if perennial, lacking tubers); style tipped by a bilobed stigma 54
54. Perennials; leaves subopposite; pedicels bibracteolate at apex **51. *Pseudonemacladus***
– Annuals; leaves alternate or in a basal rosette; pedicels ebracteolate 55
55. Cauline leaves (if any) much smaller and narrower than basal leaves; capsule apically dehiscent with 2 valves **52. *Nemacladus***
– Cauline leaves resembling basal leaves; capsule circumscissile **53. *Parishella***
56. Corolla actinomorphic, petals free almost to base **54. *Dialypetalum***
– Corolla zygmorphic (sometimes only slightly so), petals connate, forming a definite tube 57
57. Robust perennial herbs, shrubs, treelets, trees, giant rosette plants and lianas; stems woody or suffruticose, at least at base, (0.3–)1–8 m tall; corolla (1.4–)3–15 cm long, lobes all more or less similar in size and shape, or dorsal lobes larger than ventral ones 58
– Slender perennial, biennial or annual herbs; stems herbaceous throughout, 0.03–1 m tall; corolla 0.2–2.5 cm long, dorsal lobes typically smaller than ventral ones (rarely all more or less similar) 70
58. Inflorescence an axillary raceme (sometimes subumbellate) 59
– Inflorescence a terminal raceme (sometimes corymbiform or capitate) or flowers solitary in leaf axils 62
59. Corolla salverform; fruit an apically dehiscent capsule **79. *Brighamia***
– Corolla bilabiate or unilabiate; fruit a berry 60
60. Much-branched shrubs or trees; inflorescence typically 2-flowered; berries large **82. *Clermontia***
– Unbranched or sparingly branched shrubs, treelets or trees (rarely lianas); inflorescence typically 6–40-flowered; berries small 61
61. Corolla with a knob at base of dorsal slit; seeds large, white, transversely rugose **80. *Delissea***
– Corolla smooth at base of dorsal slit; seeds small, brown or black, smooth **81. *Cyanea***
62. Corolla salverform **71. *Hippobroma***
– Corolla tubular, bilabiate or unilabiate 63
63. Hypanthium and corolla distended ventrally into a large, broad, crescent-shaped nectar spur **72. *Heterotoma***
– Flower lacking a nectar spur, at most hypanthium and corolla slightly oblique or gibbous ventrally 64
64. Ovary 1-locular, placentation parietal **77. *Apetahia***
– Ovary 2-locular, placentation axile 65
65. Fruit dehiscent via pores 66
– Capsule dehiscent via apical valves, or indehiscent 67
66. Pores 2, apical; flowers solitary in leaf axils **76. *Sclerotheca***
– Pores 3–12, lateral; flowers in a raceme, commonly horizontally branched at base **78. *Trematolobelia***
67. Corolla tube cleft dorsally to base **55. *Lobelia*** (subg. *Tupa*)
– Corolla tube entire 68
68. Top of ovary conical; fruit a capsule **73. *Siphocampylus***
– Top of ovary flat; fruit a berry 69
69. Apex of anther tube occluded; pedicels typically bibracteolate; corolla, staminal column and style early deciduous on the developing fruit; seeds oblong or linear, their reticulations more or less elongate **74. *Centropogon***
– Apex of anther tube broadly open; pedicels typically ebracteolate; corolla, staminal column and style withering-persistent on the developing fruit; seeds ellipsoid or lenticular, their reticulations more or less isodiametric **75. *Burmeistera***
70. Flowers sessile, resupinate due to torsion of the hypanthium (rarely not resupinate); hypanthium pedicelliform, 5–10 times longer than wide 71
– Flowers pedicellate (rarely subsessile), resupinate due to torsion of the pedicel (rarely not resupinate); hypanthium cupulate, shorter than wide to as much as 4 times longer than wide 73
71. Corolla tube entire; ventral anthers with apical tufts of hairs **69. *Downingia***
– Corolla tube dorsally cleft at least 2/3 the distance to base; all 5 anthers with apical tufts of hairs 72
72. Leaves sessile; flowers solitary in leaf axils; stigmas round **58. *Grammatotheca***
– Leaves petiolate; flowers in axillary fascicles; stigmas filiform **59. *Dielsantha***
73. Ovary 1-locular, placentation parietal or basal 74
– Ovary 2-locular, placentation axile 77
74. Corolla tube entire (very rarely cleft dorsally to base); filament tube adnate to corolla, at least at base; capsule dehiscent by an umbonate operculum **70. *Lysipomia***
– Corolla tube dorsally cleft to base; filament tube free from corolla; capsule dehiscent with apical valves and/or irregular lateral ruptures 75
75. Plants terrestrial; leaves petiolate; hypanthium very shallow, all but obsolete; ovary almost superior; placentation basal; seed 1 **61. *Unigenes***
– Plants aquatic (submersed or emergent); leaves sessile; hypanthium 4–8 times longer than wide; ovary inferior; placentation parietal; seeds 3–20 76
76. Plants typically emergent; seeds 18–20, 1–1.8 mm long **67. *Legenere***
– Plants typically submersed; seeds 3–5, 2–4 mm long **68. *Howellia***
77. Corolla tube cleft dorsally from apex almost to base 78
– Corolla tube entire, or cleft dorsally from base half the distance to apex 80
78. Flowers not resupinate (rarely so); stigmas filiform **60. *Monopsis***
– Flowers resupinate; stigmas round 79
79. Pedicel free from subtending leaf or bract; dorsal corolla lobes shorter than ventral or about equal **55. *Lobelia*** (subg. *Lobelia*, subg. *Isolobus*)
– Pedicel adnate to subtending leaf, flower epiphyllous; dorsal corolla lobes 1.5–5 times longer than ventral **63. *Ruthiella***
80. Filaments (at least dorsal one) adnate to corolla tube 81
– Filaments free from corolla tube 83
81. Ovary more than 4/5 superior, adnate to hypanthium only at base; capsule dehiscent to about the middle **64. *Diastatea***
– Ovary less than 1/3 superior, adnate to hypanthium for all or most of its length; capsule dehiscent only at apex 82

82. Corolla tube entire; all filaments adnate to corolla **62. *Isotoma***
– Corolla tube cleft dorsally from base half the distance to apex; only dorsal filament adnate to corolla **65. *Palmerella***
83. Stems fleshy; calyx lobes 3–8(–11) mm long; all 5 anthers with apical tufts of hairs; capsules 5–10(–16) mm long; seeds c. 1 mm long **66. *Porterella***
– Stems herbaceous; calyx lobes 1–4 mm long; ventral 2 anthers with apical tufts of hairs; capsules 1–6 mm long; seeds 0.3–0.5 mm long 84
84. Stems erect, flowers solitary and axillary or terminal; pedicels with 1–3 bracteoles near the middle; filament tube 1.5–2.5 mm long; capsules 1–3 mm long; seeds ellipsoid, strophiolate, sulcate with keeled walls **56. *Solenopsis***
– Stems decumbent, flowers solitary and axillary or, if stems erect, then flowers 2–15 in a terminal raceme; pedicels bibracteolate at base; filaments 2–6 mm long; capsules 2.5–6 mm long; seeds subglobose, lacking a strophiole, sulcate with flattened walls **57. *Wimmerella***

Subfamilies and Genera of Campanulaceae

I. Subfam. Campanuloideae Burnett (1835).

Herbaceous perennials, less often annuals or biennials, herbaceous lianas, sometimes twining, pachycaul rosette plants, subshrubs or shrubs, terrestrial, rarely epiphytic. Inflorescences monotelic or polytelic, commonly appearing racemose, paniculate, spicate, umbellate or capitate, the latter two sometimes involucrate, typically terminal, or the flowers solitary in an axillary or terminal position. Calyx with the odd (unpaired) lobe in a dorsal (posterior) position. Corolla radially symmetric; lobes (4–)5(–10), valvate. Anthers distinct or connivent, rarely connate, in which case the resulting tube is symmetric. Ovary (2–)3–5(–10)-locular with axile placentation, rarely 1-locular with parietal, basal, or apical placentation. Fruit a capsule, commonly loculicidal or poricidal, or a berry.

Campanuloideae comprise 50 genera and 1,046 species. Though the subfamily is represented on all six continents, 89% of the genera and 96% of the species are endemic to the Old World. Africa and Asia each harbour about one-third of the species, Europe another one-quarter and Australasia about 4%; by contrast, just 3% of the species are North American and 1% South American.

1. *Cyananthus* Wall. ex Benth.

Cyananthus Wall. ex Benth. in Royle, Ill. Bot. Himal. Mts. 309 (1836), nom. cons.; Hong & Ma, Acta Phytotax. Sin. 29: 25–51 (1991), rev.; Shrestha, Acta Phytotax. Sin. 35: 396–433 (1997), rev.

Annual or dwarf perennial herbs, often with a large caudex. Leaves cauline, petiolate. Flowers medium-sized, solitary and terminal (rarely in cymes), short-pedicellate or rarely sessile. Calyx (3–)4–5-lobed, free from ovary and stamens. Corolla funnelform or tubular, blue (rarely yellow or white); lobes 4–5, equalling or shorter than the tube. Stamens 4–5; filaments slender; pollen (6–)7–9(–12)-colpate, minutely spinulose. Ovary superior, 3–5-locular. Fruit capsular, apically dehiscent by 3–5 valves. $2n = 14$. Twenty-three species, eastern Asia, divided by Shrestha (1997) into two subgenera: subg. *Cyananthus* (21 spp.) with sect. *Stenolobi* Franch. (9 spp.), sect. *Suffruticulosi* K. Shrestha (2 spp.), sect. *Cyananthus* (7 spp.) and sect. *Annui* (Y.S. Lian) D.Y. Hong & L.M. Ma (3 spp.), and subg. *Micranthus* K. Shrestha (2 spp.).

2. *Platycodon* A. DC.

Platycodon A. DC., Monogr. Campan. 125 (1830).

Perennial herb from tuberous roots. Leaves cauline, often subopposite or 3–4-verticillate, sessile or short-petiolate. Flowers large, pedicellate, solitary, terminal. Corolla bowl-shaped, blue-purple (rarely pink or white); lobes equalling or shorter than tube. Filaments dilated basally; anthers longer than filaments; pollen 5–6(–7)-colpate, spinulose. Ovary 5-locular, locules antesepalous. Fruit capsular, loculicidal, apically dehiscent by 5 valves; seeds large. $2n = 18, 36$. One species, *P. grandiflorus* (Jacq.) A. DC., eastern Asia and common in cultivation.

3. *Codonopsis* Wall.

Codonopsis Wall. in Roxb., Fl. Ind. 2: 103 (1824); Shen & Hong, Fl. Reip. Pop. Sin. 73, 2: 32–69 (1983), reg. rev.

Scandent, climbing or twining (rarely erect or ascending) perennials, often with a skunk-like odour; roots large, tuberous. Leaves sometimes opposite or fasciculate, petiolate or sessile. Flowers large, pendulous or rarely erect, pedicellate, solitary, terminal or axillary. Calyx lobes crowning hypanthium or inserted medially. Corolla purple, blue, green, yellow or white, often with intricate contrasting patterning, campanulate, infundibular, or tubular (rarely rotate); lobes shorter than tube. Filaments dilated basally; anthers coherent; pollen (5–)7–9(–10)-colpate, spinulose or reticulate. Ovary 3- or 5-locular, sometimes

only half-inferior. Fruit capsular, loculicidal, dehiscent by 3 or 5 apical valves, or a berry partly subtended by the persistent calyx lobes; seeds sometimes winged. $2n = 16$. Fifty-nine species, eastern Asia, divided by Shen and Hong (1983) into three subgenera: subg. *Codonopsis* (52 spp.), subg. *Obconicapsula* D.Y. Hong (1 sp.) and subg. *Pseudocodonopsis* Kom. (6 spp.).

4. *Cyclocodon* Griff.

Cyclocodon Griff., Not. Pl. Asiat. 4: 277 (1854); Hong & Pan, Acta Phytotax. Sin. 36: 106–110 (1998), rev.

Perennial herbs; root large, tuberous. Leaves opposite (rarely alternate), petiolate. Flowers small to medium-sized, erect, pedicellate, in a 3-flowered terminal cyme and solitary in leaf axils. Calyx lobes 4 or 6, subtending hypanthium. Corolla white, pale pink or lilac, campanulate or infundibular; lobes 4 or 6, equalling tube. Stamens 4 or 6; filaments distinct; anthers coherent, equalling filaments; pollen 3-colporate, spinulose. Ovary 4- or 6-locular. Fruit a berry subtended by the persistent calyx lobes. Two species, eastern Asia.

5. *Echinocodon* D.Y. Hong

Echinocodon D.Y. Hong, Acta Phytotax. Sin. 22: 183 (1984).

Small perennial herb. Leaves petiolate, pinnately lobed or parted. Flowers very small, pedicellate, solitary or in 2–3-flowered cymes in leaf axils. Calyx lobes (2–)4(–5), longer than corolla, spinose-margined. Corolla purple-blue, cupular; lobes (3–)4(–5), equalling tube. Stamens 3–5; filaments distinct, dilated at base; anthers connivent, slightly shorter than filaments; pollen 4–5-colpate, spinulose. Ovary 3–5-locular; stigmas filiform. Fruit capsular, loculicidal; seeds triquetrous. $2n = 16$. One species, *E. lobophyllus* D.Y. Hong, eastern Asia.

6. *Ostrowskia* Regel

Ostrowskia Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 8: 686 (1884).

Perennial herb; roots tuberous. Leaves whorled. Flowers large, pedicellate, in a terminal pyramidal panicle. Calyx lobes (5–)7(–9). Corolla large, bowl-shaped or funnelform, pale lilac or white; lobes (5–)7(–9), shorter than tube. Stamens (5–)7(–9); filaments dilated basally; anthers 3 times longer than filaments, apically mucronate; pollen 6–7-colpate, verrucose. Ovary (5–)7(–9)-locular. Fruit capsular, laterally dehiscent by several oblong, medial or subapical parallel slits; seeds narrowly winged. $2n = 34$. One species, *O. magnifica* Regel, central Asia.

7. *Canarina* L.

Canarina L., Mant. Pl. 148, 588 (1771), nom. cons.; Hedberg, Svensk Bot. Tidskr. 55: 17–62 (1961), rev.

Scandent (rarely epiphytic) sympodially branched perennials, climbing with twining petioles and pedicels; root tuberous. Leaves opposite or ternate, petiolate; base cordate or hastate. Flowers large, pendent, pedicellate, solitary, terminal in sympodial forks or on branches. Calyx 6-lobed. Corolla orange streaked red or yellowish purple, campanulate or funnelform; lobes 6, shorter than tube. Stamens 6; anthers distinct; pollen 3(–4)-colporate or -colporoidate, spinulose. Fruit a yellow, pale red or black berry, crowned by the persistent calyx lobes. $2n = 34$. Three species, one endemic to the Canary Islands, the other two to eastern Africa.

8. *Wahlenbergia* Schrad. ex Roth Fig. 5

Wahlenbergia Schrad. ex Roth, Nov. Pl. Sp. 399 (1821), nom. cons.; Adamson, J. S. African Bot. 21: 155–218 (1955), part. reg. rev.; Thulin, Symb. Bot. Upsal. 21: 1–223 (1975), reg. rev.; Smith, Telopea 5: 91–175 (1992), reg. rev.; Petterson, N. Z. J. Bot. 35: 9–54 (1997), reg. rev.
Lightfootia L'Hér. (1789), nom. illegit.
Cephalostigma A. DC. (1830).

Annual or perennial herbs, subshrubs and shrubs. Leaves sometimes opposite, usually sessile, cauline and often basally rosulate, rarely ericoid. Flowers small to medium-sized, sessile or pedicellate, terminal or axillary, solitary or in thyrses, panicles or fascicles, very rarely involucrate. Calyx lobes (3–)5(–6). Corolla campanulate or infundibular (rarely tubular, urceolate, or rotate), blue or white (rarely rose); lobes (3–)5(–7), much shorter to much longer than tube. Stamens (3–)5; filaments free and distinct, dilated basally; anthers coherent; pollen (2–)3(–5)-porate, spinulose. Ovary 2–5-locular, rarely superior; ovules few to many. Fruit capsular, loculicidal, apically dehiscent by 2–5 valves. $2n = 14, 16, 18, 22, 36, 42, 54, 72, 90$. Two hundred and sixty species, circumaustral.

9. *Nesocodon* Thulin

Nesocodon Thulin, Kew Bull. 34: 813 (1980).

Shrub. Leaves aggregated towards stem tips. Flowers large, pedicellate, pendent, solitary, axil-

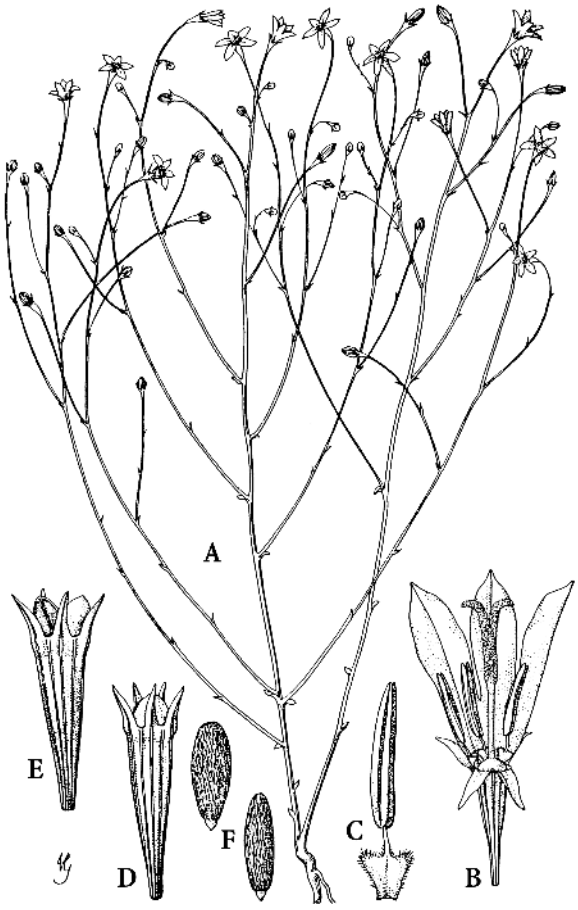

Fig. 5. Campanulaceae-Campanuloideae. *Wahlenbergia virgata*. **A** Habit. **B** Flower (two petals and stamens removed). **C** Stamen. **D**, **E** Closed and open capsule. **F** Seeds. (Thulin 1976)

lary. Corolla campanulate, pale blue with darker veins; lobes much shorter than tube. Stamens distinct, included, appressed to corolla; anthers a little shorter than filaments. Ovary 3-locular, topped by 5 scarlet ellipsoid nectaries alternating with stamens. Fruit capsular, loculicidal, apically dehiscent by 3 valves. $2n = 34$. One species, *N. mauritianus* (I. Richardson) Thulin, Mauritius.

10. *Heterochaenia* A. DC.

Heterochaenia A. DC. in Meisn., Pl. Vasc. Gen. 2: 149 (1839); Badré et al., Adansonia II, 12: 267–278 (1972), rev.

Shrubs. Leaves sessile, clustered at branch tips. Flowers large, pedicellate, in a terminal raceme or panicle. Corolla campanulate, violet, blue or yellow-white; lobes equalling or shorter than tube. Filaments distinct, the bases slender; anthers equalling filaments. Ovary 3-locular, topped by a 5-notched nectar disc. Fruit capsular, loculicidal, apically dehiscent by 3 valves, each with a pair of pores, later forming six basal pores. Three species, Mascarene Islands.

11. *Berenice* L.R. Tulasne

Berenice L.R. Tulasne, Ann. Sci. Nat., Bot. IV, 8: 156 (1857); Badré et al., Adansonia II, 15: 139–146 (1975), rev.

Delicate shrub. Leaves cauline, petiolate. Flowers very small, pedicillate, in terminal and axillary open panicles. Corolla white, tipped with rose, rotate; lobes longer than tube, recurved. Stamens exserted; anthers free, dorsifixed, about half as long as filament; pollen 3-porate, spinulose. Ovary 3-locular, topped by a nectar disc. Fruit capsular, loculicidal, apically dehiscent by 3 valves. One sp., *B. arguta* L.R. Tulasne, Mascarene Islands.

12. *Theilera* E. Phillips

Theilera E. Phillips, Gen. S. African Fl. Pl. 606 (1926).

Subshrub. Leaves fascicled. Flowers solitary, axillary, sessile. Corolla cylindric; lobes shorter than tube. Stamens included; filaments filiform, free from corolla; anthers shorter than filaments. Ovary 3(–4)-locular; ovules numerous, basal; style exserted. Fruit capsular, apically dehiscent by 3 valves. Two species, South Africa.

13. *Namacodon* Thulin

Namacodon Thulin, Bot. Notiser 127: 173 (1974).

Subshrub. Leaves sessile. Flowers small to medium-sized, terminal, solitary. Hypanthium elongate. Corolla campanulate, blue; lobes as long as tube. Stamens free; filament bases dilated; anthers apically mucronate; pollen shed in tetrads. Ovary 3-locular; style included. Fruit capsular, septicidal, dehiscing apically by 3 longitudinal fissures. One sp., *N. schinzianum* (Markgr.) Thulin, South Africa.

14. *Craterocapsa* Hilliard & B.L. Burtt

Craterocapsa Hilliard & B.L. Burtt, Notes Roy. Bot. Gard. Edinburgh 32: 314 (1973).

Perennial herbs. Stems prostrate, often matted. Leaves occasionally opposite, petiolate or sessile. Flowers small to medium-sized, solitary (rarely a few together in leaf axils), terminal. Corolla lilac or white, funnelform; lobes slightly shorter than tube. Filaments dilated at base, free; anthers distinct. Ovary (2–)3-locular; style swollen at base

or surrounded by a disc. Fruit capsular, dehiscent by a terminal operculum formed from the enlarged style base (or disc) and apex of ovary. Five species, South Africa.

15. *Roella* L.

Roella L., Sp. Pl. 170 (1753); Adamson, J. S. African Bot. 17: 93–166 (1952), rev.

Subshrubs (rarely herbs). Leaves somewhat ericoid, crowded, often in axillary fascicles. Flowers small to medium-sized, sessile, terminal, solitary or in 2–5-flowered involucrate heads; bracts sometimes pinnately spinose-lobed. Calyx lobes 4–5. Corolla campanulate; lobes 4–5. Stamens 4–5, included or slightly exserted; filaments dilated basally, free from corolla; pollen 3-porate, spinulose. Ovary 2-locular, crowned by an annular or tumid nectary; ovules numerous; style sometimes with 2 glands below stigma. Fruit capsular, dehiscent by an apical pore or operculum. Twenty species, South Africa, divided by Adamson (1952) into five series: ser. *Roella* (6 spp.), ser. *Prostratae* Adamson (6 spp.), ser. *Spicatae* Adamson (4 spp.), ser. *Squarrosae* Adamson (3 spp.) and ser. *Muscosae* Adamson (1 sp.).

16. *Gunillaea* Thulin

Gunillaea Thulin, Bot. Notiser 127: 166 (1974).

Annuals. Leaves sessile. Flowers small, pedicellate, in more or less frondose monochasia. Calyx lobes (3–)4–5. Corolla campanulate; lobes (3–)4–5. Stamens (3–)4–5, free. Ovary 2-locular; style included. Fruit capsular, dehiscing irregularly between the veins. $2n = 18$. Two species, tropical Africa.

17. *Prismatocarpus* L'Hér.

Prismatocarpus L'Hér., Sert. Angl. 1 (1789), nom. cons.; Adamson, J. S. African Bot. 17: 93–166 (1952), rev.

Subshrubs or perennial herbs. Leaves small, often ericoid. Flowers small, terminal or axillary, solitary or in clusters or sympodial panicles. Hypanthium elongate. Corolla campanulate, funnelform, subcylindric, or rarely hypocrateriform, violet, blue, pink or white; tube increasing in diameter towards mouth. Stamens included or slightly exserted; filaments long and filiform or short and basally dilated, free from corolla; pollen 3-porate, spinulose or verrucose. Ovary 2-locular, often topped by a glandular or tumid nectar disc; style included or exserted; stigma rarely cylindric, sometimes subtended by 2 glands. Fruit capsular, splitting basipetally into 5 antipetalous segments. Twenty-nine species, South Africa, divided by Adamson (1952) into two subgenera: subg. *Prismatocarpus* (25 spp.) with ser. *Prismatocarpus* (9 spp.), ser. *Stricti* Adamson (7 spp.) and ser. *Nitidi* Adamson (9 spp.), and subg. *Afrotrachelium* Adamson (4 spp.).

18. *Treichelia* Vatke

Treichelia Vatke, Linnaea 38: 700 (1874).

Dwarf annual. Flowers in dense terminal heads, subtended by long linear bracts. Corolla cylindric above a globose base, white or pale blue fading yellow. Stamens included; filaments dilated basally, free from corolla. Ovary 2-locular; ovules several; style included, with a swollen subglobose base. Fruit capsular, laterally dehiscent by medial slits, covered by the style base. One species, *T. longibracteata* (H. Buek) Vatke, South Africa.

19. *Microcodon* A. DC.

Microcodon A. DC., Monogr. Campan. 127 (1830).

Small annuals. Leaves sometimes subopposite. Flowers small, in terminal corymbs or heads. Calyx lobes foliose, enlarging in fruit. Corolla cylindric; lobes shorter than tube. Stamens included; filaments linear, adnate to base of corolla; anthers longer than filaments; pollen 3-porate, spinulose. Ovary 5-locular, the locules antipetalous; style included. Fruit capsular, loculicidal, apically dehiscent by 5 valves. Four species, South Africa.

20. *Merciera* A. DC.

Merciera A. DC., Monogr. Campan. 369 (1830); Adamson, J. S. African Bot. 20: 157–163 (1955), rev.; Cupido, Adansonia III, 25: 33–44 (2003), rev.

Dwarf subshrubs or suffruticose perennials. Leaves somewhat ericoid, dense, often fascicled. Flowers small to medium-sized, solitary, axillary, short-pedicellate or sessile, subtended by a pair of bracteoles. Calyx lobes 4–5. Corolla tube long, slender at base, gradually increasing in diameter towards mouth; lobes 4–5, shorter than tube, sometimes unequal. Stamens 4–5, included; filaments filiform, free from corolla; pollen 3-porate, spinulose. Ovary 1-locular or imperfectly 2-locular; ovules 4, basal; style exserted; stigma bilobed. Fruit dry, indehiscent, 1–2-seeded, crowned by the persistent calyx lobes. Six species, South Africa.

21. *Siphocodon* Turcz.

Siphocodon Turcz., Bull. Soc. Imp. Naturalistes Moscou 25: 175 (1852).

Subshrubs. Leaves subulate, scale-like, sparse. Flowers small, in few-flowered racemes or racemose panicles. Corolla cylindric; lobes shorter than the tube. Stamens 5, epipetalous, included; anthers almost equalling filaments. Ovary 2–3-locular; ovules 2–5 in each locule, apical. Fruit capsular, circumscissile, operculum crowned by calyx lobes. Two species, South Africa.

22. *Rhigiophyllum* Hochst.

Rhigiophyllum Hochst., Flora 25: 232 (1842).

Subshrub. Leaves small, squarrose, densely imbricate in 4 rows. Flowers small, in terminal heads, subtended by rigid leaf-life bracts. Corolla cylindric. Stamens 5, epipetalous, included; anthers longer than filaments. Ovary 3-locular; ovules several, apical; style exserted. Fruit capsular, circumscissile, operculum crowned by the persistent style base. One species, *R. squarrosum* Hochst., South Africa.

23. *Edraianthus* A. DC.

Edraianthus A. DC. in Meisn., Pl. Vasc. Gen. 2: 149 (1839), nom. cons.; Kuzmanov in Tutin et al., Fl. Eur. 4: 99–100 (1976), reg. rev.
Halacsyella Janch. (1910).
Protoedraianthus Lakušić (1988).

Caespitose perennial herbs. Flowers medium-sized, solitary or in capitula, terminal. Corolla campanulate or infundibular, blue; lobes shorter than tube. Stamens free; filament bases dilated; pollen 3-porate. Ovary (2)3-locular; style included; stigma lobes linear. Fruit capsular, dehiscing irregularly at apex. $2n = 32$. Thirteen species, south-eastern Europe.

24. *Feeria* Buser

Feeria Buser, Bull. Herb. Boissier 2: 517 (1894).

Suffruticose perennial. Leaves cauline, subsessile. Flowers small, in a terminal flat-topped corymbose cyme. Corolla infundibular, white with blue limb; lobes shorter than corolla. Stamens included; filaments slender; anthers shorter than filaments, apiculate on connective, the inner pollen sacs shorter than outer. Ovary 3-locular, crowned by a narrow annular nectary; style exserted, swollen towards apex. Fruit capsular, dehiscing apically by 3 valves; seeds ca. 10. $2n = 34$. One species, *F. angustifolia* (Schousb.) Buser, Morocco.

25. *Jasione* L.

Jasione L., Sp. Pl. 928 (1753); Tutin in Tutin et al., Fl. Eur. 4: 100–102 (1976), reg. rev.; Parnell, Watsonia 16: 249–267 (1987), part. rev.
Jasionella Stoj. & Stef. (1933).

Annual, biennial or perennial herbs. Flowers small, sessile or short-pedicellate, in terminal involucrate heads. Corolla rotate, blue (rarely white), split nearly to base. Filaments slender; anthers connate at base, longer than filaments; pollen 3-porate, spinulose. Ovary 2-locular. Fruit capsular, loculicidal, dehiscing apically by 2 valves. $2n = 12, 14, 18, 24, 36, 48, 60$. Sixteen species, Mediterranean, except one in central Europe.

26. *Musschia* Dumort.

Musschia Dumort., Comment. Bot.: 28 (1822).

Long-lived monocarpic rosette shrub or polycarpic suffruticose perennial. Flowers large, pedicellate, in many-flowered pyramidal panicle. Calyx lobes flushed with same colour as corolla. Corolla rotate, bright yellow or reddish brown; lobes equalling or longer than tube. Pollen 3–4(–8)-porate. Fruit capsular, laterally dehiscent by numerous slits. $2n = 32$. Two species, Madeira.

27. *Azorina* Feer

Azorina Feer, Bot. Jahrb. Syst. 12: 611 (1890).

Viscid rosette shrub. Leaves sessile. Flowers large, pendulous, pedicellate, in lax panicles which arise below the apical rosette. Corolla white or rose, campanulate or urceolate; lobes shorter than the tube. Stamens included; filaments dilated basally, forming a nectar chamber; anthers shorter than filaments; pollen 3–4-porate. Ovary (2–)3-locular, topped by a green nectar disc with a thickened orange rim; style included. Fruit capsular, laterally dehiscent by (2)3 valves. $2n = 56$. One sp., *A. vidalii* (H. C. Watson) Feer, Azores.

28. *Campanula* L. Fig. 6

Campanula L., Sp. Pl. 163 (1753); Fedorov, Fl. S.S.S.R. 24: 133–331 (1957), reg. rev.; Phitos, Oesterr. Bot. Z. 111: 208–230 (1964), part. rev.; Phitos, Oesterr. Bot. Z. 112: 449–498 (1965), part. rev.; Rechinger & Schimann-Czeika, Fl. Iran. 13: 7–38 (1965), reg. rev.; Charadze, Zametki Sist. Geogr. Rast. 32: 46–56 (1976), reg. rev.; Fedorov & Kovanda

in Tutin et al., Fl. Eur. 4: 74–93 (1976), reg. rev.; Damboldt, Fl. Turk. 6: 2–64 (1978), reg. rev.; Hong, Fl. Reip. Pop. Sin. 73: 78–92 (1983), reg. rev.; Carlström, Willdenowia 15: 375–387 (1986), part. rev.; Oganesian, Bot. Zhurn. (Moscow & Leningrad) 78, 3: 145–157 (1993), sect. rev.; Sáez & Aldasoro, Bot. J. Linn. Soc. 141: 215–241 (2003), subg. rev.
Roucela Dumort. (1822).
Symphyandra A. DC. (1830).
Diosphaera Buser (1894).
Tracheliopsis Buser (1894).
Campanulastrum Small (1903).
Brachycodon Fed. (1957), nom. illegit.
Astrocodon Fed. (1957).
Popoviocodonia Fed. (1957).
Brachycodonia Fed. (1961).
Annaea Kolak. (1979).
Gadellia Shulkina (1979).
Pseudocampanula Kolak. (1980).
Mzymtella Kolak. (1981).
Hyssaria Kolak. (1981).
Neocodon Kolak. & Serdyuk. (1982).
Hemisphaera Kolak. (1984).
Echinocodon Kolak. (1986), nom. illegit.
Echinocodonia Kolak. (1994).

Annual, biennial or perennial herbs, often with thickened rootstocks or rhizomes. Leaves cauline and often basally rosulate. Flowers small to large, pendulous, erect, or horizontal, pedicillate, solitary or in various racemose, spicate, paniculate or rarely capitulate inflorescences, rarely involucrate, rarely cleistogamous. Calyx lobes 5, sometimes with reflexed appendages in the sinuses. Corolla campanulate, tubular, funnelform, bowl-shaped, or rotate, violet, blue or white (rarely yellow, red or pink); lobes shorter than tube to much longer than tube. Stamens commonly included; filaments dilated basally; anthers rarely connate; pollen 3(–6)-zonoporate or rarely 6–18-pantoporate. Ovary (2–)3–5-locular; style straight or, if curved towards apex, then exserted; nectar disc absent. Fruit capsular, erect or pendent, laterally dehiscent by (2–)3–5 basal, medial, or subapical pores or valves; seeds small, numerous. $2n$ = 14, 16, 18, 20, 22, 24, 26, 28, 30, 32, 34, 36, 40, 46, 48, 50, 52, 54, 56, 58, 68, 70, 72, 80, 84, 90, 102. Four hundred and twenty-one species, circumboreal in distribution, extending as far south as eastern Africa, southern Asia and northern Mexico; many species cultivated and some naturalized outside their indigenous range. Though many infrageneric taxa have been proposed, there is no modern classification which accounts for this large genus in its entirety.

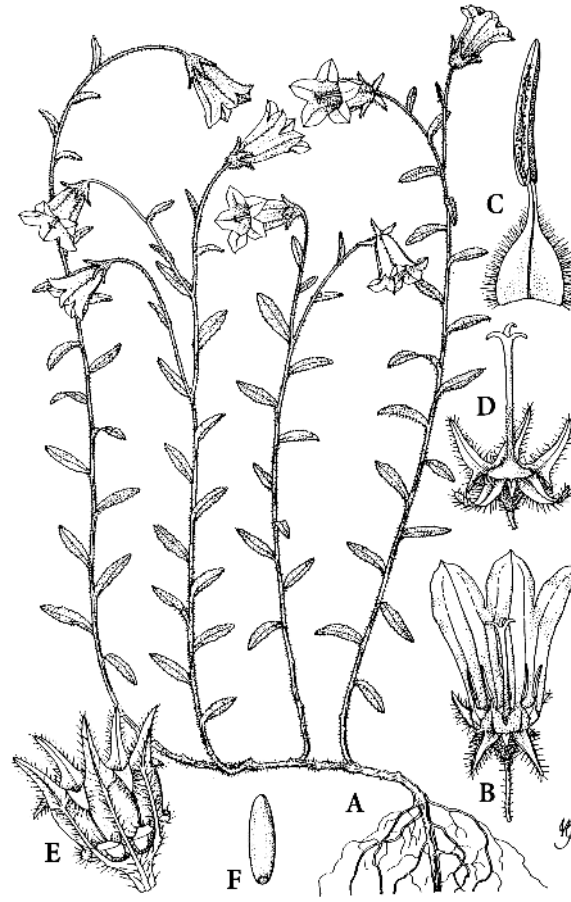

Fig. 6. Campanulaceae-Campanuloideae. *Campanula edulis*. **A** Habit. **B** Flower (two petals removed). **C** Stamen. **D** Flower (corolla and stamens removed). **E** Open capsule. **F** Seed. (Thulin 1976)

29. *Favratia* Feer

Favratia Feer, Bot. Jahrb. Syst. 12: 610 (1890).

Perennial herb. Leaves cauline and basally rosulate. Flowers small, erect or horizontal, pedicillate, solitary, terminal or axillary. Calyx lobes 5, unappendaged. Corolla urceolate, pale blue; lobes much shorter than tube, each sinus with a large conspicuous saccate appendage. Stamens included; filaments dilated basally. Ovary 3-locular; style included, curved towards apex; nectar disc absent. Fruit capsular, suberect, laterally dehiscent by 3 subapical pores; seeds small, numerous. $2n$ = 34. One sp., *F. zoysii* (Jacq.) Feer, south-eastern Alps.

30. *Zeugandra* P.H. Davis

Zeugandra P.H. Davis, Hooker's Icon. Pl. 35: pl. 3497 (1950).

Perennial herbs. Flowers medium-sized, short-pedicellate, pendent in lax panicles. Calyx lobes

alternating with recurved liguliform appendages. Corolla narrowly infundibular, blue; lobes shorter than tube. Filaments connate for half their length or more, dilated basally; anthers connate. Ovary 3-locular; style exserted. Fruit capsular, laterally dehiscent by 3 basal valves. Two species, Iran.

31. *Adenophora* Fisch.

Adenophora Fisch., Mém. Soc. Imp. Naturalistes Moscou 6: 165 (1823); Hong, Fl. Reip. Pop. Sin. 73, 2: 92–139 (1983), reg. rev.

Perennial herbs, often with large tuberous roots. Leaves cauline, rarely opposite or 3–6-verticillate. Flowers small to medium-sized, pendulous, short-pedicillate, in loose racemes or panicles. Corolla purple or blue (rarely white), campanulate, tubular, infundibular, or rarely urceolate; lobes shorter than the tube. Stamens commonly included; filaments dilated basally, forming a nectar chamber; anthers equalling or shorter than filaments; pollen 3–5-porate, echinate. Ovary 3-locular, crowned by a large, thick, annular cylindric or cupulate nectary; style exserted. Fruit capsular, laterally dehiscent by 3 pores or valves. $2n$ = 34, 36, 68, 72, 102. Sixty-five species, eastern Asia, one in western Europe and one in Crimea. Though many infrageneric taxa have been proposed, no modern classification accounts for this large genus in its entirety.

32. *Hanabusaya* Nakai

Hanabusaya Nakai, J. Coll. Sci. Imp. Univ. Tokyo 31: 62 (1911).
Keumkangsania Kim (1976), nom. illegit.

Perennial herb with a branched rhizome. Leaves cauline, petiolate, 4–6 at middle of stem. Flowers large, pedicellate, pendent, solitary or in few-flowered racemes, terminal. Corolla campanulate, light purple; lobes only 1/20 as long as tube. Stamens included; filaments dilated basally; anthers about as long as filaments, connate; pollen 4–7-porate, echinate. Ovary 3-locular, topped by a large conic or hemispheric nectary. $2n$ = 34. One sp., *H. asiatica* (Nakai) Nakai, Korea.

33. *Theodorovia* Kolak.

Theodorovia Kolak., Bot. Zhurn. (Moscow & Leningrad) 70: 7 (1985).
Fedorovia Kolak. (1980), nom. illegit.

Perennial herb with a thickened rootstocks. Leaves apically rosulate. Flowers small, pedicillate, solitary, terminal. Calyx lobes 5, with small reflexed appendages in the sinuses. Corolla tubular, dark blue; lobes much shorter than tube. Stamens included; filaments dilated basally. Ovary 3-locular. Fruit schizocarpous, the locules forming 3 mericarps which separate from the hypanthium; the 3 mericarps remain connected by the style which splits into 3 basally. One sp., *T. karakuschensis* (Grossh.) Kolak., Caucasus.

34. *Muehlbergella* Feer

Muehlbergella Feer, Bot. Jahrb. Syst. 12: 615 (1890).

Perennial herb from a thick rhizome. Leaves small, sessile, dense. Flowers small, sessile, solitary, terminal. Hypanthium narrowly obconic. Calyx lobes recurved and appressed to hypanthium after anthesis. Corolla tubular, blue, becoming scarious and hyaline, persistent; lobes equalling or shorter than tube. Filaments dilated basally. Ovary 3-locular; style included. Fruit capsular, splitting from tip to base into irregular fragments. One species, *M. oweriniana* (Rupr.) Feer, Caucasus.

35. *Sachokiella* Kolak.

Sachokiella Kolak., Soob. Akad. Nauk Gruzinsk. S.S.R. 118: 595 (1985).

Biennial herb with thick fusiform root. Leaves cauline. Flowers small, pedicillate, in an involucrate head. Corolla tubular, mauve or blue; lobes shorter than tube. Filaments somewhat dilated basally. Ovary 3 locular. Fruit capsular, splitting laterally from base into 5 elongate segments; seeds very large, few, spongy verrucose, erose winged. One sp., *S. macrochlamys* (Boiss. & A. Huet) Kolak., Caucasus.

36. *Peracarpa* Hook. f. & Thomson

Peracarpa Hook. f. & Thomson, J. Proc. Linn. Soc., Bot. 2: 26 (1858); Barnesky & Lammers, Bot. Bull. Acad. Sin. 38: 49–56 (1997), rev.

Delicate stoloniferous herb. Leaves cauline, petiolate. Flowers very small, pedicellate, terminal or less often axillary, solitary (rarely 2–17 in a fascicle). Corolla funnelform, pale blue or white; lobes about equalling tube. Stamens distinct, included; anthers half as long as filaments; pollen 4–6-porate, spinulose. Ovary (2–)3-locular, topped by a fleshy trisulcate nectar disc; ovules 4–5 pairs per placenta; style included; stigmas filiform. Fruit capsular, pendent, rupturing irregularly at the base; seeds 10–16, large. $2n$ = 28, 30. One species, *P. carnosa* (Wall.) Hook. f. & Thomson, eastern Asia.

37. *Homocodon* D.Y. Hong

Homocodon D.Y. Hong, Acta Phytotax. Sin. 18: 473 (1980).

Annuals. Stems 3-winged. Leaves cauline, petiolate. Flowers very small, sessile, solitary or paired, axillary. Calyx lobes spinose-toothed. Corolla campanulate, white or pale bluish; lobes equalling tube. Stamens included, distinct; filaments dilated at base; anthers shorter than filaments; pollen 3–4-porate, spinulose. Ovary 3-locular; style slightly exserted; stigmatic lobes linear. Fruit capsular, dehiscent by pores or by irregular tears. Two species, southern China.

38. *Legousia* Durande

Legousia Durande, Fl. Bourgogne 1: 37 (1782); Tutin in Tutin et al., Fl. Eur. 4: 94 (1976), reg. rev.
Specularia Heist. ex A. DC. (1830), nom. illegit.

Annuals. Leaves cauline, sessile or petiolate. Flowers small to medium-sized, sessile or short-pedicellate, in spike-like inflorescences. Hypanthium elongate. Corolla rotate or broadly campanulate, violet, blue, pinkish or white. Stamens 5, distinct; filaments slender; anthers much longer than filaments; pollen 3–5-porate, spinulose. Ovary 3-locular with axile placentae (rarely 1-locular with parietal placentae); stigmatic lobes filiform. Fruit capsular, dehiscing laterally by 3 medial or subapical valves. $2n$ = 20, 26. Seven species, Mediterranean.

39. *Triodanis* Raf.

Triodanis Raf., New Fl. N. Am. 4: 67 (1838); McVaugh, Wrightia 1: 13–52 (1945), rev.

Annuals. Leaves sessile or short-petiolate. Flowers medium-sized, sessile, 1–3(–8) in upper axils, forming a spike-like inflorescence, lower ones smaller and cleistogamous. Hypanthium elongate. Calyx lobes 3 in cleistogamous flowers. Corolla lavender blue, rotate; lobes longer than tube. Stamens 5, distinct, free from corolla; filaments dilated basally; anthers longer than filaments. Ovary inferior, 3-locular with axile placentae (rarely 1-locular with parietal placentae). Fruit capsular, laterally dehiscent by 3 apical, medial or basal pores. $2n$ = 28, 56, 60. Six species, North America.

40. *Heterocodon* Nutt.

Heterocodon Nutt., Trans. Amer. Philos. Soc. n.s. 8: 255 (1842).

Annual. Leaves cauline, sessile. Flowers very small, subsessile, solitary, opposite the upper leaves, the lower cleistogamous. Corolla cylindric, white with blue limb; lobes shorter than tube. Ovary 3-locular. Fruit capsular, dehiscent by irregular basal pores. One species, *H. rariflorum* Nutt., western North America.

41. *Githopsis* Nutt.

Githopsis Nutt., Trans. Amer. Philos. Soc. n.s. 8: 258 (1842); Morin, Syst. Bot. 8: 436–468 (1983), rev.

Annuals. Leaves cauline, sessile. Flowers small to medium-sized, terminal, sessile or short-pedicellate, sometimes cleistogamous. Corolla cylindric, campanulate, or funnelform, white with purple, blue or white lobes; lobes equalling or longer than tube. Stamens included; pollen 6–8-porate, spinulose. Ovary (2–)3-locular; placentation axile; style 2–3-lobed. Fruit capsular, dehiscing by 1 irregular apical pore. $2n$ = 18, 20, 36, 38, 40. Four species, western North America.

42. *Asyneuma* Griseb. & Schenk.

Asyneuma Griseb. & Schenk., Arch. Naturgesch. 18: 335 (1852); Damboldt, Boissiera 17: 1–128 (1970), rev.
Asyneumopsis Contandr., Quézel & Pamukç. (1972).

Annual, biennial or perennial herbs, with a thin rhizome or fusiform root. Leaves cauline and/or rosulate, subsessile. Flowers small to medium-sized, sessile, in a simple or branched spike or dense cylindric heads. Corolla rotate, purple, blue or white, divided nearly to base. Filaments dilated basally; pollen 4–5-porate, spinulose. Ovary (2–)3(–4)-locular; stigma lobes linear. Fruit capsular, dehiscent laterally by (2–)3 medial to subapical pores. $2n$ = 20, 22, 24, 28, 30, 32, 34, 48, 56, 68. Thirty-three species, Asia, eastern Europe, northern Africa.

43. *Cryptocodon* Fed.

Cryptocodon Fed. in Kom., Fl. S.S.S.R. 24: 474 (1957).

Perennial herb with large tuberous roots. Flowers medium-sized, subsessile, in a terminal involucrate capitulum. Calyx lobes with small recurved appendages in sinuses. Corolla blue, tubular, split nearly its entire length. Ovary 3-locular; style included. Fruit capsular, laterally dehiscent by 3 medial pores. One sp., *C. monocephalus* (Trautv.) Fed., central Asia.

44. *Petromarula* Vent. ex R. Hedw.

Petromarula Vent. ex R. Hedw., Gen. Pl. 139 (1806).

Perennial herb. Leaves petiolate, pinnate or pinnatisect, segments dentate or lobed. Flowers small, in panicles. Corolla pale blue, infundibular, split nearly to base. Filaments free, distinct, dilated basally. Ovary 3-locular; style exserted; stigma large, capitate. Fruit capsular, laterally dehiscent by 3 medial pores. $2n = 30$. One species, *Petromarula pinnata* (L.) A. DC., Crete.

45. *Cylindrocarpa* Regel

Cylindrocarpa Regel, Trudy Imp. S.-Peterburgsk. Bot. Sada 5: 258 (1877).

Perennial herb. Flowers small to medium-sized, sessile, solitary and terminal. Hypanthium cylindric. Corolla blue, split nearly its entire length. Stamens included; anthers much longer than filaments. Ovary 2–3-locular; style included; stigmatic lobes filiform. Fruit capsular, laterally dehiscent by 2–3 subapical slits. One species, *C. sewerzowii* (Regel & Herder) Regel, central Asia.

46. *Sergia* Fed.

Sergia Fed. in Kom., Fl. S.S.S.R. 24: 474 (1957).

Perennial herbs with an enlarged woody caudex. Leaves cauline, sessile or petiolate. Flowers small, pedicellate, terminal. Corolla blue, campanulate or funnelform, split for most its length. Stamens 4; anthers much longer than filaments, appearing sessile. Ovary 3-locular. Fruit capsular, laterally dehiscent by 3 basal valves. Two species, central Asia.

47. *Phyteuma* L.

Phyteuma L., Sp. Pl. 170 (1753); Damboldt in Tutin et al., Fl. Eur. 4: 95–98 (1976), reg. rev.

Perennial herbs from a fleshy rootstock. Flowers small to medium-sized, sessile or subsessile, in terminal spicate or subglobular involucrate heads. Calyx lobes 4–5. Corolla tubular, blue or lilac (rarely yellow); lobes 4–5, much longer than tube but coherent in the apical third and bowed out medially, forming five prominent fenestrations, eventually separating and spreading. Filaments dilated basally; pollen 4-porate, spinulose. Ovary 2–3-locular. Fruit capsular, laterally dehiscent by 2–3 medial pores. $2n = 16, 18, 20, 22, 24, 26, 28$. Twenty-two species, Europe.

48. *Physoplexis* (Endl.) Schur

Fig. 7

Physoplexis (Endl.) Schur, Sert. Fl. Transsilv. 47 (1853).
Synotoma (G. Don) Rich. Schulz (1904), nom. illegit.

Perennial herb. Leaves cauline and basal, petiolate. Flowers medium-sized, pedicellate, in an 8–20-flowered terminal umbel. Corolla tubular, pinkish lilac with dark violet apex; lobes much longer than tube but connate in the apical third and bowed out medially, forming five prominent fenestrations. Pollen 4-porate, spinulose. Ovary 2-locular. Fruit capsular, laterally dehiscent by 2 medial pores. $2n = 34, 68$. One species, *Physoplexis comosa* (L.) Schur, south-eastern Europe.

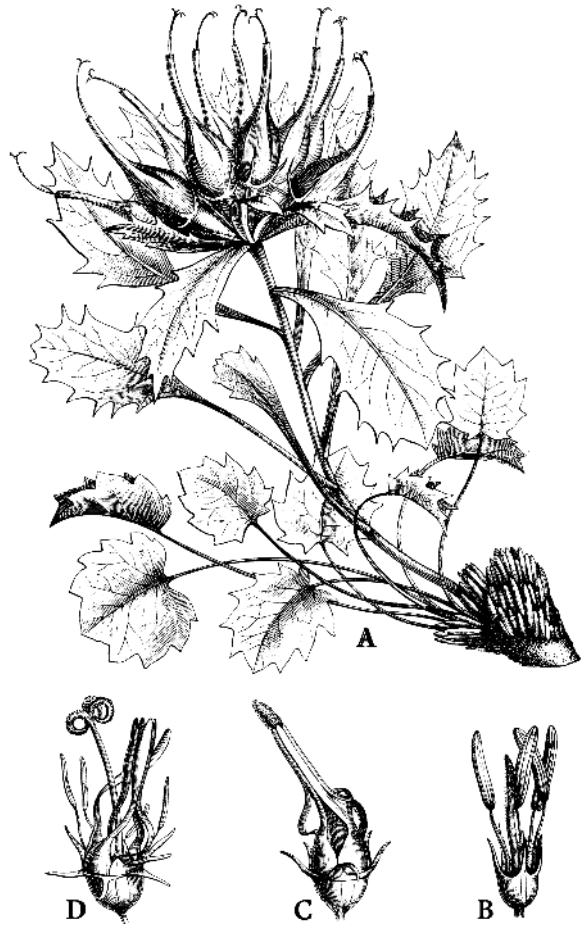

Fig. 7. Campanulaceae-Campanuloideae. *Physoplexis comosa*. **A** Habit. **B** Flower (corolla removed). **C** Flower (corolla removed, male phase). **D** Flower (corolla removed, female phase). (Schönland 1889)

49. *Michauxia* L'Hér.

Michauxia L'Hér., Michauxia (1788), nom. cons.; Rechinger & Schimann-Czeika, Fl. Iran. 13: 47–49 (1965), reg. rev.; Damboldt, Fl. Turk. 6: 81–83 (1978), reg. rev.

Robust biennials. Leaves cauline and basally rosulate, pinnately lobed or cleft. Flowers large, subsessile or short-pedicellate, in spicate racemes or panicles. Calyx lobes (6–)8–10, the sinuses appendaged. Corolla white or pale pink, rotate, split nearly to the base; lobes (6–)8–10, recurved. Stamens (6–)8–10; filaments basally dilated; anthers 3 times longer than filaments, apically mucronate or cuspidate; pollen 3-porate, spinulose. Ovary (6–)8–10-locular; style exserted; stigmatic lobes filiform. Fruit capsular, pendent, dehiscent laterally by (6–)8–10 basal valves. $2n$ = 28, 30, 34. Seven species, south-western Asia.

This genus has been called *Mindium*, though the type of that name belongs to *Canarina*.

50. *Trachelium* L.

Trachelium L., Sp. Pl. 171 (1753).

Perennial herb. Leaves petiolate. Flowers small, pedicellate, in a pedunculate corymb. Corolla tubular, blue (rarely white); lobes much shorter than tube. Style long-exserted. Fruit capsular, laterally dehiscent by basal pores. $2n$ = 32, 34. Two species, Mediterranean and often cultivated.

II. Subfam. Nemacladoideae Lammers (1998).

Annual herbs (one species perennial). Inflorescence a terminal raceme (often comprising much of the plant body) or rarely a series of 1–4 capitate clusters. Flowers not resupinate. Calyx with the odd (unpaired) lobe in a ventral (anterior) position. Corolla bilaterally symmetric, with 3 dorsal and 2 ventral lobes. Stamens epigynous, the dorsal 2 commonly alternating with three flattened, round glands; filaments connate above (rarely distinct), the dorsal 2 (sometimes 4) commonly bearing one or more transparent rod-like cells on a stipe (or rarely sessile); anthers distinct, commonly radiating at right angles to the filaments. Ovary half-inferior (rarely nearly superior), 2-locular with axile placentation (rarely 1-locular with parietal placentation); stigma 2-lobed. Fruit a loculicidal capsule, dehiscent by 2 apical valves (these sometimes splitting longitudinally at apex) or circumscissile. Seeds subglobose, ellipsoid, or cylindric, smooth or variously pitted or striate.

Nemacladoideae comprise 3 genera (2 monotypic) and 15 species endemic to the south-western United States and adjacent Mexico.

51. *Pseudonemacladus* McVaugh

Pseudonemacladus McVaugh, N. Amer. Fl. 32A: 3 (1943).

Perennial herb. Leaves cauline, opposite or the upper alternate, petiolate. Flowers very small, pedicellate, in a terminal pedunculate 5–30-flowered raceme; pedicels subapically bibracteolate. Corolla white or bluish; lobes dimorphic, the ventral larger. Filaments connate in upper half, tube strongly recurved at apex, lacking any special glands or appendages. Ovary half-inferior, 2-locular. Capsule loculicidal, dehiscent by 2 apical valves. One species, *P. oppositifolius* (B.L. Rob.) McVaugh, Mexico.

52. *Nemacladus* Nutt. Fig. 8

Nemacladus Nutt., Trans. Amer. Philos. Soc. n.s. 8: 254 (1842); McVaugh, Amer. Midl. Nat. 22: 521–550 (1939), rev.; Wimmer, Pflanzenr. IV.276c: 923–935 (1968), rev.; Morin & Milburn in Hickman, Jepson Man.: 465–468 (1993), reg. rev.

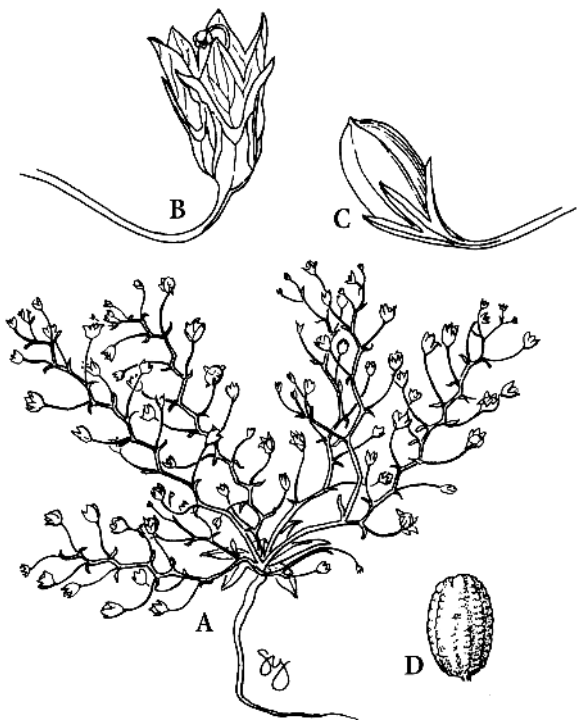

Fig. 8. Campanulaceae-Namacladoideae. *Nemacladus rigidus*. **A** Habit. **B** Flower. **C** Capsule. **D** Seed. (Hickman 1993, with permission from the Jepson Herbarium. © Regents of the University of California)

Annuals. Leaves rosulate, petiolate or sessile. Flowers very small, pedicellate, in a terminal raceme; pedicels ebracteolate. Corolla white or bluish; lobes monomorphic. Filaments distinct or connate in upper half, dorsal pair bearing one or more transparent rod-like cells on a stipe. Ovary half-inferior, 2-locular (rarely 1-locular). Capsule loculicidal, dehiscent by 2 apical valves, these sometimes splitting longitudinally. $2n = 18$. Thirteen species, western North America.

53. *Parishella* A. Gray

Parishella A. Gray, Bot. Gaz. (Crawfordsville) 7: 94 (1882).

Annual. Leaves rosulate, petiolate. Flowers very small, pedicellate, in a series of 1–3 terminal capitula; pedicels ebracteolate. Corolla white; lobes monomorphic. Filaments connate in upper half, ventral 4 bearing sessile clusters of a few transparent rod-like cells. Ovary half-inferior, imperfectly 2-locular. Capsule circumscissile. One species, *P. californica* A. Gray, western North America.

III. Subfam. Lobelioideae Burnett (1835).

Herbaceous perennials (less often annual or biennial), woody lianas (sometimes twining), pachycaul rosette plants, subshrubs, shrubs, treelets, or trees to 15 m tall, typically terrestrial, rarely aquatic or epiphytic. Inflorescences commonly racemose, or flowers solitary in an axillary (rarely terminal) position; flowers commonly resupinate by torsion of the pedicel. Calyx with the odd (unpaired) lobe in a ventral (anterior) position prior to resupination. Corolla bilaterally symmetric, with two dorsal and three ventral lobes, or all five lobes ventral. Stamens epigynous; filaments connate, tube sometimes adnate to corolla tube; anthers connate, forming an oblique tube. Ovary inferior (rarely nearly superior), 2-locular with axile placentation (rarely 1-locular with parietal or basal placentation); stigma 2-lobed. Fruit a capsule (commonly loculicidal) or berry.

Lobelioideae comprise 29 genera and 1,195 species. Though the subfamily is represented on all six continents, two-thirds of the species are endemic to the New World: South America harbours nearly half and North America 17%. Another 14% are African, 12% Polynesian, 5% Australasian, 3% Asian and less than 1% European.

54. *Dialypetalum* Benth.

Dialypetalum Benth. in Benth. & Hook. f., Gen. Pl. 2: 553 (1876).

Herbs and shrubs. Flowers small, in many-flowered terminal panicles. Corolla actinomorphic, rotate, split nearly to base, white, yellowish, greenish or purplish. Filaments distinct or connate only at apex; ventral 2 anthers with a bristle at apex. Fruit capsular, dehiscent by 2 apical valves. Five species, Madagascar.

55. *Lobelia* L. Fig. 9

Lobelia L., Sp. Pl.: 929 (1753); McVaugh, N. Amer. Fl. 32A: 35–99 (1943), reg. rev.; Braga, Trib. Farm. 32: 1–8, 41–54 (1964), 33: 3–24 (1965), reg. rev.; Mabberley, Kew Bull. 29: 535–583 (1974), reg. sect. rev.; Ayers, Syst. Bot. 15: 296–327 (1990), part. rev.; Lammers in Wagner et al., Man. Fl. Pl. Hawai'i: 473–480 (1990), sect. rev.; Wilbur, Sida 14: 555–567 (1991), reg. sect. rev.; Hong & Zhang, Acta Phytotax. Sin. 30: 146–162 (1992), reg. sect. rev.; Lammers, Sida 19: 87–110 (2000), sect. rev.; Lammers, Sida 21:591–623 (2004), sect. rev.
Pratia Gaudich. (1825).
Hypsela C. Presl (1836).
Trimeris C. Presl (1836).
Galeatella (E. Wimm.) O. Deg. & I. Deg. (1962).
Neowimmeria O. Deg. & I. Deg. (1965).
Calcaratolobelia Wilbur (1997).

Annual or perennial herbs, shrubs, trees or giant rosette plants (often pliestesial). Flowers small to large, pedicellate, solitary and axillary or in terminal racemes (rarely secund or corymbose) or panicles. Calyx lobes rarely auriculate. Corolla unilabiate or bilabiate, blue, purple, red, rose, green, yellow or white, rarely with a narrow nectar spur; tube dorsally cleft to base (rarely entire), sometimes fenestrate; lobes monomorphic (apices sometimes coherent) or dimorphic, the ventral larger. Filament tube rarely adnate to corolla; ventral or all five anthers with apical tufts of stiff hairs, ventral sometimes with minute apical appendages, rarely all nude. Ovary rarely almost superior. Plants rarely dioecious. Fruit capsular, dehiscent apically by 2 valves, or a berry. $2n = 12, 14, 18, 24, 26, 28, 38, 42, 70, 140$. Over 400 species, cosmopolitan, divided by Murata (1995) into three subgenera: subg. *Lobelia* (231 spp.), subg. *Isolobus* (A. DC.) Y.S. Lian (48 spp.) and subg. *Tupa* (G. Don) E. Wimm. (127 spp.). Subgenus *Lobelia* comprises four sections: sect. *Lobelia* (22 spp.), sect. *Heyneana* J. Murata (143 spp.), sect. *Cryptostemon* (E. Wimm.)

J. Murata (9 spp.) and sect. *Delostemon* (E. Wimm.) J. Murata (57 spp.). *Isolobus* comprises four sections: sect. *Dioica* (E. Wimm.) J. Murata (8 spp.), sect. *Pratia* (Gaudich.) J. Murata (37 spp.), sect. *Paramezleria* E. Wimm. (1 sp.) and sect. *Isolobus* (A. DC.) C.B. Clarke (2 spp.). *Tupa* comprises seven sections: sect. *Tupa* (G. Don) Benth. (4 spp.), sect. *Colensoa* (Hook. f.) J. Murata (47 spp.), sect. *Rhynchopetalum* (Fresen.) Benth. (20 spp.), sect. *Homochilus* A. DC. (6 spp.), sect. *Tylomium* (C. Presl) Benth. (37 spp.), sect. *Revolutella* E. Wimm. (9 spp.) and sect. *Galeatella* E. Wimm. (4 spp.)

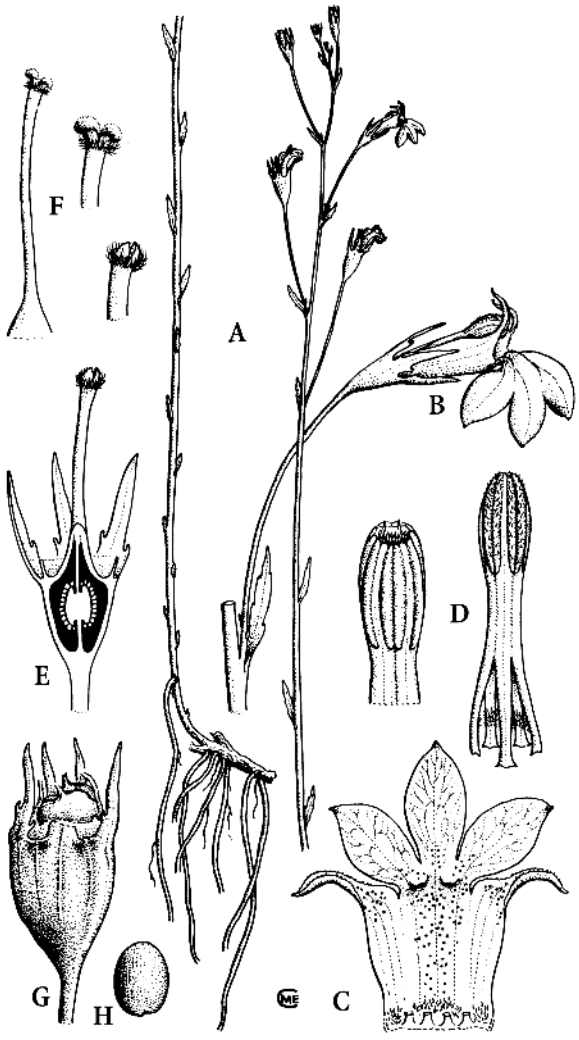

Fig. 9. Campanulaceae-Lobelioideae. *Lobelia welwitschii*. **A** Habit. **B** Flower. **C** Opened corolla. **D** Stamens and anther tube. **E** Ovary, longitudinal section. **F** Stigma at different developmental stages. **G** Capsule. **H** Seed. (Thulin 1984)

56. *Solenopsis* C. Presl

Solenopsis C. Presl, Prodr. Monogr. Lobel. 32 (1836); Crespo et al., Pl. Syst. Evol. 210: 211–219 (1998), rev.

Annual or perennial herbs, sometimes scapose. Leaves petiolate, sometimes basally rosulate. Flowers pedicellate, solitary, axillary (appearing terminal in scapose species); pedicels medially 1–3-bracteolate (rarely ebracteolate). Corolla bilabiate, blue, sometimes white or yellow on lower lip; tube entire; lobes subdimorphic, the ventral slightly larger. Filament tube free from corolla; ventral anthers aristate at apex, often also with tufts of stiff hairs. Fruit capsular, dehiscent apically by 2 valves. Seeds ellipsoid to fusiform, strophiolate, with weak longitudinal ridges, sulcate with keeled walls. $2n = 22, 28$. Six species, Mediterranean.

57. *Wimmerella* L. Serra, M.B. Crespo & Lammers

Wimmerella L. Serra, M.B. Crespo & Lammers, Novon 9: 415 (1999).

Annual or perennial herbs. Leaves petiolate or sessile. Flowers pedicellate, solitary, axillary, or in lax, often secund racemes; pedicels basally bibracteolate or ebracteolate. Corolla bilabiate, blue or white; tube entire; lobes dimorphic, the ventral slightly larger, or monomorphic. Filament tube free from corolla; ventral anthers aristate at apex, often also with tufts of stiff hairs. Fruit capsular, dehiscent apically by 2 valves. Seeds ellipsoid to subglobose, estrophiolate, sulcate with flattened walls. Ten species, South Africa.

58. *Grammatotheca* C. Presl

Grammatotheca C. Presl, Prodr. Monogr. Lobel. 43 (1836).

Repent herb. Flowers small, solitary, axillary, sessile, with a pair of bracteoles at base. Hypanthium pedicelliform, twisted 180°. Corolla bilabiate, blue-violet with white eye; tube dorsally cleft for 2/3 its length; lobes dimorphic, the ventral larger. All 5 anthers with apical tufts of stiff hairs. Fruit capsular, dehiscent apically by 2 valves and also laterally by irregular tears. One species, *G. bergiana* (Cham.) C. Presl, South Africa and Australia.

59. *Dielsantha* E. Wimm.

Dielsantha E. Wimm., Ann. Naturhist. Mus. Wien 56: 372 (1948).

Perennial herb. Flowers small, sessile, in few-flowered axillary fascicles. Hypanthium pedi-

celliform, twisted 180°. Corolla bilabiate, pale violet; tube cleft to base; lobes dimorphic, the ventral larger. Filament tube free from corolla; all 5 anthers with apical tufts of stiff hairs. Stigma lobes filiform, 1/3 as long as style. Fruit capsular, dehiscing by 5 or 6 irregular lateral ruptures. One species, *D. galeopsoides* (Engl. & Diels) E. Wimm., western Africa.

60. *Monopsis* Salisb.

Monopsis Salisb., Trans. London Hort. Soc. 2: 37 (1817).

Annual or perennial herbs. Leaves sometimes opposite or whorled. Flowers small, solitary, axillary, pedicellate or sessile and aggregated into a congested terminal raceme, commonly not resupinate; pedicels ebracteolate or basally bibracteolate. Corolla bilabiate with dimorphic lobes (the ventral larger) or subrotate with monomorphic lobes, blue, violet, yellow or orange; tube cleft dorsally to base. Filament tube sometimes adnate to corolla at base; all 5 anthers with apical tufts of stiff hairs. Stigma lobes long, filiform. Fruit capsular, dehiscent apically by 2 valves. $2n = 28$. Fifteen species, Africa. Divided by Wimmer (1953) into three sections: sect. *Monopsis* (1 sp.), sect. *Dobrowskya* (C. Presl) Urb. (11 spp.) and sect. *Parastranthus* (G. Don) E. Wimm. (3 spp.).

61. *Unigenes* E. Wimm.

Unigenes E. Wimm., Ann. Naturhist. Mus. Wien 56: 373 (1948).

Herb. Flowers very small, pedicellate, solitary, axillary; pedicels ebracteolate. Corolla bilabiate, white; tube dorsally cleft to base; lobes subdimorphic, the ventral slightly larger. Ventral anthers with minute appendages and tufts of stiff hairs at apex. Ovary nearly superior, 1-locular; placenta basal. Fruit capsular, dehiscent from apex to base by 2 valves; seed 1(2), white, large. One species, *U. humifusa* (A. DC.) E. Wimm., South Africa.

62. *Isotoma* (R. Br.) Lindl.

Isotoma (R. Br.) Lindl., Edwards' Bot. Reg. 12: pl. 964 (1826).

Annuals, sometimes dioecious. Flowers small to medium-sized, solitary, axillary, or aggregated into secund racemes; pedicels ebracteolate. Corolla bilabiate or rarely salverform, blue, rarely rose or white; tube entire; lobes monomorphic. Filament tube adnate to corolla above the middle; ventral anthers with long bristle at apex plus tufts of stiff hairs. Fruit capsular, dehiscent apically by 2 valves, or a berry. $2n = 14, 28$. Fourteen species, Australia, New Zealand.

63. *Ruthiella* Steenis

Ruthiella Steenis, Blumea 13: 127 (1965); Tuyn, Fl. Males. ser. I, 6: 137–139 (1960), rev.
Phyllocharis Diels (1919), nom. illegit.

Annuals. Flowers small, solitary; pedicels adnate to the midrib of the subtending leaf. Hypanthium dorsally oblique. Corolla bilabiate, green or yellow; tube dorsally cleft to base; lobes dimorphic, the dorsal 1.5–3 times as long as the ventral but more slender. Ventral anthers with minute apical appendages and apical tufts of stiff hairs, sometimes all nude. Fruit capsular, dehiscent apically by 2 valves. Four species, New Guinea.

64. *Diastatea* Scheidw.

Diastatea Scheidw., Allg. Gartenz. 9: 396 (1841); McVaugh, Bull. Torrey Bot. Club 67: 784–794 (1940), rev.

Annuals. Flowers small, in terminal, sometimes secund 5–30-flowered racemes (rarely solitary, axillary); pedicels ebracteolate. Corolla bilabiate, purplish, blue or white; tube entire, persistent on the developing fruit and becoming scarious and hyaline; lobes dimorphic, the ventral larger. Filament tube loosely adnate to the corolla at base; ventral 2 anthers with apical tufts of stiff hairs. Ovary nearly superior, free from hypanthium for 4/5 of its length. Fruit capsular, dehiscing to middle by 2 apical valves. Five species, Central and South America.

65. *Palmerella* A. Gray

Palmerella A. Gray, Proc. Amer. Acad. Arts 11: 80 (1876).

Perennial herb. Leaves sessile. Flowers medium-sized, in a 5–23-flowered subcapitate terminal racemes; pedicels ebracteolate. Corolla bilabiate, blue or purple; tube dorsally cleft from base for half its length at maturity; lobes dimorphic, the ventral larger. Filament tube dorsally loosely adnate to corolla; ventral anthers with a short apical appendage and apical tufts of stiff hairs. Fruit capsular, dehiscent apically by 2 valves. One species, *Palmerella debilis* A. Gray, western North America.

66. *Porterella* Torr.

Porterella Torr. in F.V. Hayden, Prelim. Rep. Geol. Surv. Montana: 488 (1872).

Annual. Leaves much smaller than bracts, sessile. Flowers small, fragrant, pedicellate, solitary, axillary. Corolla bilabiate, blue (rarely white), often marked with yellow or white on ventral lip; tube entire; lobes dimorphic, the ventral larger. Filament tube free from the corolla. Ventral anthers with a horn-like bristle, all 5 with apical tufts of stiff hairs. Ovary 2-locular with axile placentation. Fruit capsular, dehiscent apically by 2 valves; seeds fusiform, brown with dark apiculate tips. $2n$ = 22, 24. One species, *P. carnosula* (Hook. & Arn.) Torr., western North America.

67. *Legenere* McVaugh

Legenere McVaugh, N. Amer. Fl. 32A: 13 (1943); Ruiz de Ciolfi, Bol. Soc. Argent. Bot. 17: 176–178 (1976), rev.

Emergent aquatic annuals. Leaves sessile. Flowers small, both chasmogamous and cleistogamous, pedicellate, in a terminal raceme; pedicels ebracteolate. Corolla bilabiate, yellow; tube dorsally cleft to base; lobes dimorphic, the ventral larger. Staminal column included; ventral anthers with minute apical appendages. Ovary 1-locular with 2 parietal placentae. Fruit capsular, dehiscent apically by 2 valves; seeds 20 or less. One species, *L. valdiviana* (Phil.) E. Wimm., western North America, southern South America.

68. *Howellia* A. Gray

Howellia A. Gray, Proc. Amer. Acad. Arts 15: 43 (1879).

Submersed aquatic annuals. Stems branched, flaccid, floating. Leaves sessile. Flowers small, chasmogamous and cleistogamous, pedicellate, solitary, axillary; pedicels ebracteolate. Corolla bilabiate, white; tube dorsally cleft nearly to base; lobes dimorphic, the ventral larger. Staminal column included; ventral anthers with minute apical appendages. Ovary 1-locular with 2 parietal placentae. Capsule dehiscent laterally by irregular ruptures; seeds 1–5, large. $2n$ = 22. One species, *H. aquatilis* A. Gray, western North America.

69. *Downingia* Torr.

Downingia Torr., Rep. Explor. RR Pac. Ocean 4: 116 (1857), nom. cons.; McVaugh, Mem. Torrey Bot. Club 19, 4: 1–57 (1941), rev.; Ayers in Hickman, Jepson Man.: 460–462 (1993), reg. rev.

Annuals. Leaves much smaller than bracts, sessile. Flowers small, sessile, in a terminal raceme. Hypanthium pedicelliform, twisted 180° (rarely not). Corolla bilabiate, blue (rarely pinkish or white), often marked with yellow or white on ventral lip; tube entire; lobes dimorphic, the ventral larger. Ventral anthers with a horn-like bristle plus apical tufts of stiff hairs. Ovary 2-locular with axile placentation or 1-locular with 2 parietal placentae. Capsule dehiscent by 3–5 longitudinal slits. $2n$ = 12, 16, 18, 20, 22, 24. Thirteen species, western North America.

70. *Lysipomia* Kunth

Lysipomia Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 318 (1819); McVaugh, Brittonia 8: 69–105 (1955), rev.; Jeppesen, Fl. Ecuador 14: 136–151 (1981), reg. rev.
Rhizocephalum Wedd. (1858).
Dominella E. Wimm. (1953).

Dwarf perennial herbs, often forming cushions, sometimes scapose. Leaves sessile or petiolate, commonly rosulate. Flowers small to medium-sized, solitary, axillary, often not resupinate, sometimes sessile; pedicels (when present) ebracteolate. Corolla bilabiate, yellow or white; tube entire (very rarely cleft dorsally to base); lobes monomorphic or subdimorphic. Filament tube adnate to corolla, at least at base; ventral anthers commonly with long bristle at apex, sometimes also with tufts of stiff hairs. Ovary 1-locular with 2 parietal placentae. Fruit a pyxis, operculum umbonate. $2n$ = 20. Thirty species, Andean South America.

71. *Hippobroma* G. Don

Hippobroma G. Don, Gen. Hist. 3: 717 (1834); McVaugh, Bull. Torrey Bot. Club 67: 782–784 (1940), rev.

Perennial herbs. Leaves repand-dentate. Flowers large, fragrant, solitary, axillary; pedicels short, bibracteolate at base. Corolla salverform, white; tube entire; lobes monomorphic. Filament tube adnate to corolla; all anthers with apical tufts of stiff hairs. Fruit capsular, apically dehiscent by 2 valves. $2n$ = 28. One species, *H. longiflora* (L.) G. Don, originally native to the West Indies but now naturalized throughout the tropics.

72. *Heterotoma* Zucc. Fig. 10

Heterotoma Zucc., Flora 15 (2, Beibl.): 100 (1832); Ayers, Syst. Bot. 15: 296–327 (1990), rev.

Suffrutescent perennial herb. Flowers large, spurred, in a pedunculate terminal raceme. Hypanthium asymmetric, ventrally distended by the nectar spur. Ventral calyx lobes displaced to

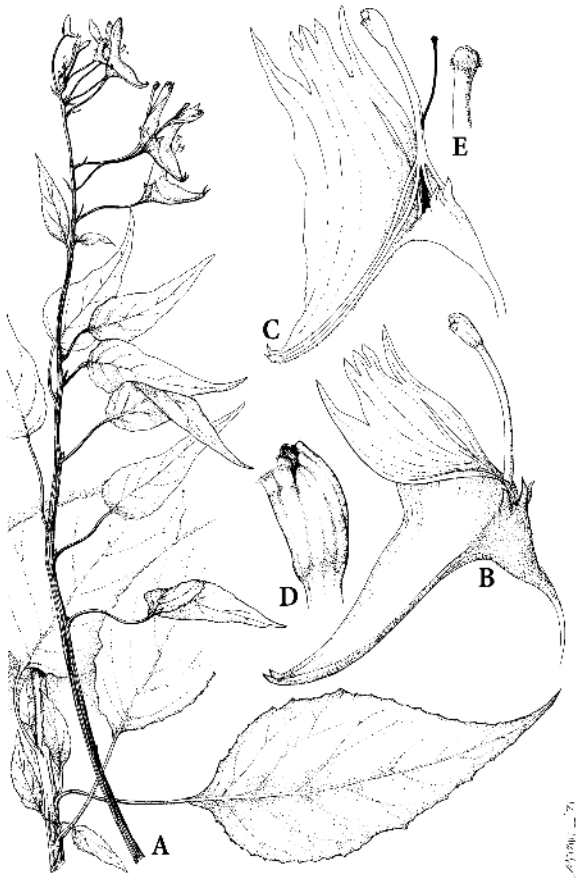

Fig. 10. Campanulaceae-Lobelioideae. *Heterotoma lobelioides*. **A** Flowering branch and leaves. **B** Flower, partly opened. **C** Flower, partly opened. **D** Anthers. **E** Stigma. (Nash 1976)

tip of spur. Corolla unilabiate, orange or red with yellow lobes, much of its length in the form of a broad calcarate nectar spur; lobes monomorphic. Ventral anthers with apical tufts of stiff hairs. Fruit capsular, dehiscent by two apical valves. $2n = 14$. One species, *H. lobelioides* Zucc., Central America.

73. *Siphocampylus* Pohl

Siphocampylus Pohl, Pl. Bras. Icon. Descr. 2: 104 (1831); Jeppesen, Fl. Ecuador 14: 151–170 (1981), reg. rev.

Suffrutescent herbs or shrubs, sometimes scandent or twining lianas. Leaves rarely opposite or whorled. Flowers medium-sized to large, solitary, axillary, rarely forming a terminal corymb or raceme. Corolla bilabiate or tubular, red, orange, pink, purple, yellow, green or white; tube entire or very rarely fenestrate; lobes dimorphic, the dorsal larger. Filament tube adnate to corolla basally or rarely free; ventral anthers (rarely all 5) with apical tufts of stiff white hair (rarely nude). Fruit capsular, apically dehiscent by 2 valves; seeds slightly longer than wide, testa reticulate. $2n = 28$. Over 230 species, Central and South America, Greater Antilles. Wimmer (1953, 1968) divided the genus into two sections: sect. *Siphocampylus* (203 spp.) with four subsections: subsect. *Hemisiphocampylus* (A. DC.) E. Wimm. (10 spp.), subsect. *Siphocampylus* (180 spp.), subsect. *Byrsanthes* (C. Presl) E. Wimm. (7 spp.) and subsect. *Isochilus* E. Wimm. (6 spp.); sect. *Brachysiphon* E. Wimm. (31 spp.) also with four subsections: subsect. *Secundiflori* E. Wimm. (10 spp.), subsect. *Altofissi* E. Wimm. (6 spp.), subsect. *Megastomi* E. Wimm. (11 spp.) and subsect. *Megalandri* E. Wimm. (4 spp.).

74. *Centropogon* C. Presl

Centropogon C. Presl, Prodr. Monogr. Lobel. 48 (1836); Jeppesen, Fl. Ecuador 14: 48–122 (1981), reg. rev.

Suffrutescent herbs or shrubs, sometimes scandent lianas. Flowers medium-sized to large, solitary, axillary, rarely forming a terminal corymb or raceme; pedicels commonly bibracteolate. Corolla bilabiate or tubular, red, orange, pink, purple, yellow, green or white; tube entire or very rarely fenestrate, often constricted at base and/or inflated at mouth; lobes dimorphic, the dorsal larger and sometimes falcate. Filament tube adnate to corolla basally; ventral anthers with apical tufts of stiff or weak hairs (sometimes concrescent into a triangular scale). Fruit a berry, sometimes inflated; seeds slightly longer than wide, reticulate. $2n = 28$. Two hundred and thirteen species, Central and South America, Lesser Antilles. Lammers (1998b, 2002) divided the genus into five sections: sect. *Centropogon* (49 spp.), sect. *Siphocampyloides* Benth. (100 spp.), sect. *Wimmeriopsis* McVaugh (40 spp.), sect. *Burmeisteroides* Gleason (21 spp.) and sect. *Niveopsis* Lammers (1 sp.). *Siphocampyloides* was divided into subsect. *Brevilimbati* E. Wimm. (89 spp.) and subsect. *Peruviani* McVaugh (11 spp.); *Wimmeriopsis* into subsect. *Falcati* McVaugh and subsect. *Colombiani* McVaugh (20 spp. each).

75. *Burmeistera* Triana Fig. 11

Burmeistera Triana, Nuev. Gen. Esp. 13 (1855); Jeppesen, Fl. Ecuador 14: 12–48 (1981), reg. rev.

Suffrutescent herbs or shrubs, sometimes scandent lianas. Flowers medium-sized to large, soli-

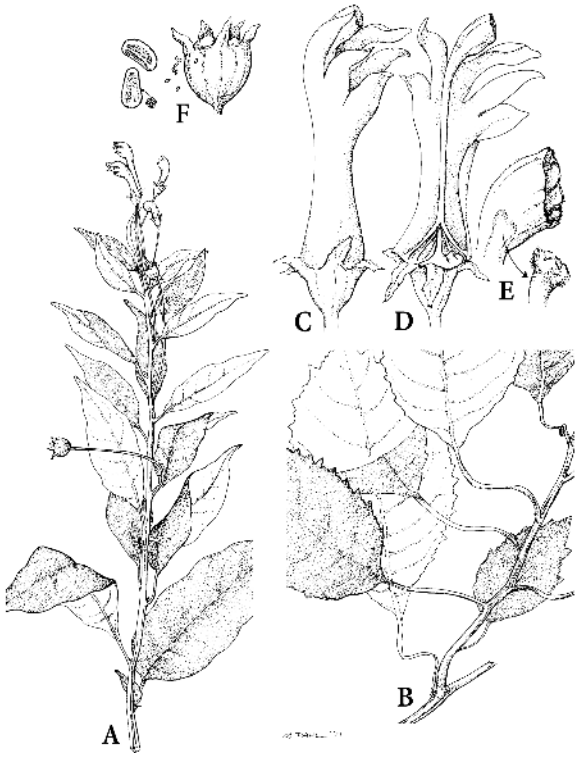

Fig. 11. Campanulaceae-Lobelioideae. *Burmeistera virescens*. **A** Flowering branch. **B** Leaves. **C** Flower. **D** Flower, opened. **E** Anther tube and stigma. **F** Berry and seeds. (Nash 1976)

tary, axillary, rarely forming a terminal corymb or raceme; pedicels ebracteolate. Corolla bilabiate, green, yellow, purple or maroon; tube entire, often inflated at base and/or mouth; lobes dimorphic, the dorsal larger and often falcate. Filament tube free or adnate to corolla basally; orifice of anther tube wide open, glabrous or with soft weak hairs on ventral anther or all anthers. Fruit a berry, sometimes much inflated; seeds much longer than wide, reticulate. Over 100 species, Central America and Andean South America. Lammers (1998b, 2002) divided the genus into two sections: sect. *Burmeistera* (54 spp.) and sect. *Barbatae* E. Wimm. (48 spp.).

76. *Sclerotheca* A. DC.

Sclerotheca A. DC. in DC., Prodr. 7: 356 (1839).

Shrubs or small trees. Flowers large, solitary, axillary; pedicels bibracteolate at or below middle. Corolla bilabiate, magenta, purple, green or yellow; tube entire or dorsally cleft to base; lobes monomorphic. Ventral anthers or all five with apical tufts of stiff hairs. Ovary 2-locular, placentae axile. Fruit capsular, dehiscent by two apical pores. Six species, Polynesia.

77. *Apetahia* Baill.

Apetahia Baill., Bull. Mens. Soc. Linn. Paris 1: 310 (1882); Florence, Allertonia 7: 248–253 (1997), rev.

Shrubs or small trees. Flowers large, solitary, axillary; pedicels bibracteolate at or above middle. Corolla unilabiate, green, white, pink or violet; tube cleft 1/4–1/5 of its length, curved slightly; lobes monomorphic, spreading, forming 1/3–2/5 of the corolla. Ovary 1-locular, placentae parietal (or appearing 2-locular/axile through intrusive growth of placentae). Fruit capsular, dehiscent by two apical valves which are often bifid. $2n = 28$. Four species, Polynesia.

78. *Trematolobelia* Zahlbr.

Trematolobelia Zahlbr. in Rock, Coll. Hawaii Publ. Bull. 2: 45 (1913); Lammers in Wagner et al., Man. Fl. Pl. Hawai'i: 485–488 (1990), rev.

Pliestesial rosette treelets. Leaves sessile or petiolate. Flowers large, pedicellate, in a terminal 50–400-flowered pedunculate panicle composed of 5–20 horizontally radiating secund racemes; pedicels bibracteolate. Corolla unilabiate or bilabiate, red, rose, pink or white; tube dorsally cleft to base; lobes monomorphic. Ventral anthers with apical tufts of stiff hairs. Fruit capsular, dehiscent laterally by 5–15 irregular pores after decomposition of the fleshy exocarp; seeds winged. $2n = 28$. Four species, Hawaiian islands.

79. *Brighamia* A. Gray

Brighamia A. Gray, Proc. Amer. Acad. Arts 7: 185 (1867); Lammers, Syst. Bot. 14: 133–138 (1989), rev.; Lammers in Wagner et al., Man. Fl. Pl. Hawai'i: 422–423 (1990), rev.

Polycarpic rosette treelets; stems unbranched, caudiciform, succulent. Leaves fleshy. Flowers large, fragrant, in axillary 3–8-flowered racemes. Corolla salverform, yellow or white; tube slender, straight, entire at anthesis but eventually cleft for c. 1/3 its length. Staminal column included; filament tube adnate to corolla tube below middle; all 5 anthers with apical tufts of stiff hairs. Capsule dehiscent by two lateral longitudinal slits per locule; seeds white, rugose. $2n = 28$. Two species, Hawaiian islands.

80. *Delissea* Gaudich.

Delissea Gaudich., Voy. Uranie: pl. 78 (1826); Lammers in Wagner et al., Man. Fl. Pl. Hawai'i: 467–472 (1990), rev.; Lammers, Syst. Bot. Monogr. 73: 1–75 (2005), rev.

Shrubs, treelets or trees; stems unbranched or sparingly branched. Flowers medium-sized to large, in 5–20-flowered axillary racemes. Corolla bilabiate or unilabiate, white or greenish (rarely lilac); tube dorsally cleft to middle, with a knob at the base of the cleft (sometimes also with a lateral pair of knobs); lobes monomorphic. Filament tube free from corolla; ventral anthers with apical tufts of stiff hairs. Fruit a purple berry; seeds white, transversely rugose. $2n = 28$. Fifteen species, Hawaiian islands. Lammers (2005) divided the genus into three sections: sect. *Delissea* (4 spp.), sect. *Rhytidospermae* Lammers (4 spp.) and sect. *Macranthae* (Hillebr.) Rock (7 spp.).

81. *Cyanea* Gaudich.

Cyanea Gaudich., Voy. Uranie: pl. 75 (1828); Lammers in Wagner et al., Man. Fl. Pl. Hawai'i: 437–467 (1990), rev.

Shrubs, treelets or trees, rarely lianas, rarely epiphytic; stems unbranched or sparingly branched, sometimes muricate or aculeate (more so in juveniles); latex sometimes yellow or tan. Leaves sometimes muricate or aculeate (more so in juveniles); margin sometimes pinnately lobed, cleft, parted, or divided (often more so in juveniles). Flowers medium-sized to large, in (3–)5–25(–40)-flowered axillary racemes, sometimes subumbellate. Corolla bilabiate or unilabiate, white, magenta, purple, pink, greenish or yellowish, sometimes longitudinally striped, rarely muricate; tube dorsally cleft to middle; lobes monomorphic. Filament tube free from corolla or dorsally adnate for 1/3–1/2 of its length; ventral anthers (rarely all 5) with apical tufts of stiff hairs. Fruit a yellow, orange or purple berry; seeds reticulate. $2n = 28$. Seventy-eight species, Hawaiian islands. Based on the phylogeny of Givnish et al. (1995), the genus can be divided into two sections: sect. *Cyanea* (61 spp.) and sect. *Delisseoideae* (Hillebr.) Rock (17 spp.); the former will eventually prove divisible into subordinate taxa.

82. *Clermontia* Gaudich.

Clermontia Gaudich., Voy. Uranie: pl. 459 (1829); Lammers in Wagner et al., Man. Fl. Pl. Hawai'i: 423–437 (1990), rev.; Lammers, Syst. Bot. Monogr. 32: 1–94 (1991), rev.

Shrubs or small trees, sometimes epiphytic. Stems branched repeatedly. Flowers medium-sized to large, in axillary, 2(–10)-flowered, subumbellate racemes. Calyx lobes frequently similar to corolla in shape, texture and colour. Corolla bilabiate, unilabiate, tubular, or rotate, white, green, purple or rose; tube dorsally cleft to near the base; lobes monomorphic. Fruit an orange or yellow berry; seeds reticulate. $2n = 28$. Twenty-two species, Hawaiian islands. Two sections were recognized by Lammers (1991): sect. *Clermontioideae* (Hillebr.) Rock (7 spp.) and sect. *Clermontia* (15 spp.). Each was divided into three series: the former into ser. *Clermontioideae* (Hillebr.) Lammers (3 spp.), ser. *Sarcanthae* Lammers (2 spp.) and ser. *Unilabiatae* Lammers (2 spp.), the latter into ser. *Kakeanae* Lammers (7 spp.), ser. *Parviflorae* Lammers (4 spp.) and ser. *Clermontia* (4 spp.).

IV. Subfam. Cyphocarpoideae Miers (1848).

Annual and perennial herbs. Leaves pinnatifid. Flowers small to medium-sized, sessile, bibracteolate at base, in a 3–15-flowered terminal spike. Hypanthium clavate or linear. Calyx with the odd (unpaired) lobe in a ventral (anterior) position; lobes pinnatifid. Corolla blue, lavender or white, bilaterally symmetric, with a single cucullate dorsal lobe bearing an apical appendage plus a 4-lobed ventral lip with a gibbous palate; tube entire. Stamens epipetalous, distinct, included. Ovary inferior, bilocular with axile placentation; stigma 2-lobed. Fruit a capsule, dehiscent via irregular rupture of the lateral walls.

83. *Cyphocarpus* Miers Fig. 12

Cyphocarpus Miers, London J. Bot. 7: 62 (1848); Wimmer, Pflanzenr. IV.276c: 922–923 (1968), rev.

See subfamily description. Three species, Chile.

V. Subfam. Cyphioideae (A. DC.) Walp. (1852).

Perennial herbs with a subglobose or elongate root tuber; stems erect or twining. Inflorescence a terminal raceme. Calyx with the odd (unpaired) lobe in a ventral (anterior) position. Corolla bilaterally symmetric, bilabiate with 3 dorsal and 2 nearly distinct ventral lobes, or tubular with 5 subequal lobes. Stamens epigynous; filaments distinct or connate; anthers distinct. Ovary inferior (rarely almost superior), 2-locular with apical

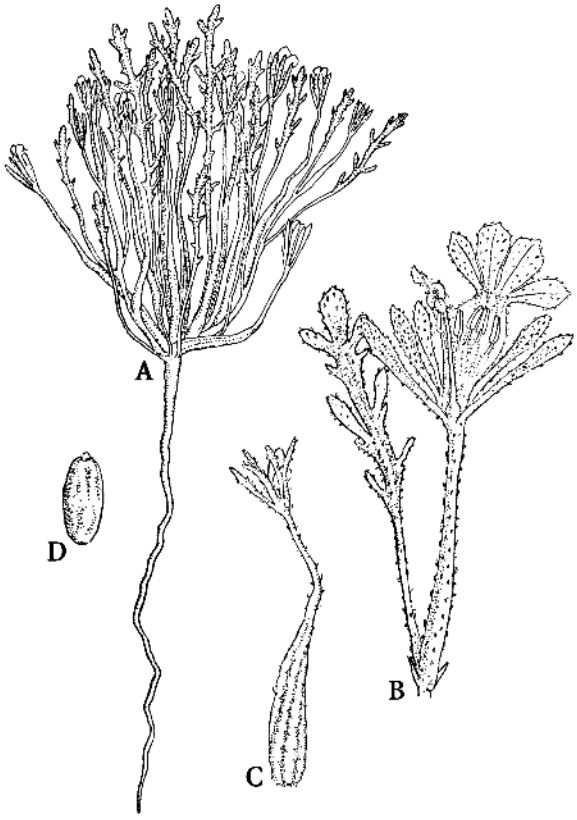

Fig. 12. Campanulaceae-Cyphocarpoideae. *Cyphocarpus psammophilus*. **A** Habit. **B** Flower, opened. **C** Capsule. **D** Seed. (Ricardi 1959)

placentation; style tipped by a fluid-filled stigmatic cavity with a lateral pore. Fruit a loculicidal capsule, dehiscent with 2 apical valves, these sometimes splitting longitudinally at apex so that the capsule appears 4-valved; seeds circumferentially winged and smooth, or 3-angled and coarsely reticulate.

Cyphioideae has sometimes been circumscribed to include *Cyphocarpus*, *Nemacladus*, *Parishella* and *Pseudonemacladus* (Schönland 1889; Wagenitz 1964; Wimmer 1968). Note that with this expanded circumscription, the name Cyphocarpoideae has priority.

84. *Cyphia* P.J. Bergius Fig. 13

Cyphia P.J. Bergius, Descr. Pl. Cap. 172 (1767); Wimmer, Pflanzenr. IV.276c: 935–1014 (1968), rev.

See subfamily description. Sixty-four species, Africa, divided by Wimmer (1968) into two sections: sect. *Cyphia* (51 spp.) and sect. *Cyphiella* C. Presl (13 spp.).

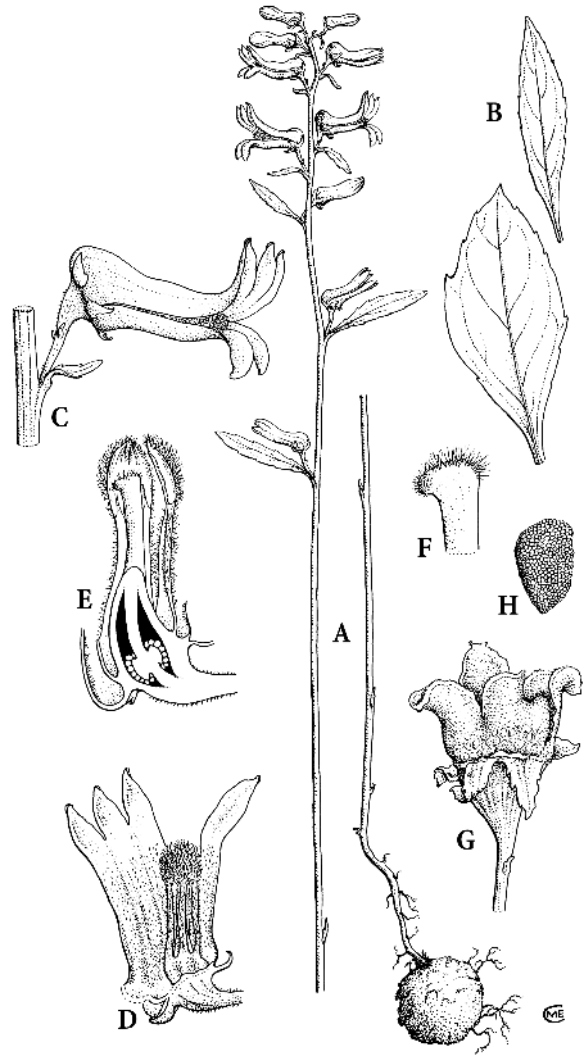

Fig. 13. Campanulaceae-Cyphioideae. *Cyphia erecta*. **A** Habit. **B** Leaves. **C** Flower. **D** Flower, perianth partly removed. **E** Flower, longitudinal section. **F** Stigma. **G** Capsule. **H** seed. (Thulin 1984)

Selected Bibliography

Adamson, R.S. 1952. A revision of the genera *Prismatocarpus* and *Roella*. J. S. African Bot. 17: 93–166.

Batterman, M.R.W., Lammers, T.G. 2004. Branched foliar trichomes of Lobelioideae (Campanulaceae) and the infrageneric classification of *Centropogon*. Syst. Bot. 29, 2: 448–458.

Bentham, G. 1875. Notes on the gamopetalous orders belonging to the campanulaceous and oleaceous groups. J. Linn. Soc., Bot. 15: 1–16.

Bentham, G. 1876. Campanulaceae. In: Bentham, G., Hooker, J.D., Genera Plantarum, vol. II. London: Reeve, pp. 541–564.

Bigazzi, M. 1986. Ultrastructural and cytochemical observations on fibrillar intranuclear inclusions in the family Campanulaceae. Caryologia 39: 199–210.

Bremer, K., Gustafsson, M.H.G. 1997. East Gondwana ancestry of the sunflower alliance of families. Proc. Natl Acad. Sci. U.S.A. 94: 9188–9190.

Candolle, A. de 1839. Lobeliaceae, Campanulaceae. In: Candolle, A.P. de, Prodromus systematis naturalis regni vegetabilis, vol. 7. Paris: Treuttel & Würtz, pp. 339–496, 784–792.

Carlquist, S. 1962. Ontogeny and comparative anatomy of thorns of Hawaiian Lobeliaceae. Amer. J. Bot. 49: 413–419.

Carlquist, S. 1969. Wood anatomy of Lobelioideae (Campanulaceae). Biotropica 1: 47–72.

Carlquist, S. 1992. Wood anatomy of sympetalous dicotyledon families: a summary, with comments on systematic relationships and evolution of the woody habit. Ann. Missouri Bot. Gard. 79: 303–332.

Carolin, R.C. 1960. The structures involved in the presentation of pollen to visiting insects in the order Campanales [sic]. Proc. Linn. Soc. New South Wales 85: 197–207.

Carolin, R.C. 1967. The concept of the inflorescence in the order Campanulales. Proc. Linn. Soc. New South Wales 92: 7–26.

Chapman, J.L. 1966. Comparative palynology in Campanulaceae. Trans. Kansas Acad. Sci. 69: 197–200.

Chase, M.W, Soltis, D.E., Olmstead, R.G., Morgan, D., Les, D., Mishler, B.D., Duvall, M.R., Price, R.A., Hills, H.G., Qiu, Y., Kron, K.A., Rettig, J.H., Conti, E., Palmer, J.D., Manhart, J.R., Sytsma, K.J., Michaels, H.J., Kress, W.J., Donoghue, M.J., Clark, W.D., Hedrén, M., Gaut, B.S., Jansen, R.K., Kim, K.-J., Wimpee, C.F., Smith, J.F., Furnier, G.R., Strauss, S., Xiang, Q., Plunkett, G.M., Soltis, P.S., Swensen, S., Eguiarte, L.E., Learn, G.H. Jr., Barrett, S.C.H., Graham, S., Dayananadan, S., Albert, V.A. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 528–580.

Cosner, M.E., Jansen, R.K., Lammers, T.G. 1994. Phylogenetic relationships in the Campanulales based on *rbcL* sequences. Pl. Syst. Evol. 190: 79–95.

Cronquist, A. 1981. An integrated system of classification of flowering plants. New York: Columbia University Press.

Dunbar, A. 1975. On pollen of Campanulaceae and related families with special reference to the surface ultrastructure. Bot. Notiser 128: 73–118.

Dunbar, A. 1984. Pollen morphology in Campanulaceae, IV. Nordic J. Bot. 4: 1–19.

Erbar, C., Leins, P. 1989. On the early floral development and the mechanisms of secondary pollen presentation in *Campanula*, *Jasione* and *Lobelia*. Bot. Jahrb. Syst. 111: 29–55.

Erbar, C., Leins, P. 1996. Distribution of the character states "early sympetaly" and "late sympetaly" within the "Sympetalae Tetracyclicae" and presumably allied groups. Bot. Acta 109: 427–440.

Fedorov, A.A. 1957. Campanulaceae. In: Shishkin, B.K. (ed.) Flora URSS, vol. 24. Moscow: Akademia Nauk, pp. 126–450, 459–475.

Gadella, T.W.J. 1966. Some notes on the delimitation of genera in the Campanulaceae. Proc. Konink. Ned. Akad. Wetensch. ser. C 69: 502–521.

Givnish, T.J., Sytsma, K.J., Smith, J.F., Hahn, W.J. 1995. Molecular evolution, adaptive radiation, and geographic speciation in *Cyanea* (Campanulaceae, Lobelioideae). In: Wagner, W.L., Funk, V.A. (eds) Hawaiian biogeography: evolution on a hot spot archipelago. Washington: Smithsonian Institution Press, pp. 288–337.

Gustafsson, M.H.G. 1995. Petal venation in the Asterales and related orders. Bot. J. Linn. Soc. 118: 1–18.

Gustafsson, M.H.G., Bremer, K. 1995. Morphology and phylogenetic interrelationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and related families (Asterales). Amer. J. Bot. 82: 250–265.

Gustafsson, M.H.G., Backlund, A., Bremer, B. 1996. Phylogeny of the Asterales sensu lato based on *rbc*L sequences with particular reference to the Goodeniaceae. Pl. Syst. Evol. 199: 217–242.

Hickey, L.J., Wolfe, J.A. 1975. The bases of angiosperm phylogeny: vegetative morphology. Ann. Missouri Bot. Gard. 62: 538–589.

Hickman, J. 1993. The Jepson Manual. Higher Plants of California. University of California Press.

Hong, D.-Y. 1995. The geography of the Campanulaceae: on the distribution centres. Acta Phytotax. Sin. 33: 521–536.

Hong, D.-Y., Lian, Y.S., Shen, L.D. 1983. Campanulaceae. In: Flora Reipublicae Popularis Sinicae, vol. 73, 2. Beijing: Science Press, pp. 1–177.

Kaplan, D.R. 1967. Floral morphology, organogenesis and interpretation of the inferior ovary in *Downingia bacigalupii*. Amer. J. Bot. 54: 1274–1290.

Kårehed, J., Lundberg, J., Bremer, B., Bremer, K. 1999. Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae. Syst. Bot. 24: 660–682.

Kolakovskii, A.A. 1987. System of the Campanulaceae family from the Old World (in Russian). Bot. Zhurn. (Moscow & Leningrad) 72: 1572–1579.

Kolakovskii, A.A. 1994. The conspectus of the system of the Old World Campanulaceae (in Russian). Bot. Zhurn. (Moscow & Leningrad) 79: 109–124.

Lammers, T.G. 1991. Systematics of *Clermontia* (Campanulaceae: Lobelioideae). Syst. Bot. Monogr. 32: 1–94.

Lammers, T.G. 1992. Circumscription and phylogeny of the Campanulales. Ann. Missouri Bot. Gard. 79: 388–413.

Lammers, T.G. 1993. Chromosome numbers of Campanulaceae. III. Review and integration of data for subfamily Lobelioideae. Amer. J. Bot. 80: 660–675.

Lammers, T.G. 1998a. Nemacladoideae, a new subfamily of Campanulaceae. Novon 8: 36–37.

Lammers, T.G. 1998b. Review of the Neotropical endemics *Burmeistera*, *Centropogon*, and *Siphocampylus* (Campanulaceae: Lobelioideae), with description of 18 new species and a new section. Brittonia 50: 233–262.

Lammers, T.G. 2002. Seventeen new species of Lobelioideae (Campanulaceae) from South America. Novon 12: 206–233.

Lammers, T.G. 2005. Revision of *Delissea* (Campanulaceae: Lobelioideae). Syst. Bot. Monogr. 73: 1–75.

Lancucka-Srodoniowa, M. 1977. New herbs described from the Tertiary of Poland. Acta Palaeobot. 18: 37–44.

Lancucka-Srodoniowa, M. 1979. Macroscopic plant remains from the freshwater Miocene of the Nowy-Sacz Basin (West Carpathians, Poland). Acta Palaeobot. 20: 3–117.

Leins, P., Erbar, C. 1990. On the mechanisms of secondary pollen presentation in the Campanulales-Asterales-complex. Bot. Acta 103: 87–92.

Leins, P., Erbar, C. 2003. The pollen box in Cyphiaceae (Campanulales). Intl J. Pl. Sci. 164 suppl. 5: S321–S328.

Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–578.

Michaels, H.J., Scott, K.M., Olmstead, R.G., Szaro, T., Jansen, R.K., Palmer, J.D. 1993. Interfamilial relationships of the Asteraceae: insights from *rbc*L sequence variation. Ann. Missouri Bot. Gard. 80: 742–751.

Murata, J. 1995. A revision of infrageneric classification of *Lobelia* (Campanulaceae-Lobelioideae) with special reference to seed coat morphology. J. Fac. Sci. Univ. Tokyo sect. 3 15: 349–371.

Nash, D.L. 1976. Campanulaceae. In: Nash, D.L., Dieterle, J.V.A. (eds) Flora of Guatemala. Fieldiana Bot. 24 (XI, 4): 396–431.

Olmstead, R.G., Michaels, H.J., Scott, K.M., Palmer, J.D. 1992. Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbc*L. Ann. Missouri Bot. Gard. 79: 249–265.

Olmstead, R.G., Bremer, B., Scott, K.M., Palmer, J.D. 1993. A parsimony analysis of the Asteridae *sensu lato* based on *rbc*L sequences. Ann. Missouri Bot. Gard. 80: 700–722.

Philipson, W.R. 1948. Studies in the development of the inflorescence, V. The raceme of *Lobelia dortmanna* L., and other campanulaceous inflorescences. Ann. Bot. II 12: 147–156, pl. 4.

Presl, C.B. 1836. Prodromus monographiae Lobeliacearum. Prague: Theophilus Haase.

Ricardi, M. 1959. Un *Cyphocarpus* nuevo para Chile. Bol. Soc. Argent. Bot. 7: 247–250.

Rosén, W. 1932. Zur Embryologie der Campanulaceen und Lobeliaceen. Acta Horti Gothob. 7: 31–42.

Rosén, W. 1949. Endosperm development in Campanulaceae and closely related families. Bot. Notiser 1949: 137–147.

Schönland, S. 1889. Campanulaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, IV, 5. Leipzig: W. Engelmann, pp. 40–70.

Shen, L.D., Hong, D.Y. 1983. *Codonopsis*. In: Hong, D.Y. (ed.) Flora Reipublicae Popularis Sinicae, vol. 73, 2. Beijing: Science Press, pp. 32–69.

Shetler, S.G. 1979. Pollen-collecting hairs of *Campanula* (Campanulaceae). I. Historical review. Taxon 28: 205–215.

Shetler, S.G., Morin, N.R. 1986. Seed morphology in North American Campanulaceae. Ann. Missouri Bot. Gard. 73: 653–688.

Shrestha, K.K. 1997. Taxonomic revision of the Sino-Himalayan genus *Cyananthus* (Campanulaceae). Acta Phytotax. Sin. 35: 396–433.

Shulkina, T.V. 1980. The significance of life-form characters for systematics, with special reference to the family Campanulaceae. Pl. Syst. Evol. 136: 233–246.

Takhtajan, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46: 225–359.

Takhtajan, A. 1997. Diversity and classification of flowering plants. New York: Columbia University Press.

Thulin, M. 1976. Campanulaceae. In: Polhill, R.M. (ed.) Flora of tropical East Africa. Rotterdam: Balkema.

Thulin, M. 1984. Lobeliaceae. In: Polhill, R.M. (ed.) Flora of tropical East Africa. Rotterdamm: Balkema.

Tjon Sie Fat, L. 1978. Contribution to the knowledge of cyanogenesis in angiosperms. 2. Cyanogenesis in Campanulaceae. Proc. Koninkl. Ned. Akad. Wetensch. C 81: 126–131.

Tobe, H., Morin, N.R. 1996. Embryology and circumscription of Campanulaceae and Campanulales: a review of literature. J. Pl. Res. 109: 425–435.

Wagenitz, G. 1964. Reihe Campanulales. In: Melchior, H. (ed.) A. Engler's Syllabus der Pflanzenfamilien, ed. 12, Band 2. Berlin: Gebrüder-Borntträger, pp. 478–497.

Wimmer, F.E. 1943. Campanulaceae-Lobelioideae, I. Teil. In: Mansfeld, R. (ed.) Das Pflanzenreich, IV.276b. Leipzig: W. Engelmann, pp. 1–260.

Wimmer, F.E. 1953. Campanulaceae-Lobelioideae, II Teil. In: Stubbe, H., Noack, K. (eds) Das Pflanzenreich, IV.276b. Berlin: Akademie Verlag, pp. 261–813.

Wimmer, F.E. 1968. Campanulaceae-Cyphioideae. In: Stubbe, H. (ed.) Das Pflanzenreich, IV.276c. Berlin: Akademie-Verlag, pp. 917–1014.

Yeo, P.F. 1993. Platycodoneae [sic], a new tribe in Campanulaceae. Taxon 42: 109.

Carpodetaceae

Carpodetaceae Fenzl, Denkschr. Königl.-Baier. Bot. Gesell. Regensburg 3: 155 (1841).
Abrophyllaceae Nakai (1943).

M.H.G. Gustafsson

Evergreen shrubs or trees with unicellular hairs. Leaves alternate, estipulate, petiolate, serrate. Inflorescences terminal and/or axillary, paniculate, bracts minute. Flowers bisexual or functionally female, actinomorphic. Sepals (4)5(7), small, free or basally fused. Petals (4)5(7), free, valvate in bud. Stamens (4)5(7), alternipetalous, free, anthers tetrasporangiate, introrse. Intrastaminal nectar-disc present or absent. Ovary superior or inferior, (3)5-locular, placentation axile. Ovules many, anatropous, unitegmic. Style simple, distally branched, or virtually absent. Stigma capitate or lobed. Fruit a berry or a loculicidal capsule. Seeds numerous, small, alveolate, with hard testa, endosperm abundant, embryo minute.

Three genera with five species in eastern Australia, New Guinea, New Zealand and the Solomon Islands.

Vegetative Morphology Juvenile plants of *Carpodetus serratus* often show a characteristic growth pattern, with slender, zigzag, divaricate branches. This type of branching is typical for a number of other New Zealand plants. Leaves are uniformly serrate (very slightly in *Abrophyllum microcarpum*), with glandular teeth. The venation is prominent on the abaxial side of the leaf, and can be described as semicraspedodromous. Domatia sometimes develop in the abaxial axils of midrib and lateral veins in *Carpodetus*.

Vegetative Anatomy. The characteristic indumentum of the three genera of Carpodetaceae was described by Al-Shammary and Gornall (1994). Hairs on young stems, leaves and inflorescences are all of one type, almost identical in the three genera: unicellular, eglandular and curved (Fig. 14E). The base of these hairs is often sunken, and they have a very thick wall and a warty cuticle. The leaf mesophyll and stem pericycle of *Abrophyllum* and *Cuttsia* contain idioblasts with granular contents, possibly some kind of latex. *Carpodetus* lacks these structures but has crystalliferous idioblasts in leaf mesophyll and floral parts (Gustafsson and Bremer 1997). The wood of *Carpodetus serratus* has both uniseriate and very large multiseriate rays. Vessel perforation plates are scalariform, with numerous (average 80) cross bars. Large rhomboidal crystals occur in the ray cells (Patel 1973).

Floral Morphology. Flowers are predominantly bisexual but *Carpodetus* is sometimes gynodioecious, i.e. some plants bear functionally female flowers with rudimentary stamens. Merosity is variable, and 4-, 5- and 6-merous flowers may occur on the same plant. The abaxial side of sepals and petals have the same kind of indumentum as is found on vegetative parts. There may be a slight basal fusion in the sepal whorl, and in *Carpodetus serratus* the calyx leaves a circular scar after abscission (Fig. 14C). At least in *Carpodetus*, petals are basally fused early in ontogeny (Tobe and Raven 1999). Filaments are short in *Abrophyllum*, not exceeding the anthers in length, while in the other genera filaments are three to several times longer, protruding from the widely open, star-like flowers (Fig. 14B, F, G). The ovary is inferior in *Carpodetus* but, after anthesis, the apical portion enlarges disproportionately, so that the locules and placentae reach above the line of perianth insertion. The ovary of *Carpodetus* is crowned by a pulvinate disc that may be radially furrowed. The stigma is deeply (3)5-lobed in *Abrophyllum* and *Cuttsia*, and in the latter genus the style is distally branched, particularly so after anthesis. In *Carpodetus*, the stigma is capitate but may have a few central pits and numerous, slight indentations along the margin.

Pollen Morphology. Pollen grains of Carpodetaceae are of two distinctive types, tetrahedral tetrads in *Carpodetus* and tricolporate monads in *Abrophyllum* and *Cuttsia* (Hideux and Ferguson 1976; Praglowski and Grafström 1985). The surface

pattern is striate to rugulate or, in *Carpodetus*, smooth or with irregular, flattened elements. The infratectum consists of wide columellae in *Abrophyllum* and *Cuttsia*, and is very thin in *Carpodetus*, consisting of scattered, small irregular elements.

Karyology. For *Carpodetus*, diploid chromosome numbers of $2n = 28$ and 30 have been reported (Hair and Beuzenberg 1960).

Pollination and Reproductive Systems. The flowers are widely open at anthesis, and the nectar (produced at least in *Cuttsia* and *Carpodetus*) is easily accessible. *Cuttsia* flowers have been referred to as an example of a generalist entomophilous syndrome (Williams and Adam 1994), and flowers of *Carpodetus arboreus* are reported to have an unpleasant odour (van Royen 1983), which could indicate adaptation to insect pollination, perhaps by flies.

Fruit and Seed. *Abrophyllum* has fleshy berries, whilst those of *Carpodetus* have a thin, leathery wall. The fruit of *Cuttsia* is a dry capsule with loculicidal dehiscence. The seeds of *Carpodetus* are much larger than those of the other genera, and tend to become angular due to dense packing in the fruit (Fig. 14D). All genera have seeds with a highly characteristic alveolate surface pattern, resulting from the presence of strong thickenings on the proximal and radial walls of the testa epidermis cells (Krach 1976; Fig. 14D). The embryo is very small, 1/6 to less than 1/10 of the length of the seed. Endosperm is abundant, and contains fatty substances and aleuron grains.

Dispersal. The dark-coloured berries of *Abrophyllum* and *Carpodetus* are presumably bird-dispersed, whilst the small seeds of *Cuttsia* lack an obvious adaptation for dispersal.

Phytochemistry. The polyphenols leucodelphinidin, quercetin and kaempferol have been detected in *Carpodetus serratus*, and a triterpene, lupeol, occurs in the bark of the same species (Hegnauer 1973).

Relationships Within the Family. *Cuttsia* and *Abrophyllum* are morphologically highly similar, and they constitute tribe Cuttsieae of Saxifragaceae-Escallonioideae in the system of Engler (1930). Molecular data confirm a close relationship between these genera (Gustafsson and Bremer 1997).

Affinities. The genera here included in Carpodetaceae have traditionally been placed in the highly heterogeneous Saxifragaceae sensu lato. Praglowski and Grafström (1985) found palynological similarities between *Carpodetus* and Ericaceae, and pointed to the possibility of a close relationship between these taxa. Findings from studies of DNA variation in the last few years (Gustafsson and Bremer 1997; Lundberg 2001) have confirmed the monophyly of Carpodetaceae as here delimited, and indicated a position distant from both Saxifragaceae and Ericaceae, viz. in Asterales sensu lato. This ordinal placement is supported by morphological characters, e.g. valvate corolla aestivation, and general characters of Asteridae such as unitegmic ovules and alternipetalous stamens. Carpodetaceae are but one of several small, woody, southern hemisphere families which have recently been found to belong in Asterales. One of these families, the monotypic Rousseaceae from Mauritius, is sister to Carpodetaceae, according to recent phylogenetic studies based on molecular data and morphology (Lundberg 2001; Lundberg and Bremer 2003). Lundberg (2001) reduced Carpodetaceae to a subfamily of Rousseaceae, and this has often been followed in later studies and classification schemes, e.g. APG II (2003). The idea of an affinity between these two taxa is not new; already Fenzl (1841) considered, on morphological grounds, Carpodetaceae to stand between Saxifragaceae and Rousseaceae. Most of the morphological characters shared by *Roussea* and Carpodetaceae are widespread in Asterales. One exception is a carpel number of five, which is otherwise seen only in some genera of Campanulaceae; most Asterales have two or three. Carpodetaceae (together with *Roussea*) are sister to Pentaphragmataceae plus Campanulaceae in the most recent, combined molecular and morphological analysis of Asterales, but this relationship is only weakly supported (Lundberg and Bremer 2003).

Distribution and Habitats. *Abrophyllum* and *Cuttsia* occur in rainforests in New South Wales and southern Queensland, particularly along watercourses. *Carpodetus arboreus* is found in montane and subalpine forests of New Guinea and the Solomon Islands, often as part of the undergrowth, and reaches altitudes above 3,500 m.

Carpodetus serratus occurs in various kinds of forest up to 1,000 m altitude in most regions of New Zealand.

Economic Importance. The wood of *Carpodetus serratus* is reported to be strong and tough, and has been used for, e.g. tool handles. Frequent damage due to wood-boring insects reduces, however, its economic importance. *Abrophyllum ornans* is occasionally cultivated as an ornamental tree in Australia.

Key to the Genera

1. Flowers epigynous, stigma capitate, seeds angular **1. *Carpodetus***
– Flowers hypogynous, stigma (3)5-lobed, seeds ovoid 2
2. Filament shorter than anther, stigma sessile, fruit baccate **2. *Abrophyllum***
– Filament longer than anther, style well-developed, fruit capsular **3. *Cuttsia***

Genera of Carpodetaceae

1. *Carpodetus* J.R. Forst. & G. Forst. Fig. 14A–E

Carpodetus J.R. Forst. & G. Forst., Char. Gen. Pl. t. 17: 33 (1776).
Argyrocalymma K. Schumann ex K. Sch. & Ltb. (1900).

Shrubs or trees to 20 m tall. Inflorescences often equalling leaves in length. Petals white, yellowish or greenish. Filaments much longer than anthers. Ovary inferior or almost so, crowned by conspicuous, intrastaminal nectar-disc. Style present, stigma capitate. Fruit a black or greyish, leathery berry. Seeds angular. Pollen grains in tetrahedral tetrads. $2n = 28, 30$. Two species, *C. arboreus* (K. Schum. & Lauterb.) Schltr. in New Guinea and the Solomon Islands, and *C. serratus* J.R. Forst. & G. Forst. in New Zealand. *C. arboreus* is very variable in size, shape and texture of the leaves, and a number of different species have been described from its area, but van Royen (1983) considered these to belong to a single, polymorphic species.

2. *Abrophyllum* Hook. f. Fig. 14F

Abrophyllum Hook. f. in Benth. Fl. Austral. II: 437 (1864).

Shrubs or small trees to 8 tall. Inflorescences much shorter than leaves. Petals yellowish. Filaments shorter than anthers. Ovary superior. Stigma (3)5-lobed, sessile. Fruit a blackish, fleshy berry. Seeds minute, ovoid. Pollen in monads, tricolporate.

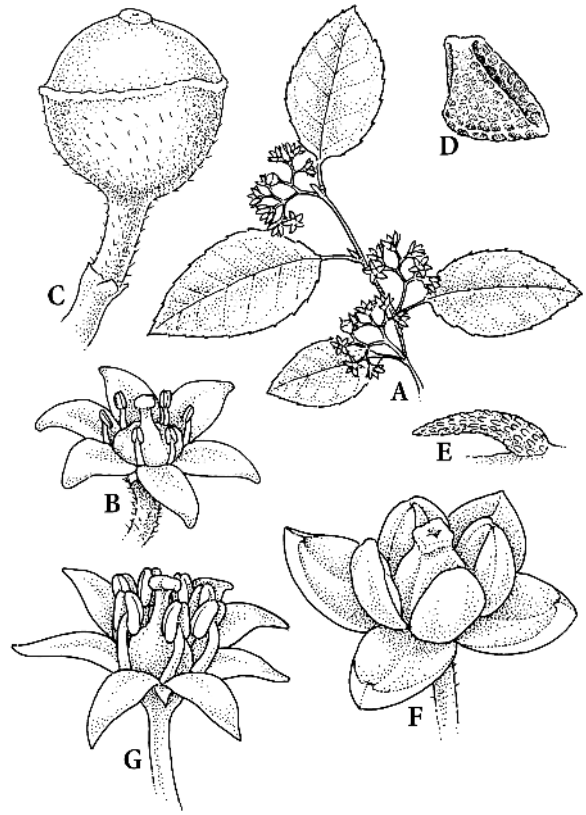

Fig. 14. Carpodetaceae. **A–E** *Carpodetus serratus*. **A** Flowering branch. **B** Flower. **C** Young fruit. **D** Seed. **E** Hair. **F** *Abrophyllum ornans*. Flower. **G** *Cuttsia viburnea*. Flower

Two species, *A. microcarpum* Domin in southern Queensland and *A. ornans* Hook f. in New South Wales and southern Queensland.

3. *Cuttsia* F. Muell. Fig. 14G

Cuttsia F. Muell., Fragm. V, t. 70: 47 (1865).

Shrub or tree to 15 m tall. Inflorescences often equalling leaves in length. Petals white. Filaments much longer than anthers. Ovary superior, with nectariferous base. Stigma 5-lobed or style distally 5-branched. Fruit a loculicidal capsule. Seeds minute, ovoid. Pollen in monads, tricolporate. A single species, *C. viburnea* F. Muell. in New South Wales and southern Queensland.

Selected Bibliography

Al-Shammary, K.I.A., Gornall, R.J. 1994. Trichome anatomy of the Saxifragaceae s.l. from the southern hemisphere. Bot. J. Linn. Soc. 114: 99–131.

APG II (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. The Angiosperm Phylogeny Group. Bot. J. Linn. Soc. 141: 399–436.

Engler, A. 1930. Saxifragaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, ed. 2, vol. 18a. Leipzig: Engelmann, pp. 74–226.

Fenzl, E. 1841. *Carpodetus* Forster. Denkschr. Königl.-Baier. Bot. Gesell. Regensburg 3: 155–173.

Gustafsson, M.H.G., Bremer, K. 1997. The circumscription and systematic position of Carpodetaceae. Austral. Syst. Bot. 10: 855–862.

Hair, J.B., Beuzenberg, E.J. 1960. Contributions to a chromosome atlas of the New Zealand flora. 4. Miscellaneous families. N. Z. J. Sci. 3: 432–440.

Hegnauer, R. 1973. Chemotaxonomie der Pflanzen, Band 6. Basel: Birkhäuser.

Hideux, M.J., Ferguson, I.K. 1976. The stereostructure of the exine and its evolutionary significance in the Saxifragaceae sensu lato. In: Ferguson, I.K., Muller, J. (eds) The evolutionary significance of the exine. London: Academic Press, pp. 327–377.

Krach, J.E. 1976. Samenanatomie der Rosifloren, 1. Die Samen der Saxifragaceae. Bot. Jahrb. Syst. 97: 1–60.

Lundberg, J. 2001. The asteralean affinity of the Mauritian *Roussea* (Rousseaceae). Bot. J. Linn. Soc. 137: 267–276.

Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–578.

Patel, R.N. 1973. Wood anatomy of the dicotyledons indigenous to New Zealand. 2. Escalloniaceae. N. Z. J. Bot. 11: 421–434.

Praglowski, J., Grafström, E. 1985. The genus *Carpodetus* (Escalloniaceae): a pollen morphological enigma. Grana 24: 11–21.

Royen, P. van 1983. The alpine flora of New Guinea, vol. 4. Vaduz: Cramer.

Tobe, H., Raven, P.H. 1999. Floral structures of Alseuosmiaceae, Argophyllaceae, Carpodetaceae, Phellinaceae and Rousseaceae: additional members in Asterales. In: Abstract Volume XVI International Botanical Congress, St. Louis, Missouri Botanical Garden, Abstract 19.13.3., p. 241.

Williams, G., Adam, P. 1994. A review of rainforest pollination and plant-pollinator interactions with particular reference to Australian subtropical rainforests. Austral. Zool. 29: 177–212.

Compositae

Compositae Adans., Fam. Pl. 2: 103 (1763), nom. alt. et cons.

Asteraceae Martynov, Tekhno-Bot. Slovar: 55 (1820), nom. cons.

A.A. Anderberg, B.G. Baldwin, R.G. Bayer, J. Breitwieser, C. Jeffrey, M.O. Dillon, P. Eldenäs, V. Funk, N. Garcia-Jacas, D.J.N. Hind, P.O. Karis, H.W. Lack, G. Nesom, B. Nordenstam, Ch. Oberprieler, J.L. Panero, C. Puttock, H. Robinson, T.F. Stuessy, A. Susanna, E. Urtubey, R. Vogt, J. Ward and L.E. Watson

Introduction with Key to Tribes

C. Jeffrey

Herbs, annual or biennial and monocarpic or perennial and polycarpic or sometimes monocarpic, subshrubs, shrubs or less often trees, leptocaul or sometimes pachycaul, often especially when herbaceous or suffruticose with tuberous roots or rhizomes or lignotuberous rootstock, sometimes lianas (vines), usually terrestrial, rarely epiphytic or aquatic, sometimes succulent, usually with one or more of various types of glandular and eglandular hairs, commonly the glandular biseriate and the eglandular uniseriate; tissues with schizogenous secretory canals (resin-ducts) and/or with articulated lacticifers; nodes (1-)3- to multilacunar. Leaves alternate or opposite, rarely whorled, usually simple but often lobed or divided, exstipulate; stomata anisocytic or anomocytic. Unit inflorescence a capitulum (head), with rare exceptions surrounded by an involucre of one to several series of protective bracts (phyllaries), capitula sometimes solitary at the apices of more or less leafless stems (scapes) but usually few to very many in often corymbiform cymose synflorescences (inflorescences, capitulescences) of various types, sometimes aggregated into often involucrate capituliform syncephalia (glomerules) of the second or even third order. Receptacle paleate with persistent or caducous vascularized scales (paleae, pales, chaff) subtending some or all of the florets, fimbrilliferous with non-vascularized fimbrils or scale-like processes surrounding the bases of the florets, setulose, hairy or naked and then smooth, areolate with polygonal areoles or alveolate with depressions in which the florets are inserted. Flowers (florets) small, 1–500 or more per capitulum, sessile or subsessile; ovary inferior, of 2 (rarely 3) united carpels, unilocular, with 1 erect, basal ovule; ovule anatropous, tenuinucellate, unitegmic; calyx represented by a pappus formed of (1–)2 to many awns, scales (squamae, squamulae), setae or hairs (rays) in 1 or more series, homomorphic or heteromorphic, or by a more or less coroniform or auriculiform structure, or completely absent, never green and herbaceous; corolla gamopetalous, of (3–)5(–6) united petals, more or less regular (actinomorphic) and equally or unequally (3–)5(–6)-lobed or -toothed with the lobes or teeth valvate, or filiform with the lobes reduced or absent or with a minute ray, or variously zygomorphic, bilabiate with a 2-lobed internal (adaxial) lip and a 3-lobed external (abaxial) lip, pseudobilabiate with an unlobed internal (adaxial) lip and a 4-lobed external (abaxial) lip, ligulate with an apically 5-dentate abaxial ligule, or radiate with an abaxial 0–3(–4)-dentate ray[1], the different types variously arranged within the capitulum, the florets either all alike (homomorphic, isomorphic, capitulum homogamous) and all regular (capitulum discoid), all ligulate (ligulate capitulum) or all bilabiate, or of more than one type (heteromorphic, anisomorphic, capitulum heterogamous) with the inner (disc florets) regular (or rarely bilabiate) and perfect (bisexual, hermaphrodite) or functionally staminate (male) and the outer (ray florets) radiate, often pistillate (female) or sometimes sterile (neuter), in one or more series (capitulum radiate), or the outer filiform pistillate, usually in several series, and the inner regular, perfect or functionally staminate (capitulum disciform), rarely the corolla absent from the pistillate florets, occasionally all the florets pistillate or staminate and the plants dioecious or monoecious, rarely the florets variously otherwise arranged. Stamens with the filaments inserted on the corolla-tube, equal in number to and alternating with the corolla-lobes; filaments

[1] In descriptions, the disposition of the corolla-lobes is sometimes indicated by a formula, giving the number of lobes forming the adaxial and abaxial parts of the limb respectively, e.g. ligulate (0/5), pseudobilabiate (1/4), radiate (0/3 or 0/4), bilabiate (2/3), regular (5/0).

usually free, rarely connate, the upper part of the filament usually with cells with thickened walls, forming a split cylindrical or balusterform anther-collar (or filament-collar); anthers united into a tube surrounding the style, very rarely free, dithecal, tetrasporangiate or rarely bisporangiate, introrse, dehiscent by longitudinal slits, usually with an apical appendage, rounded, sagittate or tailed at the base; tapetum integumentary; pollen mostly tricolporate, usually echinate (spiny), sometimes echinolophate or lophate (with a pattern of raised ridges) or spinulate (microechinate, spinulose), often caveate; nectary a thickened scale or cup surrounding the style base; style solitary, elongating through the anther-tube and extruding the pollen at its summit, apically divided (except sometimes in functionally staminate florets) into 2 (or rarely 3) short to long branches (style arms) with stigmatic areas on their inner (adaxial) surfaces, the apices of the style arms acute to rounded, truncate or variously appendaged; stigmas dry, papillose. Fruit unilocular, 1-seeded, indehiscent, usually an achene (cypsela), very rarely a drupe, crowned by the persistent pappus or the pappus caducous or absent; abscission scar surrounded by a carpopodium, distinguished by the form of its cells and the texture of its surface, of 1 to many rows of cells, indistinct to prominent, sometimes apparently absent; embryo straight; endosperm scant, forming a thin layer around the embryo.

The largest family of flowering plants, cosmopolitan except for Antarctica, with over 1,600 genera and 23,000 species (excluding apomictic microspecies), especially well represented in grassland, wooded grassland and montane vegetation, comparatively few in humid tropical lowland forests.

Vegetative Morphology. The majority of Compositae are subshrubs, shrubs or perennial herbs, adapted to moderately xeric conditions, but most life forms are represented, from ephemeral desert annuals, pyrophytes and hemicryptophytes to trees of 30 m or more, including especially in Senecioneae (Fioretto and Alfani 1988) leaf and stem succulents, also halophytes, marsh plants, lianas, epiphytes and aquatics, though the latter two life forms are comparatively infrequent and submerged aquatics rare.

Herbaceous members of the non-asteroid tribes growing in areas where grazing pressure is significant are often thistleoid, i.e. with spiny leaves and/or involucral bracts; this syndrome is mostly found in the tribes Cynareae, Gundelieae and parts of Arctotideae, and to a lesser extent in Cichorieae. Its absence from the asteroid tribes probably reflects the generally greater development of chemical defences in the latter. Subshrubby forms are usually evergreen, shrubs and trees usually also evergreen but sometimes deciduous. Pachycaul, megaphytic, polycarpic or sometimes monocarpic trees, shrubs or herbs occur widely on tropical mountains and oceanic islands, e.g. *Centaurodendron* (Cynareae, Juan Fernández Islands), *Sonchus* (Cichorieae, Macaronesia), *Dendroseris* (Cichorieae, Juan Fernández Islands), *Espeletia* (Millerieae/Heliantheae s.l., Andes), *Argyroxiphium* (Madieae/Heliantheae s.l., Hawaiian islands), *Lachanodes* (Senecioneae, St. Helena) and *Dendrosenecio* (Senecioneae, tropical east African mountains).

Underground storage organs are common in perennial herbaceous and shrubby forms and may be represented by thickened taproots, root tubers, tuberous rhizomes (or rarely a corm) or a lignotuber, the last especially common in pyrophtyic and other geoxylic forms of tropical grasslands and wooded grasslands.

The leaves of Compositae are exstipulate and commonly alternate, but opposite leaves are characteristic of most Heliantheae s.l., the Liabeae and some Vernonieae, and occur sporadically in several other tribes, e.g. Astereae and Senecioneae. The leaves may be petiolate or sessile; the lower leaves in many herbaceous perennials frequently have an attenuate petioloid base. All the leaves may be of more or less equal size or, as often in perennial herbs, the lower and basal may be larger than the upper and may form a rosette; caulirosulate forms also occur. The lamina is usually simple, although often lobed or divided, sometimes repeatedly and very deeply so, rarely truly compound with separate leaflets. In *Mutisia* (Mutisieae), the leaf-tip is modified into a tendril, in *Cissampelopsis* (Senecioneae) and a few related genera, the petioles are prehensile. The leaf venation may be parallelopinnate, pinnate, palmato-pinnate or palmate. The presence of domatia has been demonstrated (Cerana and Ariza Espinar 1995) in *Mikania* (Eupatorieae/Heliantheae s.l.). Hydathodes are common.

Vegetative Anatomy. The anatomical features of Compositae are subject to considerable homoplasy and are therefore only rarely group-definitive at or above the generic level. Like that of the leaves, the stem anatomy of Compositae (Carlquist 1966)

reflects the fact that Compositae in general are adapted to moderately dry conditions. The pith is sometimes hollow, sometimes septate and often lignified. Herbaceous stems have generally a single ring of collateral bundles which may be closely spaced or even form a complete cylinder in the more woody members; medullary bundles are frequently recorded and cortical bundles may also occur. Secondary growth is usually present, sometimes anomalous, especially in scandent (e.g. *Mikania*, Eupatorieae/Heliantheae s.l.) or secondarily woody forms. In general, the wood of Compositae is more or less indistinguishable from that of other higher asterid families. Most woody Compositae have normal wood, some (e.g. *Dendroseris*, Cichorieae, *Dendrosenecio*, Senecioneae, *Chrysanthemoides*, Calenduleae) have features indicative of secondary woodiness, derived from herbaceous ancestors. The vessels occur singly or in groups, commonly in radial chains or tangential bands. The vessel elements usually have simple perforation plates, occasionally some of them are scalariform or reticulate; the pits in the vessel element walls are alternate, often somewhat larger on the walls facing parenchyma. Helical sculpturing is often present on the vessel walls. Libriform fibres are present, they are wide to narrow, thick- or thin-walled and occasionally septate; tracheids and fibre-tracheids are absent. Wood parenchyma is scant and mostly paratracheal, usually only one layer thick. Multiseriate and uniseriate rays commonly co-occur, the former almost always the more abundant, 4–10(–18) cells wide; in a few Mutisioideae only uniseriate rays occur; a few genera have rayless wood. The multiseriate rays are heterocellular with both vertically and radially elongated cells. The ray cells are wide to narrow, with thin, unlignified or more commonly thick, lignified walls, often with conspicuous pits. Storied wood structure is rather common; it may take the form of patches of storied fibres or vessels, or may extend to all the elements of the axial xylem; in *Brachylaena* (Tarchonantheae/Mutisieae s.l.), *Gochnatia* (Gochnatieae/Mutisieae s.l.) and *Olearia* (Astereae), the rays are also storied. Growth rings are common, usually expressed as wider vessel elements at the start of a growth ring. Prismatic crystals are present in a few genera of Mutisioideae, Astereae and Anthemideae, usually in the ray parenchyma. Resin-like deposits are common, usually as minute droplets in the cell lumina. The nodes are usually 3–multi-lacunar, rarely unilacunar.

The leaves of Compositae are occasionally glabrous but both glandular and non-glandular hairs (trichomes) are frequently present, the basic types being biseriate glandular and uniseriate non-glandular. Glandular hairs may be superficial or depressed in grooves or pits; they have a 1–2-multiseriate stalk and an unicellular or multicellular head. The following types of non-glandular hairs have been documented (Metcalfe and Chalk 1950): unicellular to uniseriate base and a long, flagelliform terminal cell (a very widespread type); likewise but with an incipiently to unequally or equally 2-armed terminal cell with the arms ascending or parallel to the epidermal surface (also very widespread); stellate with uniseriate stalk and branched terminal cell; candelabriform with several tiers of stelliform branches (e.g. *Scorzonera*, Cichorieae); bladder-like, with inflated terminal cell; multiseriate, shaggy (e.g. *Vernonia*, Vernonieae); and peltate, scale-like (e.g. *Olearia*, Astereae). Many of these trichome types commonly occur also on the stems and various floral parts. Although subject to much homoplasy, indumentum types can provide taxonomically useful data. In many Heliantheae s.l., the hair bases are surrounded by a rosette of silicified cells, making the leaf surface rough to the touch. Stomata are mesogenous and usually anisocytic or anomocytic. The hydathodes of Compositae (Lersten and Curtis 1985) are always marginal, usually on the teeth, and are of a rather unspecialized type; the water-stomata are similar in size to the ordinary stomata, but are usually sunken and are permanently open. The mesophyll is usually dorsiventral, but may be isolateral or radial (e.g. in *Werneria*, Senecioneae); ecologically specialized features, such as an aqueous or lignified hypodermis and bundle sheath extensions, are commonly found. Kranz anatomy is found in Heliantheae s.l. in a monophyletic group (subtribe Chrysanthellinae) of seven genera in Coreopsidodineae, and also in *Pectis* and some species of *Flaveria*. The petiole usually has a single arc of separate vascular bundles.

Two internal secretory systems are widespread in Compositae (Carlquist 1966, 1976) – articulated lacticifers (or lacticiferous cells) with triterpene-rich latex, and schizogenous secretory canals (resin ducts) usually lined with an epithelium. Lacticifers are found in the phloem (or pericycle), secretory canals in the cortex or the region of the endodermis, usually associated with the vascular bundles (opposite or between them), occasionally also in the rays. In the asteroid tribes, secretory canals

are usually present in the roots, rhizomes, aerial stems and leaves (absent in Gnaphalieae), often in the pericarp and sometimes in the cotyledons (in Senecioneae), and lacticiferous cells are rare. In the non-asteroid tribes, various expressions of both lacticifers (or lacticiferous cells) and secretory canals are found. Lacticifers are characteristic of Cichorieae, where secretory canals are rare (found in the roots of *Scolymus* and *Scorzonera*), and Gundelieae; they are also found (or are replaced by lacticiferous cells) in some genera of Mutisieae (e.g. *Gongylolepis*), Cynareae (e.g. *Cardopatium*, *Atractylis*, *Carlina* [Carlininae] and many genera of Carduinae [Xeranthemum group]), Arctotideae (e.g. *Gazania*) and Vernonieae (e.g. *Vernonia*) and in most Liabeae. In a few genera of Barnadesioideae and Mutisioideae, both secretory systems are apparently absent. Secretory cavities, often forming translucent dots or streaks on the leaves and sometimes other organs (e.g. phyllaries), may supplement or replace the secretory canals.

Floral structure and Development. In the majority of Compositae, the capitulum (Harris 1999) is the functional flower and it usually acts as a single attraction unit. Its structure reflects a balance of various functions concerned with pollination, the breeding system, dispersal, seed germination and defence (Stuessy and Garver 1996). However, reduction and aggregation of capitula into syncephalia which function as attraction units of the second or even third order (Claßen-Bockhoff 1992, 1996) is not infrequent. Like primary capitula, these may be provided with floral (ray floret) or extrafloral (coloured phyllary) pseudocorollas. Second-order syncephalia are common in Gnaphalieae and the subtribe Nassauviinae of Mutisieae and also occur, e.g. in Cynareae-Echinopsinae, Inuleae and Heliantheae. Third-order syncephalia are exemplified by *Platycarpha* (? Arctotideae), *Gundelia* (Gundelieae), *Triplocephalum* (Inuleae) and *Lagascea* (Heliantheae). In *Gundelia*, for example, the one-flowered primary capitula are grouped into numerous secondary capitula of 5–7 primary capitula which in turn are grouped into a large syncephalium of the third order (Claßen-Bockhoff et al. 1989).

The onset of capitulum development (Harris 1995; Palmer 1996) is marked by a broadening of the apical meristem. Phyllaries, florets and receptacular bracts (when present) are initiated by subsurface periclinal cell divisions. When receptacular bracts are present, they are frequently initiated as part of a common primordium with the corresponding floret (e.g. in *Tithonia*, Heliantheae and *Xeranthemum*, Cynareae); they may also be initiated after the appearance of the floral primordium (e.g. in *Madia*, Madieae/Heliantheae s.l.); rarely, the receptacular bract is initiated first, in the axil of which the floret primordium then appears (e.g. in *Rudbeckia*, Heliantheae). Receptacular bracts may also be formed late in development, as enations from the receptacular surface (e.g. in *Chrysopsis*, Astereae); such bracts are probably not homologous with those of the other developmental types. The receptacular outgrowths characteristic of most Cynareae are likewise initiated in mid-development, and are not homologous with receptacular bracts (paleae) in terms of initiation time. Receptacular bracts (Stuessy and Spooner 1988) are found in some Mutisieae, some Cynareae (Carduinae), some Vernonieae, some Inuleae, many Heliantheae s.l. and occasionally in other tribes (e.g. Cichorieae, Liabeae, Astereae and Anthemideae).

The order of floret initiation and differentiation on the receptacle is closely associated with capitulum type (Harris 1995). In homogamous capitula, the order is almost always strictly acropetal. In heterogamous capitula, the order is often mixed, partly acropetal and partly basipetal. On the basis of primordium type, three groups of corolla types may be recognized:

1. bilabiate, ligulate and regular (disc) perfect florets – primordia radially symmetrical, usually pentagonal-circular; early stages of development similar; initiation acropetal;
2. ray and radiant florets – primordia triangular or bilaterally symmetrical; delayed in development and sometimes also in initiation with respect to the disc florets;
3. filiform florets, apically truncate, lobed or with a minute ray – primordia consistently circular and small; corollas abbreviated; all traces of stamens completely absent; initiation and/or development acropetal, basipetal, bidirectional or synchronous.

Ray-floret primordia are similar in the early stages in both the asteroid and the non-asteroid tribes in which rays occur. The development of the Mutisia type of ray floret differs least from that of the perfect types of floret.

In floral development (Leins and Erbar 1987; Harris 1995), the organogenetic order is 1, corolla, 2, androecium, 3, gynoecium. The pappus may be initiated at any stage but it is seldom the first organ

to be initiated. When pappus initiation is integral with development, three basic types of initiation are observed: sequential, in 5 (or more) sites alternate with the corolla-lobes; random, in available space; and as a ring meristem, from which many individual pappus primordia subsequently develop (a more derived state found, e.g. in Astereae and Inuleae). Alternatively, the pappus may be initiated late as enations around the summit of the ovary, during the stage of floral expansion and differentiation. Such pappi are probably not homologous with those of the other developmental types.

The corolla is initiated as a ring meristem (meristematic rim or ring wall) which develops before the more or less simultaneous initiation of the corolla-lobe primordia upon it (Leins and Erbar 2000), although in the non-asteroid tribes an irregular successional development of the corolla-lobe primordia has been reported in the development of bilabiate and ligulate corollas (Harris 1995). After initiation of the stamen primordia alternate with the corolla-lobes, intercalary growth (which occurs in the ring meristem zone when it is present) carries the stamens upwards, forming the corolla-stamen tube. The true corolla-tube (above the point of insertion of the stamens) is formed independently earlier in development. In the asteroid tribes, stamen primordia initiation may be simultaneous or in a spiral sequence; in the non-asteroid tribes, an irregular helical type of stamen initiation is commonly found.

The vascular structure of the flower (floret) of Compositae is relatively simple, and in perfect florets usually conforms to the following pattern. At the base of the ovary, the single floret vascular bundle divides into six, one of which goes to the ovule, the other five, in the ovary wall, to the summit of the ovary, where two of them each send a branch to the style and style arms. Each of the five traces then splits, sending one branch to a stamen and one to the top of the corolla to a sinus between adjacent corolla-lobes; here the corolla bundles fork to unite in pairs at the apices of the lobes. These corolla bundles represent the fused lateral bundles of adjacent petals; median petal traces are absent.

Simplification of this pattern may be observed, with reduction of the ovary wall bundles from 5 to 4 (as in *Bidens*, Coreopsideae/Heliantheae s.l.) or 2 (as in *Lactuca*, Cichorieae). More complex patterns are also found, with more bundles in the ovary wall and median corolla-lobe bundles present. Sometimes a ring of 10 bundles (5 fused laterals and 5 median bundles) is found in the ovary wall, inside of which 4 carpellary bundles extend into the style. Such and similar more complex patterns are exhibited by some Barnadesioideae (e.g. *Schlechtendalia*), Stifftieae (e.g. *Stenopadus*, *Wunderlichia*) and Vernonieae (e.g. *Proteopsis*), and here represent probable plesiomorphic states (the 10-bundle wall condition is also found in Calyceraceae). More complex venation patterns sometimes occur in other tribes (e.g. Heliantheae), are here frequently associated with an increase in size of the achene and/or corolla, and probably represent derived conditions. However, increase in size with retention of the simple 5-bundle pattern is also found (e.g. as in *Tragopogon*, Cichorieae).

The adaxial corolla epidermal cells exhibit a number of microstructural surface ornamentation patterns which, especially in ray and ligulate corollas, are broadly correlated with systematic position and functionally with the pollinator attraction mechanism – the reflexion of visible and ultraviolet light, and the nature and distribution of visible and ultraviolet light-absorbing pigments (Baagøe 1980; Hansen 1991b).

In Compositae, the stamens are typically syngenesious, with connate anthers (rarely free, in some wind-pollinated forms) and free filaments (very rarely partly or wholly connate). The upper part of the filament forms an anther-collar (or filament-collar), usually distinguished by the size, shape and wall thickness of its cells, in the form of an adaxially split cylinder or baluster (Meiri and Dulberger 1986). The anthers usually bear an apical appendage, variable in size and proportions and also consistency; it may be lignified (as in Barnadesioideae, Stifftieae, Mutisieae and Cynareae) or soft (as in Lactuceae, Arctotideae and the asteroid tribes); occasionally it is absent. At the base, the anthers may be calcarate (with a considerable portion of the thecae protruding below the filament insertion point, i.e. below the top of the anther-collar) or ecalcarate (with basal insertion of the filament). Calcarate anthers are typical of the non-asteroid tribes, ecalcarate of the asteroid tribes, although they also occur, e.g. in a few Mutisieae s.l. (Mutisieae, Gochnatieae and Dicomeae). The base of the anther may be rounded, acute, sagittate or prolonged on each side into a sterile tail, which varies from fine and unbranched to stout and branched. The endothecial cells of the pollen-sacs have walls which are variously thickened; generally the thickenings are polarized or lateral, with special states occurring in *Catananche* (Cichorieae), other Cichorieae and some Cynareae (Carduinae). Ra-

dially disposed thickenings are the most common in Eupatoriodinae (Eupatorieae), but also occur in some other Heliantheae s.l. (e.g. *Dahlia*, Coreopsideae/Heliantheae s.l.).

The nectary (when present) is commonly a thickened scale or cup alongside or surrounding the style base at the top of the ovary; it is provided with numerous stomata, through which the nectar is secreted (Galetto 1995).

The style in Compositae is single, and in perfect florets consists of a shaft divided at the apex into 2 (rarely 3) style arms. The shaft is usually glabrous, rarely hairy and may be uniform in diameter or swollen at the base (stylar node). The inner (adaxial) faces of the style arms bear the stigmatic surfaces. The stigmatic area is dry and papillose and may cover the entire inner surface of each style arm or form two marginal bands which vary from widely separated to contiguous, from broad to narrow and from free to united towards the apex of the style arm. Entire stigmatic areas are general in the non-asteroid tribes, marginal characteristic of the asteroid tribes, although this feature is subject to reversal. The style arms themselves vary in many characters, including: orientation (tangential or radial to the capitulum); disposition (erect to connivent or reflexed); length; degree of fusion; shape of apex; presence or absence of a sterile appendage above the stigmatic areas; form of apical appendage (when present); presence or absence of sweeping hairs on the outer (abaxial) surface; presence or absence of an articulation (swelling) at the base of the style arms; distribution and form of the sweeping hairs on, and character of the outer surface (papillose or smooth) of the style arms and/or upper part of the shaft. In pistillate or functionally pistillate florets, the stylar structure is generally much simpler and in staminate or functionally staminate florets, the style is commonly undivided at the apex and devoid of stigmatic areas; such styles may exhibit various elaborations of the sweeping-hair mechanism. Particular style and style arm features are characteristic of many subtribes, tribes or groups of tribes, and their variation is a reflexion of the evolutionary development and diversification of the pollen-presentation mechanism (Thiele 1988). Appendaged style arms are especially characteristic of Astereae (papillose and broadly conical to subulate) and Eupatoriodinae of Heliantheae s.l. (highly developed and conspicuous).

Embryology and Pollen development. Embryogenesis in Compositae (Batygina and Yakovlev 1987; Ahlstrand 1988, 1992) is fairly uniform, although variation in detail occurs which may be of taxonomic significance as, e.g. in the infratribal classification of Anthemideae and Arctotideae and in the tribal classification of Carduoideae. The ovule is anatropous, unitegmic and tenuinucellate; usually a solitary vascular bundle enters the chalaza and penetrates the integument to a greater or lesser extent. The micropyle is usually short. In some tribes (e.g. Cynareae, Cichorieae, Calenduleae, Heliantheae), the inner epidermis of the integument differentiates into an integumentary tapetum. The archesporium is usually unicellular but sometimes multicellular or rarely 2-cellular. The megaspore tetrad is usually linear, rarely T-shaped; most often the chalazal megaspore develops, in a few species the micropylar. The monosporic 8-nucleate Polygonum type of embryo development is most frequently found, the bisporic Allium type less frequently and almost exclusively in the asteroid tribes (with the exception of *Heterolepis*, ? Arctotideae); various tetrasporic types have also been recorded. Variation may be found even within one and the same species. In apomicts, development may be bisporic (Taraxacum type), tetrasporic (e.g. Antennaria type) or aposporic (Hieracium type). Fertilization is porogamous, double and premitotic. Endosperm development is usually cellular, less often (as in Cynareae and some representatives of some other tribes) nuclear, usually without haustoria. Both types may sometimes occur in one and the same genus. Embryogenesis is of the asteroid type with a few variations, the basic variant being the Senecio variant.

The stamens of Compositae are usually 4-locular, rarely 2-locular. The walls of the loculi develop centrifugally, and consist of epidermis, endothecium (with cell wall thickenings), a middle layer which is ephemeral, and the tapetum. The tapetum is initially cellular and multinucleate, then partial dissolution of the cell walls occurs; in the post-meiotic stage, it becomes amoeboid, sometimes forming a false periplasmodium; eventually it forms the pollenkit and is absent from the mature anther. The archesporium may be uniseriate or multiseriate, tetrad formation is of the simultaneous type and the tetrads tetrahedral, isobilateral or cruciform. The mature pollen grains are solitary and 3-celled. Abnormal meiosis is often observed in apomictic species.

Palynology. The pollen in Compositae (Stix 1960; Skvarla et al. 1977) is tricolporate or some-

times triporate, usually echinate or spinulate, generally sphaeroidal with a transverse furrow in the endexine perpendicular to each colpus and a tectate ektexine. A cavea (space), where the columellae are detached from the foot layer in the regions between the apertures or colpi, is often present. The ektexine generally consists of a foot layer, columellae (bacula) and a tectum. There is considerable and systematically significant variation on this basic pattern, especially in surface ornamentation and exine stratification. General evolutionary trends are an increase in the surface relief and in the porosity of the ektexine, both a reflection of an evolutionary increase in the capacity of the pollen grain wall to hold substances important in pollen presentation and pollination.

Spinulate pollen grains are plesiomorphic in Compositae, and are shared with Calyceraceae and some other related families (Hansen 1991a). They occur in Barnadesioideae (DeVore and Stuessy 1995; Urtubey and Telleria 1998), in Mutisioideae and some Carduoideae. The intracolpar concavities found in some Calyceraceae and Barnadesioideae may represent a synapomorphy for the two families. The apomorphic echinate condition appears to have arisen independently at least three times – in Dicomeae (Mutisieae s.l.) in the Pleiotaxis group of genera, in Cynareae (Serratula type), and in the vernonioid group of tribes (Cichorioideae and Asteroideae). Lophate pollen, in which the surface is ridged in a polygonal pattern, is found – either in the echinolophate (with echinate ridges) or the psilolophate (with smooth ridges) variant – in some Barnadesioideae and in some members of the tribes Arctotideae, Vernonieae and Cichorieae (Blackmore 1986). Its occurrences in these taxa are also examples of parallel or convergent evolution; the lophate condition must be considered derivative, as it depends upon the acquisition of a mechanism for the differential deposition of callose which is absent in the spinulate and echinate forms. It is of functional significance in, e.g. the storage and release of exine-held substances and in its mechanical attributes. Its absence from the asteroid tribes may possibly be correlated with the development of the double tectum in the latter.

Two main types of exine stratification can be recognized, lactucoid (found in the non-asteroid tribes) and asteroid. The lactucoid type exhibits one or more of the following features (Vezey et al. 1994): branched infratectal columellae (e.g. *Schlechtendalia*, Barnadesioideae; *Onoseris*, Mutisieae); infratectal columellae that appear to be continuations or branches of the basal columellae (e.g. *Gerbera*, Mutisieae) and/or more than one layer of internal tectum (e.g. *Carthamus*, Cynareae; *Arctotis*, Arctotideae); slender, widely separated basal columellae (e.g. *Tragopogon*, Cichorieae) or thick but widely separated basal columellae (e.g. *Vernonia*, Vernonieae; *Liabum*, Liabeae). Lactucoid pollen is generally ecaveate, having basal columellae which arise from the foot layer and one to several levels of slender columellae and internal tecta above the basal columellae, but caveate pollen is found in Arctotideae and in some Liabeae. Asteroid pollen is generally caveate, lacking basal columellae and having instead a cavity, the cavea, and is characterized by a double tectum. The double tectum is a synapomorphy of the asteroid tribes and does not occur in the non-asteroid tribes (except perhaps in Liabeae as a parallelism). In some asteroid tribes (e.g. Calenduleae, parts of Inuleae and Heliantheae), more complex tectal structural elements occur, which appear to be transformations of the double tectum. In most Anthemideae (except, e.g. *Ursinia*), the pollen grains are ecaveate and have a thick foot layer with basal columellae; however, these structures are not homologues of similar structures in lactucoid pollen, though in the past the lactucoid forms were also often referred to as anthemoid. Lactucoid pollen is generally larger than asteroid pollen, and has a smaller diameter/exine thickness ratio, 6.2–7.5 as opposed to 8.0–10.0, except for 6.4 in Anthemideae.

Independent of this larger-scale variation in exine structure, in some tribes of Asteroideae (and rarely also in the non-asteroid tribes) minute internal foramina are present in the structural elements of the ektexine; pollen with such foramina is commonly found in members of Heliantheae s.l. and has become known as the helianthoid type; it is also found in a few genera of Senecioneae, e.g. *Doronicum*, *Pericallis*, *Packera* (Bain et al. 1997), but the majority of Senecioneae have pollen devoid of such internal foramina, and such asteroid pollen is referred to as the senecionoid type.

The great variation in pollen form and structure in Compositae provides much taxonomically valuable information, and various pollen-type groups have been proposed by various authors. In general, the following groups are characterized by particular palynological features (or transformations of them): (1) Barnadesioideae, (2) Mutisieae s.l. (Stifftieae-Mutisieae s.s.-Dicomeae-Tarchonantheae-Pertyeae)-Echinopsinae, (3) other Cynareae, (4) Arc-

totideae, (5) Moquinieae-Gundelieae-Vernonieae-Liabeae-Cichorieae, (6) Inuleae, (7) Gnaphalieae, (8) Senecioneae-Calenduleae-Astereae-Heliantheae s.l., and (9) Anthemideae. On a more detailed level, particular pollen types may characterize one or more subtribes, groups of genera or genera; only rarely is more than one type found within a particular genus, e.g. *Munnozia* (Liabeae).

Pollination. Compositae are characterized by secondary pollen presentation (Thiele 1988; Leins and Erbar 1990; Erbar and Leins 1995; DeVore and Stuessy 1995) in which the pollen is shed into the anther-tube by introrse dehiscence of the syngenesious anthers, extruded by action of the style and presented on the outer surface of the style shaft and style arms, which then open to expose the stigmatic areas on their upper (adaxial) surfaces. In some, the filaments are insensitive and the pollen is presented merely by upgrowth of the style; in others, the filaments are sensitive (thigmotropic) and contract on being touched, so that the anthers withdraw and the pollen is exposed for transport. In all, the anther-collars, the abaxial and lateral epidermal cells of which have lignified walls, support and guide the style. Three variants of the presentation mechanism may be recognized; the pollen may be dragged out by adhesion to papillae-like microhairs on the style exterior, brushed out by sweeping hairs on the outside of the style arms and style shaft or on an appendage to the style arms, or pumped out by spreading sweeping hairs on the apices of the style arms. The drag variant is characteristic of Barnadesioideae, Stifftieae and some Mutisieae and Carduoideae, the brush variant of most Carduoideae, all Cichorioideae and some Asteroideae, and the pump variant of most Asteroideae.

The pollinator rewards are mainly nectar and pollen. The nectary is situated at the style base and the nectar is secreted through stomata. The nectar is sugar-rich (hexose or sucrose); in some, it contains amino acids which attract flies, or sometimes pyrrolizidine alkaloids which attract Lepidoptera (Brown 1984). The pollen is lipid-rich. The tapetum forms pollenkit which plays an essential role in the presentation and transfer of pollen. It keeps the pollen grains attached to the style, holds them together in clumps, facilitates adhesion to the pollinator, acts as an attractant to the pollinator, and facilitates adhesion to the stigma, the surfaces of which are papillose and dry, lacking exudate.

The majority of Compositae are adapted to specific pollinators and are not generalists, as sometimes previously thought. They exhibit intricate and precise mechanisms of pollinator attraction, species identification, pollinator rewards and reward presentation (Lane 1996). Some Barnadesioideae, Mutisioideae, Dicomeae and Cynareae with elongated corollas are pollinated by hummingbirds or sunbirds, others by long-tongued insects such as sphingids. Pollination by flies is characteristic of Compositae of some montane areas, such as the Andes and the Southern Alps of New Zealand. However, the most important pollinators of Compositae are solitary bees, with which a special relationship has developed, including learned recognition of species and orientation cues and learned manipulation for reward extraction. A few Compositae are wind-pollinated, for example, the genera *Artemisia* (Anthemideae) and *Ambrosia* (Heliantheae) and some species of *Espeletia* (Millerieae/Heliantheae s.l.; Berry and Calvo 1989).

Karyology. Haploid chromosome numbers in Compositae range from 2 to 120, although very high polyploids and very low numbers are infrequent, and species with $n = 9$, 10, 12, 17 or 18 form 50% of all Compositae for which chromosome numbers are known. The most common number is 9, and $x = 9$ is possibly the basic (plesiomorphic) number for the family as a whole. Variation in chromosome number has been brought about mainly by the processes of allopolyploidy (including amphidiploidy), aneuploid change and chromosome loss (Solbrig 1977). Dysploid reduction is most characteristic of Compositae (especially annuals) of more arid and/or disturbed areas, and appears to be correlated with speciation under such conditions. Polyploidy is more characteristic of mesic, perennial herbaceous and woody species occupying relatively stable habitats.

Breeding Systems. The majority of Compositae are sporophytically self-incompatible; the incompatibility is strong but not absolute and self-compatibility is not uncommon; a few cases of capitular cleistogamy are known. The perfect florets are protandrous but the capitulum as a whole is protogynous when the outer florets (ray or filiform) are pistillate or functionally so. Autogamy may occur with floret age. The following capitular conditions are met with: hermaphroditism (monocliny); gynomonoecy, monoecy, androdioecy, gynodioecy, dioecy and andromonoecy. Monoclinous capitula are homogamous (monomorphic) with all the flo-

rets (disc, bilabiate or ligulate) perfect; outbreeding is facilitated by the floral protandry and the centripetal maturation of the florets. Dioecious capitula are also monomorphic but either entirely pistillate or entirely staminate; outbreeding is achieved by spatial separation of the capitula, which occur on different plants. The remaining capitular types are heteromorphic (heterogamous), most commonly with the inner florets perfect or functionally staminate and the outer (filiform or ray) florets pistillate. The gynomonoecious condition, in which there are one or more outer rows of pistillate florets and central perfect florets, is very common; outbreeding is facilitated by the capitular protogyny of the outer florets. The monoecious condition is similar, but here the central florets are functionally staminate. The androdioecious, gynodioecious, andromonoecious and various intermediate conditions are less frequently observed. Apomixis is common in a number of genera, such as *Hieracium*, *Pilosella* and *Taraxacum* (all Cichorieae; den Nijs and Menken 1996), *Blumea* (Inuleae) and *Antennaria* (Gnaphalieae).

Fruit and Seed. Variation in fruit and seed characters provides much taxonomically useful information (Reitbrecht 1974; Grau 1980; Sáenz 1981; Velez 1981; Reese 1989; Short et al. 1989; Eriksson 1991; Dittrich 1996; Werker 1997). The fruit is one-seeded, normally an achene (sometimes but superfluously termed a cypsela), very rarely a drupe, usually regarded as indehiscent but often with preformed dehiscence lines opening by pressure of the germinating embryo. Achenes may be terete, angled or variously dorsiventrally obcompressed or laterally compressed, unribbed or with 2–many ribs of various degrees of prominence, apically truncate to variously attenuate or beaked, and vary in the form of the apical part of the fruit (where the pappus, when present, is inserted) and in the form of the carpopodium. Within a capitulum, the achenes may be all alike (homomorphic) or heteromorphic (of 2 or 3 kinds); such heterocarpy is quite frequent and has been recorded, for example, in 39 genera of the tribe Cichorieae (Voytenko 1989a; Voytenko and Oparina 1990). The main structural elements of the fruit are pappus (when present), pericarp, testa, endosperm and embryo.

The pericarp epidermis (epicarp) is uniseriate, sometimes papillate or otherwise surface-ornamented, sometimes lignified and commonly bears hairs of various types – uniseriate barnadesioid in Barnadesioideae, multicellular in Echinopsinae, one-celled in most other Cynareae, in other tribes twin hairs which are sometimes myxogenic; various glandular hairs may also be present. The mesocarp may consist of various elements. A hypodermis of one to several layers of sclerified or unsclerified, parenchymatous to prosenchymatous cells is often developed. Commonly, sclerenchyma is present to a greater or lesser extent; it may occur in discrete bundles or bands or form a continuous ring; often it surrounds the vascular bundles. In Heliantheae s.l., a phytomelanin layer is usually found between the hypodermis and the sclerenchymatous tissue. Schizogenous secretory canals (resin ducts) may be present, usually associated with the vascular bundles. The inner part of the mesocarp and the inner epidermis of the pericarp (endocarp) may be present at achene maturity and the endocarp even lignified, but commonly one or both become obliterated.

The testa may also become disorganized at maturity but in a number of tribes, its cellular structure is maintained and then the form of the cells of the testa epidermis and the type of thickening of their walls provide taxonomically useful variation as, for example, in the tribes Mutisieae s.l. (Stifftieae, Gochnatieae, Mutisieae, Dicomeae), Cynareae, Cichorieae and, to a lesser extent, Anthemideae and Inuleae. Endosperm is constantly present; it forms a layer 1–3 cells thick enveloping the embryo, and consists of living cells rich in oil and protein but devoid of starch. Its cell walls are thickened and composed mainly of mannose (Grau and Hopf 1985). The endosperm apparently serves as an additional protective layer for the embryo. The embryo is large, straight, dicotyledonous (rarely syncotyledonous) and with hypocotyl and radicle developed. The seed is rich in protein and oil but poor in oligosaccharides and starch; they form respectively 10–48, 4–70, 2–4 and 0–2% of the dry mass.

The pappus in its manifold forms has a protective function and may also act as a dispersal mechanism when the achene is mature. Other specialized structures associated with dispersal, such as wings, hooks and the elaiosomes of some Cynareae, may also be developed.

Dispersal. The disseminules of Compositae are dispersed mainly by wind, sometimes externally by mammals, less often by ants or other agents. The disseminule is usually the achene, sometimes enclosed by a phyllary or receptacular bract. In other cases, the capitulum is the unit of dispersal, the

achenes (one or more) being retained within the involucre. Such synaptospermy is most characteristic of Compositae of semi-arid and arid areas (Gutterman and Ginott 1994). It may be partial (as in *Crepis aculeata*, where the inner achenes are dispersed singly and the outer together, or *Didelta spinosa* where the outer are dispersed singly and the central remain in the capitulum) or complete. In *Didelta carnosa*, several-fruited capitula fragments act as disseminules, while in *Gundelia tournefortii* the disseminules are one-fruited capitula of the second order (Claßen-Bockhoff 1996); the lignified involucre is composed of the phyllaries of the 4–6 sterile lateral capitula. The capitula of Compositae suffer strongly from phytophagous insects, most of which attack the fruits. In synaptospermy, the protection afforded by the testa and pericarp is reinforced by (or transferred to) more peripheral organs in which the achenes are enclosed. Wind dispersal may be facilitated by various forms of capillary pappus, by compression of the achene, by the development of wings or (in synaptospermous species) by the development of chaffy involucral bracts. Corky ribs characterize some water-dispersed achenes, elaiosomes those dispersed by ants. The development of barbs or hooks on the pappus or other parts of the achenes or, in synaptospermous species, on the involucre (such as in *Arctium*, Cynareae) is frequent in those Compositae usually dispersed by mammals. In heterocarpic Compositae, the different achene morphs may have different dispersal strategies as well as different dormancy and germination requirements, and may thus enable the species to take advantage of a wider range of temporal and environmental conditions.

Phytochemistry. Compositae exhibit a rich and varied assortment of secondary metabolites, which serve as storage compounds or as chemical defence mechanisms, the development of which has undoubtedly been important in the evolutionary success of the family. The combined occurrence of inulin-type fructans, acetylenic fatty acid derivatives transformed into cyclic (aromatic or heterocyclic) compounds and sesquiterpene lactones is almost as characteristic of the family as is the capitulum (Hegnauer 1977).

Inulins, synthesized as a homologous series of β-2-1-linked polymers and stored in solution in the vacuole, are the main storage carbohydrates of Compositae.

The acetylenes (formerly referred to as polyacetylenes on account of their multiple acetylenic bonds; that term is now restricted by chemists to denote polymers of acetylene) of Compositae (Zdero and Bohlmann 1990) and their derivatives are nemacidal, antibiotic and toxic, and occur mainly in the resin ducts. The most common acetylene is the C_{13} pentaynene, but this is absent in Cichorieae, Astereae and Anthemideae; in the latter two tribes (except for *Ursinia* and a few related genera of Anthemideae), it is replaced by particular C_{10} and C_{17} acetylenes. The C_{17} acetylenes are also found in Cichorieae and Senecioneae, in the former another C_{10} acetylene also occurs. Thiophene derivatives of the C_{13} pentaynene occur in some Heliantheae s.l. (including Tagetodinae [Tageteae]), Inuleae, Arctotideae, Gochnatieae, Cynareae (including *Echinops*) and Mutisieae, while spiroketalenol ethers (also present as thiophene derivatives) are characteristic of Anthemideae. In their acetylene chemistry, Mutisieae and Gochnatieae resemble Cynareae, while acetylenes with pyran or furan attachments are found in Cynareae, Anthemideae, Inuleae and Heliantheae s.l. and a special type is present in Gnaphalieae. The presence of phytomelanin in the pericarp is characteristic of Heliantheae s.l., although secondarily absent in some members and occurring as a parallelism in a few Vernonieae.

Sesquiterpene lactones (Seaman 1982) are bitter and toxic and occur in the latex, in the subcuticular cavities of glandular hairs or extruded in glandular hairs. The two most significant aspects of their chemistry are the patterns of skeletal and substitutional diversity; superimposed upon each skeleton is a set of substituents which collectively define a specific compound (Seaman and Funk 1983). Three levels of biogenetic complexity may be recognized. The sesquiterpene lactone chemistry of the non-asteroid tribes is generally less complex than that of Asteroideae; the main structural types are guaianolides and germacranolides; eudesmanolides are relatively infrequent and only the bourbonolides of Vernonieae represent the highest level of biogenetic complexity. The most commonly occurring types are as follows: Stifftieae: cis-lactonized germacranolides and eudesmanolides; Mutisieae (in Nassauviinae): lactonic and non-lactonic isocedrene derivatives; Gochnatieae, Dicomeae, Pertyeae, Tarchonantheae (all Mutisieae s.l.): germacranolides, cis-cis germacradienolides, trans-lactonized eudesmanolides (in Gochnatieae and Dicomeae) and guaianolides; Cynareae: guaianolides and germacranolides; Cichorioideae: guaianolides (uncommon in Arctotideae),

germacranolides (in Moquinieae, Vernonieae, Cichorieae and Liabeae), trans-lactonized eudesmanolides (in Moquinieae) and heliangiolides (in Vernonieae). In Asteroideae, sesquiterpene lactones are absent from Heliantheae-Tagetodinae (Tageteae) and Calenduleae and rare in Astereae; they are elaborated in Inuleae, many Heliantheae s.l. (including Eupatoriodinae [Eupatorieae]), Gnaphalieae and Anthemideae. Senecioneae are very distinct in their development of furanoeremophilanes (also oxidized to lactones). The commonly occurring types are as follows: Astereae (rarely): eudesmanolides and eremophilanolides; Anthemideae: eudesmanolides, guaianolides and germacranolides; Inuleae (including Gnaphalieae): eudesmanolides, germacranolides, xantholides and guaianolides, and less frequently ambrosanolides, helenanolides, pseudoguaianolides, seco-pseudoguaianolides and seco-helenanolides; Heliantheae s.l.: ambrosanolides, helenanolides, heliangiolides, germacranolides, melampolides, eudesmanolides, guaianolides, xantholides and seco-ambrosanolides; and Senecioneae: furanoeremophilanes and aromatic furanoeremophilanes. An 8-α-oxygen function is characteristic of the germacranolides of Mutisioideae, Carduoideae, Vernonieae, Cichorieae and other non-asteroid tribes. In Heliantheae s.l., there is an 8-β function, often (in Eupatoriodinae [Eupatorieae]) an oxygenated C_5 ester. In Anthemideae, the C8 position can be free or functionalized. The guaianolides of Cynareae are mainly 6,12-olides with an 8-α-oxygen function whereas in Inuleae and Heliantheae s.l., 8,12-lactones are widespread and again the β orientation is favoured. The presence of eudesmanolides (santanolides), especially 6,12-olides and often as 11,13-dihydro derivatives, is characteristic of Anthemideae whereas 8,12-eudesmanolides predominate in Heliantheae s.l. and Inuleae. Sesquiterpene lactones are apparently absent from Barnadesioideae.

Other Compositae chemical constituents of note include triterpenes (which occur free in the latex or in the lipid fraction of tissues), steroids, essential oils, carotenoids, flavonoids, chromenes (benzopyrans) and benzofurans (prenylated acetophenones, Proksch and Kunze 1996), lignans and other phenolics, labdanes and kauranes (chemical defences), coumarins, prenylated coumarins, thymol derivatives, diterpenoids, alkaloids, cyanogenetic glycosides (both valine- and phenylalanine-derived), inositol esters, isobutyl amides (insecticidal) and seed oils. The isomeric cyclitols L-inositol and scyllitol are accumulated together. The terpenoid essential oils of Compositae are complex mixtures of steam-volatile constituents which occur in secretory glandular hairs and the resin ducts; components include acetylenes, phenylpropanols and chromenes, thymol derivatives, monoterpenoids, sesquiterpenes (widespread) and (in *Ursinia* and related genera of Anthemideae) furanosesquiterpenes. Among the flavonoids (Bohm and Stuessy 2001), quercetagetin-based yellow flavonols are characteristic of Compositae; gossypetin-based flavonols are rare. Yellow anthochlor pigments (chalcones and aurones), resorcinol-based, occur in the Heliantheae-Coreopsidodinae (Coreopsideae) and some other Heliantheae s.l., and phloroglucinol-based in some Cynareae (e.g. *Carthamus*) and Gnaphalieae (e.g. *Helichrysum* and *Gnaphalium*). Anthocyanins are important contributors to flower colour, e.g. in such ornamentals as *Chrysanthemum*, *Dahlia* and *Callistephus*. Cyanidin is the major anthocyanin, delphinidin occurs only occasionally. The anthocyanin pattern is relatively simple, acylation is rare and methylation absent.

The phytochemistry of Compositae is a rich source of potentially valuable taxonomic information; the co-occurrence (or co-absence) of specific chemical compounds (or groups of compounds) is often indicative of taxonomic affinity at the subfamily and lower levels (Zdero and Bohlmann 1990). For example, 5-methyl coumarins and onoseriolides are present in both Mutisieae-Mutisiinae and Mutisieae-Nassauviinae (Zdero et al. 1986). Mutisieae as a whole are of interest in showing some chemical similarities to the asteroid, rather than to the non-asteroid tribes. For instance, p-hydroxyacetophenones, prenyl or geranyl coumarins and nerolidol derivatives occur in Mutisieae and Asteroideae but are absent from Cichorioideae (except for the presence of nerolidol derivatives in Vernonieae) and Carduoideae; however, the presence of 5-alkyl coumarins and chromenes is shared with Vernonieae, whereas isocedrene derivatives are unique to Mutisieae. Labdanes, clerodanes and their derivatives occur in Astereae, Inuleae, Heliantheae s.l. and Senecioneae, abietanes in Inuleae and Heliantheae, beyeranes and their derivatives in all Asteroideae except Astereae, thymol derivatives in all Asteroideae except Senecioneae and most Astereae, prenyl phloroglucinols in Inuleae and Heliantheae, furanosesquiterpenes in Cynareae and Vernonieae, and (possibly as a parallelism) in *Ursinia*

and related genera of Anthemideae. Inuleae and Heliantheae are also linked by their acetylene and sesquiterpene lactone chemistry, as are Gochnatieae, Tarchonantheae, Dicomeae, Pertyeae (all Mutisieae s.l.) and Cynareae; Anthemideae and Astereae are linked by their acetylene chemistry and the co-occurrence of umbelliferone derivatives. Calenduleae relate to Inuleae and Heliantheae by the co-occurrence of special diterpenes and prenylated p-oxyacetophenones. In the rich chemistry of Compositae lies the basis of their very widespread use as medicinal plants.

Subdivisions and Relationships Within the Family. Compositae can be divided into two monophyletic groups of markedly unequal size – the small monotribal South American subfamily Barnadesioideae and the rest (Jansen and Palmer 1987, 1988; Jansen et al. 1991; Bremer and Jansen 1992; Kim et al. 1992; Kim and Jansen 1995; Panero and Funk 2002). Within the rest (here called non-barnadesioid Compositae), a number of putatively monophyletic groups have been identified, the largest of which, the asteroid group of tribes (subfamily Asteroideae) appears to be the most derived (Bremer 1987, 1994; Kadereit 1989; Kim et al. 1992); it consists of the tribes Inuleae (including Plucheeae), Heliantheae s.l. (including Eupatorieae), Gnaphalieae, Astereae, Anthemideae, Calenduleae, Corymbieae (Panero and Funk 2002) and Senecioneae. Putatively sister to this group of tribes is the cichorioid group of tribes (subfamily Cichorioideae sensu stricto) in which may be included the tribes Gymnarrheneae (Panero and Funk 2002), Moquinieae (Robinson 1994), Vernonieae, Liabeae, Cichorieae (syn. Lactuceae), Gundelieae (Karis et al. 2001) and Arctotideae. Together, Asteroideae and Cichorioideae constitute the vernonioid group of tribes, for the monophyly of which there is strong molecular as well as considerable morphological support. Tentatively, two further subfamilies may be recognized, these being Carduoideae with the tribes Gochnatieae, Hecastocleideae, Dicomeae, Cynareae and Pertyeae, and a basal Mutisioideae. Possibly, Mutisioideae and Carduoideae together form the sister group of the vernonioid group of tribes (i.e. Cichorioideae plus Asteroideae) (Bayer and Starr 1998) but it is probable that they are paraphyletic with respect to the vernonioid group (Jansen and Palmer 1988; Jansen et al. 1991; Kim et al. 1992, 2002; Karis et al. 1992; Panero and Funk 2002).

Barnadesioideae (Gustafsson et al. 2001; Urtubey and Stuessy 2001) are distinguished by a number of unique morphological features, such as the abundant 3-celled hairs – each with a short, cup-shaped basal cell, a rounded intermediate cell (Erbar and Leins 2000) and a longer, straight terminal cell – on all the floral parts, and unique types of testa-epidermis (Grau 1980) and pollen grains (Urtubey and Telleria 1998; Zhao et al. 2000). Non-barnadesioid Compositae are distinguished by the presence of a cpDNA inversion absent from Barnadesioideae and all other angiosperms (Jansen and Palmer 1987), and by the presence of twin hairs on the achenes and a bristly pappus, although these morphological features are subject to reversal, transformation and loss. Mutisioideae share with Barnadesioideae a number of plesiomorphies, such as the mutisioid and crested, smooth types of petal adaxial epidermis patterns and spinulate pollen grains (Hansen 1991a, b). The subfamily Mutisioideae can be divided into two main groups – a basal, perhaps paraphyletic group (Stifftieae) with short (or rarely long, Hyaloseris type), rounded, essentially glabrous style arms of the Wunderlichia, Stifftia and Quelchia types, and a second tribe Mutisieae s.s. (subtribes Mutisiinae, Gerberinae and Nassauviinae) with short to long, spreading-hairy style arms of the Mutisia, Trixis and Nassauvia types (Jeffrey 1967). Carduoideae, perhaps characterized by the constancy of the Gochnatia type of testa epidermal cell wall thickening (Grau 1980) or derivative types thereof (Dittrich 1996; Häffner 2000), share a number of plesiomorphies with Mutisioideae; the more plesiomorphic members (Gochnatieae, Hecastocleideae, Tarchonantheae) are marked by short to long or lipped style arms of the Gochnatia and Seris (Richterago) types, the more advanced by short to long, finely to coarsely hairy style arms, often with the upper part of the stylar shaft slightly expanded (Pertya, Dicoma and Pleiotaxis types). The more plesiomorphic members (tribe Pertyeae) of the latter group retain the mutisioid types of petal adaxial epidermis patterns, the rest (including the tribes Dicomeae and Tarchonantheae and the uncertainly placed genus *Adenocaulon*, see Katinas 2000) exhibit tabular, senecionoid or rugose patterns (Hansen 1991b), but all retain the plesiomorphic spinulate pollen, except for a few tropical African genera (*Pleiotaxis* and its allies) of Dicomeae which have apomorphic echinate pollen.

The vernonioid group of tribes (i.e. Cichorioideae and Asteroideae as here circumscribed) is

marked by a 9-base pair deletion in the *ndh*F gene (Kim and Jansen 1995), and is strongly supported as a monophyletic group also by other molecular (e.g. Jansen and Kim 1996) and by morphological data (Karis et al. 1992). Within this group, Cichorioideae, although fairly well supported by molecular data, are poorly characterized morphologically (the presence of long, acute style arms is perhaps a synapomorphy but, if so, it must be considered as subject to reversal). Asteroideae are strongly supported as monophyletic not only by molecular data, including a duplication in the *rbc*L gene (Kim et al. 1992), but also morphologically, e.g. stigmatic areas in two marginal bands and disc floret corollas regular, with short lobes, although again these features are subject to reversal.

The basal branches of non-barnadesioid Compositae, of the tribal groups within them, and of many of the subfamilies, tribes and subtribes themselves tend to be poorly resolved in both morphological and molecular cladistic analyses. This is indicative of rapid evolution in the early stages of diversification of the taxa concerned, no doubt consequent upon the attainment of new arogenetic levels providing the basis for rapid adaptive radiation and cladogenesis. Improvement in the efficiency of the pollen presentation and pollination mechanisms as well as innovations in chemical defences appear to have played particularly important roles in this respect. The sister-group relationships of the tribes within Carduoideae, Cichorioideae and Asteroideae had been largely unresolved (Bremer 1996; Jansen and Kim 1996; Bayer and Starr 1998) but Panero and Funk (2002) have recently clarified tribal relationships within the subfamilies, based on a yet to be fully published study of 13,000 base pairs of chloroplast DNA from 120 taxa across the family. There is some evidence (molecular, morphological and palynological) that, in Cichorioideae, Moquinieae are close to Vernonieae, and that Vernonieae and Liabeae may be sister groups; they are also linked to Cichorieae by the common presence of similar (vernonioid) style arms and the tangential orientation of the gynoecium (Robinson 1984). Cichorieae and Gundelieae are also sister groups (Karis et al. 2001; Panero and Funk 2002). The sister-group relationships of Arctotideae are unclear, although the tribe is undoubtedly a member of Cichorioideae.

In Asteroideae (Karis 1993b), there is fairly good evidence (chemical, molecular and morphological) that Anthemideae and Astereae may be sister groups. Inuleae (including Plucheeae) may be sister to Heliantheae s.l., a relationship more supported by molecular and chemical than by morphological data. That Anthemideae and Astereae together form a clade with Calenduleae and Gnaphalieae is fairly well supported by some molecular evidence; the sister-group relationships within this clade have been clarified by Panero and Funk (2002). Senecioneae stand apart from the other tribes of Asteroideae on both molecular and chemical grounds, and their sister-group relationships remain unresolved.

Subtribal delimitation within Compositae is currently in a state of flux and, in some tribes, satisfactory and generally accepted subtribal taxonomy is yet to be established. Currently, it would appear more prudent to recognize at subtribal level only the more well-established major clades within each tribe, to treat smaller, clearly delimited putatively monophyletic groups within them as informal, infrasubtribal groups of genera, and to leave unclassified below the tribal level those genera the affinities of which have to date not been established. In Cynareae, recent analyses (Kim et al. 1992; Susanna et al. 1995; Wagenitz and Hellwig 1996; Petit 1997; Häffner and Hellwig 1999; Häffner 2000; Petit et al. 2000; Garcia-Jacas et al. 2002), although giving somewhat conflicting results, have demonstrated the paraphyly of Carduinae, as previously constituted, with respect to Centaureinae as previously recognized; thus, only Carlininae, Cardopatiinae, Echinopsinae and the Carduinae in the broad sense are at present well-established taxa. The three subtribes of Liabeae are based largely on the results of morphological cladistic analysis but molecular data are as yet lacking. Apparently basal in Vernonieae is the yellow-flowered genus *Distephanus* but otherwise, owing mainly to the paucity of our understanding of the Old World representatives, the subtribal situation remains unclear (Keeley and Jansen 1995; Keeley and Chan 2003), in spite of recent studies (Robinson 1996, 1999a, b). In Cichorieae, well-defined at the moment, both morphologically and molecularly, are only the subtribes Scolyminae, Crepidinae sensu lato and Scorzonerinae; possibly, the large subtribe Crepidinae sensu lato (i.e. including all the other subtribes often recognized) may prove to be subdivisible into a number of smaller monophyletic subtribes; especially the New World representatives (Microseridinae sensu lato) and Hyoseridinae appear to have some evidence in favour of their recognition at subtribal level (Whitton et al. 1995; Koop-

man et al. 1998; Kim et al. 1999a; Lee et al. 2003). Of the other cichorioid tribes, Liabeae and Gundelieae are small enough to be considered monosubtribal, while the subtribes Gorteriinae and Arctotidinae of Arctotideae are more or less supported by both molecular and morphological (including developmental) data (Karis et al. 2001; Funk and Chan 2003).

Within Inuleae sensu lato, various groups at subtribal level have been recognized (Anderberg 1991b, c) but, as in other tribes, it is probable they will need considerable reassessment when the results of more detailed morphological and molecular cladistic analyses become available. In recent years, the plucheoid genera of Inuleae sensu lato have been treated by some authorities as constituting a distinct tribe, Plucheeae. In molecular analyses, however, Inuleae sensu stricto and Plucheeae always appear as sister groups (Kim and Jansen 1995; Eldenäs et al. 1998, 1999), and thus the monophyly of Inuleae is not violated by the inclusion in it of the plucheoid genera (Anderberg et al. 2005). Many small entities have been recognized at subtribal level in Heliantheae s.l. (Stuessy 1977; Turner and Powell 1977; Robinson 1981), including Eupatoriodinae as treated at tribal rank (King and Robinson 1987), but further molecular data have shown that these schemes were in need of modification, as some of the entities recognized appeared to be paraphyletic or even polyphyletic (Karis 1993a; Jansen and Kim 1996; Panero et al. 1999; Schilling et al. 1999; Schmidt and Schilling 2000; Baldwin and Wessa 2000a, b; Ito et al. 2000a, b; Baldwin et al. 2002, 2003). Recognition of putatively monophyletic taxa such as the Blepharispermum group (Eriksson 1991) and the subtribes Heleniinae, Coreopsidinae, Eupatoriinae and Tagetinae (including Flaveriinae) left what was an admittedly paraphyletic residue – Helianthinae (including Ecliptinae) – which required further analysis, now reflected in the treatments of the helianthoid tribes in this volume. Subtribal delimitation in Asteroideae is proceeding. Molecular studies in the Heliantheae alliance have provided clear evidence of subtribal relationships. With the exception of Tageteae (Tagetodinae), Eupatorieae (Eupatoriodinae) and Coreopsideae (Coreopsidodinae), subtribal delimitation is robustly established. In Gnaphalieae, the six subtribes (Anderberg 1991a) recently recognized appear to need considerable reassessment in the light of evidence from recent morphological and molecular studies (Bayer and Puttock 1999; Bayer et al. 2000, 2002, 2003). Astereae have been variously divided into subtribes on morphological grounds (Zhang and Bremer 1993; Nesom 1994c), but neither scheme is wholly supported by molecular studies (Lane et al. 1996; Noyes and Rieseberg 1999; Noyes 2000); austral genera appear to be basal, indicating a possible Gondwanan origin for the tribe, as is also the case for their putative sister tribe, Anthemideae; subtribes recently recognized (Bremer and Humphries 1993) appear in several cases not to represent monophyletic groups; again, austral (African) genera appear to be basal (among them the chemically distinctive *Ursinia* and its relatives) whereas the northern-hemisphere genera form a derived, monophyletic group (Anthemidinae sensu lato; Francisco-Ortega et al. 1997; Watson and Evans 1999; Oberprieler and Vogt 2000; Watson et al. 2000). Calenduleae are small enough to be considered monosubtribal, whereas further molecular and morphological analyses are needed to clarify the subtribal delimitation and relationships, and the affinities of problematical genera such as *Packera*, within Senecioneae (Swenson and Bremer 1999). The reference of *Corymbium* to a distinct monogeneric tribe, Corymbieae, has recently been established (Panero and Funk 2002).

The tribal and infratribal systematics adopted in this work is that accepted by the respective authors of the tribes concerned, and at the tribal rank departs from the system presented in this introduction (Jeffrey 2004) in that D.J.N. Hind treats the tribes Stifftieae, Mutisieae, Gochnatieae, Hecastocleideae, Tarchonantheae, Dicomeae and Pertyeae within a broadly circumscribed Mutisieae sensu lato, and J.L. Panero the supersubtribes i–xii and D.J.N. Hind and H. Robinson the supersubtribe xiii, of Heliantheae s.l., respectively as the tribes Athroismeae, Helenieae, Coreopsideae, Neurolaeneae, Tageteae, Chaenactideae, Bahieae, Polymnieae, Heliantheae (sensu stricto), Millerieae, Madieae, Perityleae and Eupatorieae, i.e. the tribes accepted in the subfamilial and tribal classification of Compositae given by Panero and Funk (2002), in which 11 subfamilies and 35 tribes are accepted. Here, it is considered preferable to retain the familiar, broad circumscription of Heliantheae of Cronquist (1955) and Robinson (1981), but with the addition of Eupatorieae, shown to be an ingroup of such a broadly circumscribed Heliantheae by recent molecular studies (Kim and Jansen 1995; Baldwin et al. 2002; Panero and Funk 2002). A few other genera are placed otherwise by the authors of the tribal accounts.

Family Affinities. The affinities of Compositae have been clarified in recent years by molecular taxonomic studies (Lammers 1992; Olmstead et al. 1993; Chase et al. 1993; Michaels et al. 1993; Gustafsson et al. 1996; Jansen and Kim 1996; Wagenitz 1997; Albach et al. 2001; see also introduction to this volume), supplemented by morphological cladistic analyses (Gustafsson and Bremer 1995; Hansen 1997), and there is now strong evidence that Calyceraceae, Goodeniaceae (including Brunoniaceae) and Menyanthaceae are successive sister families of Compositae. These four families together are closely related to Stylidiaceae (incl. Donatiaceae) and a clade of Alseuosmiaceae, Phellinaceae and Argophyllaceae, and more distantly related to Rousseaceae/Carpodetaceae, Campanulaceae (including Lobeliaceae) and Pentaphragmataceae (Lundberg and Bremer 2003).

The Menyanthaceae-Compositae group is characterized by the presence of scalariform perforation plates, the frequent occurrence of sclerified idioblasts, the lack of endosperm haustoria, the presence of binucleate pollen grains and binucleate tapetal cells, the production of herbivore defences by the mevalonate pathway, and the fusion of the lateral veins of adjacent petals for some part of their length, before they separate to join the mid-vein of each petal at the apex of the corolla-lobe. Compositae, Calyceraceae and Goodeniaceae are united by the presence of bifurcating columellae in the pollen grain wall and the presence of anther-collars in at least some members. With Calyceraceae, the Compositae-Barnadesioideae share a number of possible synapomorphies, such as pollen wall structure, the aggregation of pollen by pollenkit, some anther microcharacters, the unilocular ovary and the type of pollen presentation mechanism.

History and Palaeontology. The fossil record of Compositae is sparse and consists mostly of dispersed pollen grains. The earliest records are of both spinulate (mutisioid) and echinate (probably asteroid) pollen grains from the Palaeocene to mid-Eocene of the west coast of South America, of spinulate grains from the Eocene of Chile and of echinate grains from the Eocene of Brazil. Unfortunately, uncertainties of identification and/or dating attend all these pre-Oligocene records, and the earliest, definitely identified and dated records of Compositae pollen are from the early Oligocene of the western USA, the mid-Oligocene of Chile and central Europe, and the late Oligocene of North America. The late Oligocene also sees the first records of macrofossils – leaves, involucres and achenes of unknown tribal and generic affinities. From the Miocene onwards, fossils become more abundant, diverse and widespread (Graham 1996).

Because the Oligocene pollen records are of comparatively advanced types and are found on several different continents, it is reasonable to assume that the family dates back at least to the Eocene-Oligocene boundary, i.e. 38 Ma b.p. This accords well with the evidence for the age of the split between Goodeniaceae and Calyceraceae plus Compositae, which was probably connected with the isolation of South America from Antarctica and has been dated to 48 $\pm$ 5 Ma b.p. (DeVore and Stuessy 1995). Substitution rate calculations of chloroplast DNA *rbc*L gene sequences also give at least 38 Ma b.p. as the age of Compositae (Bremer and Gustafsson 1997). Late Eocene tectonic and climatic changes undoubtedly played a significant role in the early evolution of Compositae and the geographical spread of Compositae during the Miocene (10–20 Ma b.p.) was correlated with the development of extensive dry to semi-arid ecosystems with seasonal precipitation. In this respect, the storage of carbohydrate in the form of highly soluble fructans in the vacuole, giving the plants the ability rapidly to adjust vacuole size and therefore osmotic potential, enabled Compositae to exploit conditions of limited water availability under climates with seasonal rainfall or seasonally low soil water temperatures (Hendry 1996). Coupled with the development of effective dispersal mechanisms and effective chemical defences against herbivores, this enabled Compositae to flourish and spread in the grassland and wooded grassland vegetation types which became widespread during the late Miocene, and pre-adapted them to the cooler, xeric conditions which developed during the Pliocene.

Economic Importance. Compositae are prominent among the plants utilized by peoples in native cultures in all parts of the world, especially for medicinal purposes. For example, in China 500 (Huang and Ling 1996) and in Mexico 180 (Heinrich 1996) species of wild-growing Compositae are currently employed in traditional medicine. Preparations of Compositae are variously valued for their antibiotic, antifungal, antihelmintic, antiplasmodial, expectorant, sedative, diuretic, spasmolytic, haemostatic, immunostimulatory or anti-inflammatory properties. Wild Compositae species are also used as foods, fish poisons, fodder,

and sources of oil and nectar. Industrial products for which Compositae (cultivated or wild) provide raw materials include insecticides, medicines, soaps, detergents, varnishes, paints, cosmetics, rubber, perfumes, food products, and flavourings and colourants for foods and drinks (Garg and Sastry 1996; Viswanathan and Singh 1996). Many Compositae are also highly valued as ornamentals in both commercial and recreational horticulture.

Among cultivated Compositae, the following are among the more important of over 260 species currently in cultivation for other than ornamental purposes: *Cynara cardunculus*, cardoon and globe artichoke, edible leaves and capitula; *Carthamus tinctorius*, safflower, edible and industrial oil; *Cichorium intybus*, chicory, leaf vegetable, roots provide a coffee substitute and also yield fructans; *Cichorium endivia*, endive, salad vegetable; *Pterocypsela indica*, Indian lettuce, salad vegetable; *Lactuca sativa*, lettuce, salad vegetable; *Scorzonera hispanica*, Spanish salsify, scorzonera, root vegetable; *Acmella oleracea*, Para cress, culinary herb; *Echinacea purpurea*, purple coneflower, medicinal, immunostimulatory; *Helianthus annuus*, sunflower, edible and industrial oil and edible seeds, the most important crop plant of the family; *Helianthus tuberosus*, Jerusalem artichoke, root vegetable; *Smallanthus sonchifolius*, yacon, root vegetable; *Artemisia dracunculus*, tarragon, flavouring and oil used in perfumery; *Tanacetum cinerariifolium*, pyrethrum, yields the insecticidal monoterpenes called pyrethrins; *Glebionis coronarium*, crown daisy, green vegetable; and *Petasites japonicus*, butterbur, green vegetable. Among the most important of the very numerous genera cultivated as ornamentals are *Gerbera* (Mutisieae, Barberton daisy); *Dahlia* (Coreopsideae/Heliantheae s.l., dahlia); *Tagetes* (Tageteae/Heliantheae s.l., French and African marigolds), *Xerochrysum* (Gnaphalieae, everlasting), *Callistephus* (Astereae, China aster), *Symphyotrichum* (Astereae, Michaelmas daisy), *Chrysanthemum* (Anthemideae, florist's chrysanthemum) and *Pericallis* (Senecioneae, florist's cineraria).

A number of Compositae are of negative economic significance, inasmuch as they are more or less noxious weeds of gardens, cultivated fields, pastures and plantations. Among the more important weedy genera are *Acroptilon*, *Carduus*, *Cirsium*, *Centaurea* and *Onopordum* (all Cynareae), *Chondrilla* (Cichorieae), *Parthenium*, *Ambrosia*, *Chromolaena* and *Mikania* (all Heliantheae s.l.), *Chrysanthemoides* (Calendulae) and *Senecio* (Senecioneae). *Parthenium hysterophorus* causes a contact dermatitis; the pollen of *Ambrosia* species is a cause of hay fever, and many *Senecio* species are highly hepatotoxic to grazing livestock.

Classification of Compositae (Asteraceae)

I. Subfamily Barnadesioideae (D. Don) Bremer & Jansen (1992).
1. Tribe Barnadesieae D. Don (1830).
Genera 1–9

Non-Barnadesioid Compositae

II. Subfamily Mutisioideae (Cass.) Lindl. (1829).
1. Tribe Stifftieae D. Don (1830).
Genera 10–12, 19–22, 77–78
2. Tribe Mutisieae Cass. (1819) s.s.
Genera 13–18, 24–47, 50–55, 57–59, 61–64, 66–72
Genera of uncertain placement
Genera 23, 48–49, 65
III. Subfamily Carduoideae Cass. ex Sweet (1829).
1. Tribe Gochnatieae (Benth.) Panero & V.A. Funk (2002).
Genera 56, 60, 73–75
2. Tribe Hecastocleideae Panero & V.A. Funk (2002).
Genus 76
3. Tribe Tarchonantheae Kostel. (1833).
Genera 80–82
4. Tribe Dicomeae Panero & V.A. Funk (2002).
Genera 83–87
5. Tribe Cynareae Lam. et DC. (1806) syn. Tribe Cardueae Cass. (1819).
Genera 92–164
Genera of uncertain placement
Genera 165–166, 395
6. Tribe Pertyeae Panero & V.A. Funk (2002).
Genera 79, 88–91

Vernonioid group of tribes

IV. Subfamily Cichorioideae (Juss.) Chev. (1828).
1. Tribe Gymnarrheneae Panero & V.A. Funk (2002).
Genus 167
2. Tribe Moquinieae H. Rob. (1994).
Genera 168–169
3. Tribe Vernonieae Cass. (1819).
Genera 170–287
4. Tribe Liabeae (Cass. ex Dumort.) Rydb. (1927).
Genera 288–303
5. Tribe Cichorieae Lam. et DC. (1806).
Genera 304–389
6. Tribe Gundelieae DC. ex Lecoq et Juillet (1831).
Genera 390–391
7. Tribe Arctotideae Cass. (1819).
Genera 392–394, 396–408
V. Subfamily Asteroideae (Cass.) Lindl. (1829).
1. Tribe Corymbieae Panero & V.A. Funk (2002).
Genus 409
2. Tribe Senecioneae Cass. (1819).
Genera 410–559
3. Tribe Calenduleae Cass. (1819).
Genera 560–570
4. Tribe Gnaphalieae (Cass.) Lecoq et Juillet (1831).

Genera 571–755
5. Tribe Astereae Cass. (1819).
Genera 756–960
6. Tribe Anthemideae Cass. (1819).
Genera 961–1071
7. Tribe Inuleae Cass. (1819).
Genera 1072–1137
8. Tribe Heliantheae Cass. (1819) s.l.
Genera 1138–1619
i. Supersubtribe Athroismodinae (Panero & V.A. Funk) C. Jeffrey (2004) (Tribe Athroismeae)
Genera 1138–1143
ii. Supersubtribe Heleniodinae (Raf.) C. Jeffrey (2004) (Tribe Helenieae)
Genera 1144–1156
iii. Supersubtribe Coreopsidodinae (Lindl.) C. Jeffrey (2004) (Tribe Coreopsideae)
Genera 1157–1186
iv. Supersubtribe Neurolaenodinae (Rydb.) C. Jeffrey (2004) (Tribe Neurolaeneae)
Genera 1187–1191
v. Supersubtribe Tagetodinae (Cass.) C. Jeffrey (2004) (Tribe Tageteae)
Genera 1192–1223
vi. Supersubtribe Chaenactidodinae (Rydb.) C. Jeffrey (2004) (Tribe Chaenactideae)
Genera 1224–1226
vii. Supersubtribe Bahiodinae (Rydb.) C. Jeffrey (2004) (Tribe Bahieae)
Genera 1227–1246
viii. Supersubtribe Polymniodinae (H. Rob.) C. Jeffrey (2004) (Tribe Polymnieae)
Genus 1247
ix. Supersubtribe Helianthodinae (Cass.) C. Jeffrey (2004) (Tribe Heliantheae)
Genera 1248–1360
x. Supersubtribe Milleriodinae (Lindl.) C. Jeffrey (2004) (Tribe Millerieae)
Genera 1361–1394
xi. Supersubtribe Madiodinae (Benth.) C. Jeffrey (2004) (Tribe Madieae)
Genera 1395–1430
xii. Supersubtribe Perityloninae (Rydb.) C. Jeffrey (2004) (Tribe Perityleae)
Genera 1431–1437
xiii. Supersubtribe Eupatoriodinae (Cass.) C. Jeffrey (2002) (Tribe Eupatorieae)
Genera 1438–1619
Asteroid genus of uncertain tribal position
Genus 1620

Descriptions of the Subfamilies of Compositae

I. Subfam. Barnadesioideae
(D. Don) Bremer & Jansen (1992).

Shrubs, trees, or perennial or annual herbs, usually with fascicled nodal spines. Leaves variable, entire, mostly pinnatinerved, many xeromorphic. Capitula homogamous or heterogamous, discoid or pseudoradiate or ligulate, sessile or pedunculate; synflorescences variable. Receptacle pilose, rarely with pales or glabrous. Involucre cylindrical to hemispherical, phyllaries in several series. Florets 1 to numerous, isomorphic or anisomorphic, generally hermaphrodite; corollas tubular, pseudobilabiate, bilabiate, subpseudobilabiate, ligulate or subligulate, often villous. Stamens 5 (3–5 in the central flowers); filaments free or rarely fused, inserted at different levels; anthers ecaudate to tailed, with apical appendage entire, emarginate or bilobed. Pollen with or without depressions, lophate, microechinate, scabrate-microechinate or smooth. Style shortly bilobed or bifid, glabrous or papillose below bifurcation. Achenes densely villous, with straight simple hairs, rarely glabrous. Pappus uniseriate or rarely absent.

Barnadesioideae are the smallest subfamily of Asteraceae, with 91 species in 9 genera, endemic to South America. This subfamily, earlier treated at the subtribal level within Mutisieae, was newly recognized by Bremer and Jansen (1992) based primarily on molecular restriction site (and subsequent sequence, e.g. Bayer and Starr 1998) analyses. All Asteraceae (except for Barnadesioideae) have a 22-kb inversion in cpDNA (Jansen and Palmer 1987, 1988). This not only helps define the subfamily, but also places it in a basal phylogenetic position within the family. Diagnostic morphological features include the presence of axillary spines, unbranched "barnadesioid" hairs (with an epidermal cell very slightly differentiated and two other cells, one short with thick walls and the other longer with thin walls) on corollas, achenes, pappus and vegetative structures (Cabrera 1959, 1961; Bremer 1987; Bremer and Jansen 1992), and frequent occurrence of pseudobilabiate corollas (Bremer 1987, 1994). Flavonoid profiles are quite simple (Bohm and Stuessy 1995). Phylogenetic analyses of intergeneric relationships based on morphology (Urtubey and Stuessy 2001) and DNA sequences (Gustafsson et al. 2001) have given incongruent results; more study is evidently needed. Biogeographic hypotheses for the subfamily suggest a southern South American origin (Stuessy et al. 1996). Comprising only the tribe Barnadesieae.

II. Subfam. Mutisioideae
(Cass.) Lindl. (1829).

Shrubs, trees or perennial or rarely annual herbs, rarely scandent. Leaves usually alternate,

usually simple, entire, serrate, denticulate or lobulate. Capitula homogamous or heterogamous, bilabiato-radiate, bilabiate or discoid, rarely ligulate. Involucre cylindrical to urceolate-subglobose, phyllaries few- to many-seriate, imbricate, gradate. Receptacle usually epaleaceous. Florets 1–many, 5-merous, marginal usually bilabiate and often radiate, inner bilabiate or sometimes regular and corolla deeply 5-lobed, rarely all florets regular or ligulate; corolla-lobes long, with an apical tuft of minute hairs, those of inner lip of bilabiate florets coiled. Anthers calcarate and caudate, tails usually long, often variously branched or fimbriate. Pollen ecaveate, microechinate. Style shaft usually glabrous, arms mostly short, obtuse to rounded and glabrous, sometimes truncate and penicillate, with stigmatic papillae covering all inner surface. Achenes usually with twin hairs. Pappus usually present, commonly of bristles, often uniseriate.

Mutisioideae comprise c. 60 genera and 720 species, mostly South American. They here are circumscribed in the sense of Hansen (1991b), except that certain genera included by him in the subfamily (as tribe Mutisieae) are here transferred to Carduoideae.

III. Subfam. Carduoideae
Cass. ex Sweet (1826).

Perennial, biennial or less often annual herbs, shrubs or rarely trees, rarely scandent. Leaves alternate, usually simple, entire, serrate, denticulate or lobulate, especially in herbaceous members often spiny. Capitula homogamous or heterogamous, discoid or discoid with marginal florets sterile and radiant, rarely bilabiato-radiate, radiate or ligulate. Involucre narrowly cylindrical to urceolate-subglobose, phyllaries 3- to many-seriate, imbricate, often spiniferous. Receptacle epaleaceous and very often setulose, rarely paleaceous. Florets 1 to many, 5-merous, all or inner regular or subregular, outer sometimes radiant, rarely bilabiato-radiate or radiate, very rarely all ligulate; corolla-lobes long, those of inner lip of bilabiate florets straight or with incurved apex, very rarely coiled. Anthers calcarate and caudate, tails usually long, sometimes pilose or fringed. Pollen usually ecaveate, spiny or microechinate. Style arms short to long, obtuse to rarely acute, glabrous or with dorsal hairs, sometimes not divergent for most of their length, with stigmatic papillae covering all inner surface; style shaft often with an articulation at or below the branching point, marked by a ring of hairs and/or an increase in diameter, glabrous below the articulation, usually hairy above it. Achenes with twin hairs, simple hairs or glabrous. Pappus usually present, of bristles or scales, isomorphic or heteromorphic.

Carduoideae comprise at least 93 genera and 2,600 species, mostly in the Old World. The subfamily as here circumscribed includes all mutisioid genera which in molecular studies come out above Mutisieae and below the cichorioid-asteroid clade, as well as Cynareae sensu lato. The constancy of the Gochnatia type of testa epidermal cell wall thickening (Grau 1980) or its derivatives define the subfamily. Although this type also occurs, possibly as a parallelism, in some Mutisieae, it is there associated with different style and/or pollen types.

IV. Subfam. Cichorioideae
(Juss.) Chev. (1828).

Perennial, biennial or annual herbs, shrubs or trees, rarely scandent, very rarely aquatic. Leaves alternate or opposite, usually simple, entire to deeply lobed, in herbaceous members sometimes spiny. Capitula homogamous to heterogamous, discoid, ligulate or radiate. Involucre narrowly to broadly cylindrical or campanulate to subglobose, phyllaries (1-)2- to many-seriate, usually imbricate. Receptacle epaleaceous, often alveolate, or paleaceous. Florets 1–many, usually 5-merous, all regular, all ligulate or very rarely bilabiate, or inner regular and outer bilabiate or radiate; corolla-lobes usually long, not coiled. Anthers calcarate, caudate or ecaudate, tails usually simple. Pollen ecaveate or sometimes appearing caveate, spiny, sometimes echinolophate, psilolophate or lophate, globose. Style arms commonly long, tapered, acute, hairy dorsally, sometimes shaft thickened apically and arms short to long; stigmatic papillae covering all inner surface. Achenes with twin hairs. Pappus usually present, usually of bristles or scales, sometimes heteromorphic.

Cichorioideae are here accepted in the sense of Bremer (1994), comprise 241 genera and about 2,900 species, and are well represented in both the Old and the New Worlds.

V. Subfam. Asteroideae
(Cass.) Lindl. (1829).

Perennial to annual herbs or shrubs, less often trees, sometimes scandent, epiphytic or aquatic, sometimes succulent. Leaves alternate or opposite,

simple but not infrequently highly dissected, not spiny. Capitula heterogamous or homogamous, radiate, disciform or discoid, very rarely ligulate. Involucres cylindrical to subglobose, phyllaries 1- to few-, less often many-seriate, imbricate or eximbricate. Receptacle epaleaceous or paleaceous. Florets 1 to many, (3–4–)5(–6)-merous, all regular, or inner regular and outer radiate or filiform, narrowly tubular and subtruncate or microradiate, very rarely outer bilabiate or all ligulate; corolla-lobes short, deltoid, rarely long. Anthers almost always ecalcarate, caudate or ecaudate, tails simple, usually slender. Pollen almost always caveate, spiny, with double tectum. Style arms short to long, tapered and acute to obtuse or truncate, often appendaged; stigmatic papillae mostly confined to two marginal, distant to contiguous, apically confluent or separate lines, rarely covering entire inner surface of style arms. Achenes with twin hairs, in many helianthoid members with a phytomelanin layer in the pericarp ("carbonized"). Pappus present or absent, usually of bristles or scales or coroniform, sometimes auriculiform or of awns, sometimes heteromorphic.

Asteroideae, here accepted in the sense of Bremer (1994), are the largest subfamily of Compositae, comprising 1,210 genera and about 17,000 species, of which Heliantheae sensu lato form 480 and c. 5,600 respectively. They are widely distributed on all continents, except Antarctica.

Key to the Tribes and Tribally Unplaced Genera[2]

1. Corolla inside and outside and all other floral parts bearing simple, uniseriate, eglandular, 3-celled hairs, the basal cell of which has a centrally depressed, distal transverse wall **I. Barnadesieae** (p. 87)
– Corolla inside and outside and all other floral parts without such hairs, though often with hairs of various other kinds 2
2. Plant a heterocapitular amphicarpic rosulate herb, forming both subterranean cleistogamous and subaerial chasmogamous capitula **IV. Gymnarrheneae** (p. 147)
– Plant otherwise, if heterocapitular, then all capitular forms subaerial 3
3. Capitula heteromorphic, homogamous, with only pistillate (female) florets, or only functionally staminate (male) or perfect (hermaphrodite) florets, rarely pistillate capitula with a few functionally staminate florets, or staminate capitula with some marginal pistillate florets 4
– Capitula homomorphic, heterogamous (radiate or disciform) or if homogamous (discoid), then all florets perfect or rarely the outer enlarged and sterile (radiant) 16
4. Staminate and pistillate capitula borne on the same plant (plants monoecious) 5
– Staminate (or perfect) and pistillate capitula borne on different plants (plants dioecious or gynodioecious) 7
5. Herbs; achenes with a phytomelanin layer in pericarp **XXVI. Heliantheae** (p. 440)
– Shrubs; achenes without a phytomelanin layer in pericarp 6
6. Capitula 1-flowered **V. Moquinieae** (p. 148)
– Capitula many-flowered **XV. Astereae** (p. 284)
7. Leaves opposite, achenes with a phytomelanin layer in pericarp 8
– Leaves alternate, achenes without a phytomelanin layer in pericarp 10
8. Plant scandent, capitula with 4 phyllaries and 4 florets **XXX. Eupatorieae** (p. 510)
– Plant a shrub or small tree, phyllaries and florets > 4 9
9. Phyllaries dimorphic, pappus of 2–3 awns **XX. Coreopsideae** (p. 406)
– Phyllaries subequal, pappus of a few minute squamellae or absent **XIX. Helenieae** (p. 400)
10. Leaves spiny **III. Cynareae** (Cardueae) (p. 123)
– Leaves not spiny 11
11. Phyllaries in one series, with or without a few much smaller outer bracts (calyculus); pappus of bristles present **XII. Senecioneae** (p. 208)
– Phyllaries 2- or > 2-seriate, if uniseriate, then pappus absent 12
12. Phyllaries papery, brownish or coloured, not green **XIV. Gnaphalieae** (p. 246)
– Phyllaries not papery, often green, herbaceous 13
13. Anthers ecaudate, without basal tails 127
– Anthers caudate, with basal tails, often long and prominent 14
14. Capitula solitary; corollas white, anthers ecalcarate; Australia **XVII. Inuleae** (p. 374)
– Capitula few to many, variously arranged or if solitary, then corollas purple; anthers calcarate; not Australia 15
15. Style shaft slightly broadened and scabrid in upper part; style arms dorsally scabrid; South America **V. Moquinieae** (p. 148)
– Style shaft not broadened and glabrous (South America) or short-pilose (E Asia) in upper part; style arms dorsally glabrous (South America), short-papillose (Africa/Madagascar) or short-pilose (E Asia) **II. Mutisieae** (p. 90)
16. Capitula with some or all florets ligulate (0/5), with strap-shaped apically 5-toothed or 5-lobed abaxial limb 17
– Capitula without ligulate florets, florets variously regular (5/0), pseudobilabiate (1/4), bilabiate (2/3), or radiate (0/3, 0/4) 21
17. Latex (milky juice) abundantly present in all vegetative parts; all florets ligulate **VIII. Cichorieae** (p. 180)

[2] The tribes in this key (I–XXX) are those accepted by the authors of the tribal accounts. Where a final lead ends in alternative tribes, the user should try the unknown in the keys to genera of each tribe. If a plant to be identified is known or thought to be a member of the Heliantheae alliance (tribes XVIII–XXX), the user may go directly to the key to the corresponding tribes on p. 391. Stylar characters, unless otherwise stated, relate to the styles of perfect florets.

– Latex (milky juice) absent; all or some florets ligulate 18
18. Leaves opposite; achenes with phytomelanin layer in pericarp **XX. Coreopsideae** (p. 406)
– Leaves alternate; achenes without phytomelanin layer in pericarp 19
19. Outer phyllaries and leaves spiny **III. Cynareae** (Cardueae) (p. 123)
– Outer phyllaries and leaves not spiny 20
20. Herbs; style shaft with sweeping hairs in upper part **VI. Vernonieae** (p. 149)
– Shrubs or small trees; style shaft glabrous **II. Mutisieae** (p. 90)
21. Capitula with some or all florets bilabiate (2/3) or rarely pseudobilabiate (1/4) 22
– Capitula entirely without bilabiate florets 31
22. All florets of capitulum bilabiate, although outer sometimes with enlarged abaxial lip and appearing radiate 23
– Only marginal or only inner florets bilabiate or pseudobilabiate 24
23. Achenes with large, elongated crystals in epidermal cells; style arms with sweeping hairs extending to below the bifurcation; annual herbs; India **XVII. Inuleae 1136.** ***Nanothamnus*** (p. 390)
– Achenes without or with other kinds of crystals in epidermal cells; trees, shrubs or perennial herbs, if annual herbs, then New World and/or style shaft glabrous **II. Mutisieae** (p. 90)
24. Peripheral florets radiate, inner florets bilabiate; S Africa **XVI. Anthemideae** (p. 342)
– Peripheral florets bilabiate, inner florets regular 25
25. Herbs or shrubs; achenes with phytomelanin layer in pericarp 91
– Herbs, shrubs or small trees, if herbs or shrubs, then without phytomelanin layer in pericarp 26
26. Filaments connate; achenes dorsally spiny, outcurved **166.** ***Dipterocome*** (p. 147)
– Filaments free; achenes not dorsally spiny nor outcurved 27
27. Phyllaries uniseriate 28
– Phyllaries 2- or > 2-seriate 29
28. Scandent shrub; achenes without stipitate glands **XII. Senecioneae** (p. 208)
– Erect perennial herb; achenes with conspicuous stipitate glands **II. Mutisieae** (p. 90)
29. Pappus of a single plumose bristle; Africa **XIV. Gnaphalieae** (p. 246)
– Pappus otherwise, usually of numerous barbellate bristles or scarious scales 30
30. Anthers ecalcarate, ecaudate; disc florets functionally staminate **XV. Astereae** (p. 284)
– Anthers calcarate, caudate, often conspicuously so; disc florets perfect, rarely functionally staminate or pistillate 128
31. Capitula 1-flowered, or 1- to several-flowered and aggregated into secondary compound heads (syncephalia) 32
– Capitula 2- to many-flowered and not aggregated into secondary compound heads (syncephalia), although inflorescence sometimes congested 50
32. Leaves and/or phyllaries spiniferous; plant caulescent or if acaulescent, then corollas white or pale blue 33
– Leaves and/or phyllaries not spiniferous or if leaves spiniferous, then plant acaulescent and corollas purple 35
33. Syncephalia with one central perfect floret and 4–6 peripheral functionally staminate florets, further aggregated into a somewhat elongated terminal tertiary head; plant lacticiferous **IX. Gundelieae** (p. 199)
– Syncephalia with all florets perfect, not further aggregated into a somewhat elongated terminal tertiary head; plants not or only weakly lacticiferous 34
34. Individual capitula surrounded by a tuft of bristles or white plumose hairs; syncalathia globose or hemispherical, with a few small or leaf-like basal bracts; Old World **III. Cynareae** (Cardueae) (p. 123)
– Individual capitula not surrounded by a tuft of bristles or white hairs; syncalathia surrounded by ovate, marginally spiny bracts; North America **II. Mutisieae** (p. 90)
35. Achenes without a phytomelanin layer in the pericarp, usually not black 36
– Achenes with a phytomelanin layer in the pericarp, often therefore appearing black or streaked with black 42
36. Style shaft and style arms both glabrous **II. Mutisieae** (p. 123)
– Style shaft glabrous or with hairs or papillae in upper part below the bifurcation, style arms with hairs or papillae dorsally or at least apically 37
37. Phyllaries papery or cartilaginous, hyaline, brownish or coloured; style arms truncate, with apical hairs; capitula homogamous, rarely heterogamous **XIV. Gnaphalieae** (p. 246)
– Phyllary and style characters otherwise; capitula heterogamous or homogamous 38
38. Style shaft with hairs on upper part, style arms narrow, acute, unappendaged, hairy dorsally and with stigmatic papillae covering whole of inner (ventral) surface; capitula homogamous 39
– Style characters all or some otherwise; capitula heterogamous or homogamous 40
39. Plant an acaulescent rosulate herb; capitula crowded in a large syncalathium sessile in the centre of the leaf rosette; S Africa **X. Arctotideae** (p. 200)
– Plant a tree, shrub or caulescent herb; capitula distinct or if aggregated into syncephalia, then these not sessile in the centre of a leaf rosette; New World, if Old World, then capitula 4-flowered and phyllaries decussate **VI. Vernonieae** (p. 149)
40. Capitula 1-flowered, not aggregated into secondary compound heads (syncephalia), although sometimes in congested inflorescences 41
– Capitula 1- to several-flowered, aggregated into sphaerical to spiciform secondary heads (syncephalia) **XVII. Inuleae** (p. 374)
41. Plant a caulirosulate herb; leaves pinnately veined; phyllaries 5–7-seriate, imbricate; anthers with prominent tails; E Asia **II. Mutisieae** (p. 90)
– Plant a rosulate scapigerous herb; leaves parallel-veined; phyllaries 2-seriate; anthers ecaudate; S Africa **XI. Corymbieae** (p. 207)
42. Style arm appendages longer than the stigmatic lines, spathulate, or if not spathulate, then phyllaries and florets 4; syncalathia spherical clusters or glomerules; corollas not yellow **XXX. Eupatorieae** (p. 510)

– Style arm appendages otherwise, shorter than the stigmatic lines, or style arms unappendaged; corollas yellow or not 43
43. Leaves and/or phyllaries with pellucid glands or pustules, aromatic **XXII. Tageteae** (p. 420)
– Leaves and phyllaries without pellucid glands or pustules, usually not aromatic 44
44. Plant a prostrate, rosulate, annual herb; pappus of many scales, fused at the base and deciduous as a unit **XXXIII. Chaenactideae** (p. 431)
– Plant an annual or perennial herb or shrubby; pappus absent or otherwise 45
45. Capitula crowded in glomerules surrounded by leafy bracts; phyllaries uniseriate, connate; leaves opposite **XXVI. Heliantheae** (p. 440)
– Capitula otherwise; leaves opposite or alternate 46
46. Plant a shrub with brittle whitish stems; leaves opposite, succulent, glaucous **XXII. Tageteae** (p. 420)
– Plant otherwise; leaves opposite or alternate, and most subsucculent 47
47. Leaves alternate; capitula disciform or discoid; achenes tangentially flattened, laterally ciliate; anthers tailed; Africa, Madagascar, India **XVIII. Anthroismeae** (p. 395)
– Leaves opposite or at least some capitula radiate; achenes otherwise; anthers not tailed; New World, Australia, adventive elsewhere 48
48. Leaves alternate; shrubs or small trees **XXVI. Heliantheae** (p. 440)
– Leaves opposite; herbs 49
49. Capitula with peripheral tubular florets enclosed in a perigynium; styles of disc florets undivided **XXVII. Millerieae** (p. 477)
– Capitula without peripheral florets enclosed in a perigynium; styles of disc florets divided, style arms truncate **XXII. Tageteae** (p. 420)
50. Phyllaries uniseriate or varyingly uniseriate-biseriate; receptacle epaleaceous, without scales subtending florets, although sometimes with bristles or projections 51
– Phyllaries 2- to many-seriate, if uniseriate, then receptacle paleaceous, with scales subtending all or some florets, each scale subtending a single floret 72
51. Achenes without a phytomelanin layer in the pericarp, usually not black 52
– Achenes with a phytomelanin layer in the pericarp, therefore often appearing black or streaked with black 62
52. Phyllaries cartilaginous, hyaline, greenish or greenish-brown; style arm apices conical **XIV. Gnaphalieae** (p. 246)
– Phyllaries and style arm apices either or both otherwise 53
53. All or at least the disc florets with tetramerous corollas 54
– All or at least the disc florets with pentamerous corollas 56
54. Pappus of conspicuous bristles **XII. Senecioneae** (p. 208)
– Pappus coroniform or absent, not of conspicuous bristles 55
55. Leaf blades obovate, usually toothed, rarely entire **XVIII. Athroismeae** (p. 395)
– Leaf blades linear, entire, with sheathing base **XII. Senecioneae** (p. 208)
56. Pappus of bristles present, at least on some achenes 61
– Pappus absent, coroniform or of a single scale 57
57. Pappus of a single scale **XII. Senecioneae** (p. 208)
– Pappus coroniform or absent 58
58. Phyllaries with narrow hyaline margins or all or at least the inner with broad, pale membranous margins; style arms truncate, penicillate **XVI. Anthemideae** (p. 342)
– Phyllaries and style arms either or both otherwise 59
59. Achenes large, terete, triquetrous or flattened, winged or wingless, straight or curved, glabrous, smooth or aculeate, sometimes fenestrate, or fruits drupaceous; achenes homomorphic or heteromorphic; pappus absent **XIII. Calenduleae** (p. 241)
– Achenes small, columnar, angled, terete or compressed, never fenestrate, not drupaceous, unwinged, homomorphic; pappus coroniform or absent 60
60. Style arms with an ovate-lanceolate or linear appendage **XV. Astereae** (p. 284)
– Style arms without an apical appendage, truncate to obtuse, or disc floret styles undivided **XII. Senecioneae** (p. 208)
61. Involucre saucer-shaped to subglobose; marginal filiform florets 2- to many-seriate, tubular, with or without a short, narrow ray; Old World tropics **XV. Astereae** (p. 284)
– Involucre cylindrical, sometimes calyculate; marginal pistillate florets absent or uniseriate and radiate, rarely tubular; widespread **XII. Senecioneae** (p. 208)
62. Style arm appendages longer than the stigmatic lines, prominent; capitula discoid; corollas never yellow **XXX. Eupatorieae** (p. 510)
– Style arm appendages shorter than stigmatic lines; capitula radiate, disciform or discoid; corollas often yellow 63
63. Leaves and/or phyllaries with pellucid glands or pustules, aromatic **XXII. Tageteae** (p. 420)
– Leaves and phyllaries without pellucid glands or pustules 64
64. Disc corollas all 4-lobed 65
– Disc corollas 5-lobed, sometimes some also 4- or 6-lobed 67
65. Capitula radiate **XXIX. Perityleae** (p. 507)
– Capitula discoid or disciform 66
66. Achenes flattened, with wings or usually a corky, often ciliate margin **XXIX. Perityleae** (p. 507)
– Achenes 4-sided, obpyramidal, if flattened, then capitula disciform **XXIV. Bahieae** (p. 433)
67. Leaves all or some opposite or whorled, or proximal rosulate 68
– Leaves alternate 69
68. Ray corollas white; pappus of about 8 erose scales **XXIV. Bahieae** (p. 433)
– Ray corollas some shade of yellow; pappus of persistent bristles, fragile awns or awns and scales, or absent, or capitula discoid **XXVIII. Madieae** (p. 492)
69. Plant a shrub; capitula discoid **XXIV. Bahieae** (p. 433)
– Plant an annual or perennial herb, if a shrub, then capitula radiate 70
70. Plant an annual herb or shrub **XXVIII. Madieae** (p. 492)

– Plant a perennial herb 71
71. Disc florets functionally staminate; Cuba
XXI. Neurolaeneae (p. 417)
– Disc florets perfect; W North America
XXVIII. Madieae (p. 492)
72. Receptacle paleaceous, with a scale subtending each floret or each of some of the florets, scales sometimes spiniform 73
– Receptacle epaleaceous, without scales subtending the florets, although sometimes with bristles or receptacular or alveolar projections between or around the florets 129
73. Leaves all alternate 74
– Leaves some or all opposite or whorled 92
74. Style shaft with an articulation below the bifurcation, marked by a ring of hairs and/or an increase in diameter; style arms short and shortly hairy dorsally, or long and not divergent for most of their length, velvety dorsally **III. Cynareae** (Cardueae) (p. 123)
– Style shaft without an articulation below the bifurcation; style arms various 75
75. Style arms tangentially spreading, narrow, acute, unappendaged, hairy dorsally, with stigmatic papillae over whole of ventral surface; corollas not yellow; capitula homogamous; receptacular scales sometimes spiniform **VI. Vernonieae** (p. 149)
– Style arm characters otherwise; capitula homogamous or heterogamous; corollas often yellow; receptacular scales never spiniform 76
76. Plant an annual herb with heterogamous capitula sessile 2–4 together in the stem bifurcations, achenes adnate to 1 or 2 of the receptacular scales, and shortly tailed anthers; NE Asia
1620. *Symphyllocarpus* (p. 574)
– Plant otherwise 77
77. Achenes without a phytomelanin layer in pericarp, usually not black 78
– Achenes with a phytomelanin layer in pericarp, thus often black or streaked with black 93
78. Style arms with apical appendages above the stigmatic lines; anthers usually ecaudate 79
– Style arms unappendaged, rounded or truncate; anthers usually caudate 80
79. Ray florets neuter, sterile **XIX. Helenieae** (p. 400)
– Ray florets pistillate and fertile or absent
XV. Astereae (p. 284)
80. Style arms apically truncate, penicillate, with apical hairs 81
– Style arms apically rounded, with hairs or papillae dorsally, or glabrous 86
81. Phyllaries herbaceous, without scarious margins and apex 82
– Phyllaries papery or cartilaginous, hyaline, brownish or coloured, or with distinct brownish to pallid scarious membranous margins and apex 83
82. Plant a herb; North America
XIX. Helenieae (p. 400)
– Plant a shrub; S Africa **XVI. Anthemideae** (p. 342)
83. Pappus absent, a rim or a cartilaginous corona or auricle 84
– Pappus of bristles, scales or spines present 85
84. Phyllaries papery, brownish or white; pappus absent
XIV. Gnaphalieae (p. 246)
– Phyllaries with distinct brownish to pallid membranous scarious margins and apex; pappus absent, coroniform or auriculiform
XVI. Anthemideae (p. 342)
85. Phyllaries papery, hyaline, whitish to coloured; pappus of bristles, scales or 2 spines; Australia, Africa
XIV. Gnaphalieae (p. 246)
– Phyllaries not papery, but with scarious margins and apex; pappus of scales; Africa
XVI. Anthemideae (p. 342)
86. Capitula homogamous, discoid 87
– Capitula heterogamous, radiate or disciform 89
87. Style arms glabrous (South America) or coronate-papillose around apices (tropical Africa)
II. Mutisieae (p. 90)
– Style arms with sweeping hairs and papillae dorsally 88
88. Corollas yellow; tropical Africa
XVIII. Athroismeae (p. 395)
– Corollas white, cream, purplish or lavender; North America **XIX. Helenieae** (p. 400)
89. Rays purple, lilac or white
XIV. Gnaphalieae (p. 246)
– Rays yellow or absent and capitula disciform 90
90. Achenes with one large calcium oxalate crystal in each epidermal cell, or if without crystals, then capitula disciform and corolla mauve, or stems winged and receptacular paleae flattened
XVII. Inuleae (p. 374)
– Achene epidermal cells without crystals; receptacular paleae enfolding achenes
XVIII. Athroismeae (p. 395)
91. Pappus of 8–10 scales **XXIV. Bahieae** (p. 433)
– Pappus absent, of 2 scales and sometimes 2 fragile awns, or of numerous plumose bristles 107
92. Achenes without a phytomelanin layer in the pericarp 123
– Achenes with a phytomelanin layer in the pericarp, thus often black or streaked with black 93
93. Receptacular scales in one series between ray florets and disc florets **XXVIII. Madieae** (p. 492)
– Receptacular scales subtending some or all of the non-peripheral florets, but not in a single series between the ray and disc florets 94
94. Capitula discoid; corollas never yellow; style arm appendages much longer than the stigmatic surfaces, prominent, lanceolate to clavate; phyllaries all similar or gradate; pappus never of barbed awns
XXX. Eupatorieae (p. 510)
– Capitula radiate, disciform or discoid; corolla often yellow; style arm appendages usually shorter than the stigmatic surfaces, if longer, then phyllaries dimorphic and pappus of a few barbed awns 95
95. Pappus absent, or of a few teeth or awns, or of scales and minute bristles or awns, or of barbed awns, or cupuliform or coroniform, but not of 3 or more similar, conspicuous, often plumose scales or bristles 96
– Pappus of all or disc florets of 3 or more similar, conspicuous, often plumose scales or bristles 108
96. Styles of disc florets undivided, or apically very shortly bifid; disc florets functionally staminate 97
– Styles of disc florets with free style arms; disc florets perfect or functionally staminate 111

97. Plants caulirosulate herbs, shrubs or small trees, or megaphytic rosulate herbs, sometimes monocarpic; Ecuador, Colombia, Venezuela (Paramos) **XXVII. Millerieae** (p. 477)
– Plant of different habit and usually also habitat 98
98. Achenes each enfolded by a phyllary or wholly enclosed in a conceptacle formed by an adnate phyllary **XXVII. Millerieae** (p. 477)
– Achenes not enfolded by phyllaries nor enclosed in conceptacles 99
99. Capitula disciform, or if radiate, then achenes each associated with a phyllary and adjacent two disc florets and scales **XXVI. Heliantheae** (p. 440)
– Capitula radiate; achenes not so associated 100
100. Achenes obpyriform or broadly obpyramidal, not flattened parallel to the involucre **XXVII. Millerieae** (p. 477)
– Achenes more or less flattened tangentially, parallel to the involucre 101
101. Achenes winged 102
– Achenes not winged, although sometimes strongly flattened 103
102. Plant scandent **XX. Coreopsideae** (p. 406)
– Plant an annual or perennial herb or shrub, not scandent **XXVI. Heliantheae** (p. 440)
103. Pappus of 2–3 awns **XX. Coreopsideae** (p. 406)
– Pappus of a few scales, minutely coroniform or absent 104
104. Leaves alternate **XXVI. Heliantheae** (p. 440)
– Leaves opposite 105
105. Pappus a shallow corona **XXV. Polymnieae** (p. 439)
– Pappus absent 106
106. Leaf blades trilobed; S Asia **XX. Coreopsideae** (p. 406)
– Leaf blades elliptic to lanceolate, unlobed; South America **XXVII. Millerieae** (p. 477)
107. Phyllaries 2- to 5-seriate; pappus of plumose bristles, rarely absent **XXVII. Millerieae** (p. 477)
– Phyllaries 1-seriate; pappus absent or of 2 scales with or without 2 fragile awns **XXVIII. Madieae** (p. 492)
108. Leaves all or mostly alternate 109
– Leaves opposite **XXI. Neurolaeneae** (p. 417) and **XXVII. Millerieae** (p. 477)[3]
109. Leaves bipinnate, segments filiform to linear, leaves all alternate **XXIV. Bahieae** (p. 433)
– Leaves with entire to pinnatilobed margins 110
110. Proximal leaves rosulate or opposite, distal alternate **XXVIII. Madieae** (p. 492)
– Proximal and distal leaves all alternate **XXI. Neurolaeneae** (p. 417) and **XXVII. Millerieae** (p. 477)[3]
111. Leaves mostly alternate, proximal rosulate or opposite; phyllaries each enfolding the subtended ray floret proximally **XXVIII. Madieae** (p. 492)
– Leaves all alternate or all opposite, or opposite and the upper alternate; phyllaries not so enfolding the subtended ray floret, or if so, then leaves opposite 112
112. Achenes strongly 9–11-ribbed; shrubs; SW North America, N Mexico **XXII. Tageteae** (p. 420)
– Achenes otherwise; herbs, shrubs or trees; widespread 113
113. Plant a shrub with succulent, deeply dissected leaves, achenes fusiform, 4-angled; San Felix and San Ambrosio Islands, N Chile **XXIX. Perityleae** (p. 507)
– Plant and achenes otherwise; widespread 114
114. Plant aquatic or of very moist places; stem fistulose, rooting at nodes; receptacular scales wrapping tightly around florets; capitula minutely radiate or disciform, rays minute or absent; pantropical **XXI. Neurolaeneae** (p. 417)
– Plant without above combination of features; widespread 115
115. Achenes of the ray and of the disc (when present) tangentially flattened (flattened parallel to the involucre, obcompressed); receptacular scales more or less flat to navicular and sometimes cucullate 116
– Achenes of the disc radially flattened (compressed), although those of the ray sometimes tangentially flattened, or achenes of the disc not flattened; receptacular scales conduplicate, rarely more or less flat to navicular, cucullate or bristle-like 121
116. Leaves alternate, with expanded leaf-bases **XXVII. Millerieae** (p. 477)
– Leaves opposite, or if alternate, then without expanded leaf-bases 117
117. Leaves alternate 118
– Leaves all or mostly opposite 119
118. Plant with Kranz anatomy; style arm appendages as long as or longer than stigmatic surfaces **XX. Coreopsideae** (p. 406)
– Plant not with Kranz anatomy; style arm appendages much shorter than stigmatic surfaces or absent **XXVI. Heliantheae** (p. 440)
119. Style arm appendages usually vascularized, penicillate and papillose; receptacular scales more or less flat **XX. Coreopsideae** (p. 406)
– Style arm appendages non-vascularized, acute to cylindrical, papillose, or absent and represented by an apical tuft of papillae; receptacular scales more or less flat, navicular or cucullate 120
120. Capitula discoid **XXVI. Heliantheae** (p. 440)
– Capitula radiate **XXVI. Heliantheae** (p. 440) and **XXVII. Millerieae** (p. 477)[4]
121. Plant with outer phyllaries herbaceous, shortly connate and inner membranous or scarious, fusiform to linear or narrowly oblanceolate achenes with conspicuously attenuate apices, and pubescent filaments **XX. Coreopsideae** (p. 406)
– Plant without above combination of features 122
122. Leaves alternate, at least in part **XXVI. Heliantheae** (p. 440)
– Leaves all opposite **XXVI. Heliantheae** (p. 440) and **XXVII. Millerieae** (p. 477)[4]
123. Style arms with a lanceolate to linear, papillose appendage above the stigmatic areas **XV. Astereae** (p. 284)
– Style arms without appendages 126
124. Stigmatic papillae covering entire inner surface of style arms; style arms dorsally and upper part of shaft with long sweeping hairs 125
– Stigmatic papillae confined to two marginal or submarginal lines on inner surface of style arms; style

[3] See also key to the Heliantheae alliance tribes, p. 391.

[4] See also key to the Heliantheae alliance tribes, p. 391.

arms truncate, with hairs apically, or rounded with hairs dorsally 126
125. Capitula radiate; disc florets yellow; Americas **VII. Liabeae** (p. 175)
– Capitula discoid; florets purplish; tropical Africa **VI. Vernonieae** (p. 149)
126. Pappus absent or an entire or denticulate rim; capitula radiate, disciform or discoid **XVI. Anthemideae** (p. 342)
– Pappus of scales or awns, sometimes connate; capitula radiate, rays yellow with purple bands dorsally, or blue or white **XIV. Gnaphalieae** (p. 246)
127. Pappus bristles, if present, whitish to tawny; New World **XV. Astereae** (p. 284)
– Pappus bristles purple; Sinohimalaya **165. *Cavea*** (p. 146)
128. Inner phyllaries whitish to pinkish-violet or purple, or ending in a long, pungent, often pink or purple apex **III. Cynareae** (Cardueae) (p. 123)
– Inner phyllaries otherwise **II. Mutisieae** (p. 90)
129. Pappus of at least some achenes at least in part of one or more conspicuous scabrid, barbellate, plumose or smooth capillary bristles as long as or longer than the corolla 171
– Pappus absent, rim-like, coroniform, auriculiform or of short to long and conspicuous free or variously connate scales (sometimes dissected distally into bristles), aristae or awns, devoid of conspicuous bristles at least as long as the corolla, or if bristles present, then these shorter than the corolla, inconspicuous and often caducous 130
130. Achenes with a phytomelanin layer in the pericarp, thus often black or streaked with black 131
– Achenes without a phytomelanin layer in pericarp, usually but not always not black 154
131. Leaves and/or phyllaries with pellucid glands or pustules, if without them, then plant a perennial herb with 3-seriate involucres with the outer phyllaries broad and herbaceous (Mexico, SE North America), or phyllaries succulent or achenes strongly 9–11-ribbed **XXII. Tageteae** (p. 420)
– Leaves and phyllaries without pellucid glands or pustules, plant and/or phyllaries and achenes otherwise, achenes mostly with 5 or fewer ribs 170
132. Pappus absent, or of a few teeth or awns, or of small scales and minute bristles and awns, or cupuliform or coroniform, but not of 3 or more conspicuous, often erose, plumose or lanciniate scales nor of numerous, sometimes erose awns 133
– Pappus of at least the disc florets of 3 or more conspicuous, often erose, plumose or lanceolate scales, sometimes dissected into bristles distally, or of numerous, sometimes erose awns 144
133. Pappus present 138
– Pappus absent 134
134. Leaves all or mostly alternate 135
– Leaves all opposite, or if alternate, then viscid, or glandular and achenes 4-angled 137
135. Capitula discoid **XXIII. Chaenactideae** (p. 431)
– Capitula radiate 136
136. Rays orange-yellow; receptacle flat to shallowly convex **XXIV. Bahieae** (p. 433)
– Rays yellow or white; receptacle convex to conical **XXVIII. Madieae** (p. 492)
137. Leaves sessile, clasping or shallowly to strongly perfoliate **XXVIII. Madieae** (p. 492)
– Leaves petiolate or if sessile, then not clasping nor perfoliate 142
138. Pappus of numerous scales, erose and fused at the base, ciliate or erose and free or lanceolate and laciniate and free 140
– Pappus of a few awns or scales or coroniform 139
139. Capitula disciform, or if radiate or discoid, then pappus of 2–3 awns fused to the wings of the achenes, or outer phyllaries 1/10th of the length of the inner, and inner enclosing the achenes **XXVI. Heliantheae** (p. 440)
– Capitula radiate, if discoid, then pappus and phyllaries otherwise; pappus of 1–2 pairs of opposite scales, of 2–4 bristles or awns and small scales, or a small corona of fimbriate scales 143
140. Pappus scales united at base, pappus shed as a unit **XXIII. Chaenactideae** (p. 431)
– Pappus scales free, persistent 141
141. Achenes obconical or obpyramidal, black or brown; disc florets usually numerous **XXI. Neurolaeneae** (p. 417)
– Achenes obovoid, terete and slightly flattened to quadrangular, black; disc florets 1–6 **XXVI. Heliantheae** (p. 440)
142. Leaves viscid, or glandular and achenes 4-angled **XXIX. Perityleae** (p. 507)
– Leaves not viscid, or if glandular, then achenes not 4-angled **XXVI. Heliantheae** (p. 440)
143. Capitula radiate; pappus of 1–2 pairs of opposite scales or of 2 (rarely 3–4) awns and small scales **XXVIII. Madieae** (p. 492)
– Capitula radiate or discoid; pappus of 4 scales alternating with bristles or a small corona of fimbriate scales **XXIX. Perityleae** (p. 507)
144. Pappus of 5–10 or many erose scales, fused at the base and deciduous as a unit **XXIII. Chaenactideae** (p. 431)
– Pappus of (2–)4 to many scales or awns, free and persistent, rarely fused at the base and persistent 145
145. Scales of pappus with thickened, often excurrent midrib **XXIV. Bahieae** (p. 433)
– Scales of pappus without prominent thickened midrib, or pappus of awns or of awns and scales 146
146. Scales and/or awns several (usually 4–10) 147
– Scales and/or awns numerous 150
147. Pappus of 2–4 opposite, erose scales or awns **XXVIII. Madieae** (p. 492)
– Pappus otherwise 148
148. Plant a rosulate perennial herb; disc florets functionally staminate; Cuba **XXI. Neurolaeneae** (p. 417)
– Plant an annual or non-rosulate perennial herb or shrub; disc florets perfect, rarely functionally staminate, or capitula discoid; New World 149
149. Leaves mostly alternate, entire to pinnately or deeply lobed **XXVIII. Madieae** (p. 492)
– Leaves opposite, if alternate, then leaves 1–3-pinnate with linear segments **XXIV. Bahieae** (p. 433)
150. Capitula discoid 151

– Capitula radiate or disciform 152
151. Leaves alternate **XXI. Neurolaeneae** (p. 417)
– Leaves opposite **XXI. Neurolaeneae** (p. 417) or **XXIV. Bahieae** (p. 433) or **XXVI. Heliantheae** (p. 440)[5]
152. Leaves opposite **XXI. Neurolaeneae** (p. 417) or **XXVI. Heliantheae** (p. 440)[5]
– Leaves all or mostly alternate 153
153. Achenes with large glands **XXVIII. Madieae** (p. 492)
– Achenes without large glands **XXI. Neurolaeneae** (p. 417)
154. Style arms with entire inner surface covered with stigmatic papillae 155
– Style arms with stigmatic papillae confined to two submarginal, distant to almost contiguous, distinct or apically confluent bands 159
155. Style shaft with an articulation below the bifurcation, marked by a ring of hairs and/or an increase in diameter, hairy above the articulation; style arms hairy or velvety dorsally, short to long and, when long, often not divergent for much of their length; leaves and/or phyllaries often spiny 158
– Style shaft without an articulation below the bifurcation, of uniform diameter, glabrous or hairy in upper part; leaves and phyllaries not spiny 156
156. Arms of style short, with hairs or papillae dorsally, style shaft glabrous; capitula disciform, few-flowered (temperate South America) or discoid, 1–3-flowered (E Asia) **II. Mutisieae** (p. 90)
– Arms of style usually long, with long sweeping hairs dorsally extending down shaft to below bifurcation; widespread 157
157. Capitula radiate; corollas usually yellow; leaves opposite; latex usually present; New World **VII. Liabeae** (p. 175)
– Capitula discoid; corollas never yellow; leaves alternate or rarely (Old World) opposite; latex usually absent; widespread **VI. Vernonieae** (p. 149)
158. Capitula radiate, rarely discoid; corollas usually yellow; tropical and S Africa **X. Arctotideae** (p. 200)
– Capitula discoid or radiant; if corollas yellow, then plant not African **III. Cynareae** (Cardueae) (p. 123)
159. Achenes large, terete, triquetrous or flattened, winged or wingless, straight to curved, glabrous, smooth or aculeate, sometimes fenestrate, homomorphic or heteromorphic, or fruits drupaceous; pappus absent; phyllaries herbaceous **XIII. Calenduleae** (p. 241)
– Achenes usually small, columnar, angled, terete or compressed, never fenestrate, usually but not always homomorphic, never drupaceous; pappus present or absent; phyllaries various 160
160. Style arms with an apical papillose appendage above the stigmatic bands, hairy dorsally below the appendage 161
– Style arms usually obtuse to truncate, rarely acute or with a much prolonged apex, hairy or papillose apically and/or dorsally, not appendaged 162
161. Receptacle strongly alveolate, alveolae forming aristate baskets or cups around achenes, or densely setose; achene epidermal cells with large, quadrate or isodiametric crystals **XIX. Helenieae** (p. 400)
– Receptacle alveolate or not, if alveolate, then alveolae not forming baskets or cups around achenes, nor densely setose; achene epidermal cells usually with raphides **XV. Astereae** (p. 284)
162. Disc floret corollas 4-lobed 163
– Disc floret corollas 5-lobed 164
163. Phyllaries rather dry and scarcely herbaceous, often with pale or brownish scarious margins and/or apices; style arms truncate, penicillate **XVI. Anthemidae** (p. 342)
– Phyllaries herbaceous or membranous; style arms short, acute to obtuse, apically papillose **XVIII. Athroismeae** (p. 395)
164. Capitula radiate 166
– Capitula disciform or discoid 165
165. Plant a perennial herb with alternate leaves, herbaceous 4–5-seriate phyllaries, zygomorphic peripheral florets, achenes with 4 strongly thickened ribs and pappus of basally fused scales; SW tropical Africa **XVIII. Athroismeae** (p. 395)
– Plant not with above combination of features 167
166. Phyllaries papery or cartilaginous; style arms truncate with apical hairs or obtuse with dorsal hairs; rays yellow or yellow with purple bands abaxially; pappus absent or of free scales; S Africa **XIV. Gnaphalieae** (p. 246)
– Phyllaries, style arms, rays and pappus not providing the above combination of features; widespread 167
167. Style arms more or less acute, with stigmatic papillae in two submarginal, rarely almost contiguous, apically confluent bands; style arms with acute sweeping hairs ending above the bifurcation or obtuse sweeping hairs extending down to below the bifurcation; phyllaries herbaceous **XVII. Inuleae** (p. 374)
– Style arms and phyllaries not with above combination of characters 168
168. Phyllaries papery or cartilaginous at least in part, hyaline, whitish, brownish or variously coloured, very rarely herbaceous; capitula discoid or disciform; style arms truncate, hairy apically, or rounded or with a much prolonged apex and hairy dorsally **XIV. Gnaphalieae** (p. 246)
– Phyllaries herbaceous, or rather dry and usually with scarious margins and/or apices; capitula radiate, discoid or disciform; style arms truncate, apically penicillate or with a tuft of papillae 169
169. Phyllaries herbaceous; cells of apical anther appendages heavily sclerified, appendages carinate; style arms with apical tuft of papillae **XIX. Helenieae** (p. 400)
– Phyllaries rather dry and scarcely herbaceous, usually with scarious margins and/or apices; cells of anther appendages not sclerified, appendages soft, flat; style arms penicillate **XVI. Anthemideae** (p. 342)
170. Capitula discoid, although rarely abaxial lobes of marginal floret corollas enlarged and ray-like; corollas never yellow; style arm appendages usually much longer than the stigmatic bands, prominent, lanceolate to clavate **XXX. Eupatorieae** (p. 510)
– Capitula radiate, disciform or discoid; corollas often yellow; style arm appendages usually shorter than stigmatic bands or style arms unappendaged 132

[5] See also key to the Heliantheae alliance tribes, p. 391

171. Achenes with a phytomelanin layer in the pericarp, therefore often black or streaked with black 189
– Achenes without a phytomelanin layer in the pericarp, not black or if black, then for some other reason 172
172. Style shaft with an articulation below the bifurcation, marked by a ring of hairs and/or an increase in diameter, usually hairy or papillose above the articulation; style arms with hairs or papillae dorsally, with stigmatic papillae covering the whole inner surface, sometimes long and united for most of their length; capitula homogamous, radiant or radiate 177
– Style shaft uniform in diameter below the bifurcation or rarely somewhat narrowed in upper part, without an articulation, glabrous or with sweeping hairs in upper part below the bifurcation; capitula never radiant 173
173. Style arms usually long, with long sweeping hairs dorsally extending down shaft below the bifurcation, unappendaged; stigmatic papillae covering entire inner surface of style arms 174
– Style arm and shaft characters otherwise; style arms unappendaged or appendaged, with stigmatic papillae over entire inner surface or more usually confined to two submarginal bands 178
174. Leaves opposite; South America **VII. Liabeae** (p. 175)
– Leaves alternate; Old and New Worlds 175
175. Corollas not yellow, or if of some shade of yellow, then leaves triplinerved; capitula discoid; widespread **VI. Vernonieae** (p. 149)
– Corollas yellow; leaves pinnately veined; capitula discoid or radiate; Old World 176
176. Capitula radiate or discoid, sessile; leaves dentate-spinulate, spine-tipped; S Africa **X. Arctotideae** (p. 200)
– Capitula discoid, pendunculate; leaves dentate-lobulate, unarmed; NW Africa **IX. Gundelieae** (p. 199)
177. Capitula radiate; S Africa **X. Arctotideae** (p. 200)
– Capitula discoid or radiant 182
178. Stigmatic papillae covering whole of inner surface of style arms 184
– Stigmatic papillae confined to two free or apically confluent, distant to almost contiguous submarginal bands 179
179. Style arms ending in a sterile appendage above the stigmatic bands 183
– Style arms unappendaged, although sometimes ending in a more or less conical tuft of papillae or hairs, apex acute, obtuse or truncate 180
180. Anther appendages carinate, with cells strongly sclerified; North America **XIX. Helenieae** (p. 400)
– Anther appendages flat, soft, cells not sclerified; widespread 181
181. Phyllaries with broad, pale to dark brown or black scarious margins; C Asia **XVI. Anthemideae** (p. 342)
– Phyllaries without broad scarious margins, although sometimes wholly or partly papery or cartilaginous, often herbaceous 185
182. Capitula numerous, in inflorescences with densely racemose branches; shrub; leaves not spiny; Brazil **V. Moquinieae** (p. 148)
– Capitula variously arranged, but not in inflorescences with densely racemose branches; habit various, usually herbaceous, rarely shrubby; leaves spiny or unarmed; Old World, if not Old World, then not Brazil **III. Cynareae** (Cardueae) (p. 123)
183. Plant a broom-like shrub or treelet with small, yellow, discoid capitula and sagittate or caudate anther bases; SW North America, Mexico **XII. Senecioneae** (p. 208)
– Plant of various habit; capitula discoid, radiate or disciform, yellow or not; anther bases commonly rounded or truncate, rarely caudate; worldwide **XV. Astereae** (p. 284)
184. Capitula discoid, or if radiate, then rays red; corolla-lobes much longer than wide; anther bases strongly tailed **II. Mutisieae** (p. 90)
– Capitula radiate, with yellow rays, if discoid, corollas yellow, lobes about as long as wide; anther bases not tailed **XII. Senecioneae** (p. 208)
185. Phyllaries papery or cartilaginous at least in part, hyaline, white, brownish or variously coloured, often yellow or pink; style arms truncate and hairy apically, or rounded or with a much prolonged apex and hairy dorsally and apically; stigmatic bands not confluent apically **XIV. Gnaphalieae** (p. 246)
– Phyllaries usually herbaceous and green, style arms apically conical, rounded, obtuse, acute or truncate, with hairs or papillae apically or dorsally and sometimes extending downwards on to shaft below the bifurcation; stigmatic bands confluent or not confluent apically 186
186. Stigmatic bands apically confluent; style arms more or less acute, with usually acute sweeping hairs dorsally ending above the bifurcation, or usually obtuse sweeping hairs extending to below the bifurcation 187
– Stigmatic bands distant, not confluent apically; style arms apically conical, obtuse or truncate; sweeping hairs otherwise distributed **XII. Senecioneae** (p. 208)
187. Plant a scandent shrub; Cuba **XVII. Inuleae 1137. *Feddea*** (p. 390)
– Plant a herb, subshrub, non-scandent shrub or tree 188
188. Pappus purple, of numerous uniseriate barbellate bristles, bristles in staminate florets shorter and apically slightly dilated; corolla externally with robust, acute, multicellular hairs; Sinohimalaya **165. *Cavea*** (p. 146)
– Pappus otherwise, not purple; corollas without such hairs; widespread **XVII. Inuleae** (p. 374)
189. Capitula discoid, although rarely abaxial lobes of peripheral floret corollas enlarged and ray-like; corollas never yellow; style arm appendages usually much longer than the stigmatic bands, prominent, lanceolate to clavate **XXX. Eupatorieae** (p. 510)
– Capitula radiate, disciform or discoid; corollas often yellow; style arm appendages usually shorter than stigmatic bands or style arms unappendaged 190
190. Leaves and/or phyllaries with pellucid glands or pustules, if without them, then plant a perennial herb with 2–3-seriate involucres with the outer phyllaries broad and herbaceous (Mexico, SE North America) or achenes 9–10-ribbed and leaves succulent, opposite, or if alternate, then receptacle setose **XXII. Tageteae** (p. 420)
– Leaves and phyllaries without pellucid glands or pustules; plant and/or phyllary and achene features otherwise, achenes usually with 5 or fewer ribs 191

191. Achenes 4–5-angled, cylindrical to obconical 193
– Achenes tangentially or radially flattened 192
192. Plant an annual herb; achenes tangentially flattened, without wings or corky ciliate margin; disc floret corollas 5-lobed **XXIV. Bahieae** (p. 433)
– Plant a shrub or perennial or annual herb; achenes tangentially or radially flattened, with wings or a well-developed corky, ciliate margin; disc floret corollas 4- or 5-lobed **XXIX. Perityleae** (p. 507)
193. Pappus of 4 scales alternating with 4 bristles **XXIX. Perityleae** (p. 507)
– Pappus of numerous bristles 194
194. Phyllaries 2–3-seriate and subequal or 3–5-seriate and gradate **XXIV. Bahieae** (p. 433)
– Phyllaries (1–)2-seriate, outer herbaceous and each opposite a ray floret, inner membranous or absent **XXVIII. Madieae** (p. 492)

I. Tribe Barnadesieae D. Don (1830).

T.F. Stuessy and E. Urtubey

Shrubs, trees, or perennial or annual herbs. Stems erect or decumbent, with or without axillary spines. Basal leaves sometimes rosulate. Cauline leaves alternate, fasciculate, opposite or whorled, often with spinescent apex, sessile to petiolate, entire, often xeromorphic. Synflorescences solitary or aggregated (cymose-racemose or cymose-corymbose heads). Involucre campanulate, cylindrical, turbinate or hemispherical; phyllaries in 4–14-series, frequently apically spinulose, velutinous to glabrous. Receptacle pilose, rarely with pales or glabrous. Capitula homogamous or heterogamous, discoid, pseudoradiate or ligulate. Florets 1–c. 135, white, yellow, orange, pink, purple to violet, isomorphic, generally hermaphrodite or sometimes unisexual or with only marginal florets unisexual; corolla 5-merous, actinomorphic or zygomorphic (pseudobilabiate, bilabiate, subpseudobilabiate, ligulate or subligulate), or anisomorphic, with marginal flowers hermaphrodite (with pseudobilabiate 1/4 corollas), and with central flowers hermaphrodite or unisexual (with actinomorphic or zygomorphic, i.e. pseudobilabiate, bilabiate, ligulate or subligulate, corollas), often villous. Anthers ecaudate to tailed; apical appendage entire, emarginate or bilobed; filaments free or connate, inserted at apex or base of corolla (rarely in between), Style shortly bilobed or bifid, glabrous or papillose below bifurcation. Achenes villous ("barnadesioid hairs"), rarely only at the apex. Pappus often plumose, sometimes scaly, barbellate or setaceous. Pollen with or without depressions, microechinate, scabrate-microechinate, granulate (sparsely microechinate), spinulate, smooth, or rarely lophate. $2n$ = 16, 48, 50, 54, 100, 108.

Exclusively South American, in the Andes from Venezuela to Patagonia in Argentina, in central Chile and eastwards into Brazil. Nine genera and 91 species.

Key to the Genera

1. Herbs 2
– Subshrubs, shrubs or trees 4
2. Plants erect; leaves long and strap-shaped, hairy **1. *Schlechtendalia***
– Plants spreading; leaves various 3
3. Pappus plumose **2. *Doniophyton***
– Pappus scaly, ciliate **3. *Duseniella***
4. Capitula one-flowered **4. *Fulcaldea***
– Capitula with more than one flower 5
5. Capitula heteromorphic; pollen lophate 6
– Capitula isomorphic; pollen various 7
6. Shrubs or trees, 0.6–20 m tall; spiny **5. *Barnadesia***
– Subshrubs to 5 cm tall; unarmed **6. *Huarpea***
7. Apical appendage emarginate or bilobed **7. *Dasyphyllum***
– Apical appendage entire 8
8. Corollas pseudobilabiate (1/4); stamens inserted on throat of corolla tube **8. *Arnaldoa***
– Corollas tubular, rarely pseudobilabiate or pseudoligulate; stamens inserted at base of corolla tube **9. *Chuquiraga***

Genera of Barnadesieae

1. *Schlechtendalia* Less. Fig. 15A–E

Schlechtendalia Less., Linnaea 5: 242 (1830), nom. cons.

Perennial herbs, unarmed, to 1 m. Leaves basally rosulate, on stems opposite, linear, sessile, amplexicaul, at apex mucronate, entire, parallel-nerved with numerous nerves. Capitula homogamous, discoid, pedunculate, in racemose or cymose clusters. Involucre hemispherical, c. 5-seriate. Receptacle flat, pilose. Florets numerous, yellow, isomorphic, hermaphrodite; corollas 5-merous, pseudobilabiate (1/4), pilose. Stamens inserted near base of corolla; filaments free; anthers shortly sagittate, with apical appendage entire. Styles bifid, papillose below bifurcation. Achenes turbinate, villous. Pappus plumose. Pollen with 1 depression per mesocolpus, microgranulate, sparsely microechinate. $2n$ = 16. One species, *S. luzulaefolia* Less., endemic to Brazil, Uruguay and Argentina.

2. *Doniophyton* Wedd. Fig. 15F–J

Doniophyton Wedd., Chloris Andina 1: 7, 8 (1855); Katinas & Stuessy, Pl. Syst. Evol. 206: 33–45 (1997), rev.

Chuquiraga Juss. "*anomale*" DC. (1838).
Chuquiraga Juss. sect. *Gymnophoranta* Remy (1848).

Herbs with some secondary growth, 2.5–8 cm. Stems ascendent or decumbent, fasciculate spines present or absent. Leaves alternate, sessile, linear to linear-lanceolate, at apex spiny, entire, 1-nerved, involute or plicate. Capitula heterogamous, discoid, sessile, solitary. Involucre hemispherical to campanulate, 4–5-seriate. Receptacle flat or convex, pilose. Florets 40–135, yellow, isomorphic; corollas 5-merous, tubular, pilose. Marginal florets female. Central florets hermaphrodite. Stamens inserted at base of corolla tube; filaments free; anthers long-sagittate, with apical appendage entire. Style shortly bifid, papillose below bifurcation. Achenes turbinate, densely villous. Pappus plumose. Pollen without depressions, scabrate-microechinate. $2n = 48$, 50. Two species in northern Chile and Patagonian Argentina.

3. ***Duseniella*** K. Schum. Fig. 15K–O

Duseniella K. Schum., Just's Bot. Jahresber. 28, 1: 475 (1902).

Annual herbs, unarmed, to 10 cm. Leaves basally opposite, becoming alternate further up, sessile, linear to linear-lanceolate, at apex mucronate, entire, 3-nerved. Capitula heterogamous, discoid, sessile, solitary. Involucre campanulate, c. 4-seriate. Receptacle convex, naked. Florets 30–35, yellow, isomorphic, corollas 5-merous, tubular, pilose. Marginal flowers female. Central flowers hermaphrodite. Stamens inserted near base of corolla; filaments free; anthers long-sagittate, with apical appendage entire. Style bifid, papillose below bifurcation. Achenes cylindrical, villous. Pappus scaly, ciliate. Pollen without depressions, microechinate. One species, *D. patagonica* K. Schum., endemic to Patagonian Argentina.

4. ***Fulcaldea*** Poir. ex Lam.

Fulcaldea Poir. ex Lam., Encycl. Meth. Bot. suppl. 5: 375 (1817).

Shrubs or small trees, 3–4 m. Stems erect, spiny. Leaves alternate, petiolate, elliptic, at apex spiny, entire, glabrous, 3-nerved. Capitula one-flowered, sessile, in corymbose cymes. Involucre cylindrical, 5–7-seriate. Receptacle flat, pilose. Florets violet or white, hermaphrodite; corolla 5-merous, tubular, pilose. Stamens 5, inserted between throat and base of corolla; filaments free; anthers obtuse, with

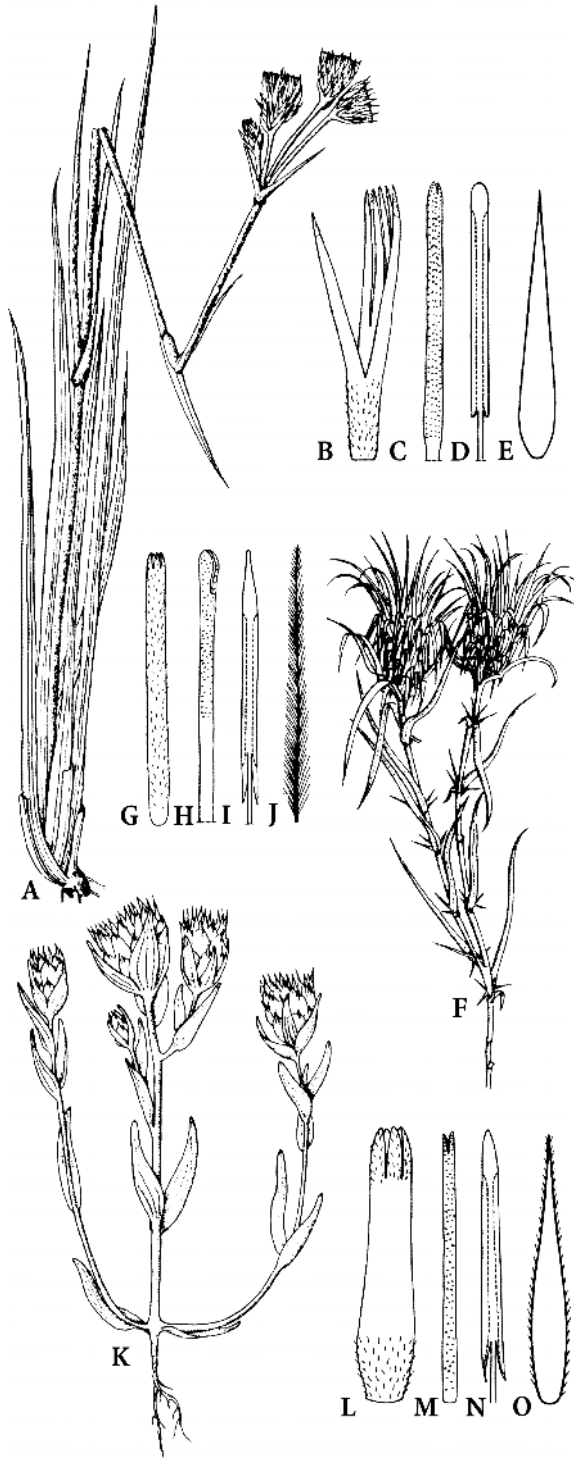

Fig. 15. Compositae-Barnadesieae. **A–E** *Schlechtendalia luzulaefolia*. **A** Habit. **B** Pseudobilabiate corolla. **C** Style. **D** Shortly sagittate anther. **E** Lanceolate pappus trichome. **F–J** *Doniophyton anomalum*. **F** Habit. **G** Tubular corolla. **H** Style. **I** Long sagittate anther. **J** Plumose pappus trichome. **K–O** *Duseniella patagonica*. **K** Habit. **L** Tubular corolla. **M** Style. **N** Long sagittate anther. **O** Lanceolate pappus trichome

apical appendage entire. Style shortly bifid, papillose and distinctly swollen below lobes. Achenes cylindrical, villous. Pappus plumose. Pollen without depressions, spinulose. One species, *F. laurifolia* Poir. ex Lam., endemic to southern Ecuador and north-western Peru.

5. ***Barnadesia*** Mutis Fig. 16A–K

Barnadesia Mutis in L. f., Suppl. Pl. 55 (1782); Urtubey, Ann. Missouri Bot. Gard. 86: 57–117 (1999), rev.
Bacasia Ruiz & Pav. (1794).
Diacantha Less. (1830), non Lag. (1811).
Penthea (D. Don) Spach (1841), non Lindl. (1838).

Shrubs or trees, 0.6–20 m. Stems erect, spiny. Leaves alternate or fascicled, sessile to petiolate, ovate, elliptic to obovate, at apex mucronate or spinescent, at base usually obtuse, entire, 1- or 3-nerved. Capitula heterogamous or homogamous, pseudoradiate, sessile or pedunculate, solitary or in cymose aggregates. Involucre campanulate, turbinate or cylindrical, 6–14-seriate. Receptacle flat, pilose. Florets 9 or 16, pink, red, purple, rarely white, iso- or 2–3-morphic, hermaphrodite or unisexual. Stamens inserted on throat (or rarely at base of corolla tube or between throat and base of corolla tube); filaments free or fused; anthers obtuse or bulging, with apical appendage entire. Style bilobed, smooth below bifurcation. Achenes turbinate or cylindrical, villous. Marginal florets 8 or 13, hermaphrodite; corollas pseudobilabiate (1/4). Stamens 5. Pappus plumose. Central florets 1 or 3, iso- or anisomorphic, hermaphrodite or unisexual; corollas tubular (3, 5-merous), pseudobilabiate (1/4), bilabiate (1/3 or rarely 2/3), subligulate or ligulate (0/5). Stamens 3–5. Pappus plumose, barbellate or setaceous. Pollen lophate, radially symmetric or asymmetric, smooth. $2n$ = 50, 100. Nineteen species distributed from the eastern Andes in Colombia southwards into north-western Argentina and south-eastern Brazil.

6. ***Huarpea*** Cabrera

Huarpea Cabrera, Bol. Soc. Argent. Bot. 4, 1/2: 129 (1951).

Subshrubs, unarmed, c. 5 cm. Leaves alternate, subrosulate, sessile, amplexicaul, linear, at apex spiny, entire, 1-nerved, revolute, xeromorphic. Capitula heterogamous, sessile, solitary. Involucre cylindric-campanulate, c. 4-seriate. Receptacle flat, pilose. Florets 6, white, dimorphic, 5-merous. Marginal florets 5, hermaphrodite; corollas pseudobilabiate (1/4). Central flower 1, male; corolla

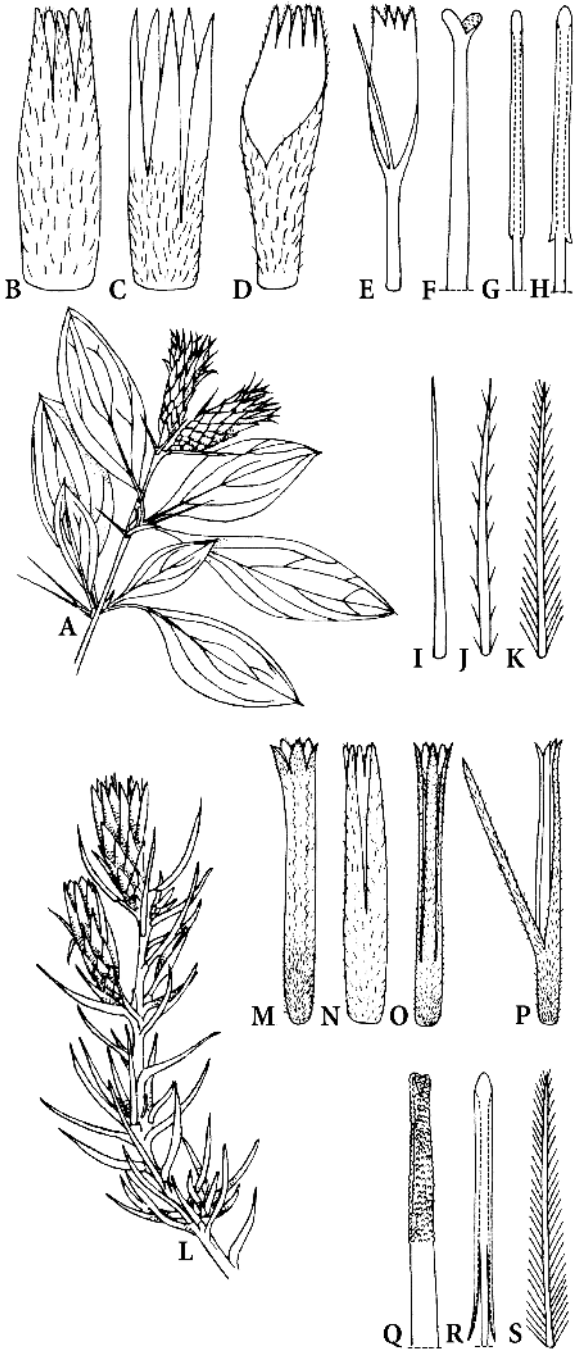

Fig. 16. Compositae-Barnadesieae. **A–K** *Barnadesia odorata*. **A** Habit. **B** Tubular corolla. **C** Subligulate corolla. **D** Ligulate corolla. **E** Pseudobilabiate corolla. **F** Style. **G** Anther. **H** Shortly sagittate anther. **I** Simple pappus trichome. **J** Barbellate pappus trichome. **K** Plumose pappus trichome. **L–S** *Chuquiraga erinacea* var. *erinacea*. **L** Habit. **M** Tubular corolla. **N** Subligulate corolla. **O** Subpseudobilabiate corolla. **P** Pseudobilabiate corolla. **Q** Style. **R** Long sagittate anther. **S** Plumose pappus trichome

tubular. Filaments of stamens free; anthers obtuse or shortly sagittate, with entire apical appendage. Style bilobed, smooth below bifurcation. Achenes turbinate or cylindrical. Pappus plumose (central florets with a single villous bristle or without pappus). Pollen lophate, radially symmetrical, smooth. One species, *H. andina* Cabrera, endemic to San Juan Province of Argentina.

7. *Dasyphyllum* Kunth

Dasyphyllum Kunth in Humb., Bonpl. &. Kunth, Nova Gen. Sp. ed. folio 4: 13, tab. 308 (1818); Cabrera, Revista Mus. La Plata, secc. Bot. 9: 21–100 (1959), rev.
Flotovia Spreng. (1826).
Chuquiraga sect. *Erinesa* D. Don (1830).
Piptocarpha Hook. & Arn. (1835).
Flotowia Endlicher (1838).

Shrubs or trees, 0.5–20 m. Stems erect or decumbent, with or without spines. Leaves alternate, fasciculate or whorled, sessile to petiolate, ovate, elliptic to obovate, at apex mucronate or spiny, entire, 1- or 3-nerved. Capitula homogamous or heterogamous, discoid, sessile or pedunculate, solitary, glomerate, cymose or racemose. Involucre campanulate, turbinate or cylindrical, 6–14-seriate. Receptacle flat, pilose, sometimes with paleae. Florets 6–90, white to yellowish, isomorphic, hermaphrodite or unisexual; corollas 5-merous, tubular, pseudobilabiate (1/4), subpseudobilabiate, rarely bilabiate (2/3), subligulate or ligulate, pilose, rarely glabrous. Stamens inserted on throat or near base of corolla tube; filaments free; anthers sagittate, with apical appendage emarginate or bilobed. Style bifid, papillose (rarely hairy) below bifurcation. Achenes turbinate or cylindrical, villous, rarely glabrous. Pappus plumose. Pollen with 3–23 depressions (rarely lacking), sparsely microechinate. Forty species, distributed from Venezuela south to Chile and Argentina and eastwards to Brazil.

8. *Arnaldoa* Cabrera

Arnaldoa Cabrera, Bol. Soc. Argent. Bot. 10: 21–45 (1962); Sagástegui Alva & Stuessy, Arnaldoa 1: 9–21 (1993), rev.

Shrubs, 1–4 m. Stems erect, with axillary spines. Leaves alternate, shortly petiolate, ovate, elliptic or obovate, at apex mucronate or spiny, at base attenuate or obtuse, entire, 3-nerved. Capitula homogamous, discoid, sessile, solitary. Involucre campanulate, 8–15-seriate. Receptacle flat, pilose. Florets 30–95, cream-white, light orange to orange or purple, isomorphic, hermaphrodite; corollas pseudobilabiate (1/4). Stamens inserted on the throat of the corolla tube; filaments free, with or without barnadesioid hairs; anthers sagittate, with apical appendage entire. Style bifid, papillate bellow bifurcation. Achenes turbinate or cylindric, densely hirsute. Pappus plumose. Pollen with 4 paraporal depressions for mesocolpi, microechinate. $2n = 48$, 54. Three species endemic to northern Peru and southern Ecuador, in xerophytic habitats.

9. *Chuquiraga* Juss. Fig. 16L–S

Chuquiraga Juss., Gen. Pl.: 178 (1789); Ezcurra, Darwiniana 26: 219–284 (1985), rev.
Johannia Willd. (1803).
Joannesia Pers. (1807), orth. var.
Joannea Spreng. (1818), orth. var.

Intricately branched shrubs, 0.25–2 m. Stems erect or compressed into cushions, often spiny. Leaves alternate, opposite, whorled or fasciculate, sessile, ovate, linear to obovate, at apex spiny; 1- or 3-nerved, flat or revolute, xeromorphic. Capitula homogamous, discoid, sessile, solitary. Involucre campanulate, turbinate or cylindrical, 4–8(–12)-seriate. Receptacle alveolate, pilose. Florets 5–100, yellow to orange, isomorphic, hermaphrodite; corollas 5-merous, tubular, rarely pseudobilabiate (1/4), subpseudobilabiate or subligulate, pilose. Stamens inserted at base of corolla tube; filaments free; anthers sagittate, with apical appendage entire. Style bifid, papillate bellow bifurcation. Achenes turbinate, villous. Pappus plumose. Pollen without depressions, microechinate. $2n = 54$, 108. Twenty-three species from the Andes of Colombia south into Argentina and Chile, frequently in xeromorphic habitats.

II. Tribe Mutisieae Cass. (1819).

D.J.N. Hind

Herbs, subshrubs, shrubs, trees, rarely climbers or ramblers, glabrous or with simple, glandular, malpighiaceous or stellate hairs, often glabrescent. Leaves usually evenly spaced, sometimes rosulate or densely spiralled, usually alternate, rarely opposite, lamina simple, variously shaped, usually herbaceous, venation trinervate, pinnate, sometimes parallel or very rarely palmate, margins entire or lobed, serrate or denticulate, rarely spiny or pinnatisect, lamina rarely pinnate or impar-

ipinnate with a simple or branched tendril. Inflorescences scapose or scapiform, cymose or of corymbose or paniculate, axillary or terminal clusters, sometimes of glomerules, very rarely of true syncalathia. Capitula small to very large, usually chasmogamous, very rarely cleistomagous, usually monoecious, homogamous or heterogamous, radiate, very rarely ligulate, rarely disciform or discoid, one- to many-flowered; involucres cylindrical to globular or urceolate; phyllaries imbricate, few- to many-seriate, sometimes uniseriate, rarely calyculate, rarely distant, usually gradate, often chartaceous or herbaceous, usually homomorphic; receptacles flat, convex or rarely conical, scrobiculate, foveolate, fimbrillate or alveolate, glabrous or variously pubescent, usually epaleaceous. Florets rarely all actinomorphic, usually marginal and disc florets distinct; marginal florets usually variously bilabiate (2/3) or pseudobilabiate (1/4), and often distinctly rayed, sometimes ligulate (0/5), hermaphrodite, female or neuter, corollas glabrous or variously pubescent; staminodes rarely present; disc florets usually bilabiate (2/3), sometimes actinomorphic (5/0), usually fertile; corollas glabrous or variously pubescent, lobes short or long. Stamens usually conspicuously exserted from corolla; filaments glabrous or rarely pubescent or papillate, collars inconspicuous or sometimes distinct and variously enlarged or flattened; anther appendages usually acuminate or apiculate and several times as long as wide, sometimes thickened at apex and knob-like, sometimes truncate or rounded; anthers calcarate and caudate, rarely ecalcarate, tails usually long-acute, entire or variously laciniate, sometimes conspicuously branched or pilose. Pollen tricolporate, exine tectate, perforate, psilate, spinulose or echinate, tectum poorly differentiated or with distinct columellae. Styles usually well exserted from corolla and anther cylinder; style base sometimes with conspicuous nectary, with or without distinctive basal node, glabrous, style shaft usually glabrous, rarely papillose in upper part, style arms usually relatively short, apices acute, obtuse to rounded, or (Nassauviinae) truncate and usually penicillate, often with a lip around inner margins, usually apically pilose, hairs acute or obtuse to rounded. Achenes fusiform or sometimes distinctly beaked, terete, ribbed or angled or very rarely flattened, glabrous or variously setuliferous, commonly with twin-hairs, or rarely tomentose with long tortuous hairs, or appearing papillate, very rarely with stalked and sticky glands (*Adenocaulon*); carpopodium sometimes absent, more usually a narrow annulus, sometimes cylindrical; pappus sometimes absent but usually of uniseriate, sometimes biseriate to multiseriate, simple, barbellate, subplumose or plumose bristles, sometimes flattened or scale-like, persistent or deciduous, separate or sometimes basally connate.

Eighty-two genera with more than 950 species, most in South America but also in North America, Africa/Madagascar and Asia; one genus in Australia.

Panero and Funk (2002) placed several genera of Mutisieae into separate tribes and subfamilies. This treatment is not recognized here.

Classification of Mutisieae s. l.

1. Stifftia group
   Genera 10–12
2. Stenopadus group
   Genera 13–23
3. Subtribe Nassauviinae
   Genera 24–47
   Problematic placement (probably within Nassauviinae)
   Genera 48–49
4. Subtribe Mutisiinae
   Genera 50–65
5. Subtribe Gerberinae
   Genera 66–72
6. Subtribe Gochnatiinae
   Genera 73–75
7. Hecastocleis group
   Genus 76
8. Nouelia group
   Genera 77–78
9. Catamixis group
   Genus 79
10. Subtribe Tarchonanthinae
    Genera 80–81
11. Dicoma group
    Genera 82–87
12. Pertya group
    Genera 88–91

Key to the Genera

1. All capitula ligulate, or rarely with mixtures of ligulate and bilabiate florets in one capitulum as well as ligulate capitula on one plant 2
– Capitula containing actinomorphic, bilabiate, or pseudobilabiate florets, or mixtures thereof 4
2. Corollas red; leaves buff-tomentose beneath; Guyana Highlands **14. *Glossarion* (*G. rhodanthum*)**
– Corollas cream or yellow; leaves glabrous, glabrescent or arachnoid pubescent; Argentina and Bolivia or Himalayas 3
3. Achenes glabrous or with moderately long setulae and stipitate-glandular; style arms long; capitula few to several in terminal or axillary clusters or solitary and terminal; leaves usually opposite (sometimes fasci-

culate on axillary brachyblasts); phyllaries yellow; pappus setae few-seriate; Argentina and Bolivia **11. *Hyaloseris***

– Achenes densely long-setuliferous and appearing sericeous; style arms short; capitula numerous in large terminal corymbs; leaves alternate; phyllaries greenish often with purplish apices; pappus setae uniseriate; western Himalayas, India **79. *Catamixis***

4. Style arm apices flattened (subtribe **Tarchonanthinae**) 5
– Style arm apices cylindrical or swollen 6
5. Pappus absent; capitula usually hemispherical or globular **81. *Tarchonanthus***
– Pappus present; capitula turbinate or campanulate **80. *Brachylaena***
6. Receptacles entirely (or partially) paleaceous 7
– Receptacles epaleaceous 15
7. Pappus absent (or reduced to a few (3–5) caducous flattened setae); achene setulae basally forked twin-hairs **85. *Erythrocephalum***
– Pappus of capillary, or flattened, barbellate or plumose setae (rarely absent on central achenes); achene setulae, when present, twin-hairs (apices connate or forked) 8
8. Florets all actinomorphic; style arm apices acute or obtuse 9
– Florets all bilabiate; style arm apices truncate (subtribe **Nassauviinae** p.p.) 11
9. Corollas magenta, sometimes with golden lobes **21. *Stenopadus***
– Corollas cream to yellowish 10
10. Corollas glabrous; pappus setae subpaleaceous with margins densely plumose towards apices, straw-coloured; corolla lobes tightly coiled; Brazil (Bahia and Goías southwards) **12. *Wunderlichia***
– Corollas with dense tufts of hairs at bases of sinuses of lobes; pappus setae flattened with barbellate margins, cream-coloured; corolla lobes erect or slightly recurved; Guyana Highlands **20. *Stomatochaeta***
11. Leaves linear, margins strongly revolute, entire; corollas yellow; pappus biseriate **37. *Pleocarphus***
– Leaves lanceolate, ovate or orbicular, margins flat, entire, lobed or pinnatisect, sometimes spiny; corollas white, pink, purple, rarely yellow; pappus setae uniseriate 12
12. Leaves reduced to spiny segments **29. *Oxyphyllum***
– Leaves with relatively broad, unarmed lamina 13
13. Leaves (at least lower) sessile **43. *Marticorenia***
– Leaves usually distinctly petiolate 14
14. Leaf margins pinnatisect; florets 2 per capitulum; phyllaries biseriate, outer foliaceous; annual herbs **46. *Moscharia***
– Leaf margins entire or lobed; florets few to many per capitulum; phyllaries uniseriate, sometimes with an outer calyculus, never foliaceous; perennial herbs, shrubs or lianes **36. *Jungia***
15. Style arms truncate or rarely rounded; style hairs obtuse to rounded (subtribe **Nassauviinae** p.p.) 16
– Style arms acute or obtuse; style hairs mostly acute 37
16. Achenes epappose 17
– Achenes pappose 20
17. Achenes rostrate; inflorescences scapiform, capitula usually solitary; receptacle pubescent **47. *Cephalopappus***
– Achenes erostrate; inflorescences lax cymes, corymbs, panicles or capitula solitary, axillary; receptacle glabrous 18
18. Achenes (of female florets) conspicuously stipitate-glandular (of male florets, glandular) **48. *Adenocaulon***
– Achenes glabrous, sparsely papillose or densely lanose 19
19. Corollas bilabiate; annual herbs; leaves petiolate, leaf bases not amplexicaul; inflorescences lax few-headed corymbs; all florets hermaphrodite and fertile **45. *Pamphalea***
– Corollas actinomorphic, 5-lobed; perennial rhizomatous herbs; leaves sessile and pseudopetiolate, leaf bases amplexicaul; inflorescences solitary axillary capitula; marginal florets female, disc florets hermaphrodite and functionally male **49. *Eriachaenium***
20. Inflorescence scapiform (or with few capitula) and arising from a basal rosette of leaves 21
– Inflorescences glomerules, cymes, panicles or capitula solitary, terminal on leafy stems 22
21. Leaf bases vaginate about scape; corollas white; pappus setae plumose **30. *Macrachaenium***
– Leaf bases clasping stem but not vaginate; corollas orange; pappus setae coarsely barbellate **41. *Criscia***
22. Inflorescences glomerules 23
– Inflorescences cymes, corymbs, panicles or capitula solitary 25
23. Pappus of coarse setae; leaf lamina pinnately lobed or pinnatisect, margins unarmed, arachnoid or tomentose; capitula 2-(rarely 3-)flowered **31. *Polyachyrus***
– Pappus of caducous scales; leaf lamina entire or pinnatisect with denticulate spiny margins, or with few long spines; capitula 3–6-flowered 24
24. Pappus scales linear or with broad flattened rachis, margins ciliate to plumose; corollas white or rarely violet or yellowish **27. *Nassauvia***
– Pappus scales apically lacerate-plumose; corollas white or blue, often both on same plant **28. *Triptilion***
25. Pappus of caducous scales **27. *Nassauvia***
– Pappus setae capillary or broadened at base 26
26. Receptacles always glabrous 27
– Receptacles usually pubescent (with hairs or papillae) 30
27. Annual or perennial rosulate herbs; corollas white, pink, lilac or purple 28
– Low shrubs; corollas yellow 29
28. Pappus setae biseriate, capillary, barbellate; corollas white **44. *Holocheilus***
– Pappus setae usually uniseriate, flattened and broadened at base, barbellate or plumose; corollas white, pink, lilac or purple **35. *Leucheria***
29. Achenes with stipitate-glandular beak; leaves pinnatisect, sparsely to moderately stipitate-glandular; capitula large and on elongated pedicels **39. *Dolichlasium***
– Achenes cylindrical and lacking stipitate-glandular setulae; leaves coarsely dentate and glandular-punctate; capitula relatively small and short-pedicellate **40. *Ameghinoa***
30. Stems armed either with pairs of recurved spines at nodes or with spines terminating branches or axes of inflorescences 31
– Stems and inflorescence axes completely unarmed 32

31. Clambering woody vine-like plants; stems bearing a pair of recurved persistent spines at each node; inflorescences axillary cymes; corollas yellow; Greater Antilles **25. *Berylsimpsonia***
– Stems and side branches often terminating in a spine, but otherwise unarmed; inflorescences racemes or panicles; corollas pink or purple; Argentina, Bolivia, Chile, Peru **24. *Proustia***
32. Densely caespitose dwarf shrubs; leaves acicular with expanded bases, margins highly revolute; Argentina (Patagonia) **34. *Burkartia***
– Herbs, subshrubs, shrubs or small trees; leaves with relatively broad lamina, ovate, broadly ovate, oblanceolate, spathulate, cordate or lyrate-pinnatifid 33
33. Rosettiform sometimes caespitose herbs, rarely tall and leafy; inflorescences solitary and sessile in leaf rosette, scapiform with solitary or few capitula or few-headed panicles; stem leaves, if present, sessile and amplexicaul but never decurrent; corollas blue, purple, violet, red, or crimson, sometimes yellow, but rarely white or cream **32. *Perezia***
– Subshrubs, shrubs (sometimes scandent or trailing) or small trees or, if herbaceous, then inflorescences corymbose and stem winged or with decurrent based leaves 34
34. Corollas typically pinkish light purple or purple, rarely white; subshrubs (stems with basal rosette of leaves, appearing scapiform) or densely leafy scandent shrubs; style arms > 1 mm long with rounded apices **33. *Acourtia***
– Corollas white, yellow or orangish; non-scapiform subshrubs, laxly leafy scandent shrubs or often densely leafy shrubs; style arms < 1 mm long and rounded or > 1 mm long and truncate or if > 1 mm long and rounded, then capitula solitary, large and terminal 35
35. Low subshrubs; inflorescence large terminal solitary capitula; leaves and phyllaries with excentrically branched 'T'-shaped and stipitate-glandular hairs; phyllaries biseriate and almost distant; anther cylinder exserted from corolla throat; pappus setae broadened at base and often branched, off-white; Chile **42. *Leunisia***
– Herbs, subshrubs, scandent or trailing shrubs or small trees and, if subshrubs, then capitula never large nor solitary; leaves and phyllaries glabrous or with flagellate eglandular and stipitate-glandular hairs; phyllaries (1–)2–5-seriate and usually imbricate; anther cylinder only partially exserted from corolla throat; pappus setae of ± uniform diameter and simple, white, straw-coloured, yellowish or reddish 36
36. Inflorescences usually terminal cymes, corymbs or panicles, sometimes pseudoglomerules; style arms > 1 mm long, apices truncate; receptacle pilose or densely long-pubescent; corollas yellow, orange or rarely white, variously pubescent or sometimes glabrous; pappus setae 2–3(–4)-seriate **38. *Trixis***
– Inflorescences terminal solitary or tightly grouped clusters of small capitula; style arms < 1 mm long, apices rounded; receptacle papillate; corollas white or yellowish white, glabrous; pappus setae uniseriate **26. *Lophopappus***
37. Florets all actinomorphic 38
– Florets clearly bilabiate, pseudobilabiate or pseudoligulate, capitula sometimes heterogamous and radiate 55
38. Plants dioecious, capitula with only staminate or only pistillate flowers 39
– Plants not dioecious, capitula otherwise 40
39. Corollas whitish or cream; style shaft glabrous; inflorescences many-headed, usually leafy panicles or corymbs, capitula sessile or short-pedicellate **73. *Gochnatia*** (sect. ***Moquiniastrum***)
– Corollas purple; style shaft short-pilose beneath style arms; inflorescence of solitary sessile or subsessile capitula on brachyblasts subtended by bud and leaf-scales in 2–3 series **91. *Myripnois***
40. Plants soon appearing leafless (leafy only on young shoots); stems terminating in spine **60. *Cyclolepis***
– Plants conspicuously leafy; stems unarmed 41
41. Basal half of stem with only scale leaves; normal leaves (large and obovate or trilobed) rosulate or alternate at base of inflorescence; pappus setae usually somewhat flattened and dilated at apices **89. *Macroclinidium***
– Leaves rosulate at base or apex of stem or alternate and descrescent upwards or leaves similar throughout, sometimes with axillary brachyblasts, leaves small or medium-sized; pappus setae of uniform width, if flattened, then narrowing towards apex or reduced to a corona 42
42. Pappus a scale-like corona; capitula clustered in centre of secondary spiny foliaceous bracts; USA (Nevada and California) **76. *Hecastocleis***
– Pappus of capillary or paleaceous setae or absent; capitula free or in aggregations lacking outer secondary foliaceous bracts; outside USA 43
43. Corolla lobes stiff and erect and sinuses of lobes densely pubescent; inflorescences solitary terminal capitula embedded in densely tomentose, densely leafy stem apices **19. *Chimantaea***
– Corolla lobes usually recurved or tightly coiled and sinuses of lobes glabrous; inflorescences multi-headed or if one-headed, then stem apices not densely tomentose and capitulum not embedded in apical leaves 44
44. Capitula solitary on relatively long, slender multibracteolate axillary pedicels, bracteoles scale-like; corolla lobes tomentose; receptacle with alveolae margins ciliate or fimbriate between achenes; corollas bright yellow **65. *Chucoa***
– Capitula in corymbs or panicles and sessile or short-pedicellate, if solitary, then sessile or on short pedicels and terminal or axillary and bracteoles scale-like or leaf-like; corolla lobes glabrous, glandular-punctate or pilose; receptacle with alveolae margins scarcely discernible or appearing honeycombed; corollas white, cream red, violet, purple, brownish, rarely yellow and then often pale 45
45. Pappus uniseriate and plumose (rarely absent); plants with basal rosettes of leaves, or with short naked basal portion of stem beneath leaf rosette or rarely leafy throughout; inflorescences usually spiciform, racemose or narrow-paniculate; achene setulae, when present, short or long twisted twin-hairs **90. *Ainsliaea***
– Pappus usually 2- to 3-seriate, barbellate or plumose or combinations of barbellate and plumose setae or

if uniseriate, then barbellate and setae united at base; inflorescences of solitary axillary or terminal capitula, or of many-headed panicles or compound corymbs; achene setulae, when present, straight twin-hairs 46

46. Phyllary apices pungent, outer phyllaries narrow and usually squarrose **84. *Dicoma***
– Phyllary apices acute, obtuse or rounded, outer phyllaries usually erect and never pungent 47
47. Leaves congested and sometimes fasciculate on brachyblasts, or evenly spaced on stems and uniform; capitula usually solitary and sessile or short-pedicellate on brachyblasts or stem apices or in few-headed panicles; leaves small and subulate, lanceolate or oblong to ovate; anther thecae drying brownish or blackish **88. *Pertya***
– Stems basally or apically rosulate or stems leafy throughout and leaves often descrescent towards inflorescence; inflorescences scapiform (single- or few- to many-headed), cymose, pseudocorymbose or pseudopaniculate with many capitula or capitula large terminal and solitary; leaf laminas medium to large; anther thecae not drying brownish or blackish 48
48. Capitula with 1 floret 49
– Capitula with 2 or more florets 50
49. Pappus setae straw-coloured; plants poorly branched shrubs or monopodial small trees **22. *Quelchia***
– Pappus setae magenta; plants clambering shrubs or vines **10. *Stifftia* (*S. uniflora*)**
50. Apical anther appendages acuminate to long-caudate and knob-like at very tip **86. *Pleiotaxis***
– Apical anther appendages apiculate or lanceolate to long-acute 51
51. Leaves usually sticky and distinctly pockmarked and glandular-punctate; corollas lilac or white; pappus setae broad and flattened at base; inflorescences dense glomerules or pseudoracemes **74. *Pentaphorus***
– Plants lacking glandular punctae; corollas yellow to orange, cream or white; pappus setae capillary, sometimes coarse; inflorescences corymbs, racemes, sometimes capitula solitary, terminal or axillary 52
52. Inflorescences dense terminal corymbs or glomerules; achene setulae long twisted twin-hairs; Old World (Asia) **78. *Leucomeris***
– Inflorescences scapiform, of solitary terminal capitula or of cymes or panicles; achenes glabrous or setuliferous and setulae straight twin-hairs, stipitate-glandular, or uniseriate; New World (Central and South America) 53
53. Style arms markedly divergent, relatively long; apical anther appendages lanceolate to long-acute; achenes cylindrical, glabrous or very sparsely setuliferous, setulae short stipitate glands or eglandular uniseriate and multicellular; pappus setae 4–5-seriate, usually spreading, of plants with dense axillary or terminal cymes straw-coloured, of those with solitary capitula highly coloured and orange, reddish, purple or magenta **10. *Stifftia***
– Style arms scarcely bifid and very short; apical anther appendages usually apiculate; achenes usually turbinate, usually densely setuliferous, setulae twin-hairs and sometimes stipitate glands; pappus setae 1–2-seriate, erect, straw-coloured 54
54. Shrubs or trees; inflorescences solitary or clustered terminal capitula or capitula in many-headed cymes, pseudocorymbs or pseudopanicles; capitula usually sessile, subsessile or short-pedicellate; pappus setae free to base **73. *Gochnatia***
– Small subshrubs; inflorescences scapiform with a long, distinct peduncle above leaves; capitula usually long-pedicellate; pappus setae basally connate into distinct annulus **75. *Richterago***
55. Plants appearing leafless, minute linear-spathulate leaves falling rapidly **58. *Aphylloclados***
– Plants conspicuously leafy, stems leafy throughout or with apical or basal rosettes of leaves 56
56. Plants dioecious, capitula with only pistillate or only staminate flowers **55. *Lycoseris***
– Plants not dioecious, capitula otherwise 57
57. Pappus setae dimorphic, outer series multiseriate, capillary and barbellate, inner series of awn-like scales with laciniate margins **51. *Urmenetia***
– Pappus setae monomorphic, all barbellate or plumose 58
58. Achenes obcompressed with 2 or 4 ribs **64. *Lulia***
– Achenes cylindrical, fusiform or turbinate 59
59. Leaves with simple or branched tendrils at apices, leaves often pinnate, sometimes simple **50. *Mutisia***
– Leaves lacking tendrils at apices 60
60. Capitula radiate and marginal (ray) florets with conspicuous ray limb, either with marginal floret corollas bilabiate and disc floret corollas actinomorphic, or marginal and disc floret corollas bilabiate 61
– Capitula discoid and all floret corollas bilabiate and hermaphrodite 82
61. Marginal (ray) floret and disc floret corollas all bilabiate 62
– Marginal (ray) floret bilabiate and disc floret corollas actinomorphic 72
62. Pappus setae plumose 63
– Pappus setae barbellate 64
63. Prostrate rhizomatous rosettiform perennial herbs or subshrubs; leaves fleshy **52. *Pachylaena***
– Erect, ascending or clambering subshrubs or shrubs; leaves usually herbaceous **50. *Mutisia*** (sect. ***Holophyllum***, sect. ***Fruticosa***)
64. Leafy-stemmed erect or prostrate annual or perennial herbs or dense caespitose or lax subshrubs or shrubs; inflorescences of solitary sessile or subsessile terminal capitula or a short few-headed cyme; ray florets female and lacking staminodes, neuter or hermaphrodite 65
– Acaulescent rosulate scapigerous herbs; scapes usually very long and with few to several scale-like bracteoles, scapes often markedly elongating in fruit; ray florets usually with staminodes (subtribe **Gerberinae**) 66
65. Densely caespitose shrubs with sessile capitula; outer phyllaries not foliaceous; corolla tube arachnoid-pubescent or glabrescent, usually sparsely glandular-punctate **53. *Brachyclados***
– Herbs or very rarely small shrubs with more or less pedicellate capitula; outer phyllaries often foliaceous; corolla tube glabrous **54. *Chaetanthera***
66. Plants with stout rhizomes; involucres mostly broad and hemispherical; achenes short and ovoid; anther filaments papillate; achene setulae flattened and spathulate; ray limbs pubescent and sometimes glandular-punctate **66. *Trichocline***
– Plants usually with slender rhizomes and often wiry or fibrous roots; involucres mostly turbinate; achenes

usually long, cylindrical, sometimes beaked; anther filaments glabrous; achene setulae inflated or short or very long twin-hairs or absent; ray limbs usually glabrous 67

67. Receptacles fimbriate 68
– Receptacles alveolate 69
68. Achenes densely silky setuliferous with abundant, very long, white pointed setulae; capitula conspicuously radiate and limb of ray florets long and conspicuous, exceeding pappus, pink; length of scape at least twice leaf length; Turkish Armenia and central Asia **69. *Uechtritzia***
– Achenes glabrous or densely papillate; capitula appearing discoid with limb of ray florets very short, slender, strap-shaped, white; length of scape scarcely exceeding leaf length; South Africa **71. *Perdicium***
69. Capitula with only ray and disc florets 70
– Capitula with ray, submarginal and disc florets 71
70. Plants with vernal (radiate and chasmogamous) and autumnal (cleistogamous) generations of capitula; achene setulae fine with acute apices, apices scarcely divided or rarely divided to base; ray limbs concolorous above and beneath but sometimes with limb (pink or purple) differently coloured from tube (white or cream); Central America and Asia **68. *Leibnitzia***
– Plants with only one generation of capitula; achene setulae 'sausage-shaped' with rounded apices, apices never divided; ray limbs discolorous, white above and pink or purple beneath; Australia **70. *Amblysperma***
71. Pappus setae usually uniseriate and often united at base, setae fine; ray limbs shorter than involucre; corollas usually white, rarely purplish; capitula either nodding or erect in bud and flower becoming erect in fruit; plants often with vernal (radiate and chasmogamous) and autumnal (cleistogamous) generations of capitula; Central and South America **67. *Chaptalia***
– Pappus setae usually biseriate, setae relatively coarse; ray limbs usually considerably longer than involucre; corollas white, yellow, pink, red, purple; capitula always erect; plants with only chasmogamous capitula; East and South Africa, Madagascar, southern Asia **72. *Gerbera***
72. Corollas intense orange to orange-red; phyllaries with scarious apical appendages or linear to linear-lanceolate **56. *Cnicothamnus***
– Corollas white, yellow, pink, reddish or purple; phyllaries lacking apical appendages 73
73. Leaves filiform; ray florets purple; Chile **59. *Gypothamnium***
– Leaves round, elliptic, lanceolate, hastate or lyrate; ray florets usually white or pink (if violet, then leaves broad) 74
74. Pappus setae purple **62. *Ianthopappus***
– Pappus setae whitish, straw-coloured or fawn 75
75. Pachycaul shrubs or small trees with very densely tomentose, poorly branched stems; South Africa **82. *Oldenburgia***
– Annual to perennial herbs or well-branched shrubs or trees, sometimes simple-stemmed or poorly branched subshrubs and inflorescences appearing scapiform 76
76. Achene base with dense tuft of setulae, otherwise setuliferous between ribs; ray corollas deep red (rarely white); ray florets neuter **83. *Passacardoa***
– Achenes glabrous, glandular-punctate or uniformly setuliferous; ray corollas white, pink, purple or violet; ray florets hermaphrodite or female 77
77. Florets few (5–6); leaf pubescence of malpighiaceous hairs; leaves linear-lanceolate to oblong-lanceolate **93. *Hyalis***
– Florets numerous (> 10); leaf pubescence absent or of simple hairs; leaves round, ovate, hastate or lyrate 78
78. Ray or marginal floret corollas pink, purple or violet **61. *Onoseris***
– Ray or marginal floret corollas white 79
79. Tall shrubs or small trees; capitula large; Old World (China) **77. *Nouelia***
– Small shrubs or subshrubs; capitula medium; Old World (Madagascar) or New World (Argentina, Bolivia, Brazil, Chile, Peru) 80
80. Inflorescences scapiform with solitary capitula or few capitula in panicles; achenes setuliferous, setulae twin-hairs; New World (Brazil) **75. *Richterago***
– Inflorescences solitary, terminal and sessile and surrounded by apical leaves; achenes glabrous or glandular-punctate; Old World (Madagascar) or New World (Argentina, Bolivia, Chile, Peru) 81
81. Stems and leaves densely white- to grey-tomentose, leaves concolorous; achenes glandular-punctate; Old World (Madagascar) **87. *Gladiopappus***
– Stems resinous and short-pubescent, leaves sticky and glabrous above and densely pubescent beneath; achenes glabrous; New World (Argentina, Bolivia, Chile, Peru) **57. *Plazia***
82. Pappus setae plumose; corollas yellow **50. *Mutisia*** (sect. ***Isantha***)
– Pappus setae barbellate; corollas white, red or purple, rarely pale yellow 83
83. Phyllaries subequal and pubescent throughout; pappus setae caducous; capitula solitary on long, very sparsely bracteolate peduncles **16. *Eurydochus***
– Phyllaries gradate and glabrous or pubescent only at apices; capitula, if solitary, on relatively short peduncles with leaf-like bracts, otherwise few to many capitula in corymbs or cymes 84
84. Florets few (2–5, rarely 6) 85
– Florets several to numerous (8–60) 87
85. Inflorescences terminal and many-headed; corollas reddish; achenes setuliferous; Dominican Rep. **23. *Salcedoa***
– Inflorescences axillary; corollas white; achenes glabrous; Guyana Highlands 86
86. Outer phyllaries with densely pubescent apices; sinuses of corolla lobes sparsely to moderately pubescent; phyllaries c. 4-seriate; adjacent basal anther appendages distinct; inflorescences axillary, of solitary capitula or few-headed cymes, often obscured by subtending leaves or in terminal clusters on ascending, leafy subterminal flowering stems, capitula usually erect **17. *Achnopogon***
– Outer phyllaries pubescent throughout; sinuses of corolla lobes glabrous; phyllaries 6–8-seriate; adjacent basal anther appendages connate; inflorescences axillary of few (1–)2–9 capitula, capitula usually pendulous **18. *Neblinaea***
87. Leaves linear or linear-lanceolate and conspicuously 1-veined; corollas white, reddish or purple; achenes glabrous or setuliferous **13. *Duidaea***

– Leaves broadly lanceolate, oblanceolate or obovate, with reticulate, pinnate or subparallel venation; corollas white, pale yellow or red; achenes glabrous 88
88. Corollas red; inflorescence of subsessile or short-pedunculate solitary terminal capitula; outer phyllaries floccose or glabrescent; leaves buff-tomentose beneath; florets 12–22 **14. *Glossarion***
– Corollas white or pale yellow; inflorescence of long-pedunculate large solitary terminal capitula or few- to many-headed and corymbiform or umbelliform; outer phyllaries glabrous; leaves glabrous or pubescent beneath; florets 6–60 **15. *Gongylolepis***

II.1. Stifftia Group

Tribe Stifftieae D. Don (1830).

Shrubs, vines or trees. Leaves alternate or opposite, coriaceous. Inflorescence solitary terminal capitula or paniculate or racemose; capitula discoid; phyllaries few- to many-seriate; involucres cylindrical, campanulate or globose; receptacle epaleaceous or paleaceous. Florets few to many, rarely solitary; corollas bilabiate, actinomorphic or rarely ligulate. Achenes cylindrical or fusiform, glabrous or sparsely setuliferous; carpopodium annular to short-cylindrical; pappus setae 3–5-seriate, capillary and barbellate or subpaleaceous and densely plumose.

10. *Stifftia* J.C. Mikan

Stifftia J.C. Mikan, Delec. Fl. Faun. Brasil. I 1, tab. 1 (1820), nom. cons., Robinson, Syst. Bot. 16: 685–692 (1991), key; Hind & Semir, Kew Bull. 53: 617–622 (1998), part. rev.

Shrubs, vines or trees. Leaves persistent, alternate, simple, lamina herbaceous or coriaceous. Capitula in dense axillary cymes, few-headed apical clusters, or solitary, 1- to many-flowered, homogamous, discoid; involucres narrowly cylindrical to turbinate; phyllaries few- to many-seriate, subimbricate to imbricate, usually with many smaller bracts grading down pedicels; receptacle flat to slightly convex, epaleaceous. Florets actinomorphic, hermaphrodite; corollas deeply 5-lobed, whitish to yellow or orangish yellow, lobes linear, tightly coiled; basal anther appendages long-caudate, short-papillate or laciniate; style base lacking basal node, glabrous, shaft glabrous, arms short, divergent, rounded to acute, glabrous. Achenes cylindrical, glabrous or sparsely setuliferous; carpopodium annular to short-cylindrical; pappus setae 4–5-seriate, persistent, prominent, often brightly coloured. Eight species, Brazil, French Guyana. One species is relatively widely cultivated in the Tropics.

11. *Hyaloseris* Griseb.

Hyaloseris Griseb., Symb. Fl. Argent.: 212 (1879); Ariza Espinar, Kurtziana 7: 195–211 (1973), rev.
Dinoseris Griseb. (1879).

Shrubs or small trees. Leaves opposite, simple, lamina lanceolate, narrowly elliptic to elliptic, denticulate or entire, apices acute or obtuse. Capitula two to several subsessile in dense terminal or axillary clusters or terminal, homogamous, few- or many-flowered, usually appearing ligulate; involucre cylindrical (in *Hyloseris* s.str.) or campanulate (in *Dinoseris*), usually surrounded by dense scale-like bracteoles; phyllaries 6–7-seriate, imbricate, gradate, all straw-coloured; receptacle small, epaleaceous, glabrous. Corollas off-white or cream to yellow, glabrous, ligulate or bilabiate and then with 3- to 4-toothed outer lip; basal anther appendages extremely long, long-caudate, retrorsely long-pilose towards base; style base lacking basal node, glabrous, shaft glabrous, arms long, divergent and often recurved, acute and short-papillose. Achenes fusiform to long-fusiform, 5- or 10-ribbed; carpopodium large, procurrent in upper part with body; pappus setae few-seriate, persistent, coarsely barbellate, off-white to straw-coloured. Seven species, Argentina, Bolivia.

12. *Wunderlichia* Riedel ex Benth. & Hook. f.

Fig. 17

Wunderlichia Riedel ex Benth. & Hook. f., Gen. Pl. 2, 1: 489 (1873); Barroso & Maguire, Revista Brasil. Bot. 33: 379–406 (1973), rev.

Shrubs or trees. Leaves alternate, deciduous, lamina elliptic, oblong-elliptic or broadly obovate to orbicular, coriaceous. Capitula solitary, terminal, or few to several in dense panicles or lax racemes to scorpioid cymes, usually erect, medium or large, homogamous, discoid; involucre campanulate, globose or infundibuliform; phyllaries 4–10-seriate, gradate, imbricate, persistent; receptacle flat to convex, paleaceous. Florets actinomorphic, many (to 300+), yellowish to cream; corollas glabrous, lobes linear, coiled throughout or only at apex; filaments long, often 'swan-necked' at anthesis; basal anther appendages caudate, usually entire or appearing somewhat contorted; style base with enlarged basal node, or node absent

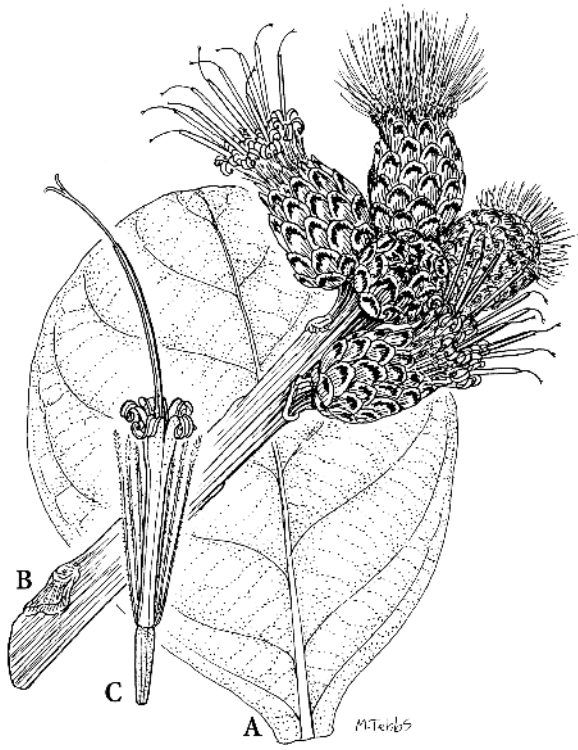

Fig. 17. Compositae-Mutisieae. *Wunderlichia cruelsiana*. **A** Leaf. **B** Inflorescence. **C** Floret. (Drawings by Margaret Tebbs)

and distinctive nectary present, glabrous, style glabrous, long-exserted from anther cylinder, arms short, scarcely divided, or appearing connate/adnate. Achenes 10-ribbed; carpopodium very narrow, pale; pappus setae 3–4-seriate, falling as a unit, subpaleaceous, sometimes barbellate below and densely plumose above, straw-coloured. Five species, endemic to Brazil (Bahia, Espírito Santo, Goiás, Minas Gerais, Rio de Janeiro).

II.2. Stenopadus Group

Small to large shrubs or trees. Leaves alternate, coriaceous. Inflorescence solitary axillary or terminal capitula or cymes, corymbs or glomerules; capitula homogamous, discoid or ligulate; involucres campanulate or cylindrical; phyllaries 3–8-seriate; receptacles usually paleaceous; florets hermaphrodite, few to many, rarely solitary; corollas actinomorphic and deeply 5-lobed or ligulate or bilabiate. Achenes cylindrical, ribbed, glabrous or setuliferous; pappus setae capillary and barbellate or flattened with barbellate to subplumose margins.

13. *Duidaea* S.F. Blake

Duidaea S.F. Blake, Bull. Torrey Bot. Club 58: 496 (1931); Pruski, Fl. Venez. Guayana 3: 261–263 (1997), reg. rev.

Shrubs (with extremely woody bases) or dwarf trees. Leaves alternate or densely spiralled, simple, lamina linear, linear-lanceolate or oblanceolate. Capitula usually solitary, axillary or subterminal, or on medium-length pedicels, homogamous; involucre hemispherical or cylindrical to campanulate; phyllaries c. 3-seriate, imbricate, gradate; receptacle scarcely convex, epaleaceous, pubescent. Florets few to many (8–24), bilabiate, hermaphrodite, fertile; corollas white, red or reddish purple, outer lip short 3-toothed, scarcely curved or apparently strongly coiled, inner of two long coiled lobes; basal anther appendages caudate (sometimes very long), rough or pilose, obtuse or acute; style base lacking obvious basal node, glabrous, shaft glabrous, arms moderately long, usually recurved/coiled at maturity, apices obtuse to truncate. Achenes c. 10-ribbed, cylindrical; carpopodium annular; pappus setae biseriate, flattened at base, margins almost subplumose, coarsely barbellate above, straw-coloured. Four species, Venezuela (Venezuelan Guyana).

14. *Glossarion* Maguire & Wurdack

Glossarion Maguire & Wurdack, Mem. New York Bot. Gard. 9: 390 (1957); Pruski, Fl. Venez. Guayana 3: 279–281 (1997), reg. rev.
Guaicaia Maguire (1967).

Shrubs or small trees. Leaves alternate, short-petiolate, lamina elliptic to narrowly lanceolate, entire. Capitula solitary, axillary, homogamous, discoid or ligulate; involucre turbinate to narrowly campanulate or cylindrical; phyllaries imbricate, gradate, persistent; receptacle slightly convex, epaleaceous, scarcely alveolate, long-pilose. Florets bilabiate or ligulate, bilabiate corollas with 3-toothed outer lip and inner lip of 2 long linear lobes, lobes somewhat coiled, glabrous, ligulate corollas usually with limb tightly rolled in apical portion; corollas rose-coloured to orange-red; basal anther appendages appearing truncate, densely short-pilose, often appearing retrorsely so; style with small glabrous basal node, shaft glabrous, arms moderately long or short, spreading to coiled or erect. Achenes glabrous, 10-ribbed, cylindrical; carpopodium narrow, pale; pappus setae multiseriate, capillary, barbellate, cream or

rust-coloured. Two species, northern Brazil and southern Venezuela in the Guyana Shield.

15. *Gongylolepis* R.H. Schomb.

Gongylolepis R.H. Schomb., Linnaea 20: 759 (1847); Pruski, Bol. Mus. Para. Emilio Goeldi, ser. Bot. 7: 352–367 (1991), rev.; Fl. Venez. Guayana 3: 284–293 (1997), reg. rev.

Small to large shrubs or trees. Leaves simple, alternate or densely spiralled, lamina usually large, broadly lanceolate to obovate, entire. Capitula solitary, sessile or pedicellate, or few to many corymbose to subumbellate, homogamous, few- to many-flowered (6–150), large; involucre hemispherical or campanulate; phyllaries imbricate, gradate, 4–6-seriate; receptacle convex, epaleaceous. Florets hermaphrodite; corollas bilabiate, white or pale yellow, sometimes yellowish or reddish, outer lip tightly rolled outwards, apex with three short teeth, glabrous, inner of two long, linear, tightly rolled lobes; basal anther appendages long-caudate, adjacent pairs fused, usually smooth; style base with large nectary, glabrous, shaft glabrous throughout, cream or purple, arms bifid, short and scarcely bifid, or of moderate length and usually recurved, glabrous, apices truncate or obtuse, usually purplish. Achenes cylindrical, usually 10-ribbed; carpopodium annular; pappus setae biseriate to few-seriate, setae about as long as corolla tube, finely barbellate, cream, pale yellow or rust-coloured. Fourteen species, Brazil, Colombia, Guyana (Guyana Highlands) Venezuela (Venezuelan Guyana).

16. *Eurydochus* Maguire & Wurdack

Eurydochus Maguire & Wurdack, Bol. Soc. Venez. Ci. Nat. 20: 57 (1958).

Trees or treelets. Leaves simple, alternate, usually in terminal clusters at stem apices, lamina large, elliptic or oblanceolate. Capitula solitary, subterminal on long sparsely bracteolate pedicels, homogamous; involucre hemispherical to campanulate; phyllaries imbricate, few-seriate (c. 6–8), subequal; receptacle broad, naked, convex. Florets numerous (40–50), hermaphrodite; corollas bilabiate, red, outer lip three-toothed at apex, usually partially to wholly tightly coiled, inner of two tightly rolled linear lobes; basal anther appendages long-caudate, free (Pruski 1997) or connate (Maguire and Wurdack 1958), puberulous; style base with pronounced basal nectary, shaft glabrous, arms relatively short, recurved, apices truncate to obtuse. Achene 10-ribbed; carpopodium annular; pappus setae 2–3-seriate, barbellate, fragile, caducous, shorter than corolla tube, usually bronze-coloured. One species, *E. bracteatus* Maguire & Wurdack, Brazil, Venezuela (Guyana Highlands).

17. *Achnopogon* Maguire, Steyermark & Wurdack

Achnopogon Maguire, Steyermark & Wurdack, Mem. New York Bot. Gard. 9: 437 (1957); Pruski, Fl. Venez. Guayana 3: 197–199 (1997), reg. rev.

Shrubs or small trees. Leaves densely spiralled or rosulate, lamina coriaceous, elliptic, oblanceolate or obovate, entire. Capitula solitary, sessile, axillary or in few-headed cymes or in axillary cymes at apices of long flowering branches, homogamous, bilabiate; involucres narrow-cylindrical; phyllaries c. 4-seriate, imbricate, gradate; receptacle small, epaleaceous, naked. Florets few (2–6), hermaphrodite; corollas white, zygomorphic, outer lip of three long lobes, inner of two long, often tightly rolled lobes; basal anther appendages caudate, retrorsely pilose; style base with distinct glabrous basal node, shaft glabrous throughout, arms long, eventually coiled, truncate, mammillose outside at apices. Achenes cylindrical, obscurely 10-ribbed; carpopodium distinct, annular; pappus setae 3–5-seriate, flattened at base, margins finely barbellate throughout, straw-coloured. Two species, Venezuela (Guyana Highlands).

18. *Neblinaea* Maguire & Wurdack

Neblinaea Maguire & Wurdack, Mem. New York Bot. Gard. 9: 391 (1957).

Poorly branched shrubs or trees/treelets. Leaves alternate to ± densely spiralled, pseudopetiolate, oblanceolate, entire. Capitula solitary or few to several in cymes, homogamous, bilabiate; involucre narrow-cylindrical; phyllaries c. 6-seriate, imbricate, gradate; receptacle small, epaleaceous. Florets few (2–5), hermaphrodite, fertile; corollas white, glabrous; outer lip short 3-toothed, inner of two long rolled lobes; basal anther appendages caudate, pilose; style base with glabrous node, arms short, slightly recurved, obtuse to rounded. Achenes cylindrical, obscurely ribbed; carpopodium large, merging with and procurrent on to base of achene; pappus setae c. 2–3-seriate, somewhat flattened at base, coarsely barbellate, straw-coloured, vaguely pinkish. One species, *N. promontorium* Maguire

& Wurdack, Venezuela (Guyana Highlands) and neighbouring Brazil.

19. *Chimantea* Maguire, Steyerm. & Wurdack

Chimantea Maguire, Steyerm. & Wurdack, Mem. New York Bot. Gard. 9: 428 (1957); Maguire et al., Mem. New York Bot. Gard. 9: 428–434 (1957), rev.; Pruski, Fl. Venez. Guayana 3: 239–245 (1997), reg. rev.

Small shrubs or rather low trees/treelets (to c. 9 m). Leaves sessile or pseudopetiolate, spiralled, lamina linear, oblanceolate, broadly elliptic or obovate, entire. Capitula solitary, sessile, terminal, discoid, homogamous; involucre campanulate; phyllaries multiseriate, persistent; receptacle flat or slightly concave, epaleaceous or with a few outer paleae, alveolate. Florets hermaphrodite, few to many (7–35, rarely to 100); corollas actinomorphic, 5-lobed, yellowish or yellowish-green, lobes stiff, very long, erect; basal anther appendages caudate, entire or scarcely 'erose'/pilose; style base lacking basal node but immersed in large lobed nectary, glabrous; style glabrous throughout, arms short to medium, acute or obtuse. Achene 10-ribbed; carpopodium absent; pappus setae 3-seriate, flattened at base, barbellate, straw-coloured. Nine species, Venezuela (Guyana Highlands).

20. *Stomatochaeta* (S.F. Blake) Maguire & Wurdack

Stomatochaeta (S.F. Blake) Maguire & Wurdack, Mem. New York Bot. Gard. 9, 3: 388 (1957); Pruski, Brittonia 41: 35–40 (1989), rev.; Pruski, Fl. Venez. Guayana 3: 370–374 (1997), reg. rev.
Stenopadus S.F. Blake subg. *Stomatochaeta* S.F. Blake (1931).

Trees, treelets (or possibly shrubs). Leaves alternate or sometimes pseudowhorled, simple, sessile or pseudopetiolate, lamina oblanceolate, obovate, entire. Capitula solitary, terminal, often surrounded by a pseudowhorl of leaves, homogamous, discoid; involucres cylindrical to hemispherical; phyllaries few-seriate, imbricate, gradate; receptacle sparsely paleaceous or epaleaceous, glabrous, flat to slightly concave. Florets few to many, hermaphrodite, all fertile; corollas actinomorphic, cream-coloured, corolla lobes stiff, erect, long; basal anther appendages caudate, long, apices coarsely and irregularly short-papillose; style base lacking basal node, glabrous, shaft glabrous, arms relatively short, ascending, scarcely divided, acute or possibly subobtuse. Achenes often 4-ribbed; carpopodium absent; pappus setae 3-seriate, unequal, persistent, flattened throughout, coarsely barbellate, straw-coloured. Six species, Brazil, Guyana, Venezuela.

21. *Stenopadus* S.F. Blake

Stenopadus S.F. Blake, Bull. Torrey Bot. Club 58: 489 (1931); Maguire & Wurdack, Mem. New York Bot. Gard. 9: 366–392 (1957), reg. rev.; Pruski, Bol. Mus. Para. Emlio Goeldi, ser. Bot. 7: 372–384 (1993), reg. rev.; Fl. Venez. Guayana 3: 364–370 (1997), reg. rev.

Trees or shrubs. Leaves alternate or loosely spiralled, simple, oblanceolate or round, entire. Capitula solitary, terminal or rarely in few-headed cymes, homogamous, discoid; involucre campanulate, sometimes subtended by a pseudowhorl of reduced leaf-like bracts; phyllaries multiseriate (c. 8-seriate), imbricate, gradate; receptacle flat to slightly concave or slightly convex, epaleaceous or paleaceous with narrowly lanceolate paleae. Florets few to many (5–100), actinomorphic, hermaphrodite; corolla magenta, lobes straight, partially coiled or strongly coiled; apical anther appendages long-acute; basal anther appendages caudate, short or long, entire, irregular or antrorsely short-papillose, sometimes connate with adjacent anthers; style base lacking basal node, glabrous, shaft glabrous, arms relatively short or of medium length, scarcely separated or obviously bifid and coiled, short-papillose outside, obtuse, usually with marginal lip. Achenes c. 10-ribbed (sometimes obscurely); carpopodium absent; pappus setae 3-seriate, flattened throughout, barbellate, apices somewhat broadened, straw-coloured. Fifteen species, Brazil, Colombia, Ecuador, Venezuela (Guyana Highlands).

22. *Quelchia* N.E. Br.

Quelchia N.E. Br., Trans. Linn. Soc. London, Bot. 6: 41 (1901); Maguire & Steyermark, Mem. New York Bot. Gard. 9: 428–434 (1957), reg. rev.; Pruski, Bol. Mus. Para. Emílio Goeldi, ser. Bot. 7: 370–372 (1993), reg. rev.; Fl. Venez. Guayana 3: 353–355 (1997), reg. rev.

Poorly branched shrubs or small trees. Leaves simple, alternate, sometimes densely clustered towards branch apices, lamina elliptic, oblanceolate or obovate, entire. Capitula in dense terminal or subterminal cymes of glomerules, single-flowered, homogamous; involucres usually cylindrical, sometimes slightly constricted at apex; phyllaries c. 3–4-seriate, imbricate; receptacle small, epalea-

ceous, naked. Florets hermaphrodite, usually actinomorphic; corollas red or white to cream, lobes 5, long, spreading to slightly recurved; basal anther appendages sagittate, acute or obtuse, somewhat papillose; style base with basal node, glabrous, shaft purplish, glabrous throughout, arms short, recurved. Achenes c. 10-ribbed; carpopodium a narrow annulus; pappus setae multiseriate, usually united at base into prominent callus, persistent, barbellate, straw-coloured or sometimes reddish. Four species, endemic to Guyana Shield in southern Venezuela.

23. *Salcedoa* F. Jiménez R. & Katinas

Salcedoa F. Jiménez R. & Katinas, Syst. Bot. 29: 991 (2004).

Moderately branched treelet. Leaves alternate, lamina simple, margins entire, obtuse. Inflorescence terminal, pseudocorymbose, many-headed (20–30), capitula pedicellate, erect, discoid, homogamous, medium to large; involucre cylindrical; phyllaries 4–5-seriate, imbricate, gradate; receptacle glabrous, alveolate, epaleaceous. Florets few (4–5), hermaphrodite, fertile; corollas reddish or cream-coloured, bilabiate or rarely actinomorphic and 5-lobed, glabrous; anther cylinder exserted; apical anther appendages oblong-lanceolate, apices apiculate; basal appendages caudate, tails pilose; style base glabrous; style shaft glabrous; style arms short and short-bifid. Achenes cylindrical to turbinate, setuliferous, setulae long twin-hairs, apices unequal and undivided; carpopodium annular(?); pappus setae biseriate, barbellate, outer series capillary, inner flattened, reddish. One species, *S. mirabaliarum* F. Jiménez R. & Katinas, Dominican Republic.

II.3. Subtribe Nassauviinae (Cass.) Dumort. (1829).

Annual or perennial herbs, subshrubs, shrubs, sometimes clambering, or trees. Leaves alternate, rarely in a basal rosette or densely clustered on brachyblasts. Inflorescences short leafy axillary cymes, dense, few- to many-headed terminal corymbs, or appearing glomerulate with capitula densely aggregated, or sometimes scapiform; capitula homogamous and discoid or sometimes appearing almost radiate; involucres turbinate, cylindrical, campanulate or hemispherical, very rarely acetabuliform or cochleariform; phyllaries (1–)3–5-seriate; receptacles epaleaceous or paleaceous, paleae enclosing accompanying floret. Florets 3–70, rarely 2, heteromorphic, or homomorphic and all with bilabiate corollas, hermaphrodite and fertile; style arm apices rounded, obtuse or truncate, short-papillate, sometimes penicillate. Achenes fusiform or cylindrical, very rarely compressed, ribbed or terete, very rarely rostrate, glabrous or setuliferous; carpopodium a narrow annulus or short-cylindrical, or absent; pappus rarely absent or setae 2–4-seriate, sometimes uniseriate, barbellate throughout or apically subplumose, or entirely plumose.

24. *Proustia* Lag.

Proustia Lag., Amen. Nat. Españ. 1, 1: 33 (1811); Fabris, Revista Mus. La Plata n.s., Secc. Bot. 11: 23–49 (1968), rev.

Scandent or erect shrubs or rarely small trees, stems unarmed or spiny. Leaves simple, alternate, lamina elliptic, ovate or oblong, entire, denticulate or dentate-spinose. Capitula racemose or paniculate, erect or pendent, pedunculate or sessile, homogamous, few-flowered; involucre campanulate; phyllaries few-seriate, imbricate, gradate; receptacle flat. Florets few, hermaphrodite, sweet-smelling; corollas bilabiate, outer lip with expanded 3-toothed limb, inner 2-dentate, pink or purple; basal anther appendages caudate; style with basal node, glabrous, arms truncate, papillose. Achenes fusiform, 4-ribbed; carpopodium annular; pappus biseriate, barbellate, apically subplumose, straw-coloured, yellow, pink, or purplish. $n = 26, 27$. Three species, Peru, Bolivia, Chile, Argentina.

25. *Berylsimpsonia* B.L. Turner

Berylsimpsonia B.L. Turner, Phytologia 74: 351 (1993); Turner, Phytologia 74: 349–355 (1993), key.

Clambering woody shrubs, 1–5 m tall, stems with recurved spines at each node. Leaves alternate, simple, very short-petiolate, lamina entire to serrulate, scarcely spinulose. Capitula in short leafy axillary cymes, sessile or very short-pedicellate; involucres turbinate; phyllaries 3–4-seriate, gradate; receptacle pubescent. Florets 3–6 per capitulum; corollas yellow, glabrous, bilabiate, outer lip short three-toothed, inner deeply 2-lobed, lobes strongly coiled; basal anther appendages long-tailed, bases irregularly 'bearded'; style base slightly expanded but lacking basal node, shaft glabrous, arms glabrous, rounded or obtuse, short-papillate.

Achenes fusiform to narrowly oblanceolate, ribbed; carpopodium cylindrical, procurrent on base of ribs; pappus 2–3-seriate, setae numerous, barbellate, tawny. Two species, Cuba, Dominican Republic, Haiti, Puerto Rico, Santo Domingo.

26. *Lophopappus* Rusby

Lophopappus Rusby, Bull. Torrey Bot. Club 21: 487 (1894); Cabrera, Bol. Soc. Argent. Bot. 5: 37–50 (1953), reg. rev.; Faúndez & Macaya, Not. Mens. Mus. Nac. Hist. Nat. 332: 3–6 (2000), reg. rev.

Well-branched shrubs. Stems often viscous. Leaves alternate or in dense axillary clusters, simple, often viscous, lamina often viscous and shiny when covered in exudate, entire or dentate, sometimes minutely so. Capitula solitary or in tight clusters at apices of branches, sessile or short-pedicellate, homogamous; involucres cylindrical to narrowly campanulate; phyllaries few-(3-)seriate, with apical spine; receptacles small, flat to slightly convex, papillate. Florets usually few, yellowish white to white, usually sweet-smelling, hermaphrodite, fertile; corollas distinctly two-lipped, either outer lip short to moderately 3-toothed or deeply 3-lobed, inner of two long, usually coiled lobes or 2-toothed with teeth moderately long, or corolla actinomorphic and deeply 5-lobed; basal anther appendages caudate, entire; style base sometimes with distinct node, glabrous, shaft gradually thickening upwards and then contracting beneath branching point of arms or uniformly cylindrical, arms moderately long, divergent, often coiled at maturity, acute, mammillose outside. Achenes 5-ribbed, usually narrowed to almost attenuate at base; carpopodium cylindrical; pappus uniseriate, setae barbellate at base, becoming subplumose towards apices, usually straw-coloured. Six species, Argentina, Bolivia, Chile, Peru.

Lophopappus is rather similar to *Proustia* but differs in its solitary or few, grouped capitula, the lack of terminal spines on short branches, to some degree corolla colour (white in *Lophopappus*, pink or purple in *Proustia*). The setulae on the achenes of *Proustia*, when present, are long, twisted or spiralled twin-hairs. Preliminary molecular work (Funk et al., pers. comm.) supports their separation, although they are clearly closely related. The recent treatment of genera for the Flora of Peru (Ferreyra 1995) has suggested that *Lophopappus* be treated as congeneric with *Proustia*. They are treated as separate genera here.

27. *Nassauvia* Comm. ex Juss. Fig. 18

Nassauvia Comm. ex Juss., Gen. Pl.: 175 (1789); Cabrera, Darwiniana 24: 283–379 (1982), rev.
Calopappus Meyen (1834).

Perennial herbs, subshrubs or shrubs, often compact and caespitose. Leaves alternate, sessile, usually densely crowded, lamina ovate, lanceolate, rarely spathulate, entire, dentate, denticulate-spiny, or with few long spines. Capitula generally in complex, terminal, often dense, sometimes globular synflorescences, rarely solitary or in few-headed dichasia, rarely with solitary short-pedicellate axillary capitula forming a terminal 'spike', capitula sessile or subsessile, homoga-

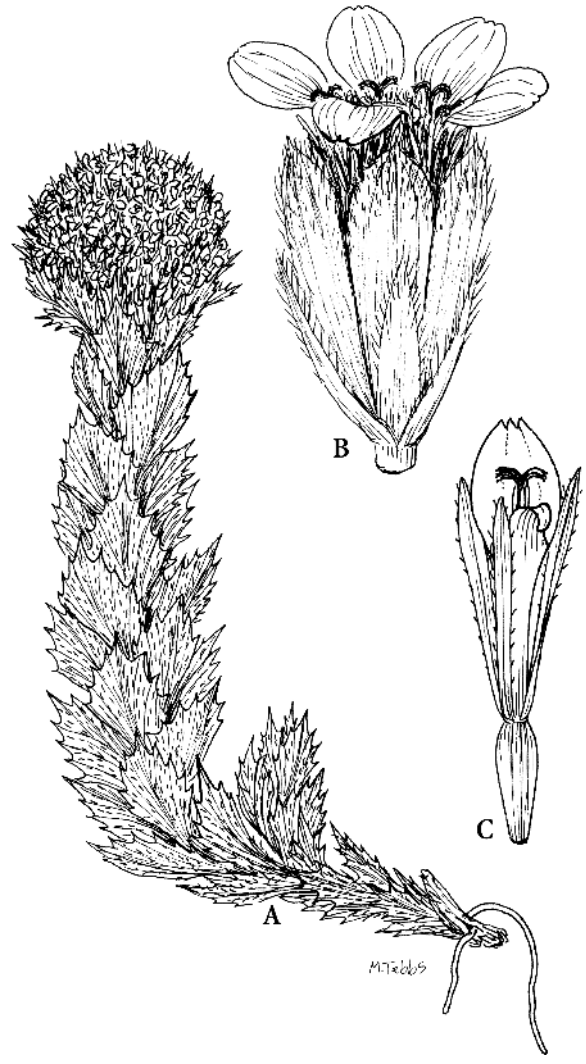

Fig. 18. Compositae-Mutisieae. *Nassauvia dentata*. **A** Flowering shoot. **B** Capitulum. **C** Floret. (Drawings by Margaret Tebbs)

mous; involucre cylindrical; phyllaries biseriate; receptacle epaleaceous, glabrous. Florets few, (2–4–)5, hermaphrodite; corollas white, rarely violet-pinkish or yellowish, bilabiate, outer lip with a conspicuous 3-toothed limb, inner bilobed, lobes recurved; basal anther appendages caudate, usually acute with scarcely finely laciniate margins; anther collar thickened and markedly constricted at base; style base with distinct node, glabrous, shaft glabrous, arms linear, truncate, penicillate. Achenes turbinate or obovate, ribbed or sometimes conspicuously compressed with two lateral ribs; carpopodium usually an inconspicuous, narrow white annulus; pappus uniseriate, of few (5) caducous linear scales or several setae with broad flattened rachis and margins ciliate to plumose, white to straw-coloured. n = 11, 22, c. 44. Circa 40 species, Argentina, Bolivia, Chile, Falkland Islands.

The genus has been divided into two subgenera and the type subgenus into four sections by Cabrera (1982).

28. *Triptilion* Ruiz & Pav.

Triptilion Ruiz & Pav., Fl. Peruv. Prodr.: 102, t. 22 (1794).

Annual or perennial herbs or subshrubs. Leaves alternate, in basal rosettes in some herbaceous plants, lamina entire or pinnatisect with denticulate spiny margins. Capitula densely aggregated into paniculate glomerules, sessile to short-pedicellate, few-flowered, discoid, homogamous; involucre biseriate, ovoid to cylindrical; phyllaries with pungent apices; receptacle convex, long-ciliate or rarely naked. Florets hermaphrodite; corollas glabrous, white or blue, bilabiate, outer lip 3-toothed, inner 2-toothed, strongly coiled; basal anther appendages sagittate, entire; style shaft glabrous, apically bifid, arms truncate, penicillate. Achenes cylindrical, attenuate towards base; carpopodium absent; pappus of few (3–5) apically lacerate-plumose caducous scales. Circa 12 species, Argentina and Chile.

29. *Oxyphyllum* Phil.

Oxyphyllum Phil., Fl. Atacam.: 28, tab. 4 (1860).

Erect shrub, each leaf axil with a dense cluster of simple, linear, spine-tipped immature leaves. Stem leaves pinnatifid, rarely entire, segments and apices spiny. Capitula in a terminal, dense, few- to many-headed corymb, homogamous, discoid; involucre cylindrical to narrowly campanulate; phyllaries 3-seriate, imbricate, gradate, with distinct apical spine; receptacle glabrous, small, scarcely convex in centre portion, paleaceous, paleae few (3), broad. Florets few, dimorphic, outer florets apparently sterile and each subtended by an internal palea, inner florets fertile; corollas pinkish-white; outer florets bilabiate, outer lip a large limb, short 3-toothed at apex, inner of one coiled lobe; basal anther appendages very long-caudate, entire; anther collar distinctly broadened; style base swollen, glabrous, shaft glabrous, arms divergent, truncate, usually with a slight corona of short papillae; inner florets similar to outer but inner lip of two long, tightly coiled lobes. Achenes of outer florets apparently abortive, those of inner florets dark brown; carpopodium absent; pappus uniseriate, setae plumose, white. One species, *O. ulicinum* Phil., Chile (Atacama Desert).

30. *Macrachaenium* Hook. f.

Macrachaenium Hook. f., Fl. Antarctica 2: 321 (1847).

Perennial herb. Leaves mostly in loose basal rosette, alternate, lamina oblong, ovate or broadly ovate, coarsely and deeply, often irregularly, lobed, sometimes pinnatifid to almost runcinate-pinnatifid, often irregularly subdentate. Capitula solitary on scapiform peduncles, homogamous, usually discoid, sometimes conspicuously radiate, apparently nodding; involucre campanulate; phyllaries biseriate, outer usually much shorter than inner; receptacle flat to slightly convex, epaleaceous, glabrous. Florets bilabiate, all hermaphrodite and fertile; corollas white. Ray florets (when present) two-lipped, outer lip conspicuous, short 3-toothed, inner of two long coiled lobes; basal anther appendages absent, base of thecae rounded; style base lacking basal node, glabrous, shaft glabrous, arms short to moderate, acute with marginal thickening, mammillose, glabrous outside. Disc florets two-lipped, outer not conspicuous, short 3-toothed, inner of two long coiled lobes; basal anther appendages caudate, entire; style base and shaft as in ray florets, arms short, acute, mammillose. Achenes of ray and disc florets identical, cylindrical; carpopodium evident or not; pappus usually biseriate, setae plumose, off-white, straw-coloured or sometimes pale rust-coloured. One species, *M. gracile* Hook. f., Argentina and Chile.

31. *Polyachyrus* Lag.

Polyachyrus Lag., Amen. Nat. Españ. 1, 1: 37 (1811); Ricardi & Weldt, Gayana, Bot. 26: 1–41 (1974), rev.

Decumbent, scandent or prostrate subshrubs or shrubs, rarely herbs. Leaves alternate, lamina pinnate-lobed or pinnatisect, entire or coarsely dentate. Capitula in solitary apical glomerules or glomerules in pseudocorymbs, each subtended by one bract; capitula numerous, sessile, 2- or rarely 3-flowered; involucres cochleariform; phyllaries 5, outer enclosing outer floret, inner two including inner floret; receptacle naked. Florets hermaphrodite, fertile, sweet-smelling; corollas bilabiate, outer lip expanded to a 3-toothed limb, inner deeply 2-lobed, revolute/coiled, white or pink; basal anther appendages caudate, margins laciniate (glabrous?); style with distinct basal nectary (possibly node in some species), glabrous, arms divergent, truncate or obtuse, dorsally papillose, appearing penicillate. Achenes terete; carpopodium indiscernible or absent; pappus uniseriate, often detached as unit, plumose, white. $n = 21$. Seven species, Peru, Chile.

32. *Perezia* Lag.

Perezia Lag., Amen. Nat. Españ. 1, 1: 31 (1811); Vuilleumier, Contr. Gray Herb. 199: 1–163 (1969), sect. rev.

Perennial, usually strongly rosettiform, sometimes caespitose herbs, rarely tall leafy-stemmed herbs. Leaves simple, radical or alternate, entire or lyrate, lamina linear, narrowly lanceolate, spathulate to broadly ovate, often ciliate to lacerate, entire, coarsely serrate or dentate to biserrate, pinnatifid or deeply lobed, often spinous. Capitula on 1–(2)-headed scapes arising from basal rosette, or in few- to many-headed dense or lax and spreading panicles; capitula appearing radiate but being discoid, homogamous, usually erect, rarely nodding; involucre broadly cylindrical, turbinate or hemispherical; phyllaries few-seriate to multiseriate, gradate, imbricate, often with terminal spine; receptacle convex, epaleaceous, usually pubescent. Florets usually several to many (8–40); corollas bilabiate, yellow, blue, purple, violet, red, or crimson, rarely white or cream, occasionally with outer lip of one colour and inner of another (usually yellow); outer lip a 3-toothed limb, inner usually tightly rolled, linear and short 2-toothed at apex; basal anther appendages very long-sagittate, often poorly laciniate; style base with distinct glabrous basal node, shaft glabrous throughout, arms relatively short, truncate, purplish or white. Achenes cylindrical to fusiform; carpopodium short-cylindrical or scarcely evident; pappus setae numerous, persistent, slightly longer than corolla tube, 2- or few-seriate, barbellate, brownish. $n = 4$, 8, 12. Circa 32 species, South America (Argentina, Bolivia, Brazil, Chile, Paraguay, Peru, Uruguay).

33. *Acourtia* D. Don

Acourtia D. Don, Trans. Linn. Soc. London 16: 203 (1830); Bacigalupi, Contr. Gray Herb. 97: 1–81 (1931), rev. (sub *Perezia*); Turner, Phytologia 38: 456–468 (1978), part. rev.

Scandent shrubs or subshrubs. Leaves few in a basal rosette, or many, cauline and alternate, simple, lamina small to large, narrowly ovate, oblanceolate, oblong, spathulate, cordiform, lyrate-pinnatifid or broadly elliptic to broadly ovate, serrate, spinous, coarsely dentate or rarely entire. Capitula 1–(2–3), arising on scape from basal rosette, few to many in dense terminal or axillary clusters, or many in a dense thyrse or in broad thyrsoid panicle well exceeding upper stem leaves, homogamous, few- to many-flowered (4–60), rarely appearing radiate when outer florets bilabiate and inner florets actinomorphic; involucre turbinate to campanulate; phyllaries imbricate, gradate, 3–8-seriate; receptacle usually glabrous, sometimes appearing fimbriate or sparingly short-pubescent, epaleaceous, flat to slightly convex. Florets hermaphrodite; corolla cream, white, pinkish, light purple or purple, usually bilabiate, outer lip 3-toothed, inner of two linear lobes, rarely few inner florets with actinomorphic corollas (with 5 linear lobes); basal anther appendages long-caudate, entire or varyingly sparingly laciniate, long-acute; style base somewhat expanded into node, glabrous, shaft purplish, glabrous, arms purplish, recurved (sometimes strongly so), truncate, papillate, occasionally appearing coronate. Achenes cylindrical to fusiform, usually with narrowed apex and apical callus, obscurely ribbed or with distinct paler ribs/lines; carpopodium annular; pappus setae 1–2-seriate, numerous, persistent, barbellate, fawn, whitish or sometimes dark greyish brown. $n = 27$, 28. Circa 80 species, USA, Mexico.

34. *Burkartia* Crisci

Burkartia Crisci, Bol. Soc. Argent. Bot. 17, 3/4: 242 (1976).

Dwarf caespitose shrub forming hemispherical cushions. Leaves sessile, densely spiralled, acicular, margins strongly revolute. Capitula solitary, terminal, usually appearing sessile although shortly pedunculate, few-flowered, radiate, homogamous; involucre turbinate to campanulate; phyllaries 2–3-seriate, imbricate; receptacle slightly convex,

epaleaceous, densely short-pubescent. Florets hermaphrodite, fertile; corollas white, bilabiate, outer lip glabrous, short 3-toothed, inner long 2-lobed (scarcely short 2-toothed in some florets), lobes coiled; basal anther appendages caudate, pilose; anther collar slightly thickened; style base with basal node, shaft glabrous, arms markedly divergent, truncate, short-papillate outside. Achenes cylindrical, obscurely ribbed; carpopodium short-cylindrical or conical, straw-coloured; pappus usually 3-seriate, setae barbellate, off-white. One species, *B. lanigera* (Hook. & Arn.) Crisci, Argentina (Patagonia).

35. *Leucheria* Lag.

Leucheria Lag., Amen. Nat. Españ. 1, 1: 32 (1811); Crisci, Darwiniana 20: 9–126 (1976), rev.

Annual or perennial herbs. Leaves alternate, rosulate, lamina linear, narrowly lanceolate, spathulate, oblong or ovate, entire, dentate, coarsely lobed, pinnatisect or pinnatifid. Capitula solitary or in few- to many-headed corymbs or panicles, pedicellate, appearing radiate; involucre campanulate; phyllaries usually biseriate; receptacle convex, glabrous, epaleaceous. Florets several to many, homomorphic, hermaphrodite, fertile, outer lip white, pink, lilac or wine-coloured; corollas 2-lipped, outer short 3-toothed, often slightly more prominent, inner usually very shortly 2-toothed, often rolled; basal anther appendages caudate, entire or somewhat erose; anther collar cylindrical, usually markedly narrowed beneath and then expanding to flattened filament; style base with basal node, glabrous, shaft glabrous, arms moderately long, truncate, short-papillate outside. Achene terete; carpopodium annular, straw-coloured; pappus setae usually uniseriate, setae flattened and united at base, barbellate or rarely plumose, white or whitish. $n = 20$. Forty-six species, Argentina, Bolivia, Chile, Peru.

36. *Jungia* L. f. Fig. 19

Jungia L. f., Suppl. Pl.: 58 (1782), nom. cons.; Harling, Acta Regiae Soc. Sci. Litt. Gothob. Bot. 4: 1–133 (1995), rev.
Tostimontia Diaz Piedrahita (2001).

Perennial herbs, rarely rosulate, subshrubs, shrubs or lianes. Leaves alternate, lamina cordate, usually lobed, entire, serrate, dentate or crenate. Capitula in usually terminal corymbs or panicles, sometimes with dense glomerules, homogamous, appearing radiate by enlarged outer lip of marginal florets; involucre narrowly cylindrical, turbinate, campanulate or hemispherical; phyllaries uniseriate, subequal, each enclosing a marginal floret. Florets few to many, hermaphrodite, all fertile; corollas white, violet pink, purple or rarely yellow, bilabiate, outer lip enlarged into 3-toothed limb, inner usually deeply bifid, lobes revolute to coiled; basal anther appendages caudate, entire; style base with basal node, glabrous, shaft glabrous, arms markedly bifid and recurved through upper part of anther cylinder, truncate, penicillate. Achenes slender, fusiform to turbinate, 5-ribbed; carpopodium a broad annulus with somewhat lobed upper margin; pappus uniseriate or biseriate, setae barbellate, subplumose or plumose, usually white or straw-coloured, rarely grey or bright orange red, sometimes variable. $n = 18, 21$. Circa 32 species, Central and South America.

Harling (1995) recognized four sections in the genus.

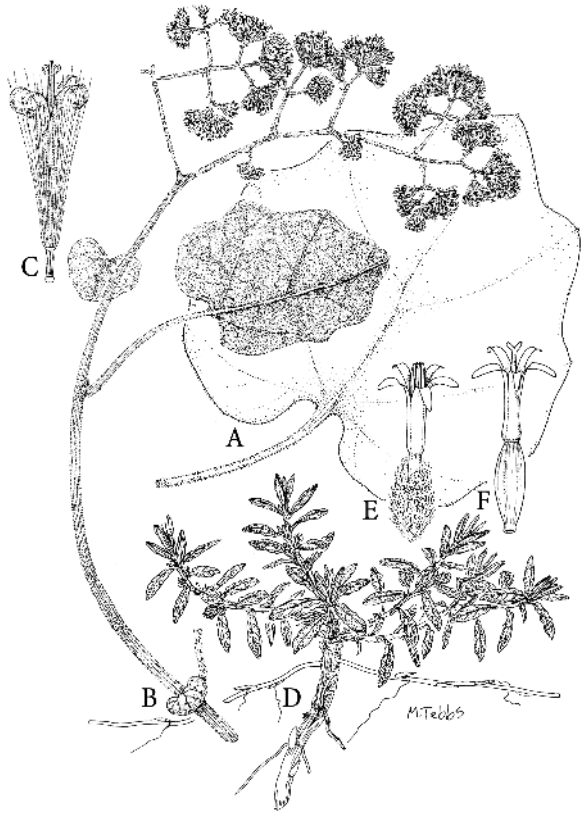

Fig. 19. Compositae-Mutisieae. **A–C** *Jungia woodii*. **A** Mature leaf. **B** Flowering shoot. **C** floret. **D–F** *Eriachaenium magellanicum*. **D** Plant with stolons. **E** Floret showing pubescent achene. **F** Floret with naked achene. (Drawings by Margaret Tebbs)

37. *Pleocarphus* D. Don

Pleocarphus D. Don, Trans. Linn. Soc. London 16: 228 (1830).

Shrub. Leaves sessile, linear, entire, margins conspicuously revolute. Capitula many to numerous in an elongated panicle, pedicellate, homogamous; involucre turbinate to campanulate; phyllaries 2–(3)-seriate, imbricate; receptacle scarcely convex, pubescent, paleaceous, paleae few, usually surrounding central florets. Florets homomorphic, hermaphrodite, fertile; corollas yellow, essentially two-lipped, outer lip of a 2- or 3-short-toothed limb, inner of 3 or 2 long coiled lobes; basal anther appendages extremely long-caudate, entire or sparsely short-pilose/papillose; style base with basal node, glabrous, shaft glabrous, arms long, apically truncate with a corona of short papillae. Achenes long, apically and basally attenuate, 5-ribbed; carpopodium cylindrical, upper margins procurrent with ribs; pappus setae biseriate, setae numerous, barbellate, straw-coloured. $n = 26$. One species, *P. revolutus* D. Don, Chile.

38. *Trixis* P. Browne Fig. 20

Trixis P. Browne, Civ. Nat. Hist. Jamaica: 312 (1756); Anderson, Mem. New York Bot. Gard. 22: 1–68 (1972), reg. rev.; Katinas, Darwiniana 34: 27–108 (1996), reg. rev.

Perennial herbs, subshrubs, shrubs, scandent/trailing shrubs or small trees. Leaves alternate, lamina simple, narrowly lanceolate, elliptical, oblanceolate or obovate to oblong, entire or often denticulate. Capitula in usually terminal, sometimes axillary, lax cymes, corymbs or panicles, occasionally aggregated into pseudoglomerules, homogamous; involucre cylindrical, campanulate or hemispherical, sometimes an outer calyculus present; phyllaries imbricate, pubescent, (1–)2–(3–5)-seriate; receptacle flat, alveolate, pilose or densely long-pubescent. Florets few to many (5–c. 70), hermaphrodite, all fertile; corollas yellow to orange, rarely white, bilabiate, outer lip 3-toothed, inner deeply bifid; basal anther appendages caudate, glabrous or papillose; style base with distinct basal node, glabrous, shaft glabrous, arms truncate, penicillate. Achenes 5-ribbed, cylindrical to turbinate, ± beaked and usually with distinct expanded apical callus above beak; carpopodium annular to short-cylindrical; pappus setae 2–3(–4)-seriate, markedly longer than phyllaries, barbellate, persistent, white, yellowish or reddish. $n = 27$. Circa 50–60 species, Argentina, Bolivia, Brazil, Chile, Colombia, Costa Rica, Cuba, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Paraguay, Peru, Uruguay, USA, Venezuela, West Indies.

39. *Doliclasium* Lag.

Doliclasium Lag., Amen. Nat. Españ. 1, 1: 33 (1811).

Small, moderately branched low shrub. Leaves alternate, petiolate, lamina pinnatisect, pinnae opposite, ovate. Capitula large, terminal, solitary, homogamous, erect; involucre narrowly campanulate; phyllaries biseriate to 3–4-seriate with outer two series often well separated from inner subequal series; receptacle epaleaceous, glabrous. Florets hermaphrodite, numerous, homogamous, fertile; corollas yellow, bilabiate, with outer distinct 3-toothed limb and inner lip of two long rolled lobes; basal anther appendages

Fig. 20. Compositae-Mutisieae. *Trixis vauthieri*. **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

long-caudate, usually acute, margins laciniate to short-pilose; style base with basal node, glabrous, shaft glabrous, arms long, dilated at very apices, obtuse to truncate, papillate outside and appearing coronate. Achenes fusiform, slender, rostrate; pappus biseriate to multiseriate, setae with thickened and flattened rachis at base, subplumose to very coarsely barbellate, more densely so towards base, off-white to white. One species, *D. lagascae* D. Don, Argentina (Patagonia).

40. *Ameghinoa* Speg.

Ameghinoa Speg., Revista Fac. Agron. La Plata 3: 539 (1897).

Low, densely branched shrub. Leaves often in dense clusters on brachyblasts, simple, coarsely dentate. Capitula few in terminal clusters, short-pedicellate, homogamous; involucre narrow-campanulate; phyllaries 2-seriate, gradate, imbricate; receptacle flat, epaleaceous, alveolate, glabrous. Florets hermaphrodite, isomorphic, 20–30; corollas yellow, bilabiate, outer lip a scarcely enlarged limb with 3 short apical teeth, inner of 2 long linear lobes, often rolled; basal anther appendages long-caudate, sparsely pilose/laciniate; style base somewhat swollen, glabrous, shaft glabrous, arms short, slightly bifid, truncate and papillate around edge outside, appearing coronate. Achenes cylindrical; carpopodium dark, procurrent with base of achene; pappus setae uniseriate, somewhat fragile and easily detached, coarsely barbellate, off-white. $n = 26$. One species, *A. patagonica* Speg., endemic to Argentina (Patagonia).

41. *Criscia* Katinas

Criscia Katinas, Bol. Soc. Argent. Bot. 30: 60 (1994).

Perennial herb or subshrub. Leaves rosulate, lamina obovate to broadly obovate, entire. Capitula solitary or 2–4 on scapes, large, bilabiate, homogamous; involucre hemispherical or broadly campanulate; phyllaries c. 4-seriate, imbricate, gradate; receptacle epaleaceous, glabrous. Florets all bilabiate, hermaphrodite, fertile; corollas orange, marginal florets with more pronounced, shortly 3-toothed outer lip, inner divided into 2 often straight (at least when young) or somewhat rolled long linear lobes; inner florets similar to marginal but with shorter outer lip; basal anther appendages caudate, entire or somewhat contorted/irregular; style base with distinct basal node, glabrous, shaft glabrous, arms moderately long, recurved to coiled, rounded to truncate, papillate and appearing almost 'crowned' by short papillae. Achene obscurely constricted towards apex almost into a short rostrum; carpopodium short-cylindrical; pappus setae c. 3–4-seriate, setae flattened towards base, coarsely barbellate, pinkish- to light rusty-brown. One species, *C. stricta* (Spreng.) Katinas, Argentina, Brazil and Uruguay.

42. *Leunisia* Phil.

Leunisia Phil., Linnaea 33: 120 (1864).

Viscid low 'subshrub' or perennial herb. Leaves alternate to loosely spiralled, irregularly toothed or sometimes entire. Capitula terminal, solitary, homogamous, discoid; involucre turbinate; phyllaries biseriate, scarcely imbricate, subequal; receptacle epaleaceous, convex, densely pubescent. Florets numerous, hermaphrodite, fertile; corollas yellow, bilabiate, outer lip short 3-toothed, inner long 2-lobed; basal anther appendages caudate, pilose; style base with node, glabrous, shaft glabrous, arms short, connate, short-papillate outside. Achenes cylindrical; carpopodium concolorous and procurrent with base of achene; pappus setae biseriate, broad, united at base, barbellate, often branched, off-white. One species, *L. laeta* Phil., Chile.

43. *Marticorenia* Crisci

Marticorenia Crisci, J. Arnold Arb. 55: 38 (1974).

Shrub with short woody caudex. Leaves alternate, lamina ovate, lobulate, becoming lanceolate above. Capitula in a lax many-headed corymb, homogamous; involucre hemispherical; phyllaries biseriate; receptacle ± concave, slightly pubescent, paleaceous, paleae conduplicate about florets, apices laciniate. Florets hermaphrodite; corollas violet-pink, bilabiate, outer lip 3-toothed, inner bifid, of two revolute lobes; basal anther appendages tailed; style shaft glabrous, arms truncate, penicillate. Achenes cylindrical; pappus uniseriate, of numerous white plumose setae. $n = 22$. One species, *M. foliosa* (Phil.) Crisci, Chile.

44. *Holocheilus* Cass.

Holocheilus Cass., Bull. Sci. Soc. Philom. 1818: 73 (1818); Cabrera, Revista Mus. La Plata, Secc. Bot. 11: 1–15 (1968), rev.

Perennial rosulate herbs. Leaves usually few, loosely rosulate, lamina medium and coarsely

dentate, crenate or entire, or large and pinnatisect or coarsely lobed. Capitula in large, few- to many-headed terminal corymbs or cymes, rarely scapose, homogamous, small to medium, erect; involucre hemispherical; phyllaries uniseriate to biseriate; receptacle epaleaceous, glabrous. Florets hermaphrodite, bilabiate; corollas white, outer lip an enlarged limb with three short apical teeth, inner of 2 medium to short, usually coiled lobes; basal anther appendages long-caudate, entire, anther collar prominent, distinctly narrowed compared with rest of filament; style base enlarged (probably into node, rather than nectary), glabrous, shaft glabrous, arms short, truncate, papillae forming corona. Achenes fusiform; carpopodium a distinct annulus, of same colour as achene; pappus setae biseriate, persistent, barbellate, spreading to ascending, white or straw-coloured. $n = 11, 18$. Seven species, Argentina, Brazil, Paraguay, Uruguay.

45. *Pamphalea* Lag.

Pamphalea Lag. (orig. *Panphalea*), Amen. Nat. Españ. 1, 1: 34 (1811); Cabrera, Notas Mus. Eva Perón, Bot. 16: 225–237 (1953), rev.

Slender annual or perennial rhizomatous herbs. Leaves mostly basally rosulate, alternate, entire and linear-lanceolate to orbicular, coarsely lobed or lyrate-pinnatifid. Capitula in lax, relatively few-headed corymbs, small, appearing radiate (although all florets identical), homogamous; involucre campanulate to hemispherical; phyllaries few, 1–2-seriate, imbricate, subequal (uniseriate) or gradate (biseriate); receptacle flat, epaleaceous, glabrous, sometimes fimbriate. Florets hermaphrodite, many; corollas white, bilabiate, outer lip with an expanded 3-toothed limb, inner of two fairly wide linear rolled lobes; basal anther appendages sagittate, entire, anther collar slightly narrower than rest of filament and constricted at base; style base with distinct basal node, glabrous, shaft glabrous, arms truncate, penicillate. Achenes often included within involucre, inflated, usually with apical corona/callus; carpopodium a narrow annulus; epappose. $n = 8$. Nine species, Argentina, Brazil, Paraguay, Uruguay.

46. *Moscharia* Ruiz & Pav.

Moscharia Ruiz & Pav., Fl. Peruv. Prodr.: 91 (1794), nom. cons.; Crisci, Contr. Gray Herb. 205: 163–173 (1974), rev.

Annual odiferous herbs. Leaves alternate, simple, lamina elliptic, entire, coarsely dentate or lobed to pinnatisect. Capitula in lax, terminal corymbs, discoid, homogamous; involucre biseriate; phyllaries dimorphic, outer foliaceous, inner convolute and enclosing marginal florets; receptacle convex, glabrous, paleaceous, paleae narrowly lanceolate. Florets few, hermaphrodite, bilabiate; corollas pink or violet, outer florets hermaphrodite with 3-toothed outer limb, inner lip bifid, inner florets sterile; basal anther appendages long-caudate, entire; style base with distinct basal node/nectary, glabrous, shaft glabrous, arms bifid, truncate, penicillate. Achenes fusiform; carpopodium short-cylindrical; pappus setae uniseriate, short, flattened, persistent, with long-ciliate/subplumose margins, brownish, sometimes absent on central florets. $n = 20$. Two species, Chile.

47. *Cephalopappus* Nees & Mart. Fig. 21

Cephalopappus Nees & Mart., Nova Act. Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12, 1: 5, tab. 1 (1824).

Perennial rosulate stoloniferous herbs. Leaves with ovate to narrowly obovate lamina, coarsely dentate. Capitula solitary, scapose, rarely scape branched with two (or few) capitula, homogamous; involucre

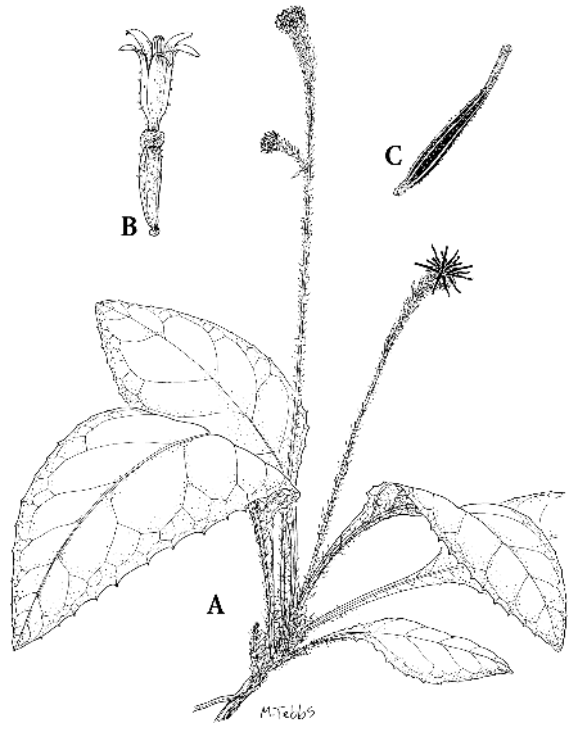

Fig. 21. Compositae-Mutisieae. *Cephalopappus sonchifolius*. **A** Flowering plant. **B** Floret. **C** Mature achene. (Drawings by Margaret Tebbs)

broadly saucer-shaped; phyllaries 2–3-seriate; receptacle epaleaceous, glabrous, scarcely alveolate. Florets many, hermaphrodite, all fertile; corollas white, few opening at a time and lost very rapidly, leaving green achene, bilabiate when open, lobes spreading; basal appendages sagittate, entire (or sometimes subentire); anther collars markedly enlarged; style base lacking basal node, glabrous, shaft glabrous, arms obtuse and rounded, apically densely to moderately short-pilose. Achenes slender, glabrous; carpopodium apparently absent; pappus absent. One species, *C. sonchifolius* Nees & Mart., endemic to Brazil.

Genera of Problematic Placement (Probably Within Nassauviinae)

48. ***Adenocaulon*** Hook.

Adenocaulon Hook., Bot. Misc. 1: 19 (1830); Bittman, Candollea 45: 389–420, 493–518 (1990), rev.

Perennial herbs. Leaves alternate or forming basal rosette, lamina ovate, broadly triangular or lyrate-pinnatifid, entire to coarsely lobed. Capitula many in lax panicles, peduncles and pedicels with persistent and moderately long stipitate-glandular hairs; capitula small, few-flowered, disciform, heterogamous, hemispherical, erect; involucre distant; phyllaries uniseriate, in many species a cupule with phyllaries 'connate' in bottom half; receptacle convex to almost conical in some species, epaleaceous, glabrous. Marginal florets uniseriate, female, fertile; corollas actinomorphic or slightly zygomorphic (bilabiate), 4- or 5-lobed, whitish or yellowish-white, staminodes present, style bifid; central florets few, hermaphrodite, functionally male, usually lacking achene, corollas actinomorphic, 5-lobed, style undivided; basal anther appendages caudate but without distinct tails; style arms scarcely divided or connate, papillate outside. Achenes of female florets obovoid, with conspicuous stipitate glands densest in upper half, achenes of male florets, when present, usually glabrous; carpopodium on base of basal constriction of achene, annular; pappus absent. $n = 23$. Five species, Argentina, Chile, eastern Asia, Nepal, western Canada and USA, Guatemala.

49. ***Eriachaenium*** Sch. Bip. Fig. 19

Eriachaenium Sch. Bip., Flora 38: 120 (1855).

Perennial rhizomatous herbs. Leaves alternate, lamina obovate to elliptic, undulate, sometimes serrate. Capitula solitary, axillary, small, sessile or on short-bracteolate side shoots; involucre campanulate; phyllaries 1–(2)-seriate, few, subequal, not imbricate; receptacle very small, epaleate, glabrous. Marginal florets female, few; corollas white (pinkish in some herbarium material), actinomorphic, usually 5-lobed; anthers absent; style base lacking basal node, glabrous, shaft glabrous, arms short, short-papillose outside. Achenes inflated, conspicuously densely lanose; carpopodium not evident; pappus absent. Central florets very few, hermaphrodite, functionally male; corollas white, actinomorphic, 5-lobed; basal anther appendages scarcely caudate, short-pilose; style base lacking basal node, glabrous, shaft glabrous, arms short, markedly divergent, usually with lip around margins, short-papillose outside. Achenes sterile, pappus absent. $n = 23$. One species, *E. magellanicum* Sch. Bip., Argentina and Chile (Patagonia and Tierra del Fuego).

II.4. Subtribe Mutisiinae (Cass.) Dumort. (1829).

Annual or perennial herbs, subshrubs, shrubs or trees, sometimes climbers. Leaves alternate, sometimes rosulate, simple or rarely pinnate or imparipinnate with a simple or branched tendril. Inflorescences solitary terminal or leaf-opposite capitula, or few- to many-headed corymbs or panicles; capitula radiate and homogamous or heterogamous, discoid and homogamous or very rarely disciform; involucres cylindrical, turbinate, campanulate or hemispherical; phyllaries 2–8-seriate; receptacle epaleaceous, alveolate; ray florets, when present, female, rarely neuter, uniseriate, corollas bilabiate; disc florets hermaphrodite, actinomorphic and corollas deeply 5-lobed, or bilabiate; style arms short, glabrous. Achenes cylindrical or fusiform, very rarely obcompressed, glabrous or setuliferous; carpopodium absent, annular or stopper-shaped; pappus setae uniseriate to multiseriate, persistent, barbellate, subplumose or plumose.

50. ***Mutisia*** L. f. Fig. 22

Mutisia L. f., Suppl. Pl.: 57 (1781); Cabrera, Opera Lilloana 13: 1–227 (1965), rev.

Plants perennial subshrubs or shrubs, often climbers. Leaves simple, subulate, narrowly lanceolate or ovate, entire or dentate, apices with or without terminal tendril, rarely deeply pinnatisect

or coarsely lobed or deeply partite, or pinnately compound with few to several pairs of leaflets and rachis always with a terminal simple, 3- or 5-fid tendril. Capitula small to large, solitary, leaf-opposed or terminal, erect or pendulous, homomorphic with all florets hermaphrodite or heteromorphic with marginal florets female, 'subligulate' and disc florets hermaphrodite and bilabiate; involucre short- or long-cylindrical or campanulate, sometimes very broadly so; phyllaries multiseriate, imbricate, gradate; receptacle epaleaceous, naked, convex to almost flat. Ray florets absent or few to many, female; corollas yellow, orange, pink, purple or white, bilabiate, outer lip a conspicuous, short 3-toothed limb, inner of 2 shorter linear lobes, sometimes strongly reduced; anthers rudimentary or present only as filaments; style base lacking basal node but with enlarged basal portion, arms shortly bifid or apparently adnate. Disc florets few to numerous, hermaphrodite; corollas usually clearly bilabiate with outer three-toothed limb and inner lip of two linear, usually long straight lobes, rarely subligulate with all lobes appearing on one limb but one lobe separated by deeper sinus, usually yellow; anther collar sometimes discernible as abrupt change in colour of filament near connection with anther; basal anther appendages extremely long-caudate, usually entire, sometimes sparsely laciniate, often somewhat contorted; style base lacking distinct basal node but with enlarged basal portion, shaft glabrous, arms relatively short, short-papillose outside, adnate, subacute. Achenes fusiform, indistinctly ribbed; pappus setae uniseriate, with broad, flattened rachis, margins plumose, white or greyish, usually about as long as corollas. n = 13, 23, 24, 26. Circa 62 species, Argentina, Brazil, Bolivia, Chile, Colombia, Ecuador, Paraguay, Peru, Uruguay.

Six sections have been recognized by Cabrera (1965).

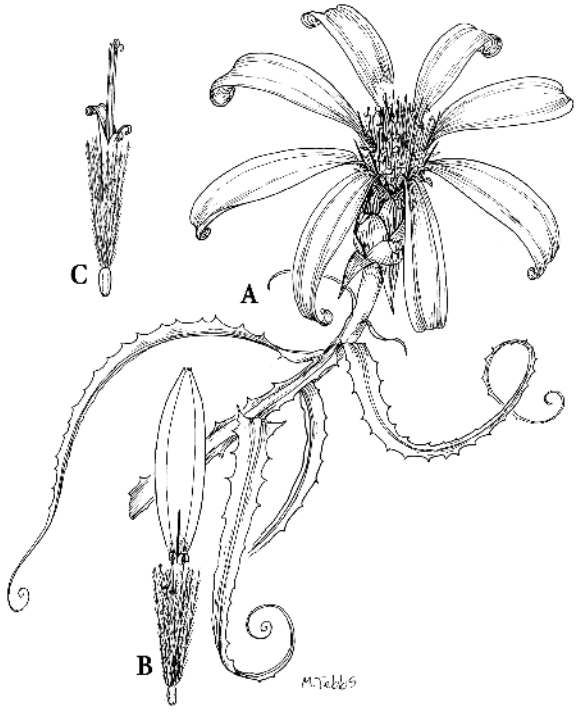

Fig. 22. Compositae-Mutisieae. *Mutisia subspinosa*. **A** Flowering shoot. **B** Ray floret. **C** Disc floret. (Drawings by Margaret Tebbs)

51. *Urmenetia* Phil.

Urmenetia Phil., Fl. Atacam.: 26, tab. 3 (1860).

Subshrub or perennial herb. Leaves alternate and loosely rosulate, lamina broadly elliptic or ovate, denticulate. Capitula terminal on scape, radiate, homogamous; involucre turbinate to campanulate and hemispherical; phyllaries few-seriate, gradate, imbricate; receptacle epaleaceous, glabrous, flat to slightly convex, alveolate. Ray florets uniseriate, female; corollas bilabiate, white or pink, outer lip short 3-toothed at apex, inner of two long twisted filiform lobes; anther cylinder reduced to apparently free staminodes; style base with distinct basal node, shaft glabrous, expanding considerably to middle, upper half considerably thicker, purple, arms short, short-pilose outside, with distinct labia. Disc florets numerous, hermaphrodite, fertile; corollas yellow, actinomorphic, short 5-lobed, lobes erect to slightly spreading; basal anther appendage caudate, short-pilose; style base with distinct basal node, surface very short-papillate, shaft glabrous, expanding gradually upwards, arms short, somewhat enlarged, acute, short-pilose. Achenes apparently 5-ribbed; carpopodium indistinct; pappus heteromorphic, ferrugineous, outer series capillary, multiseriate, unequal, of numerous finely and sparsely barbellate setae, inner series of few awn-like scales with laciniate margins and long-attenuate apices. One species, *U. atacamensis* Phil., Chile and Argentina.

52. *Pachylaena* D. Don ex Hook. & Arn. Fig. 23

Pachylaena D. Don ex Hook. & Arn., Companion Bot. Mag. 1: 106 (1835).

Prostrate, rhizomatous rosulate herbs or subshrubs. Leaves simple, lamina spathulate, fleshy,

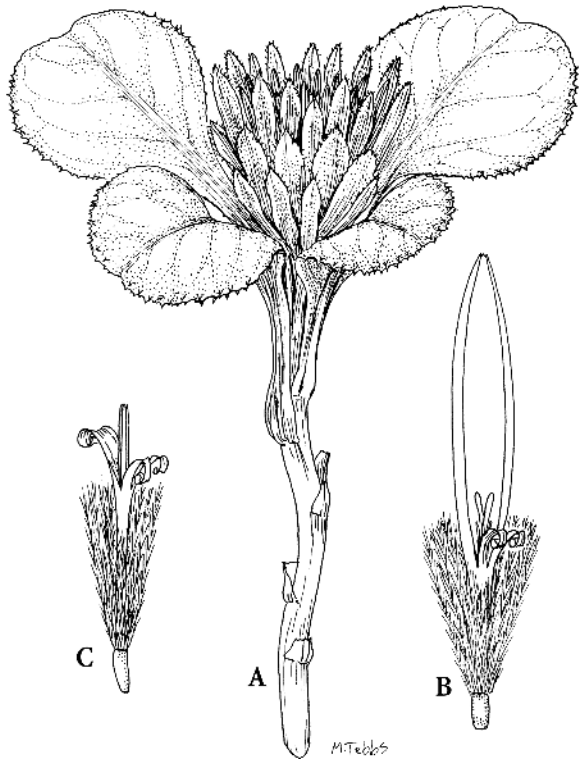

Fig. 23. Compositae-Mutisieae. *Pachylaena atriplicifolia*. **A** Flowering plant. **B** Ray floret. **C** Disc floret. (Drawings by Margaret Tebbs)

finely to coarsely and often irregularly denticulate, apices rounded or obtuse. Capitula solitary, terminal, sessile to subsessile, radiate, large; involucre broadly campanulate to hemispherical; phyllaries 3–5-seriate, imbricate, gradate; receptacle flat to concave, epaleaceous, alveolate to reticulate, naked. Florets heteromorphic, marginal florets female, disc florets hermaphrodite; corollas of marginal florets yellowish-red to pink, bilabiate, outer lip an enlarged 3-toothed limb, corollas of disc florets yellow, bilabiate, outer lip scarcely enlarged, 3-toothed, inner bifid, lobes coiled; basal anther appendages caudate, pilose; style lacking basal node, glabrous, arms short, scarcely bifid, obtuse. Achenes cylindrical; pappus 2–3-seriate, setae broad and flattened at base, margins plumose, somewhat fragile, whitish. Two species, Argentina, Chile.

53. *Brachyclados* D. Don

Brachyclados D. Don, Philos. Mag. 11: 391 (1832); Cabrera, Fl. Patagonica 7: 316–318 (1971), key.

Dwarf caespitose or lax shrubs. Leaves alternate, simple, lamina linear-lanceolate, entire. Capitula solitary, terminal, sessile or short-pedicellate, radiate, heterogamous; involucre campanulate or hemispherical; phyllaries 3–4-seriate, imbricate, gradate; receptacle flat to slightly convex, naked, alveolate. Florets numerous, marginal female, disc hermaphrodite; corollas yellow, of marginal florets bilabiate, outer lip an enlarged 3-toothed limb, inner deeply bifid, lobes spiralled to coiled, corollas of disc florets bilabiate but lacking markedly enlarged limb, outer lip 3-toothed, inner bifid, lobes coiled or recurved; basal anther appendages sagittate, tails pilose; style lacking basal node, glabrous, shaft gradually thickening towards style arms, arms scarcely separating, short, obtuse, apices very short-papillose. Achenes cylindrical; carpopodium obscure; pappus biseriate, barbellate, whitish or yellowish. $n = 23 + 2B$. Three species, Chile, Argentina.

54. *Chaetanthera* Ruiz & Pav.

Chaetanthera Ruiz & Pav., Fl. Peruv. Prodr.: 106, tab. 23 (1794); Cabrera, Revista Mus. La Plata, ser. 2, 1: 87–210 (1937), rev.
Luciliopsis Wedd. (1856).

Erect or prostrate annual or perennial herbs or subshrubs, monoecious, rarely dioecious. Leaves opposite and decussate with connate bases, subulate, or alternate and linear, oblanceolate or spathulate, entire, finely serrate or dentate, sometimes almost pectinate. Capitula terminal, solitary, sessile, rarely 2 or 3 in a cyme, radiate or disciform, heterogamous, rarely homogamous, small to medium; involucre campanulate or cylindrical; phyllaries 2–4-seriate; receptacle usually flat, epaleaceous, glabrous. Ray florets female; corollas white, yellow, rarely orange or reddish, bilabiate, outer lip an enlarged usually 3-toothed limb, rarely lacking teeth, inner of two very short, rarely long lobes, style as in disc florets. Disc florets hermaphrodite or female; corollas yellow, bilabiate, outer lip usually only slightly longer than inner, 3-toothed at apex, inner of two short lobes; basal anther appendages caudate, pilose; style base glabrous and lacking basal node, shaft glabrous, arms short, bifid, short-papillose outside. Achenes terete or sometimes compressed, marginal sometimes filiform and sterile; carpopodium annular; pappus 1–2-seriate, often flattened at base, barbellate or subplumose or almost plumose towards base, whitish to fawn. $n = 11, 12, 14$. Circa 42 species, Argentina, Bolivia, Chile, Peru.

Seven subgenera were recognized by Cabrera (1937).

55. *Lycoseris* Cass.

Lycoseris Cass., Dict. Sci. Nat. 33: 474 (1824); Egeröd & Ståhl, Nordic J. Bot. 11: 549–574 (1991), rev.

Dioecious subshrubs or shrubs, usually scandent. Leaves alternate, simple, lamina ovate, elliptic, lanceolate, entire or serrulate. Capitula solitary, terminal or few to several in corymbs or racemes, large, many-flowered, female often considerably larger than male; involucre hemispherical to campanulate; phyllaries c. 6-seriate in male plants, c. 8-seriate in female plants, in female capitula usually longer; receptacle flat to convex, alveolate from coalesced acicular bristles between achenes. Florets usually numerous, heteromorphic; corollas orange to orange-red, sometimes yellow or violet. Ray florets uniseriate, sterile, bilabiate, outer lip an expanded (1–)3(–5)-toothed limb, inner apparently absent or a single linear lobe; disc florets actinomorphic, relatively short 5-lobed, lobes sometimes of varying lengths, glabrous; functional anthers present only in disc florets of male capitula; basal anther appendages caudate, long-entire, sometimes with 'erose' margins; style base glabrous, of female florets scarcely enlarged but lacking basal node, of male florets with distinct node, shaft of male and female florets glabrous, arms of female florets spreading, flattened, margins papillose, of male florets scarcely divergent or sometimes divergent in ray florets. Achenes cylindrical, ±5-ribbed; carpopodium annular, narrow; pappus setae numerous (150–200) in female florets, few to many (−50) in male florets, flattened, margins barbellate, sometimes with ± dilated apices, fragile, whitish. Eleven species, Central America (Guatemala), northern and western South America (Bolivia, Colombia, Brazil), Mexico, USA.

56. *Cnicothamnus* Griseb.

Cnicothamnus Griseb., Abhand. Königl. Gesell. Wissensch. Göttingen 19: 196 (1874); Cabrera, Fl. Prov. Jujuy, Rep. Argent. X: 576–579 (1978), key.

Shrubs or small trees. Leaves alternate, simple, lamina broadly elliptic or ovate, dentate. Capitula solitary, terminal, large, ± sessile; involucre broadly campanulate to globose; phyllaries multiseriate, imbricate, gradate; receptacle glabrous, convex, naked, scarcely reticulate. Florets numerous, hermaphrodite, heteromorphic; corollas intense orange to orange-red, marginal bilabiate with expanded 3-toothed outer lip, inner lip profoundly bilobed, lobes spiralled or recurved only at apex, disc corollas deeply divided, lobes erect, recurved at apex; basal anther appendages sagittate, tails long, linear, glabrous; style lacking basal node, glabrous, arms scarcely divided, short, obtuse, glabrous. Achenes cylindrical, densely long-setuliferous; carpopodium annular, indistinct; pappus setae 3-seriate, flattened in lower part, barbellate, straw-coloured. $n = 22$. Two species, Argentina, Bolivia.

57. *Plazia* Ruiz & Pav.

Plazia Ruiz & Pav., Fl. Peruv. Prodr.: 104 (1794); Cabrera, Darwiniana 9: 363–386 (1951), rev.
Harthamnus H. Rob. (1980).

Shrubs, often resinous. Leaves spiralled, lamina ovate or oblong, entire. Capitula solitary, terminal, surrounded by leaves, radiate; involucre campanulate; phyllaries few-seriate, imbricate, gradate; receptacle flat to slightly convex, epaleaceous, naked. Florets numerous, hermaphrodite, all fertile; corollas white to pink, glabrous, marginal florets bilabiate, outer lip distinctly 3-toothed, inner profoundly bifid, lobes coiled, inner florets actinomorphic, deeply divided; basal anther appendages caudate, short-pilose, base ± penicillate; style with basal node, glabrous, shaft glabrous, arms scarcely bifid, obtuse, glabrous or short-papillose outside. Achenes glabrous, attenuate towards base and narrowed beneath apical callus; carpopodium almost indiscernible from body of achene, upper margins procurrent on base of achene; pappus multiseriate, setae barbellate, tawny to straw-coloured. $n = 27$. Three species, Peru, Bolivia, Argentina, Chile.

58. *Aphylloclados* Wedd.

Aphylloclados Wedd., Chloris And. 1: 11 (1855); Cabrera, Darwiniana 9: 363–386 (1951), rev.

Almost leafless, well-branched odoriferous shrubs. Leaves alternate, simple, sessile, minute, rapidly falling, linear-spathulate, entire. Capitula solitary, terminal rarely in few-headed scorpioid-like cymes, radiate or disciform; involucre campanulate; phyllaries 3–5-seriate, imbricate, gradate; receptacle flat, naked, alveolate, fimbriate. Florets several to many (c. 10–40), heterogamous or homogamous; corollas lilac to purple, outer florets bilabiate, with an outer 3-toothed limb, inner lip profoundly 2-lobed, lobes linear, recurved to coiled, disc florets actinomorphic, profoundly 5-lobed, lobes recurved, pubescent at apices;

basal anther appendages sagittate, long-pilose; style with basal node, glabrous, shaft glabrous, purplish, arms short, scarcely divergent, apices obtuse. Achenes turbinate; carpopodium short-cylindrical; pappus 2–3-seriate, setae barbellate to subplumose especially near apices, straw-coloured. Five species, Bolivia, Chile, Argentina.

59. *Gypothamnium* Phil.

Gypothamnium Phil., Fl. Atacam.: 27, t. 3C (1860).

Moderately branched glabrous shrubs. Leaves spiralled, often ascending, simple, linear, somewhat fleshy, entire. Capitula terminal, solitary, radiate, medium to large; involucres cup-shaped; phyllaries glabrous; receptacle flat, naked. Florets heteromorphic, heterogamous, marginal florets uniseriate, female, spreading, ± reflexed; disc florets numerous, hermaphrodite; corollas glabrous, purple or pinkish-purple, marginal bilabiate, outer lip enlarged, narrow, 3-toothed, inner profoundly bifid, lobes coiled, disc actinomorphic, profoundly 5-fid, lobes coiled; basal anther appendages caudate, tails sparsely long-pilose; style base scarcely enlarged but lacking basal node, shaft glabrous, arms short, obtuse, scarcely bifid, glabrous or sparsely short-pilose outside. Achenes ± turbinate; carpopodium scarcely discernible; pappus 2–4-seriate, setae straw-coloured, outer series capillary, barbellate, inner series flattened, margins barbellate, apices ± inflated. $n = 36$. One species, *G. pinifolium* Phil., Argentina, Chile.

60. *Cyclolepis* D. Don

Cyclolepis D. Don, Philos. Mag. 11: 392 (1832).

Gynodioecious spiny shrubs. Leaves alternate, simple, lamina small, coriaceous, entire. Capitula few to several on short side shoots, sessile, spicate, discoid, heterogamous; involucre campanulate; phyllaries few-seriate, lowermost scale-like; receptacle small, glabrous, flat to slightly convex. Female florets few, fertile; corollas yellowish, equally five-lobed, or sometimes with one much longer lobe; anther cylinder lacking; style base without basal node, glabrous, shaft glabrous, arms relatively long, bifid, glabrous, edges prominent. Hermaphrodite florets few, fertile; corolla yellowish, equally five-long-lobed, lobes somewhat rolled; anther collar inconspicuous; basal anther appendages caudate, pilose; style base lacking basal node, glabrous, shaft glabrous, arms long, glabrous. Achenes densely setuliferous; carpopodium annular; pappus setae biseriate, long-barbellate below, barbellate to subplumose towards apices, straw-coloured. $n = 27$. One species, *C. genistoides* D. Don, Argentina, Bolivia, Chile(?), Paraguay.

61. *Onoseris* Willd.

Onoseris Willd., Sp. Pl. 3, 3: 1702 (1803); Ferreyra, J. Arnold Arb. 25: 349–395 & Lam. I–IX (1944), rev.

Annual or perennial herbs, subshrubs or suffrutices. Leaves radical or alternate, lamina small to large, linear to broadly ovate or subrhomboid, sometimes hastate, sagittate or lyrate. Capitula solitary or few to many in panicles, usually radiate, rarely discoid, erect; involucre hemispherical, campanulate or turbinate; phyllaries many-seriate, imbricate, gradate, persistent and spreading after loss of achenes; receptacle flat, glabrous or long-pilose, sometimes fimbrillate. Ray florets, when present, uniseriate, female; corollas violet or purple, bilabiate, outer lip enlarged, 3-toothed, inner inconspicuous, usually 2-lobed, sometimes rudimentary or even lacking, anthers rudimentary; style base with basal node, glabrous, shaft glabrous, arms appearing adnate or scarcely divergent at very apices, often distinctly clavate, glabrous. Disc florets hermaphrodite, fertile, numerous; corollas usually yellow, reddish or purple, tubular, 5-lobed, lobes equal or unequal, or sometimes subligulate with an enlarged 4-toothed limb and inner lip a single long, linear lobe; basal anther appendages long-caudate, often sparsely retrorsely short-papillate, anther collar with obvious constriction at base; style base with distinct basal node, glabrous, shaft glabrous, arms short, obtuse, papillate at least around margin. Achenes cylindrical, 3–6-ribbed, sometimes very conspicuously, narrowed beneath distinct apical callus; carpopodium a distinct annulus with upper margins procurrent on base of achene body, sometimes eccentric; pappus setae 2-seriate to multiseriate, barbellate, isomorphous and capillary or heteromorphous with inner series larger and broader, more numerous and sometimes darker than outer series, yellowish, straw-coloured or off-white. $n = 18$. Circa 32 species, Central and South America (Argentina, Bolivia, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Peru).

62. *Ianthopappus* Roque & D.J.N. Hind

Ianthopappus Roque & D.J.N. Hind, Novon 11: 97 (2001).

Subshrub. Leaves alternate, lamina coriaceous, elliptic to orbicular. Capitula few to many in

lax corymbs, radiate, heterogamous; involucre few-seriate; phyllaries densely sericeous outside, apices long-acute; receptacle convex, glabrous, naked. Ray florets female, fertile; corolla glabrous, bilabiate, outer limb white, often purplish beneath, short three-toothed, inner lip of two long rolled lobes; basal anther appendages caudate, long-attenuate, margins pilose; style base with basal node, glabrous, shaft glabrous, arms purple, short, with thickened margins. Disc florets hermaphrodite, fertile, actinomorphic; corollas purplish, lobes revolute; basal anther appendages caudate, long-attenuate, margins pilose; style base with basal node, glabrous, shaft glabrous, arms purple, short-bifid, with thickened margins. Achenes long-cylindrical, obscurely 10-ribbed; carpopodium annular; pappus setae 3-seriate, barbellate, apices slightly dilated, purplish to red wine-coloured. One species, *I. corymbosus* (Less.) Roque & D.J.N. Hind, northern Argentina, the extreme south of Brazil, Uruguay.

63. *Hyalis* D. Don ex Hook. & Arn.

Hyalis D. Don ex Hook. & Arn., Companion Bot. Mag. 1: 108 (1835).

Rhizomatous shrubs. Leaves alternate, simple, lamina linear-lanceolate to oblong-lanceolate, entire. Capitula few in corymbs, radiate, pedicellate; involucre narrowly campanulate; phyllaries 3-seriate, imbricate, gradate; receptacle flat, naked. Florets hermaphrodite, 5–6, fragrant; corollas glabrous, usually pink, sometimes white or purplish, marginal florets 4–5, bilabiate, outer lip 3-toothed, inner profoundly bilobed, lobes coiled, central floret solitary, actinomorphic, deeply divided, lobes revolute to tightly coiled; basal anther appendages sagittate, tails laciniate to long-pilose; style shaft glabrous, arms scarcely bifid, obtuse, glabrous. Achenes obovoid to turbinate, 10-ribbed; carpopodium a narrow annulus; pappus multiseriate, setae numerous, barbellate, often slightly inflated and ± subplumose towards apices, whitish. $n = 27$. Two species, Bolivia, Paraguay, Argentina.

64. *Lulia* Zardini

Lulia Zardini, Bol. Soc. Argent. Bot. 19: 255 (1980).

Subshrub or perennial herb. Leaves alternate, simple, lamina coriaceous, entire. Capitula solitary, terminal on scapes, radiate; involucre campanulate or hemispherical; phyllaries 4–5-seriate, imbricate, gradate; receptacle glabrous, concave to flat, alveolate. Ray florets uniseriate, female; corollas yellow or orangish, glabrous, bilabiate, outer lip a ray, 3-toothed at apex, considerably longer than inner, inner strongly 2-lobed, lobes linear, often twisted along their length; staminodes present; style base lacking basal node, expanding gradually towards upper part, shaft glabrous, arms short, short-papillose outside, margins thickened. Disc florets hermaphrodite; corollas yellow, bilabiate, lips equal, outer 3-toothed at apex, inner 2-lobed, lobes long-acute, erect, filaments glabrous; basal anther appendages very long-caudate, pilose; style base lacking basal node, glabrous, shaft glabrous, arms short-pilose outside, margins somewhat thickened. Achenes obcompressed with 2 or often 4 ribs, rostrate; pappus setae 2–3-seriate, flattened, barbellate, off-white, apices dilated and conspicuously darker than main stipe, often fawn. One species, *L. nervosa* (Less.) Zardini, Brazil.

65. *Chucoa* Cabrera

Chucoa Cabrera, Bol. Soc. Argent. Bot. 6, 1: 40 (Nov. 1955). *Weberbaueriella* Ferreyra (1955), non *Weberbauerella* Ulbr. (1906) [Leguminosae-Papilionoideae].

Poorly and laxly branched shrubs. Leaves alternate, lamina oblanceolate, spinose-dentate with few spines, apices spiny. Capitula solitary, long-pendunculate, axillary, or two capitula in divaricately branched axillary inflorescence, discoid, homogamous, slightly nodding before anthesis but erect in flower; involucre turbinate to narrowly campanulate; phyllaries 4–5-seriate, gradate, imbricate, subulate, ending in a long spine; receptacle flat to slightly convex, epaleaceous, alveolate, margins of alveolae ciliate. Florets actinomorphic, hermaphrodite, several; corollas 5-lobed, yellow; basal anther appendages long-sagittate, usually entire, sometimes appearing laciniate/rough; style base with glabrous basal node, shaft glabrous throughout, arms short, usually adpressed, short-papillate outside. Achenes cylindrical; carpopodium stopper-shaped with thickened upper margin; pappus setae multiseriate (3+), persistent, barbellate, more densely so towards apices. One species, *C. ilicifolia* Cabrera, endemic to Peru.

II.5. Subtribe Gerberinae Benth. & Hook. f. (1873).

Rosettiform herbaceous annuals or perennials, rarely shrubs. Leaves alternate, rosulate. Inflorescences scapiform, peduncles usually elongating

as achenes ripen; capitula chasmogamous or rarely cleistogamous; involucres hemispherical, campanulate or turbinate; phyllaries 2–7-seriate; receptacles epaleaceous, glabrous or rarely with fimbriate scales; florets usually homomorphic and all fertile; style shaft rarely papillose in upper part, arms short, apices rounded. Achenes fusiform or cylindrical, apices truncate or beaked, setuliferous or rarely papillate; carpopodium annular or absent; pappus setae 2–3-seriate, rarely uniseriate or multiseriate, capillary, barbellate.

66. *Trichocline* Cass.

Trichocline Cass., Bull. Sci. Soc. Philom. 1817: 13 (1817); Zardini, Darwiniana 19: 618–733 (1975), rev.

Perennial scapigerous herbs or shrubs, rarely caespitose. Leaves rosulate, lamina linear, linear-lanceolate, oblanceolate, elliptic, oblong or occasionally orbicular, lyrate or pinnatipartite to pinnatisect, entire, lobed, dentate or rarely undulate. Capitula solitary on scapes, radiate, erect; involucre hemispherical; phyllaries 3–7-seriate, outer series usually foliaceous, inner series imbricate, gradate, rarely all phyllaries gradate; receptacle flat or sometimes concave, epaleaceous, smooth, with ridge around insertion point of achenes or alveolate with fimbriate scales between achenes. Ray florets female, uniseriate, yellow to orangish yellow or rarely reddish, outer lip conspicuous, spreading, apices very short 3-toothed, inner of two long linear spiralled lobes; staminodes with sterile anthers; style base lacking basal node, glabrous, shaft glabrous, arms short, undivided or slightly divergent and spreading. Disc florets numerous, hermaphrodite; corollas bilabiate, outer lip short 3-toothed, inner of two short linear lobes; basal anther appendages long-sagittate, very long-papillose or pilose; style base lacking basal node, glabrous, shaft glabrous, arms scarcely divided to slightly recurved, rounded or obtuse, very short-papillose. Achenes ovoid, densely setuliferous; pappus setae multiseriate, persistent, barbellate, sometimes with dilated apices, occasionally with crisped apices, white or off-white. $n = 18, 20$. Twenty-one species, Argentina, Bolivia, Brazil, Chile, Colombia, Paraguay, Peru, Uruguay.

67. *Chaptalia* Vent. Fig. 24

Chaptalia Vent., Descr. Pl. Jard. Cels: tab. 61 (1802); Burkart, Darwiniana 6: 505–594, pl. i–x (1944), reg. rev.; Nesom, Brittonia 36: 396–401 (1984), part. rev.; Phytologia 78: 153–188 (1995), reg. rev.

Scapigerous perennial, rarely annual, herbs. Leaves rosulate, simple, often relatively few, lamina elliptic to obovate, unlobed or lyrate-pinnatifid, entire, finely toothed or lobed. Capitula solitary, terminal on scapes, conspicuously or inconspicuously radiate, heterogamous, nodding at first becoming erect in flower and fruit, sometimes nodding in

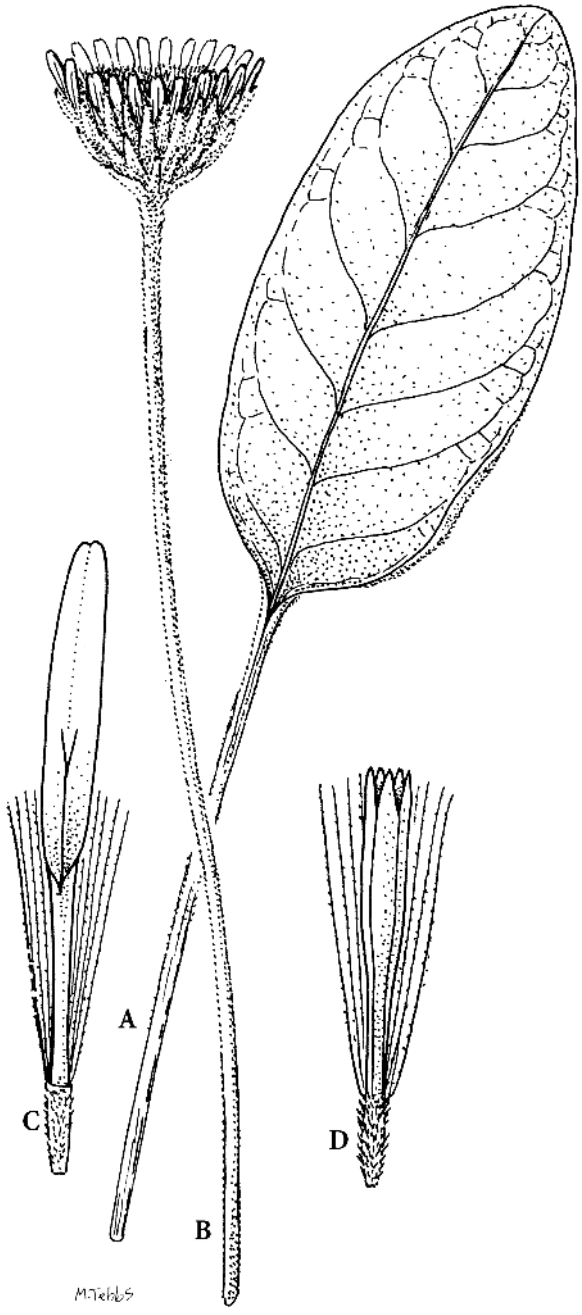

Fig. 24. Compositae-Mutisieae. *Chaptalia chapadensis*. **A** Rosette leaf. **B** Scapose inflorescence. **C** Ray floret. **D** Disc floret. (Drawings by Margaret Tebbs)

fruit or always erect, chasmogamous or sometimes cleistogamous; involucre turbinate to campanulate or hemispherical, elongating in fruit; phyllaries imbricate, gradate, 3–6-seriate; receptacle flat to slightly concave, foveolate/alveolate or smooth, glabrous, epaleaceous. Florets many, usually trimorphic, sometimes dimorphic without intermediate florets, marginal florets 1–2(–3)-seriate, female; corollas usually white or creamy white, rarely purplish, sometimes with purplish midstripe beneath limb, bilabiate, outer lip an enlarged limb, apices short 3-toothed, inner present or absent, if present, then of 2 relatively small linear to narrowly lanceolate lobes; style shaft glabrous, arms linear to elliptic, acute, papillose inside; intermediate florets female, corollas often bilabiate with distinct ray and sometimes with abortive staminodes or sometimes corolla reduced to filiform tube surrounding style; central/disc florets, when present, hermaphrodite, usually functionally male, corollas white, cream or pinkish, sometimes with a purplish stripe if bilabiate and appearing radiate, bilabiate or actinomorphic with erect or reflexed short lobes; basal anther appendages caudate, tails usually entire; style base lacking basal node, glabrous, shaft glabrous, arms short, scarcely spreading. Fertile achenes fusiform or rostrate with distinctive prolonged beak, usually 5-ribbed (4–12-ribbed), glabrous or setuliferous; pappus setae uniseriate, numerous, connate into small cup at apex of beak, barbellate, pale straw-coloured. n = 16, 24. Circa 60 species, southern USA, West Indies, Central and South America, with one species from Texas south to Argentina.

68. *Leibnitzia* Cass.

Leibnitzia Cass., Dict. Sci. Nat. 25: 420 (1825); Hansen, Nordic J. Bot. 8: 61–76 (1988), reg. rev.; Nesom, Brittonia 35: 126–139 (1983), reg. rev.

Perennial scapose herbs. Leaves rosulate, appearing concurrently with first capitula, lamina discolorous, entire to lyrate-lobed. Capitula solitary on long scapes, usually chasmogamous, radiate, heterogamous, sometimes cleistogamous, erect; involucre turbinate; phyllaries imbricate, usually 3–4-seriate, gradate; receptacles flat to slightly convex, foveolate. Florets all with fertile ovaries; corollas white, cream, pink or purple-tinged, bilabiate, marginal florets with an expanded limb, female, those of cleistogamous heads with reduced limb, disc florets tubular, hermaphrodite, those of chasmogamous heads strongly bilabiate, those of cleistogamous heads ± actinomorphic with very short lobes; basal anther appendages caudate; style base lacking basal node, glabrous, shaft glabrous, arms short, scarcely divergent, rounded, dorsally pilose. Achenes fusiform, short- or long-rostrate in some species, moderately setuliferous, setulae adpressed and ascending; carpopodium a minute annular ring; pappus setae 2–3-seriate, numerous, finely barbellate, capillary, persistent, straw-coloured or purple. n = 23. Six species, China, Guatemala, India, Japan, Nepal, Siberia, Taiwan, and Mexico and the south-western USA.

69. *Uechtritzia* Freyn

Uechtritzia Freyn, Oesterr. Bot. Z. 42: 240 (1892); Hansen, Nordic J. Bot. 8: 61–76 (1988), rev.

Scapose perennial herbs. Leaves rosulate, lamina lyrate, pinnatifid or entire and ± sinuate. Capitula solitary on terminal scape, radiate, usually homogamous; involucre hemispherical; phyllaries imbricate, gradate, 5–7-seriate; receptacle alveolate, margins fimbriate-laciniate. Ray florets uniseriate, female with staminodes; corolla pale pink or purple, bilabiate, outer lip limb-like, short 3-toothed, inner of two long, sometimes coiled lobes, glabrous; basal appendages of staminodes caudate, scarcely pilose; style base lacking basal node, glabrous, shaft glabrous, arms short, connate, short-papillose outside. Disc florets numerous, hermaphrodite, fertile; corollas pink or purple, glabrous, bilabiate with two subequal lips, outer short 3-toothed, inner of two long tightly coiled lobes (or outer 2-toothed, inner with 3 long coiled lobes); basal anther appendages long-caudate, short-pilose; style base lacking basal node, glabrous, shaft glabrous, arms short, scarcely separated, short-papillose outside. Achenes often obscurely 6–11-ribbed; pappus setae 2–3-seriate, barbellate, apices more coarsely and densely barbellate, white to off-white. Three species, Armenia, Turkey, Afghanistan, China, India and Kashmir.

70. *Amblysperma* Benth.

Amblysperma Benth., Enum. pl.: 67 (1837).

Perennial rosulate herbs. Leaves probably seasonal, lamina oblanceolate, sinuate to lobulate or sometimes very broadly serrate with mucronate lobes, sometimes entire. Capitula solitary on terminal scapes, radiate; involucre turbinate to campanulate; phyllaries 3–5-seriate, gradate, imbricate; receptacle epaleaceous, glabrous, flat to slightly convex, scarcely ridged between achenes.

Florets numerous, all fertile, heteromorphic. Ray florets functionally female, uniseriate; corollas glabrous with prominent well-developed outer lip forming ray, apex short 3-toothed, white above and pink to brownish purple beneath, inner of two long linear lobes, usually tightly coiled, often somewhat dissimilar; basal appendages of staminodes decurrent on the filament; style base lacking basal node, glabrous, shaft glabrous, arms adnate. Disc florets with poorly developed outer lip of three longish teeth or sub-bilabiate to actinomorphic with five subequal lobes; basal anther appendages long-caudate, usually smooth; style base lacking basal node, glabrous, shaft glabrous, arms relatively short, scarcely divided, short-papillate outside towards apices. Achenes cylindrical, densely covered in long papillae with rounded/blunt apices; pappus setae few-seriate, persistent, barbellate, off-white. Two species endemic to western Australia.

71. *Perdicium* L.

Perdicium L., Pl. Rar. Afric.: 22 (1760).

Perennial scapigerous herbs. Crown usually white-lannose. Leaves rosulate, few, lamina narrowly obovate, coarsely lobed, sometimes almost runcinate, lobes sparsely serrate. Capitula solitary, terminal on scapes, disciform, heterogamous; involucre campanulate, few-seriate; phyllaries gradate, imbricate; receptacle epaleaceous, convex. Florets bilabiate, corollas white, glabrous; marginal florets uniseriate, female; corollas with short 3-toothed outer lip, inner of two long lobes; staminodes absent; style shaft glabrous; style arms moderately long, short-papillose outside, obtuse; central/disc florets probably bilabiate at first, but appearing long 5-lobed in some material; basal anther appendages long-caudate, entire; style base lacking basal node, but often with a nectary disc, glabrous, shaft glabrous, cylindrical, arms short, scarcely divided, short-papillose outside. Achenes terete, densely papillate or glabrous, papillae with obtuse apices; pappus setae multiseriate, barbellate, usually united into a distinct cupule-like callus at base and detached as a unit. Two species, South Africa.

72. *Gerbera* L.

Gerbera L., Opera Varia: 214/247 (1758), nom. cons.; Hansen, Opera Bot. 78: 1–36 (1985), sect. rev.; Nordic J. Bot. 5: 451–453 (1985), sect. rev.; Nordic J. Bot. 8: 61–76 (1985), sect. rev.; Humbert, Fl. Madag. III: 854–868 (1963), reg. rev. *Piloselloides* (Less.) C. Jeffrey (1967).

Scapigerous perennial herbs from woody rootstocks. Rootstock/crowns lanate or villous. Leaves rosulate, lamina elliptic, ovate or subcircular, herbaceous or coriaceous, entire, serrulate, dentate, pinnatifid or pinnatisect. Capitula solitary on terminal scapes, erect, heterogamous, bilabiate-radiate; involucre broadly obconic, cylindrical to broadly campanulate; phyllaries 2-seriate to multiseriate, numerous, imbricate, gradate; receptacle flat to convex, epaleaceous, shallowly alveolate. Corollas white, yellow, pink or red (paler-coloured corollas often tinged pink or violet beneath), all 2-lipped, outer lip strap-shaped or shortly elliptic and 2–3-toothed, inner of 2 small linear lobes. Marginal florets female, radiate, submarginal florets female, equally bilabiate, central florets hermaphrodite, equally bilabiate; basal anther appendages caudate, tails entire or 'ciliate'; style base lacking basal node, glabrous, shaft glabrous except for portion just beneath style arms which has scattered to moderate short papillae, style arms of hermaphrodite florets short and broadly lanceolate, rounded or sub-acute with short pollen sweeping-hairs outside. Achenes fusiform to narrowly flask-shaped, of outer florets sometimes filiform to narrowly cylindrical and infertile, ± attenuate above or distinctly rostrate, sometimes very long-beaked, 4–10-ribbed, sparsely setuliferous, setulae, when without divided apices, acute or obtuse; pappus multiseriate, setae minutely barbellate, white, cream, straw-coloured, pinkish or reddish. n = 23, 25. Circa 30 species, China, Kenya, Malawi, Madagascar, Mozambique, South Africa, Tanzania, Uganda, Yemen, Zimbabwe. One species, *G. hieracioides* (Kunth) Zardini, is native in South America (Ecuador and Peru) but its inclusion in the genus is disputed (Jeffrey 1967; Zardini 1974; Hansen 1985a, b, 1990, 1991b).

The genus has been divided into six sections by Hansen (1985a, b, 1988, 1990; cf. Jeffrey 1967).

II.6. Subtribe Gochnatiinae Benth. & Hook. f. (1873).

Gynodioeceous, hermaphrodite, gynomonoeceous or polygamous subshrubs, shrubs or trees. Leaves alternate or rosulate. Inflorescences scapiform, paniculate or corymbose; capitula homogamous (hermaphrodite or female) or heterogamous (hermaphrodite and female, radiate or discoid;

involucre campanulate or turbinate; phyllaries 3–10-seriate; receptacle glabrous, epaleaceous; florets few to many, female, male or hermaphrodite, corollas bilabiate (1/3, 2/3, 1/4) or actinomorphic and deeply 5-lobed; style arms short, glabrous. Achenes cylindrical to turbinate; ribbed, densely setuliferous; carpopodium cylindrical or annular; pappus setae 1–3-seriate, barbellate, whitish, yellowish or reddish.

73. *Gochnatia* Kunth Fig. 25

Gochnatia Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. (folio ed.) 4: 15 (1818); Cabrera, Revista Mus. La Plata, Secc. Bot. 12: 1–160 (1971), rev.

Monoecious shrubs or trees. Leaves alternate, simple, lamina narrowly lanceolate, elliptic, ovate or obovate, entire, dentate or denticulate (sometimes only in upper part of leaf), rarely spiny. Capitula solitary, terminal or few to many in dense terminal clusters or (sect. *Hedraiophyllum*) numerous in panicles, cymes, corymbs or 'glomerules', small to relatively large, often subtended by numerous reduced leaf-like bracts; involucres cylindrical, turbinate or campanulate; phyllaries 4–10-seriate (sometimes many-seriate and decrescent in size down pedicel or towards base), imbricate, gradate; receptacle epaleaceous, sometimes alveolate or foveolate, glabrous or with short hairs and sometimes glands. Florets few to many (4–c. 150), hermaphrodite; corollas actinomorphic, profoundly 5-lobed, white to cream or yellow, ± orangish; basal anther appendages long-caudate, sometimes very long, finely pilose or glabrous/entire; style base lacking basal node, glabrous, shaft glabrous, arms short and scarcely separating to somewhat bifid, rounded to truncate. Achenes cylindrical to turbinate, often ribbed; carpopodium a distinct annulus or short to distinct cylinder; pappus setae 2(–3)-seriate, setae persistent, barbellate, straw-coloured, yellowish to reddish. $n = 23$. Circa 60 species, mostly from Cuba and the Caribbean Islands, including Puerto Rico, Haiti, Dominican Republic, Bahamas, few species in South America (Brazil, Bolivia, Peru, Argentina, Paraguay), and USA and Central America (Mexico).

Six sections have been recognized by Cabrera (1971), and eight by Freire et al. (2002).

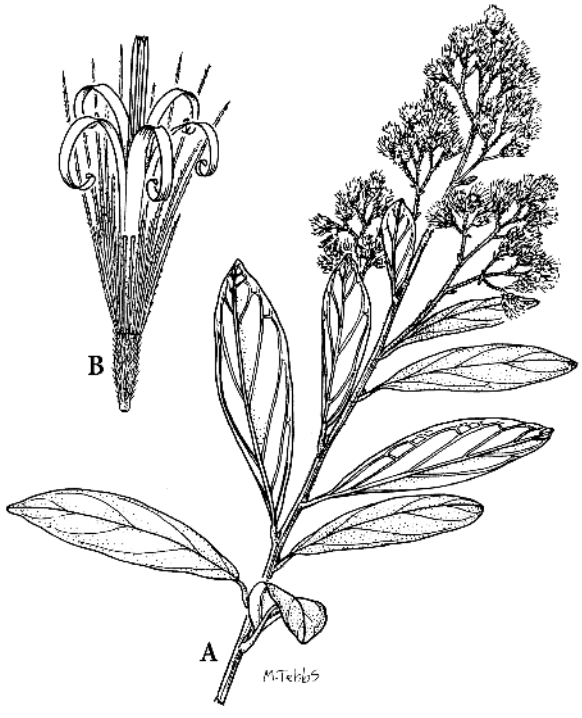

Fig. 25. Compositae-Mutisieae. *Gochnatia floribunda*. **A** Flowering branch. **B** Floret. (Drawings by Margaret Tebbs)

74. *Pentaphorus* D. Don

Pentaphorus D. Don, Trans. Linn. Soc. London 16: 296 (1830).

Monoecious shrubs. Leaves alternate, sessile, entire, coriaceous, glandular-punctate. Capitula in dense terminal clusters, sessile or subsessile, discoid; involucre cylindrical to turbinate; phyllaries 4–5-seriate, gradate, imbricate; receptacle glabrous, epaleaceous. Florets few to several, (3–)5–20, hermaphrodite; corollas deeply 5-lobed, lobes erect to partially coiled; basal anther appendages caudate, entire or antrorsely laciniate; style base lacking basal node, glabrous, shaft glabrous, arms rounded, scarcely separate, glabrous. Achenes turbinate; carpopodium a pale or dark cylinder; pappus setae numerous, biseriate, subequal, ascending to spreading, flattened with barbellate margins, pale straw-coloured. Two species, Argentina, Chile.

Cabrera (1971) and Freire et al. (2002) treated *Pentaphorus* as a section of *Gochnatia*. I prefer to recognize it as a separate genus.

75. *Richterago* Kuntze Fig. 26

Richterago Kuntze, Rev. Gen. Pl. 1: 360 (1891); Roque & Pirani, Taxon 50: 1155–1160 (2001), rev.
Seris Less. (1830), nom. illegit.
Actinoseris Cabrera (1970).

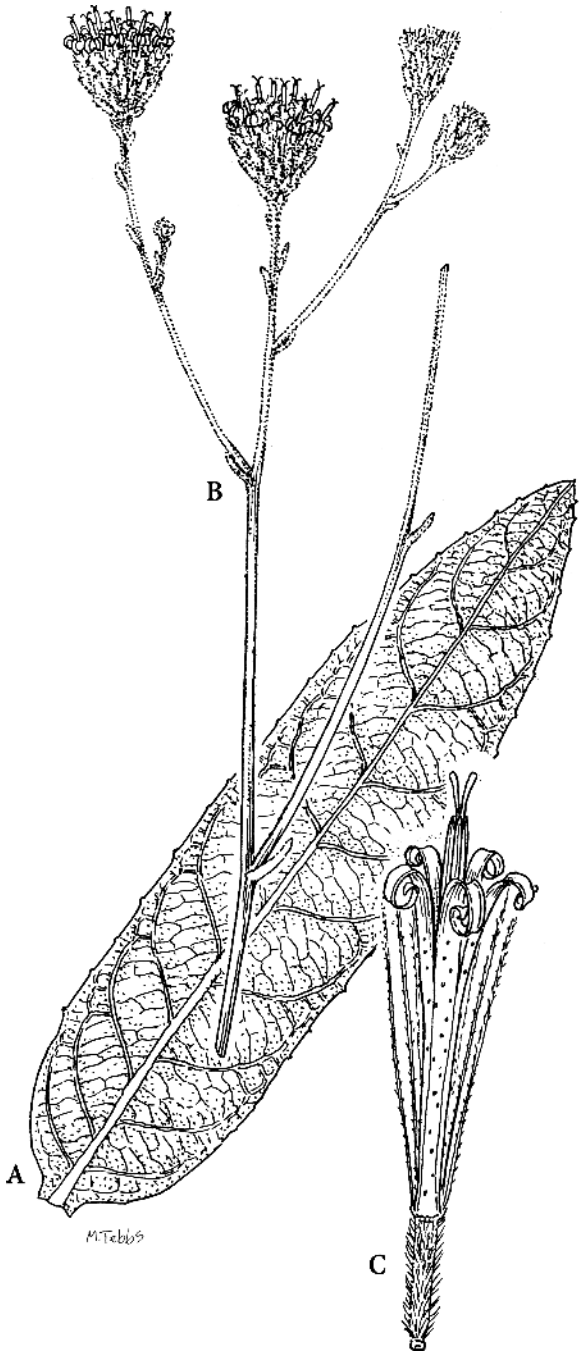

Fig. 26. Compositae-Mutisieae. *Richterago discoidea*. **A** Rosette leaf. **B** Inflorescence. **C** Floret. (Drawings by Margaret Tebbs)

Subshrubs or shrubs, often single-stemmed. Leaves alternate, rosulate, lamina linear, obovate or spathulate, entire or denticulate. Capitula solitary on scapes or in few-headed panicles, radiate or discoid; involucre campanulate to hemispherical or turbinate; phyllaries multiseriate, gradate, imbricate; receptacle flat to slightly convex, alveolate, glabrous, epaleaceous. Ray florets when present uniseriate, white, pink, or purplish; corolla bilabiate, outer lip 3- or sometimes 4-toothed, inner of two long, tightly coiled lobes (or one, if outer lip 4-toothed); staminode bases caudate and pilose; style base glabrous with basal node, shaft glabrous, arms glabrous, moderately long, scarcely divergent. Disc florets numerous, multiseriate, fertile, white, creamish or pink; corollas actinomorphic, deeply 5-lobed; basal anther appendages caudate, laciniate; style base with basal node, glabrous, shaft glabrous, arms relatively short, sometimes scarcely divergent. Achenes cylindrical; carpopodium annular, sometimes excentric; pappus setae uniseriate, barbellate, white to off-white or straw-coloured. Nine species, Brazil.

II.7. Hecastocleis Group

Tribe Hecastocleideae Panero & V.A. Funk (2002).

Shrubs. Leaves dimorphic, primary alternate, margins spiny, secondary fasciculate at bases of brachyblasts, apices spiny. Inflorescences solitary, terminal and surrounded by broad foliaceous spinescent bracts forming a secondary involucre enclosing several capitula; capitula discoid, single-flowered; involucre narrowly cylindrical; phyllaries 3–4-seriate, spiny; receptacle glabrous, epaleaceous; florets hermaphrodite; corollas actinomorphic, deeply 5-lobed; style arms short. Achenes glabrous; carpopodium inconspicuous; pappus a scale-like corona.

Only one genus:

76. *Hecastocleis* A. Gray

Hecastocleis A. Gray, Proc. Amer. Acad. Arts Sci. 17: 221 (1881).

Characters of the group. $n = 8$. One species, *H. shockleyi* A. Gray, USA (Nevada and California).

II.8. Nouelia Group

Large shrubs or treelets. Leaves alternate. Inflorescence terminal solitary capitula or capitula in dense corymbs or glomerules; capitula homogamous, radiate or discoid; involucres turbinate or campanulate; phyllaries 4–7-seriate; receptacles epaleaceous; florets all hermaphrodite and fertile,

ray florets bilabiate, disc florets and those of discoid capitula actinomorphic and deeply 5-lobed; style arms short to moderately long. Achenes cylindrical to turbinate, setuliferous; carpopodium annular; pappus setae 2–3-seriate, capillary, barbellate.

77. *Nouelia* Franch.

Nouelia Franch., J. Botanique 2, 5: 66 (1888).

Shrub to small tree. Leaves alternate, lamina elliptic, entire or minutely serrate. Capitula solitary, terminal, radiate, homogamous; involucre turbinate to campanulate; phyllaries multiseriate (6–7), coriaceous, imbricate, gradate; receptacle flat to convex, glabrous, alveolate. Florets all hermaphrodite, fertile, marginal florets uniseriate, bilabiate, outer lip 3-toothed to long 3-lobed at apex, inner of two long lobes, tightly rolled, disc florets numerous, actinomorphic, deeply 5-lobed, lobes tightly rolled; basal anther appendages pilose; style base glabrous, gradually narrowing upwards into glabrous shaft, arms short, glabrous. Achene with annular carpopodium; pappus setae 2–3-seriate, many, barbellate, fawn. $n = 27$. One species, *N. insignis* Franch., China (Sichuan–Yunnan region).

78. *Leucomeris* D. Don

Leucomeris D. Don, Prodr. Fl. Nepal.: 169 (1825).

Large shrubs or small trees. Leaves alternate, lamina broadly lanceolate to elliptic, entire. Capitula in a dense terminal cyme or panicle or in a dense many-headed terminal glomerule; involucres narrowly turbinate; phyllaries 4–5-seriate; receptacle small, epaleaceous, scarcely alveolate. Florets few to several, (4–)6–10, hermaphrodite; corollas actinomorphic, deeply 5-lobed, white, lobes long, usually recurved, sometimes strongly coiled; basal anther appendages caudate, sometimes contorted, entire to very irregularly and sparsely short-laciniate; style base lacking basal node but slightly swollen towards base, shaft glabrous, arms moderate, linear, obtuse. Achenes cylindrical to turbinate, often ribbed; carpopodium a distinct pale cylinder; pappus setae 2–3-seriate, somewhat flattened at base, barbellate, straw-coloured yellowish to reddish. $n = 27$. Two species, Burma, China, India, Nepal, Pakistan, Thailand, Vietnam.

II.9. Catamixis Group

Small shrubs. Leaves alternate, coriaceous. Inflorescences corymbose; capitula homogamous, ligulate; involucre turbinate; phyllaries 4–5-seriate, scarcely imbricate; receptacle epaleaceous; corollas yellow; apical anther appendages narrow-triangular; style arms short, acute. Achenes densely long-setuliferous, apices acute; carpopodium annular; pappus setae uniseriate, long-barbellate, white.

Only one genus:

79. *Catamixis* T. Thomson

Catamixis T. Thomson, J. Linn. Soc., Bot. 9: 342 (1865).

Characters of the group. One species, *C. baccharoides* T. Thomson, India and the Himalayas.

II.10. Subtribe Tarchonanthinae Cass. ex Dumort. (1829).

Dioecious trees or shrubs. Leaves alternate. Inflorescences terminal capitula or axillary panicles or racemes, or glomerulous; capitula unisexual, discoid or disciform; involucres campanulate, hemispherical or globular; phyllaries 1–5-seriate; receptacle glabrous or with long silky hairs; corollas 5-lobed, white, lobes villous; apical anther appendages attenuate; style arms short, flat, acute. Achenes of female florets fusiform, ribbed, densely setuliferous; carpopodium annular; pappus absent or setae uniseriate and barbellate.

80. *Brachylaena* R. Br.

Brachylaena R. Br., Trans. Linn. Soc. London 12: 115 (1817); Beentje, Kew Bull. 55: 1–41 (2000), rev.

Semi-deciduous, deciduous or evergreen dioecious trees or shrubs. Leaves alternate, lamina elliptic to obovate, entire, denticulate, repand or coarsely dentate to sinuate towards apex. Capitula numerous, terminal in axillary panicles or racemes, or in clusters or glomerules, unisexual, disciform, few- to several-flowered; phyllaries imbricate, few-seriate (usually 3–5); receptacle epaleaceous, small, scarcely ridged. Female capitula few- to many-flowered, (1–)4–80, involucre campanulate; corollas filiform, 5-lobed, lobes loosely coiled to ascending; staminodes occasionally present; style base glabrous, arms exserted, short to medium, flat, spreading to coiled, acute, papillate outside; achenes fusiform, 4–8-ribbed; carpopodium a narrow annulus; pappus setae 2–3-seriate, setae subequal or with several outer much shorter, barbellate, pale straw-coloured. Male capitula

smaller than female, involucre turbinate or campanulate; florets few to many, (1–)4–40; corollas funnel-shaped, 5-lobed, white, lobes relatively short, usually coiled; basal anther appendages moderately short-tailed, entire to slightly laciniate, style base lacking basal node but with prominent nectary, glabrous, shaft glabrous, arms short-bifid, short-papillose, acute; achenes rudimentary; pappus setae uniseriate, barbellate, off-white to straw-coloured. Eleven species, Angola, Botswana, Kenya, Madagascar, Mozambique, South Africa, Swaziland, Tanzania, Uganda, Zimbabwe.

81. *Tarchonanthus* L.

Tarchonanthus L., Sp. Pl.: 842 (1753); Pope, Fl. Zamb. 6, 1: 9–11 (1992), reg. rev.; Beentje, Kew Bull. 54: 81–95 (1999), rev.; Herman, Bothalia 32: 21–28 (2002), reg. rev.

Dioecious trees or shrubs, often aromatic, evergreen. Leaves alternate, lamina elliptic to narrowly obovate, entire to coarsely irregularly serrate or rarely apically 3-lobed towards apex. Capitula numerous in terminal or axillary panicles, unisexual, discoid; involucre campanulate to hemispherical or globular; phyllaries 1–3-seriate, imbricate, gradate; receptacle ± convex, epaleaceous, sometimes with long silky hairs. Male capitula many-flowered; corollas cream, tubular or funnel-shaped, longer than female, lobes 5, relatively short, apices recurved; basal anther appendages short-caudate, entire, connate with neighbouring appendage; style base lacking basal node but with prominent nectary, glabrous, shaft glabrous, relatively short, style simple or shortly bifid. Female capitula 1-, 2- or 3-flowered; corolla lobes 4–5, equalling tube and usually recurved, anthers absent; style base without node, glabrous, shaft glabrous, arms exserted, short, flat, glabrous. Achenes obovoid or ellipsoid, densely long-setuliferous; pappus absent. Two species, Angola, Botswana, Ethiopia, Kenya, Lesotho, Mozambique, Namibia, Saudi Arabia, Somalia, South Africa, Swaziland, Tanzania, Uganda, Yemen, Zambia.

II.11. Dicoma Group

Tribe Dicomeae Panero & V.A. Funk (2002).

Annual or perennial herbs, subshrubs, shrubs or small trees. Leaves alternate. Inflorescences of solitary or many terminal capitula, or terminal and scapose, corymbose or racemose; capitula homogamous and discoid, heterogamous and radiate, or rarely heterogamous and disciform; involucre campanulate to almost hemispherical or urceolate; phyllaries 4–10-seriate, sometimes spinescent; receptacles very rarely paleaceous; ray florets, when present, uniseriate, usually female, bilabiate (2/3); disc florets hermaphrodite, numerous, actinomorphic; style shaft glabrous, style arms short, scarcely divided, acute, obtuse or rounded, sometimes with a subapical fringe of hairs or papillae Achenes turbinate or fusiform to cylindrical, glabrous or densely long-setuliferous; carpopodium annular or apparently absent; pappus setae 1–many-seriate, capillary or sometimes flattened and squamelliform, barbellate or subplumose to plumose, rarely laciniate.

82. *Oldenburgia* Less.

Oldenburgia Less., Linnaea 5: 252 (1830); Bond, S. African J. Bot. 53: 493–500 (1987), rev.

Shrubs or small trees. Leaves alternate, rosulate at branch apices, simple, lamina thick and coriaceous, narrowly oblanceolate to oblanceolate or narrowly obovate, entire. Capitula solitary or in few-headed cymes, medium to large, homogamous, radiate, sessile or pedicellate; involucre campanulate to almost hemispherical or urceolate; phyllaries imbricate, 'subgradate' with shorter outer but subequal middle and inner series, or entirely gradate, 4–10-seriate; receptacle flat to concave, epaleaceous, alveolate, alveole margins somewhat fimbriate. Ray florets uniseriate, female; corollas white or rarely pink, bilabiate, outer lip an elongated limb, short 3-toothed, inner of two long linear coiled lobes; basal anther appendages long-caudate; style base slightly inflated, glabrous, shaft glabrous, arms short, scarcely divided, truncate. Disc florets hermaphrodite, numerous; corollas white, actinomorphic, deeply 5-lobed, lobes strongly coiled; basal anther appendages extremely long-caudate, entire, rough or long-laciniate; style base slightly inflated but without basal node, glabrous, shaft glabrous, apices short, scarcely bifid, truncate or acute. Achenes fusiform to cylindrical, ribbed; carpopodium a narrow annulus; pappus setae uniseriate, long-barbellate to subplumose or plumose, straw-coloured to off-white. $n = 18$. Four species, South Africa.

83. *Pasaccardoa* Kuntze

Pasaccardoa Kuntze, Rev. Gen. 1: 354 (1891); Lisowski, Flor. Geobot. Ann. 36, pars 1, suppl. 1: 535–541 (1991), reg. rev.; Pope, Fl. Zamb. 6, 1: 26–29 (1992), reg. rev.

Annual to perennial herbs or weak shrubs or subshrubs. Leaves alternate, simple, lamina narrowly oblanceolate to obovate, finely denticulate or subentire. Capitula solitary, terminal or in axillary and terminal obscurely scorpioid cymes, medium to large, radiate; involucre campanulate to turbinate; phyllaries multiseriate, gradate, imbricate; receptacle convex, epaleaceous, markedly alveolate, alveole margins fimbriate. Ray florets uniseriate, neuter; corollas deep red, occasionally creamy white, limb short 3-toothed, inner lip absent. Disc florets hermaphrodite, fertile; corollas actinomorphic, glabrous or glandular-punctate, deeply 5-lobed, red or creamish; lobes long, usually recurved; basal anther appendages long-caudate, retrosely (upwardly) pilose/laciniate; style base scarcely swollen, although sometimes with a basal nectary, glabrous, shaft glabrous to just below branching of arms and then pilose with a band of short hairs/papillae, arms relatively short, acute, glabrous. Achenes ribbed, base with a dense tuft of setulae; pappus setae subequal or very unequal with outer shorter, united at base, broadly winged and scale-like and narrowly lanceolate, midrib usually very distinct, finely laciniate, acute or acuminate. Four species, tropical Africa (Angola, Tanzania, Zaire, Zambia).

84. *Dicoma* Cass.

Dicoma Cass., Bull. Soc. Philom.: 12 (1817); Humbert, Fl. Madag. III: 844–851 (1963), reg. rev.; Lawalrée & Mvukiyumwami, Bull. Jard. Bot. Nat. Belg. 52: 151–163 (1982), reg. rev.; Lisowski, Fragm. Flor. Geobot. Ann. 36, pars 1, suppl. 1: 541–555 (1991), reg. rev.; Pope, Fl. Zamb. 6, 1: 29–44 (1992), reg. rev.; Ortiz & Tadesse, Ann. Missouri Bot. Gard. 85: 440–459 (1998), reg. rev.; Jeffrey & Beentje, Fl. Trop. E. Afr. Compositae, part 1: 13–19 (2000), reg. rev.
Macledium Cass. (1825).
Hochstetteria DC. (1838).
Cloiselia S. Moore (1906).

Perennial, sometimes acaulescent, or sometimes annual herbs, subshrubs or shrubs. Leaves alternate, rarely rosulate (in one Madagascan species), densely set and imbricate, lamina linear, linear-lanceolate, oblanceolate or spathulate, entire to serrulate. Capitula solitary, terminal or in terminal corymbs or racemes, sometimes precocious in acaulescent species, erect, homogamous and discoid or sometimes heterogamous and disciform, rarely radiate; involucre campanulate or turbinate, often with numerous gradate bracts running down pedicel; phyllaries 4- to many-seriate, imbricate, gradate; receptacle epaleaceous, moderately to deeply alveolate, honeycombed, margins of alveoli toothed, at least at angles. Ray florets, when present, few, neuter; corolla bilabiate, outer lip short 3-toothed and not larger than inner 2-toothed lip or pseudoligulate with one long sinus and a 5-toothed lip (only in Madagascan taxa), otherwise all florets hermaphrodite, few to many; corollas white, cream, yellow, violet to reddish, deeply divided into 5 narrow equal lobes, only apices coiled; basal anther appendages caudate, retrorsely long-pilose; nectary usually conspicuous; style base lacking basal node in some species (and these with obvious nectary), glabrous, shaft glabrous, arms short, scarcely separating, obtuse, short-papillose. Achenes turbinate, 5–10-ribbed, glabrous or glabrous and with dense basal tuft of setulae, otherwise densely setuliferous usually between ribs; pappus usually multiseriate, outer setae coarse and barbellate or plumose, median often with narrow hyaline margins and barbellate to almost scabrid along rachis, inner (when present) scale-like with broad hyaline margins, rachis scabrid, or pappus uniseriate, of spreading to ascending scale-like setae; setae white, straw-coloured or rarely purplish. $n = 11$. Between 32 and 65 species, South Africa and tropical Africa, Madagascar, north-eastern Africa, Asia.

85. *Erythrocephalum* Benth. & Hook. f.

Erythrocephalum Benth. & Hook. f., Gen. Pl. 2: 488 (1873); Lisowski, Fragm. Flor. Geobot. Ann. 36, pars 1, suppl. 1: 528–535 (1991), reg. rev.; Pope, Fl. Zamb. 6, 1: 20–26 (1992), reg. rev.; Jeffrey & Beentje, Fl. Trop. E. Afr. Compositae, part 1: 26–35 (2000), reg. rev.
Achyrothalamus O. Hoffm. (1893).

Annual herbs or subshrubs. Leaves alternate, narrowly linear-lanceolate to obovate or broadly obovate, dentate. Capitula one to many, terminal, often on several short side branches, homogamous and discoid or heterogamous and radiate, ray florets hermaphrodite, functionally male; involucre hemispherical to campanulate; phyllaries imbricate, outer series often with foliaceous, often coarsely dentate apical appendages; receptacle paleaceous, convex; paleae linear-lanceolate. Ray florets usually present, uniseriate, few to many (5–16); corollas usually red, sometimes white or pink, bilabiate, outer lip an expanded 3-toothed limb, teeth relatively broad and long or very short, inner of two long, usually erect linear lobes; basal anther appendages long-caudate and retrorsely long-pilose, anther collar somewhat pronounced; style base and

shaft as in disc florets, arms short, truncate, appearing coronate with long papillae around apices. Disc florets usually many (20–80), hermaphrodite; corollas actinomorphic, red, deeply 5-lobed, lobes erect; basal anther appendages long-caudate, long-pilose, retrorsely so except at base, base somewhat truncate, anther collar somewhat pronounced; style base with prominent basal nectary, glabrous, shaft glabrous, arms short to moderate, truncate, usually appearing coronate with larger papillae around edge, often with papillae along margins for short distance. Achene usually somewhat inflated, 5-angled, straw-coloured; pappus setae uniseriate, often few (3–5), flattened, caducous, barbellate, straw-coloured. Circa 13 species, eastern, central and southern tropical Africa.

86. *Pleiotaxis* Steetz

Pleiotaxis Steetz in Peters, Reise Mossamb., Bot. 2: 499 (1864); Jeffrey, Kew Bull. 21: 180–200 (1967), rev.; Lisowski, Fragm. Flor. Geobot. Ann. 36, pars 1, suppl. 1: 501–527 (1991), reg. rev.; Pope, Fl. Zamb. 6, 1: 11–20 (1992), reg. rev.; Jeffrey & Beentje, Fl. Trop. E. Afr. Compositae, part 1: 21–26 (2000), reg. rev.

Perennial herbs or more usually subshrubs. Leaves alternate, upper margin of base usually coarsely toothed, lamina linear, elliptic, ovate-lanceolate or obovate, toothed, sometimes finely so, rarely almost entire. Capitula solitary, terminal or few to many in racemes or racemose panicles, discoid, homogamous; involucre campanulate, turbinate or cylindrical; phyllaries 5–7-seriate, gradate, imbricate, broad; receptacle epaleaceous, alveolate, sometimes with scarcely or distinctly bordered pits, flat to slightly convex. Florets numerous, actinomorphic, hermaphrodite; corollas red or yellowish-white, or white in 'albino forms', lobes long, linear; style base glabrous, lacking basal node, shaft glabrous, arms short to moderately long, usually short-papillate outside above branching point, obtuse; basal anther appendages caudate, pilose; Achenes 4- to many-ribbed; carpopodium annular; pappus setae multiseriate, usually flattened, barbellate, sometimes coarsely so or subplumose, rarely with dilated and flattened apices, off-white to fawn. $n = 10$. Circa 26 species, tropical Africa.

87. *Gladiopappus* Humbert

Gladiopappus Humbert, Bull. Soc. Bot. France 95: 181 (1948).

Small branched shrub. Leaves alternate, simple, lamina broadly obovate, entire. Capitula solitary, terminal, sessile, surrounded by dense cluster of leaves, radiate, homogamous; involucre campanulate; phyllaries c. 4-seriate; receptacle flat to slightly convex, fimbriate between achenes (acc. to Humbert – but not seen in Kew isotype). Ray florets uniseriate, several (c. 9–10); corollas white, 2-lipped, outer lip a conspicuous limb with 3 short teeth, inner of 2 linear, coiled lobes; basal anther appendages long-caudate and conspicuously densely retrorsely pilose. Disc florets many (25–30), actinomorphic, 5-lobed; corollas with white lobes and reddish-black tubes, lobes linear, strongly coiled; basal anther appendages long-caudate, retrorsely pilose but less so than in ray florets; style base with distinct glabrous basal node, shaft glabrous, arms short. Achenes obovoid or turbinate, terete; pappus setae biseriate, persistent, flattened and squamelliform, white, outer series shorter than inner, of variable length and width, laciniate, acute, inner series subequal, laciniate and more coarsely so towards apices, acute, sometimes irregularly divided into 2 lobes. One species, *G. vernonioides* Humbert, endemic to Madagascar.

II.12. Pertya Group

Tribe Pertyeae Panero & V.A. Funk (2002).

Herbs or scandent shrubs, rarely dioecious shrubs. Leaves alternate. Inflorescences paniculate, spiciform or racemose, or of solitary capitula on brachyblasts; capitula 1–16-flowered, discoid, very rarely cleistogamous; involucres cylindrical or campanulate; phyllaries 5–7-seriate; receptacles epaleaceous; florets hermaphrodite and deeply 5-lobed or zygomorphic with one deeper sinus; style arms short, acute or obtuse to rounded. Achenes fusiform, ribbed or terete, glabrous or setuliferous; carpopodium annular; pappus setae 2–3-seriate, rarely absent, barbellate or subplumose.

88. *Pertya* Sch. Bip.

Pertya Sch. Bip., Bonplandia 10: 109 (1862).

Perennial rhizomatous herbs, shrubs or scandent shrubs. Leaves alternate, sometimes fasciculate on brachyblasts, lamina subulate to lanceolate or oblong to ovate, entire, dentate or divided. Capitula racemose, paniculate or solitary, generally few-flowered, discoid, homogamous; involucre campanulate; phyllaries multiseriate, imbricate, membranous or coriaceous; receptacle flat, glabrous or villous, epaleaceous. Florets (1–)5(–16), hermaphrodite, fertile; corollas actinomorphic,

deeply 5-lobed, usually equally lobed, usually white, sometimes slightly pinkish towards base; lobes loosely coiled above; basal anther appendages caudate, tails conspicuously pilose or finely laciniate; style base with distinct node, glabrous, shaft glabrous, arms short, dorsally with short hairs or papillae. Achenes obovoid-oblong, 10-ribbed; carpopodium annular; pappus setae 2–3-seriate, finely barbellate, off-white, fawn or pinkish. n = 12, 13, 14. Fifteen species, Afghanistan, China, Thailand, Japan, Taiwan.

89. ***Macroclinidium*** Maxim.

Macroclinidium Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 15: 375 (1871).

Perennial herbs. Leaves more or less rosulate or alternate at base of inflorescence, lamina large, obovate or trilobed, grossly dentate or serrate. Capitula numerous in panicles, compound corymbs or spikes, single- to several-flowered (1 or 6–11), discoid, homogamous; involucres 5–7-seriate, cylindrical to campanulate; phyllaries imbricate; receptacle convex, glabrous or setose, alveolate. Florets hermaphrodite, fertile; corollas actinomorphic, deeply 5-lobed, white, lobes long, usually coiled towards apices; basal anther appendages caudate, tails conspicuously pilose or finely laciniate; anther collar indistinct; style base with conspicuous node, glabrous, shaft glabrous, arms short, with short hairs or papillae beneath, acute. Achenes terete or sometimes striate; carpopodium annular; pappus 2–3-seriate, setae barbellate, white, apices usually somewhat flattened and dilated. Three species, Japan.

90. ***Ainsliaea*** DC.

Ainsliaea DC., Prodr. 7: 13 (1838).
Diaspananthus Miq. (1866).

Perennial herbs. Leaves usually alternate, lamina linear to very narrowly lanceolate, elliptic, ovate or orbicular, entire, crenate, dentate or lobed. Capitula many in spikes, racemes or elongated panicles, solitary or in dense clusters, often nodding, discoid, homogamous; involucres cylindrical; phyllaries few-seriate to multiseriate, imbricate, gradate; receptacle small, epaleaceous, glabrous. Florets few (1–3), hermaphrodite, usually all fertile, rarely cleistogamous or sterile; corollas deep rose-purple, sometimes white, actinomorphic and deeply 5-lobed with lobes erect to reflexed, or sometimes zygomorphic with deeper sinus between two lobes and almost ligulate; basal anther appendages caudate with connate short-pilose/laciniate or entire tails; style base scarcely swollen or with distinct basal node, glabrous, shaft glabrous, arms short, truncate, dorsally with short hairs or papillae. Achenes fusiform to oblanceolate, sometimes flattened; carpopodium annular, usually whitish; pappus uniseriate, setae plumose, brownish or purplish, rarely absent. n = 6, 8, 12, 13, 14, 15. Circa 50 species, China, India, Japan, Nepal, Taiwan, southeast Asia.

91. ***Myripnois*** Bunge

Myripnois Bunge, Enum. Pl. China bor. collegit.: 38 (1833).

Dioecious shrub. Leaves scattered and alternate or few (1–5) verticillate on brachyblasts, lamina simple, entire. Capitula solitary and sessile or very short-pedicellate, on brachyblasts, usually subtended by bud and leaf-scales in 2–3 series. Male and female capitula few-flowered, homogamous, male smaller than female; involucre narrowly campanulate to cylindrical, subtended by one phyllary-like subinvolucral bract; phyllaries 5–7, biseriate, both series of ± equal size, not imbricate; receptacle small, naked, epaleaceous. Female florets lacking anther cylinder; corollas purple, 5-lobed with much deeper sinus between fourth and fifth lobe, sometimes subligulate; style base not inflated, style glabrous in lower half and with short hairs in upper part, arms short, divergent, with short hairs outside. Male florets with abortive achene; corollas purple, irregularly 3-lipped, two of two short lobes and a third of the remaining long lobe; style base with prominent nectary, otherwise lacking basal node, glabrous, shaft glabrous in lower part and short-pilose in upper part beneath arms, arms slightly divergent, pilose outside; basal anther appendages caudate, finely laciniate or short-pilose. Achenes of female florets long-setuliferous; carpopodium annular; pappus setae barbellate to subplumose, white to off-white. One species, *M. dioica* Bunge, Mongolia and China.

III. Tribe Cardueae Cass. (1819).[5]

A. Susanna and N. Garcia-Jacas

Perennial, biennial, or monocarpic herbs or shrubs, less often annual herbs, very rarely small

[5] The authors of the tribal account prefer to adopt the name Cardueae Cass. (1819) for the tribe, but the name Cynareae Lam. & DC. (1806) is validly published under Articles 32.1 and 19.6 of the

trees, often spiny. Leaves alternate, frequently rosetted, rarely in terminal whorls. Resin-ducts always present in roots, less frequent in aerial parts; laticiferous cells often present but only in aerial parts. Capitula scapose-solitary or diversely corymbose, often aggregate, usually many-flowered, rarely glomerate in secondary capituliform compound inflorescences and then one-flowered. Involucral bracts in many rows, spiny or unarmed, foliaceous or membranous, often prolonged into a membranous, variously fimbriate, lacerate or pectinate, spiny or unarmed appendage. Receptacle variously chaffy or more often setose, rarely naked (*Alfredia* pro parte, *Dolomiaea*, *Onopordum*, *Myopordon*, *Russowia* and *Tugarinovia*). Florets usually tubular, very rarely peripheral florets ligulate (*Atractylis* and *Carlina*); all fertile or the peripherals sterile through abortion and radiant; sterile peripheral florets often absent (especially in subtribe Carduinae). Corollas usually almost actinomorphic, very rarely zygomorphic, divided into a tube and a campanulate limb, straight or s-shaped. Anthers sagittate, apically extending into a rigid, lignified, lanceolate appendage, basally caudate, often with long divisions; anther filaments glabrous or papillose; in many derived groups (especially in subtribe Centaureinae), the stamens are strongly thigmotropic, making up an elaborate mechanism of pollen presentation. Pollen tricolporate, oblate, spherical or more or less prolate; ektexine formed by two layers of columellae, sometimes caveate (in subtribe Centaureinae), spiny (Fig. 27A), verrucate, scabrate (Fig. 27B) or almost smooth. Style with a papillose-pilose thickening (functionally a pollen brush) below the branches; stigmatic areas confined to the inner surfaces of the style arms; nectary present at the base of the style. Achenes very variable, with parenchymatous pericarp (in Carlininae, Cardopatiinae and Echinopsinae, rarely in Carduinae) or radially lignified (in Carduinae and all Centaureinae), hirsute in subtribes Carlininae, Cardopatiinae and Echinopsinae, glabrous in most of Carduinae and Centaureinae. Insertion areole basal, basal-lateral or lateral. Pappus of scales or bristles, directly attached to the pericarp wall (subtribes Cardopatiinae, Carlininae, and Echinopsinae; *Berardia*, *Staehelina* and the Xeranthemum group of Carduinae) or connate by means of a parenchymatous ring to the apical plate; pappus in two structurally different rows (double pappus) in subtribe Centaureinae. Pinnules shorter than width of palea (scabrate), as long as width of palea (pinnulate) or much longer and capillary (plumose). Apical caruncle present in many genera of subtribe Carduinae, basal elaiosome in subtribe Centaureinae, associated with myrmecochory.

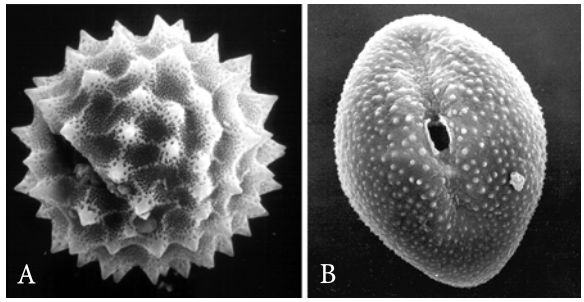

Fig. 27. Compositae-Cardueae. Pollen grains. **A** *Serratula*-type (*Cheirolophus sempervirens*). **B** *Centaurea scabiosa*-type (*Centaurea prolongi*; Garcia-Jacas 1992)

The tribe contains 73 genera and over 2,360 species.

Chromosome numbers show complex dysploid series within natural groups. As a general rule, chromosome numbers in subtribe Carlininae range from $x = 12$ in the basal *Atractylodes* to $x = 10$ in *Carlina*. In subtribe Echinopsinae, basic chromosome numbers are $x = 7, 14, 15$ and 16. Subtribe Carduinae shows also complicated dysploid patterns, not fully correlated with phylogeny. The Xeranthemum group shows a dysploid series with $x = 6, 7, 10$ and 11. Many groups (e.g. *Onopordum*, *Cynara* and *Cirsium*) have $x = 17$, while $x = 13$ seems widespread in *Saussurea* and even $x = 11$ is present in *Galactites*. In subtribe Centaureinae, the relationship between dysploidy and phylogeny was thoroughly studied by Garcia-Jacas et al. (1996). Basal groups have chromosome numbers ranging from $x = 13$ to $x = 15$, whereas the complex of genera with derived features (pollen usullay caveate, crystals in the phyllaries, and hilum basal) show base chromosome numbers from $x = 7$ to $x = 12$. Secondary metabolites include predominantly lipophilic compounds (especially sesquiterpene lactones); hydrophilic compounds are scarcely represented. Only some genera have been investigated in depth (*Centaurea*, *Cirsium*). Subtribes Carduinae and mainly Centaureinae show higher structural differentiation than the remaining subtribes (Wagner 1977). Geographical

International Code of Botanical Nomenclature, and under Article 11.1 must be adopted as correct (C. Jeffrey, ed.).

distribution is mainly Mediterranean in its widest sense (including the Irano-Turanian region), with a major centre of diversification in central Asia. The mountains of central Asia (Tian-Shan, Pamir and the Himalayas) constitute the eastern boundary for most of the genera. The tribe becomes less frequent in central Africa, and disappears in equatorial and southern Africa. Three genera are native to North America (*Cirsium*, *Plectocephalus* and *Saussurea*), only two to temperate South America (*Centaurodendron* and *Plectocephalus*), and two species are (with reservations) native to Australia. The tribe contains many subcosmopolitan and noxious weeds (*Acroptilon*, species of *Carthamus*, *Carduus*, *Centaurea*, *Cirsium* and *Onopordum*).

The traditional classification of Cardueae into four subtribes (Carduinae, Carlininae, Centaureinae and Echinopsinae) is extremely controversial (reviewed by Dittrich 1977; Susanna et al. 1995; Petit 1997); many doubts are centred in subtribes Carlininae and Echinopsinae, often treated as separate tribes, Carlineae and Echinopeae. However, molecular evidence of diverse origin (cpDNA restriction sites, Jansen 1991; *rbc*L, Kim et al. 1992; nuclear-ribosomal DNA, Susanna et al. 1995; combined ribosomal-nuclear and chloroplast DNA, Garcia-Jacas et al. 2002; Susanna et al. 2006) consistently groups Cardueae in a robust monophyletic clade. A limited cladistic-morphological analysis by Bremer (1994) also supported the monophyly of the group. However, none of these analyses has solved the relative position of the subtribes; they have suggested only that Carlininae, the restored subtribe Cardopatiinae, and Echinopsinae probably form a grade basal to subtribes Carduinae to Centaureinae; Centaureinae are a highly derived monophyletic group, and Carduinae are a paraphyletic assemblage. These results suggest that the compound inflorescence of *Echinops* is without systematic relevance. The trend towards grouping uniflowered capitula into compound inflorescences is common in all subtribes of Cardueae: in Carlininae (*Atractylis polycephala* has only three flowers per head), in Cardopatiinae (*Cardopatium*), in Carduinae (*Cousinia congesta*, *Cirsium congestum*) and even in Centaureinae (*Centaurea aggregata*). Subtribe Echinopsinae should not include Xerantheminae, a separate tribe in Cassini's earliest classification, usually included in Carlininae, moved to Carduinae by Petit (1997), and moved again to Echinopsinae by Garcia-Jacas et al. (2002). The Xeranthemum group is here placed in Carduinae, together with *Staehelina*. In the classical delimitation of the tribe (e.g. Bremer 1994), *Staehelina* and the Xeranthemum group were placed in Carlininae.

Most recent studies have also confirmed the paraphyly of Carduinae when the monophyletic Centaureinae alone, or Centaureinae plus their sister group (Cousinia and Saussurea groups), are moved to a different subtribe. In view of the strong support for the monophyly of the tribe, we have followed the traditional classification in one tribe Cardueae, even if broadly redefined and with the restoration of subtribe Cardopatiinae. However, taking into account the very probable paraphyly of Carduinae, this classification is a conservative approach and not fully satisfactory. The alternative solution, i.e. to combine subtribes Carduinae and Centaureinae, would be impractical because the resulting Carduinae would encompass nearly 2,300 species representing more than 90% of the tribe.

We have organized the genera of Carduinae in five informal groups. This classification follows partly the suggestions of Dittrich (1977), Häffner and Hellwig (1999) and Häffner (2000), strongly modified on the basis of Garcia-Jacas et al. (2002) and Susanna et al. (2006). However, the position of some genera from central Asia is only tentative. All of them are poorly represented in Western World herbaria (cf. we have not seen any material), and the diagnoses and descriptions are not conclusive. In Centaureinae, we have organized the genera into several informal groups which recent molecular studies have confirmed as natural. Regarding generic limits, we have acted more as "lumpers" than as "splitters" in *Cousinia*, *Jurinea* and *Saussurea*. Many small genera described from central Asia fall within the broad range of variability of one of these three large genera, and the lack of a recent, comprehensive revision of any of the three makes the suggested segregates only hypothetical.

Finally, there is the problem of the treatment of *Centaurea*. In the present account, the small group previously classified as *Centaurea* sect. *Centaurea* is named *Rhaponticoides*, and we have used *Centaurea* for the remainder of the genus (the Acrocentron, Cyanus and Jacea groups, as defined in Garcia-Jacas et al. 2001).

Key to the Subtribes

1. Capitula one-flowered, clustered in second-order spherical or hemispherical compound inflorescences
3. Echinopsinae (p. 128)

– Capitula not one-flowered, sometimes clustered in flat-topped corymbs but never forming second-order heads 2
2. Achenes soft, with parenchymatous pericarp, sericeous, rarely glabrous. Receptacle with broad scales, very rarely naked (*Tugarinovia*) 3
– Achenes hard, lignified, usually glabrous. Receptacle with bristles, rarely naked 5
3. Capitula usually subtended by pectinate-pinnatisect leaf-like bracts. Corolla lobes 1–3 mm long. Pappus of long, plumose bristles, often connate at the bases into broader, robust scales **1. Carlininae** (p. 126)
– Capitula usually subtended by entire or dentate bracts or on leafless pedicels. Corolla lobes usually longer than 3 mm. Pappus of free bristles or scales, very rarely connate at the bases 4
4. Pappus of two rows of short lanceolate scales. Corollas filiform, blue **2. Cardopatiinae** (p. 127)
– Pappus of one or two rows of pinnulate or plumose long scales or bristles. Corollas not filiform, never blue **4. Carduinae** (p. 129)
5. Insertion areole of the achenes straight, basal or basal-abaxial, without elaiosome. Achenes often with apical caruncle. Pappus rarely differentiated into two rows, usually deciduous **4. Carduinae** (p. 129)
– Insertion areole of the achenes concave, lateral-abaxial, often with an elaiosome. Caruncle absent. Pappus differentiated into two rows (sometimes aborted), more often persistent **5. Centaureinae** (p. 138)

III.1. Subtribe Carlininae Dumort. (1827).

Perennial herbs or shrubs, plants less often annual. Leaves often spiny, deeply pinnatisect, rarely entire. Capitula frequently subtended by pectinate leaf-like bracts, homogamous or heterogamous with radiate florets. Inner involucral bracts often showy, radiant and coloured. Receptacle densely covered with large scales, absent only in *Tugarinovia*. Anther filaments glabrous, appendages long and sericeous. Corolla and style often very short. Achenes with parenchymatous pericarp, densely sericeous. Pappus of plumose bristles, often connate into stout scales, persistent or deciduous.

Key to the Genera

1. Plants dioecious. Receptacle naked, foveoloate. Male heads much smaller than female, both scapose on leafless pedicels laterally arising from a basal rosette of leaves **96. *Tugarinovia***
– Plants monoecious. Receptacle with scales. Capitula not scapose on leafless pedicels laterally arising from a basal rosette of leaves 2
2. Receptacular scales connate, enclosing the achenes. Innermost involucral bracts showy, rarely absent 3
– Receptacular scales free, not enclosing the achenes. Innermost involucral bracts inconspicuous 4
3. Annual herbs with innermost involucral bracts spiny-tipped **94. *Thevenotia***
– Perennial or annual herbs with unarmed innermost involucral bracts **92. *Carlina***
4. Leaves entire or 3–5-lobate, finely serrulate. Involucral bracts green, foliose. Achenes with a basal glabrous thickening **95. *Atractylodes***
– Leaves usually pinnatisect, spiny-toothed or rarely entire and unarmed. Involucral bracts scarious. Achenes without basal glabrous thickening **93. *Atractylis***

Genera of Carlininae

92. *Carlina* L. Fig. 28

Carlina L., Sp. Pl. 2: 828 (1753); Petit, Bull. Mus. Natl Hist. Nat., B, Adansonia 9: 407–440 (1987), part. rev.; Meusel & Kästner, Österr. Akad. Wissensch., Math.-Naturwissensch. Kl., Denkschr. 127, 128 (1990–1994), rev.
Chamaeleon Cass. (1827).

Annual or perennial herbs or shrublets. Leaves dentate to pinnatisect, spiny, rarely entire and unarmed. Capitula homogamous or heterogamous. Outer involucral bracts similar to upper leaves, dentate to pinnatisect, spinulose; innermost narrowly linear, longer than florets, radiant and brightly coloured, rarely not radiant. Receptacular scales connate into a honeycombed structure covering the receptacle and enclosing the achenes. Florets from whitish to pink or purple, or yellow. Corolla lobes papillose on the margins. Achenes oblong-obconical, sericeous or villous. Pappus of plumose, basally stout and connate scales. $x = 10$, rarely $x = 9$. Twenty-eight species, central Europe, Mediterranean region (2 species in the Canary Islands, 1 species in the Caucasus).

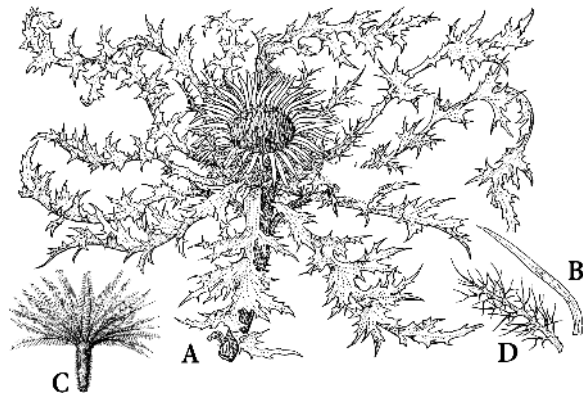

Fig. 28. Compositae-Cardueae. *Carlina acaulis*. **A** Habit. **B** Inner involucral bract. **C** Achene. **D** Plumose pappus hair. (Font Quer 1962)

93. *Atractylis* L.

Atractylis L., Sp. Pl. 2: 829 (1753); Meusel & Kästner, Österr. Akad. Wissensch., Math.-Naturwissensch. Kl., Denkschr. 127, 128 (1990–1994), part. rev.; Petit, Bull. Soc. Bot. France 134: 165–184 (1987), part. rev.

Annual or perennial herbs or shrublets. Leaves dentate to pinnatisect, spinulose, rarely unarmed. Capitula heterogamous, sessile in involucels of leaf-like bracts. Outer involucral bracts winged; innermost linear-lanceolate, often appendiculate with brown, scarious, wide appendages. Receptacle with large, scarious, laciniate-fimbriate scales. Florets whitish to violet, pink, purple, or yellow. Peripheral ligulate florets sometimes present, with staminodes and stylodia. Achenes oblong-obconical, sericeous. Pappus of plumose free scales. $x = 10$. Thirty species, mainly Mediterranean (Europe and northern Africa); also Eurasia and Canary Islands.

94. *Thevenotia* DC.

Thevenotia DC., Arch. Bot. (Paris) 2: 331 (1833).

Annual herbs. Leaves white-tomentose, coriaceous, somewhat fleshy, with prominent veins, spiny-toothed, densely tomentose or lanate. Capitula homogamous, subtended by leaf-like bracts. Receptacle with fimbriate scales, basally connate. Outer involucral bracts dentate-spinulose, woolly; middle bracts entire, oblong; innermost ending in a dark purple spine. Florets purple. Achenes oblong-obconical, sericeous. Pappus of plumose, basally stout and connate bristles. Two species, Irano-Turanian and central Asia semi-deserts.

95. *Atractylodes* DC.

Atractylodes DC., Prodromus 7: 48 (1838); Zarembo & Boyko, Comp. Newslett. 33: 61–72 (1999), part. rev.

Perennial herbs. Leaves simple or pinnately 3- to 5-lobed, marginally finely serrulate-spinulose. Capitula often heterogamous. Outer involucral bracts green and foliose, widely winged; medium bracts with a narrow translucent margin; innermost linear-lanceolate. Receptacle with linear, entire scales. Florets white, yellow, pink or purple; female florets sometimes present. Anther filaments thick, basally flattened. Apical appendages very long, slender. Achenes linear or oblong, sericeous, with a basal, glabrous, thickened lip. Pappus of easily deciduous, basally connate plumose bristles. $x = 12$. Five species, eastern Asia (Siberia, China, Korea and Japan).

96. *Tugarinovia* Iljin

Tugarinovia Iljin, Izv. Glavn. Bot. Sada S.S.S.R. 27: 356 (1928); Dittrich et al., Bot. Jahrb. Syst. 108: 167–186 (1987), rev.

Dioecious perennial herb with stout woody stock. Leaves rosulate, deeply dentate, spiny. Capitula on decumbent peduncles arising laterally from the rosette, subscapose, homogamous, male or female; male capitula smaller than female. Receptacle naked, alveolate. Achenes obconical, very densely sericeous. Pappus of scabrid bristles basally connate into larger scales, double, inner longer than outer. One species, *T. mongolica* Iljin, montane steppes of Mongolia.

III.2. Subtribe Cardopatiinae Less. (1832).

Spiny perennial or annual herbs. Leaves spiny-dentate or pinnatisect. Capitula either few-flowered and clustered in corymbs, or many-flowered. Involucral bracts with spiny pectinate-fimbriate appendages. Anther filaments glabrous. Florets deep blue, filiform. Style very shortly bilobed. Achenes with parenchymatic pericarp, densely sericeous; pappus double, of two rings of short scales.

Key to the Genera

1. Robust perennials. Heads few-flowered, clustered in flat-topped corymbs **97. *Cardopatium***
– Delicate annuals. Heads many-flowered, not clustered in flat-topped corymbs **98. *Cousiniopsis***

97. *Cardopatium* Juss. Fig. 29

Cardopatium Juss., Ann. Mus. Natl Hist. Nat. 6: 324 (1805). *Broteroa* DC. (1836).

Robust perennial herbs. Leaves pinnatisect, very spiny. Capitula numerous in a flattened corymb subtended by leaf-like spiny bracts, very small and few-flowered, homogamous. Involucral bracts with pectinate, very spiny appendages, gradually less divided inwards, outer leaf-like, innermost scarious and lanceolate. Receptacle densely setose with very thin fimbriae. Style shortly bilobed with a subapical ring of longer hairs. Achenes obconical-oblong, villous. Pappus of apically fimbriate scales with a few lateral fimbriae. $x = 18$. One or two species, eastern Mediterranean region, from the Caucasus to

Fig. 29. Compositae-Cardueae. *Cardopatium corymbosum*. **A** Habit and leaf. **B** Involucral bract. **C** Floret. **D** Achene. (Fiori and Paoletti 1895–1899)

Italy and northern Africa. Robust colonizing ruderal plants with an easily sprouting rootstock.

98. *Cousiniopsis* Nevski

Cousiniopsis Nevski, Trudy Bot. Inst. Akad. Nauk S.S.S.R. ser. 1, 4: 288 (1937).

Small annual herb, branched from the base. Leaves pinnatisect, spinulose. Capitula homogamous, solitary, sessile, one or two basal, two more subterminal, subtended by an involucel of leaf-like bracts. Outer involucral bracts with a pectinate-spinulose appendage, innermost with a brown, scarious, cuspidate appendage. Receptacle densely setose with laciniate scales. Anther appendages laciniate, with divisions as long as the filament. Corolla lobes rolled outwards. Achenes obovoid, sericeous-villous. Pappus of membranous scales in two series; outer linear-lanceolate, laciniate; inner subulate and connate. One species, *C. atractylodes* (C. Winkler) Nevski, semi-desert steppes of central Asia.

III.3. Subtribe Echinopsinae (Cass.) Dumort. (1829).

Perennial herbs, less often annuals, spiny or unarmed. Capitula one-flowered, aggregated in secondary inflorescences. Bracts spiny. Anther filaments glabrous, basal appendages short, laciniate. Achenes with parenchymatous pericarp, densely sericeous. Pappus of broad, short scales directly attached to the apical plate.

Key to the Genera

1. Secondary capitula spherical. Leaves pinnatifid or pinnatisect, rarely entire, spiny **99. *Echinops***
– Secondary capitula hemispherical. Leaves entire, unarmed **100. *Acantholepis***

99. *Echinops* L. Fig. 30

Echinops L., Sp. Pl. 2: 814 (1753); Garnatje et al., Folia Geobot. 40: 407–419 (2005), mol. phylog.

Stout annual or perennial herbs. Leaves entire or dentate to pinnatisect, spiny. Capitula surrounded by a tuft of bristles, aggregated in globose secondary capitula subtended by small bracts. Involucral bracts in many rows. Outer bracts strongly keeled, winged, apically slightly fimbriate. Median more broadly winged, spinose. Innermost usually green or green-brown, polished, linear-lanceolate, often partly or totally connate with only the apical appendages free, not spinose. Florets violet-blue, red, greenish or white. Corolla lobes often apically scarious, densely denticulate. Achenes oblong. $x = 14, 15, 16$. About 120 species, Eurasia, northern and central Africa; introduced elsewhere.

100. *Acantholepis* Less.

Acantholepis Less., Linnaea 6: 88 (1831).

Unarmed annual herb. Leaves sessile, linear-oblong, entire or marginally denticulate-spinose, white-woolly. Capitula single-flowered, each capitulum surrounded by a tuft of white plumose hairs, aggregated in semi-globose terminal secondary capitula subtended by leaf-like bracts. Involucral bracts in many rows, very densely woolly, especially apically, free. Outer bracts bristly. Florets pink. Achenes linear-oblong, many-angled. $x = 7$. One species, *A. orientalis* Less., central Asia. Probably not different from *Echinops*.

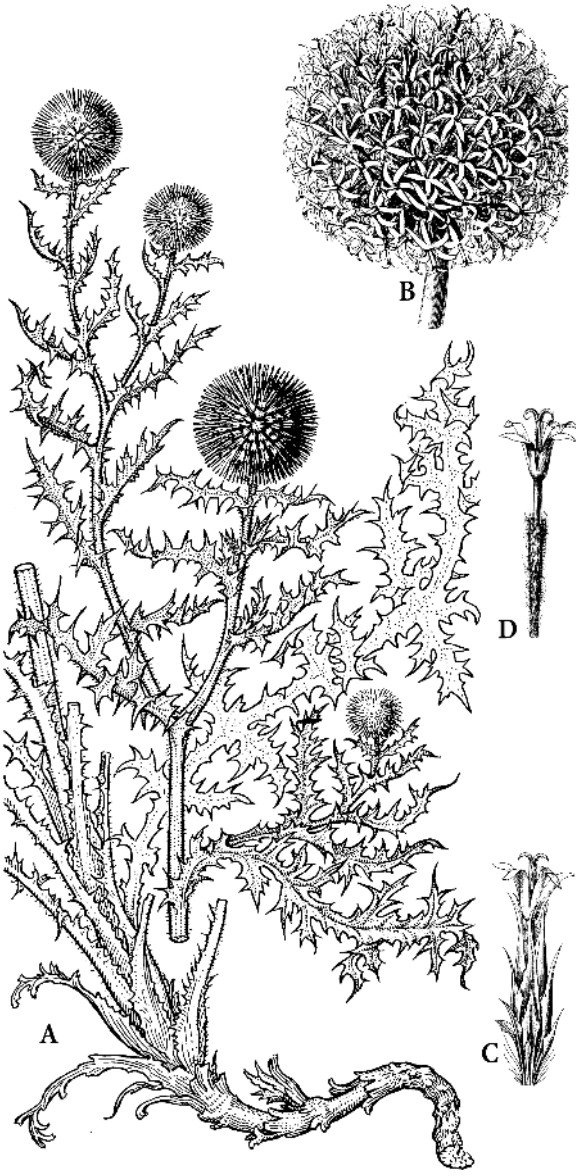

Fig. 30. Compositae-Cardueae. *Echinops ritro*. **A** Habit. **B** Compound head. **C** Individual capitulum. **D** Floret. (Font Quer 1962)

III.4. Subtribe Carduinae (Cass.) Dumort. (1827).

Perennial, biennial or annual spiny herbs or subshrubs, rarely unarmed. Capitula homogamous, very rarely peripheral florets sterile and radiant. Bracts usually spiny, innermost exappendiculate or with rudimentary appendages. Achenes with radially sclerified pericarp (absent in *Staehelina* and the Saussurea group), often with apical caruncle. Insertion areole straight or lateral-abaxial. Apical plate very often inclined adaxially. Pappus inserted on a parenchymatous ring in the apical plate, simple or in many undifferentiated rows, deciduous.

Key to the Genera

1. Leaves spiny or spinulose 2
– Leaves unarmed 22
2. Receptacle naked, honeycombed (foveolate) 3
– Receptacle with bristles 5
3. Robust biennial herbs with spiny-winged stems, rarely acaulescent. Achenes tetrangular, often fringed or pitted **117. *Onopordum***
– Perennial herbs with stems not spiny-winged; achenes compressed, ridged 4
4. Leaves spiny-pinnatifid. Bracts with bright-coloured appendages **118. *Alfredia***
– Leaves entire, hastate, spiny-toothed. Bracts linear, without appendages **121. *Synurus***
5. Capitula sessile on a broad tubular stem, clustered, covered with woolly hairs **127. *Schmalhausenia***
– Capitula not sessile on a tubular stem, not covered with woolly indument 6
6. Receptacle with strongly twisted bristles. Pappus bristles free, individually deciduous 7
– Receptacle with straight bristles. Pappus bristles basally connate in a ring, deciduous as a single piece 8
7. Corollas glandular **128. *Hypacanthium***
– Corollas eglandular **126. *Cousinia***
8. Pappus plumose 9
– Pappus scabrid or barbellate 17
9. Receptacle fleshy. Involucral bracts orbicular. Achenes tetragonous **108. *Cynara***
– Receptacle not fleshy. Involucral bracts lanceolate. Achenes rounded or compressed 10
10. Peripheral florets sterile, radiant. Pericarp hygrophanous **112. *Galactites***
– Peripheral florets not radiant. Pericarp not hygrophanous 11
11. Anther filaments glabrous. Achenes ridged, with apical rim 12
– Anther filaments papillose. Achenes smooth, usually without apical rim 13
12. Leaves linear, subglabrous. Pappus bristles s-shaped **119. *Ancathia***
– Leaves broadly elliptic, lanate below. Pappus bristles usually straight **124. *Lamyropappus***
13. Achenes broadly ovoid, not compressed, without nectary **113. *Ptilostemon***
– Achenes oblong, compressed, often with apical nectary 14
14. Leaves green above, white-lanuginose beneath. Nectary cylindrical **116. *Lamyropsis***
– Leaves glabrous or uniformly pilose. Nectary globose 15
15. Leaves white-veined. Corolla more deeply split on the abaxial side **115. *Notobasis***
– Leaves not white-veined. Corolla regularly split 16
16. Annual, much-branched plant. Capitula almost concealed by densely araneose bracts. Involucral bracts with pectinate appendages **110. *Picnomon***

– Perennial or robust biennials, little-branched. Capitula not concealed by bracts. Involucral bracts ending in a single spine **109. *Cirsium***
17. Outer involucral bracts with stout spines to 50 mm. Leaves white-variegated **111. *Silybum***
– Outer involucral bracts with spines less than 30 mm. Leaves not white-variegated 18
18. Anther filaments glabrous. Achenes without caruncle 19
– Anther filaments papillose. Achenes carunculate 21
19. Leaves linear or narrowly lanceolate, spinulose-dentate **122. *Syreitschikovia***
– Leaves broadly lanceolate or oblong in outline, spinose-pinnatisect 20
20. Achenes smooth. Capitula with a leaf-like involucel **120. *Olgaea***
– Achenes ridged. Capitula without involucel **118. *Alfredia***
21. Capitula on long leafless peduncles. Pappus bristles s-shaped **114. *Tyrimnus***
– Peduncles foliose. Pappus bristles straight **107. *Carduus***
22. Achenes soft, parenchymatous 23
– Achenes hard, lignified 32
23. Pappus of up to 15 pinnulate scales. Capitula heterogamous 24
– Pappus of barbellate or plumose bristles. Capitula homogamous 27
24. Dwarf shrubs **106. *Amphoricarpos***
– Annuals 25
25. Achenes dimorphic, outer dorsiventrally compressed, keeled or winged, innermost linear-oblong, subcylindrical **104. *Chardinia***
– Achenes not dimorphic 26
26. Outer florets with liguloid corollas. Innermost bracts unarmed **103. *Xeranthemum***
– Outer florets not liguloid. Innermost bracts spiny-tipped **105. *Siebera***
27. Leaves lanate on both faces, with prominent veins below. Pappus bristles retrorsely twisted **101. *Berardia***
– Leaves usually green above, without prominent veins below. Pappus bristles straight 28
28. Pappus very long, showy, exceeding involucral bracts 29
– Pappus not exceeding involucral bracts[6] 32
29. Annual plants. Leaves somewhat fleshy, sparsely glandular-hirsute above **132. *Polytaxis***
– Perennial plants, very rarely annuals. Leaves not fleshy, not glandular-hirsute above 30
30. Receptacle naked, foveolate **131. *Dolomiaea***
– Receptacle setose 31
31. Nectary prominent, detachable as a single piece with the pappus. Leaves not decurrent. Achenes usually plicate, ribbed or foveolate **130. *Jurinea***
– Nectary not prominent. Leaves usually decurrent. Achenes ridged or costate **129. *Saussurea***
32. Dwarf shrubs. Leaves green above, white beneath. Pappus very long, exceeding involucral bracts, usually persistent **102. *Staehelina***
– Perennial herbs or shrubs. Leaves not bicoloured. Pappus short, never exceeding involucral bracts, deciduous 33
33. Achenes smooth, broadly ovoid, subglobose. Apical plate slanted. Pappus detachable as a single piece **113. *Ptilostemon***
– Achenes often ridged, keeled or winged, oblanceolate, never globose. Apical plate straight. Pappus bristles individually deciduous 34
34. Leaves often hastate, very large, to 70 cm. Involucral bracts usually hooked **125. *Arctium***
– Leaves small, never hastate. Involucral bracts without hooks **126. *Cousinia***

[6] Except in **102. *Staehelina***

Genera of Carduinae

Unplaced Genera

101. *Berardia* Vill.

Berardia Vill., Prosp. Hist. Pl. Dauphiné 27 (1779); Dittrich, Ann. Naturhist. Mus. Wien 99, B: 329–342 (1996), rev.

Acaulescent, unarmed perennial herb. Leaves rounded, entire or denticulate, densely woolly, with veins prominent beneath, white above. Capitula solitary, sessile, homogamous. Involucral bracts subulate, scarious, woolly, ending in a slender flat point. Receptacle areolate. Florets yellowish or pinkish. Staminal connective very long, apiculate. Achenes oblong, glabrous, slightly sulcate. Pericarp not sclerified. Pappus of scabrid cylindric bristles retrorsely twisted, directly attached to the apical plate. $x = 18$. One species, *B. subacaulis* Vill., high Alps (France, Italy and Switzerland).

102. *Staehelina* L.

Staehelina L., Sp. Pl. 2: 840 (1753).
Hirtellina Cass. (1827).

Unarmed dwarf shrubs or subshrubs. Leaves entire or dentate-pinnatifid, linear to obovate, dark green above, white-woolly beneath. Capitula corymbose or rarely solitary, homogamous. Involucral bracts ovate to lanceolate, mucronate, sometimes minutely hirsute. Receptacle with wide, basally connate scales. Florets whitish or pink-purple. Corolla lobes very long. Anther filaments glabrous; basal appendages very long, sericeous. Achenes linear-oblong, glabrous or sericeous, with minute apical coronula. Pappus of bristles basally connate into broader paleae, more or less divided apically into pinnulate fimbriae (into capillary hairs in *Staehelina dubia* L. and *S. baetica* DC.), always overtopping involucre, sometimes deciduous in a ring. $x = 15, 17$. Eight species, Mediterranean region.

III.4. a. Xeranthemum Group

Unarmed annual herbs, rarely dwarf shrubs. Leaves always entire, velvety underneath. Capitula heterogamous. Receptacle with large scarious scales. Anther filaments glabrous, anther appendages short, laciniate. Corolla lobes very short. Achenes often dimorphic, with pappus of long tapering or subulate scales, rarely reduced to a corona in *Chardinia*.

103. *Xeranthemum* L. Fig. 31

Xeranthemum L., Sp. Pl. 2: 857 (1753).

Unarmed annual herbs. Leaves entire, elliptic-linear, usually greyish-hairy. Capitula solitary, pedunculate. Involucral bracts scarious, ovate-lanceolate to obovate; inner bracts elongated, erect or spreading and radiate, white, pink-violet or purple. Receptacle with linear-lanceolate, scarious, densely glandular-punctate scales. Outer florets sterile, with a very long pink stylodium and corollas deeply cleft, bilabiate; central florets perfect. Achenes narrowly obconical to obovoid, sericeous. Pappus of wide, scarious, subulate, apically pinnulate scales. $x = 6, 7, 10$. Five species, Mediterranean region, from northern Africa to western Asia.

104. *Chardinia* Desf.

Chardinia Desf., Mém. Mus. Hist. Nat. 3: 455 (1817).

Unarmed cleistogamous herb. Capitula solitary, pedunculate. Involucral bracts ovate-lanceolate to obovate, scarious. Receptacle with lanceolate, subulate scales. Outer florets female, central florets perfect. Corollas shorter than the scales of the pappus. Achenes dimorphic; outer dorsiventrally flattened with an adaxial keel, obovate, with broad, lacerate-fimbriate wings apically elongated into two horns, glabrous; central achenes obconical, apically sulcate and minutely pilose, basally sericeous. Pappus of the external achenes formed by prolongations of the wings; in central achenes a denticulate corona. $x = 11$. One species, *C. orientalis* (L.) Kuntze, Turkey, Middle East, Iran, Afghanistan and Pakistan.

105. *Siebera* J. Gay

Siebera J. Gay, Mém. Soc. Hist. Nat. Paris 3: 344 (1827).

Annual herbs. Capitula solitary or aggregated, subtended by a small verticel of leaves. Involucral bracts scarious, inner with a long lanceolate,

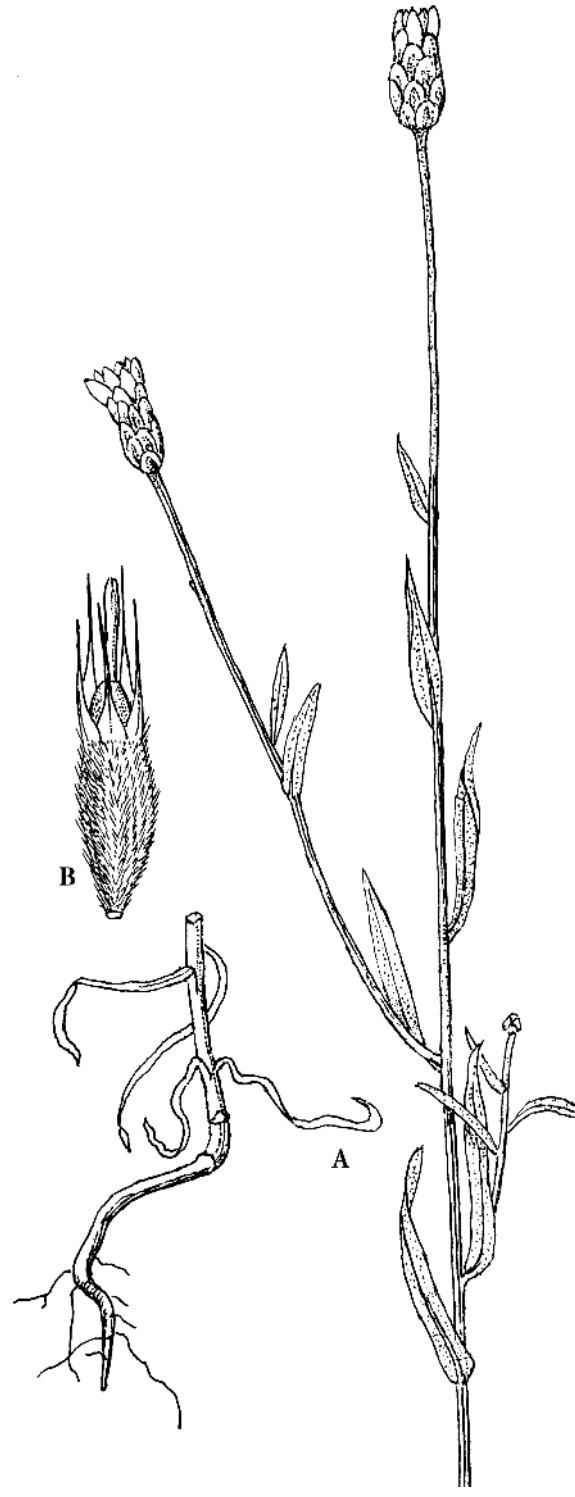

Fig. 31. Compositae-Cardueae. *Xeranthemum cylindraceum*. **A** Habit. **B** Achene. (Feinbrun-Dothan 1977)

subulate appendage usually pink to purplish; median bracts with a slender spine; outer bracts with a minimal spine, finely tomentose. Outer florets sterile, bilabiate; central florets perfect. Achenes narrowly oblong-obconical, sericeous. Pappus of scarious scales ending in a barbellate or plumose bristle. $x = 10$. Two species, Turkey, Middle East, Iran, Afghanistan and Pakistan.

106. *Amphoricarpos* Vis.

Amphoricarpos Vis., Fl. Dalmat. 2: 27 (1847); Schwarz, Phyton (Horn) 14: 125–133 (1970), part. rev.

Unarmed dwarf shrubs. Leaves green above, white-tomentose beneath, entire or denticulate. Capitula solitary, pedunculate or scapose. Involucral bracts scarious, ovate-lanceolate to obovate. Receptacle with linear-lanceolate, long-subulate, apically twisted scales. Florets violet to pink or white, outer florets female, central florets perfect or functionally male. Achenes dimorphic; outer achenes compressed, winged, sericeous; inner achenes narrowly oblong-obconical, sericeous. Pappus of subulate, bristle-like scales. $x = 12$. Four species, Balkan Peninsula, Turkey and Caucasus.

III.4. b. Carduus Group

Spiny perennial, biennial or annual herbs or subshrubs, rarely unarmed. Leaves often decurrent; stem frequently winged. Capitula homogamous, rarely outer florets sterile. Florets usually purple, pink or white, less often yellow. Anthers very shortly caudate, with papillose filaments. Achenes smooth, narrowly obovoid, oblong or orbiculate, often with apical nectary. Pappus detachable as a single piece.

107. *Carduus* L.

Carduus L., Sp. Pl. 2: 820 (1753); Kazmi, Mitt. Bot. Staatsamml. München 5: 139–198, 279–550 (1963–1964), rev.

Annual, biennial or perennial herbs with spiny-winged stems. Leaves dentate-pinnatisect, rarely entire, spiny (very rarely unarmed in *C. personatus* Gaertn.). Involucral bracts long-spinose-acuminate, rarely muticous. Florets red, purple or pink. Achenes obovoid-oblong, smooth, glabrous, umbonate, with an apical, globose, obscurely 5-lobulate, small caruncle, rarely absent (*C. nutans* L.). Pappus bristles from almost smooth (*C. collinus* Waldst. & Kit.) to serrulate. $x = 8$, 9, 10, 11. About 90 species, Eurasia (mainly in the Mediterranean region), also in northern and central Africa (however, central African species should belong to *Cirsium*; see Häffner and Hellwig 1999), introduced elsewhere.

108. *Cynara* L.

Cynara L., Sp. Pl. 2: 827 (1753); Wiklund, Bot. J. Linn. Soc. 109: 75–123 (1992), rev.
Arcyna Wiklund (2003).

Spiny stout perennial herbs. Leaves pinnatisect, very spiny (unarmed in cultivated *C. cardunculus* L.). Capitula large, globose, solitary or clustered in lax corymbs. Involucral bracts oval, entire, coriaceous, usually spine-tipped. Receptacle fleshy, densely setose. Florets purplish or violet. Anther filaments papillose. Achenes glabrous, very faintly angular; apical rim and nectary absent. Pappus of very long, plumose bristles, basally connate in a ring, deciduous or persistent. $x = 17$. Eight species, Mediterranean region. One species, *C. cardunculus*, widely cultivated from Roman times for its edible fleshy receptacles.

109. *Cirsium* Mill. Fig. 32

Cirsium Mill., Gard. Dict., ed. 4, 1 (1754).
Breea Less. (1832).
Cephalanophlos Fourr. (1869).

Perennial or biennial herbs, rarely to 4 m high (*Cirsium subcoriaceum* (Less.) Sch. Bip.). Leaves dentate-pinnatisect, spiny, sometimes entire, often semi-amplexicaul. Stems less often than in *Carduus* spiny-winged. Outer involucral bracts few, spiny; inner bracts without spines, leaf-like, often appendiculate and coloured. Florets red, purple or pink, rarely yellow. Achenes obovoid-oblong, smooth, glabrous, with an apical rim and a small obconical caruncle. Pappus of plumose, usually deciduous bristles. $x = 17$ (Eurasia) and $x = 15$ (North America). About 250 species, Eurasia, North America, northern and eastern Africa, frequent in wet waste grounds; some noxious cosmopolitan weeds (*Cirsium vulgare* (Savi) Ten., *C. palustre* (L.) Scop.).

110. *Picnomon* Adans.

Picnomon Adans., Fam. Pl. 2: 116 (1763), nom. cons. prop.
Acasma Vaill. (1754), nom. rej. prop.

Annual herb. Leaves dentate-pinnatifid, spinulose. Stem winged. Capitula solitary or few clustered together, sessile, overtopped by the

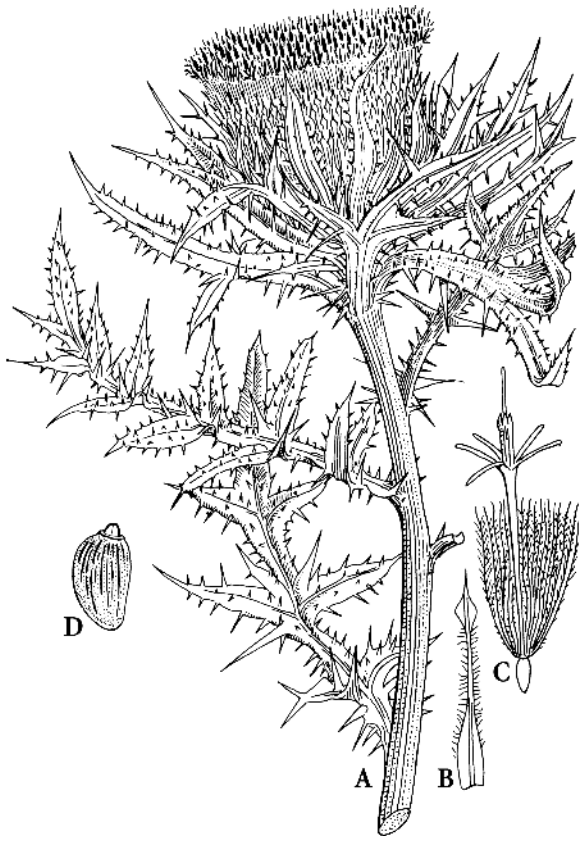

Fig. 32. Compositae-Cardueae. *Cirsium eriophorum*. **A** Habit. **B** Involucral bract. **C** Floret. **D** Achene. (Folch 1986)

uppermost leaves. Receptacle densely setose. Involucral bracts marginally spiny, densely covered with woolly-arachnoid hair. Florets purple. Achenes obovoid-oblong, smooth, glabrous, with a small apical rim. Caruncle small, 5-lobed. Pappus plumose, deciduous, basally connate in a ring. $x = 16$. One species, *P. acarna* (L.) Cass., Mediterranean region; introduced elsewhere.

111. *Silybum* Vaill.

Silybum Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 173 (1754), nom. cons.

Biennial herbs. Leaves coarsely dentate-pinnatifid, semi-amplexicaul, white-veined or variegated, spiny. Capitula solitary. Involucral bracts with spinose margin and spine-tipped appendages. Florets purple. Anther filaments adnate. Achenes obovoid, compressed, smooth, glabrous, with a white apical rim and a large apical nectary. Pappus of scabrid, deciduous bristles, basally connate in a parenchymatous ring forming a cupule with long hairs, mimicking a double pappus (the same as in *Tyrimnus* Cass. and *Cirsium ciliatum* Moench). $x = 17$. Two or three species, Mediterranean region, introduced elsewhere.

112. *Galactites* Moench

Galactites Moench, Methodus: 558 (1794), nom. cons.

Annual spiny herbs. Leaves pinnatifid-pinnatisect, spiny. Capitula solitary or corymbose, heterogamous, radiate. Outer florets sterile and radiant, flattened, patent, much exceeding the involucre, purple or pink; central florets perfect, whitish. Anther filaments concrescent with very short tails. Achenes obovoid, slightly compressed, smooth, glabrous, hygrophanous, with an apical rim and a large hemispherical stipitate nectary. Pappus of plumose, deciduous bristles. $x = 11$. Two species, western Mediterranean region.

113. *Ptilostemon* Cass.

Ptilostemon Cass., Bull. Sci. Soc. Philom. Paris 1816: 200 (1816); Greuter, Boissiera 22: 9–215 (1973), rev.
Lamyra Cass. (1822).

Perennial or annual spiny herbs, rarely unarmed shrublets. Leaves dentate-pinnatisect with divaricate spines, rarely entire and unarmed. Capitula homogamous, sometimes functionally heterogamous. Leaves always white-variegated above and snow-white beneath. Involucral bracts almost unarmed to spiny, innermost often coloured. Florets red, purple, pink, perfect or the outer functionally male. Anther filaments papillose. Achenes not or only slightly compressed, smooth, glabrous. Pappus of plumose, deciduous bristles, basally connate in a ring, in outer florets sometimes of barbellate to scabrid bristles. $x = 16$, rarely $x = 12$. Fourteen species, dry stony places in the Mediterranean region.

114. *Tyrimnus* Cass.

Tyrimnus Cass., Bull. Sci. Soc. Philom. Paris 1818: 168 (1818).

Annual spiny herb with spiny-winged stems. Leaves coarsely dentate-pinnatifid. Capitula solitary on long leafless peduncles, heterogamous. Florets purple or pink; outer sterile, sometimes absent. Anther filaments concrescent. Achenes obovoid, sometimes flattened, with four ribs, glabrous, myxogenic in the concavities between ribs. Pappus of smooth or minutely scabrid deciduous

bristles, inserted downwards and bent upwards, basally connate in a very large parenchymatous ring with long hairs on the inner rim. $x = 17$. One species, *T. leucographus* Cass., Mediterranean region.

115. *Notobasis* Cass.

Notobasis Cass., Dict. Sci. Nat. 25: 225 (1822), nom. cons. prop.
Polyacantha Vaill. (1754), nom. rej. prop.

Annual herb. Leaves semi-amplexicaul, dentate to pinnatisect, spiny. Stem not winged. Capitula heterogamous, usually in racemose clusters, sessile. Involucral bracts sharply spine-tipped. Florets purple. Central florets perfect, peripheral florets sterile. Corolla more deeply cleft on the abaxial side. Achenes obliquely and broadly obovoid, strongly compressed, smooth, glabrous, with hygrophanous surface. Apical rim and nectary absent. Pappus simple, of pluriseriate, plumose bristles, basally connate in a parenchymatous cupuliform ring. As in *Tyrimnus* Cass. and *Silybum* Adans., inner margin of the basal ring hirsute. $x = 17$. One species, *N. syriaca* (L.) Cass., Mediterranean region.

116. *Lamyropsis* (Kharadze) Dittrich

Lamyropsis (Kharadze) Dittrich, Candollea 26: 98 (1971).

Perennial herbs. Leaves dentate-pinnatisect, spinulose, green above, white beneath. Capitula solitary or clustered. Involucral bracts spinulose, with a short membranous appendage. Florets red, purple or pink. Anther filaments papillose. Basal appendages very long, filiform, with two narrow divisions. Achenes oblong, sulcate, slightly compressed, with a smooth apical rim. Nectary 5-lobed. Pappus plumose, deciduous, basally connate in a ring. $x = 13$. Six species, eastern Mediterranean region, Balkan Peninsula to Caucasus.

III.4. c. Onopordum Group

Robust biennial or perennial herbs, usually spiny-toothed, rarely unarmed. Capitula homogamous. Receptacular bracts very often absent; receptacle foveolate, margins of foveoles with short scales, rarely setose. Pappus bristles always deciduous and basally connate in a ring.

117. *Onopordum* L.

Onopordum L., Sp. Pl. 2: 827 (1753).

Stout, erect, very spiny biennial herbs with winged stems, rarely acaulescent. Leaves dentate-pinnatisect or pinnatilobed, rarely undivided, spiny. Capitula solitary or rarely corymbose. Receptacle foveolate; foveoles with short marginal scales. Involucral bracts very deeply serrulate, spiny. Florets reddish, purple or pink. Anther filaments minutely papillose. Achenes obovoid-oblong, somewhat tetrangular, glabrous, often transversally fringed, sometimes with a short apical rim. Pappus of plumose, barbellate or scabrid bristles. $x = 17$. About 60 species, western and central Asia, Europe, northern Africa and the Canary Islands; introduced elsewhere.

118. *Alfredia* Cass.

Alfredia Cass., Bull. Sci. Soc. Philom. Paris 1817: 33 (1817).
Xanthopappus C. Winkl. (1893).

Perennial spiny herbs. Leaves long-petiolate, entire-hastate, lobed or spiny-dentate, green above, silver-white beneath. Capitula solitary or corymbose, often nodding at anthesis. Involucral bracts with a large membranous appendage. Receptacle foveolate in *A. cernua* Cass., setose in *A. acantholepis* Kar. & Kir. and *A. nivea* Kar. & Kir.; unknown in remaining species. Florets pink or cream-white. Corolla lobes apically thickened and incurved. Achenes obovoid, glabrous, ridged, with a denticulate apical rim. Pappus of scabrid-barbellate bristles. $x = 13$. Four species, central and eastern Asia.

119. *Ancathia* DC.

Ancathia DC., Arch. Bot. (Paris) 2: 331 (1833).

Perennial herb. Leaves linear or linear-lanceolate, entire, spinulose. Capitula solitary, terminal. Involucral bracts linear to subulate, innermost brown-purple. Receptacle setose. Florets purple-orange. Anther filaments glabrous. Anther appendages convolute with very long tails. Achenes deeply sulcate-ridged and minutely verrucose, foveolate between ridges, with a long denticulate apical rim, umbonate. Pappus of plumose s-shaped bristles. One species, *A. igniaria* (Spreng.) DC., mountains of central Asia, China and Mongolia.

120. *Olgaea* Iljin

Olgaea Iljin, Bot. Mater. Gerb. Glavn. Bot. Sada S.S.S.R. 3, 36: 142 (1922).

Perennial herbs. Leaves coriaceous, dentate-pinnatisect, spiny; cauline leaves semi-amplexicaul.

Capitula solitary or clustered, with a leaf-like involucel. Involucral bracts spiny, innermost with short, scarious, coloured appendage. Receptacle densely setose. Florets red, blue, white or purple. Corolla lobes apically somewhat thickened, anther filaments glabrous, appendages long and laciniate. Achenes linear-oblong, glabrous, smooth, with a long dentate apical rim. Pappus of barbellate bristles apically widened-incrassate. $x = 13$. Sixteen species, Afghanistan, central and eastern Asia (China and Mongolia). Very closely related to *Alfredia* Cass.

121. *Synurus* Iljin

Synurus Iljin, Not. Syst. Herb. Hort. Bot. U.S.S.R. 6: 35 (1923).

Perennial herbs. Leaves very big (30–40 cm), long-petiolate, entire-hastate, spiny-dentate, green above, silver-white beneath. Capitula solitary, often nodding at anthesis. Involucral bracts linear, spiny-tipped, densely araneose. Receptacle foveolate. Florets pink. Corolla lobes apically thickened and incurved. Achenes obovoid, glabrous, ridged, with a denticulate apical rim. Pappus of scabrid-barbellate bristles. $x = 13$. Four species, eastern Asia, from Mongolia to Japan. Very closely related to *Alfredia*.

122. *Syreitschikovia* Pavlov

Syreitschikovia Pavlov, Repert. Spec. Nov. Regni Veg. 31: 192 (1933).

Perennial herbs or dwarf shrubs. Basal leaves rosetted, petiolate; cauline leaves sessile, coriaceous, green above, grey-tomentose beneath, spinulose-dentate. Capitula solitary, terminal. Involucral bracts linear, acute, spinulose, often reddish. Receptacle setose. Florets pink. Anther filaments glabrous. Achenes obpyramidal, compressed, glabrous, with a small denticulate apical rim. Pappus double; outer of filiform bristles; inner longer and paleaceous with bristles apically incrassate, barbellate-scabrid. $x = 12$. Two species, central Asia.

123. *Takeikadzuchia* Kitag. & Kitam.

Takeikadzuchia Kitag. & Kitam., Acta Phytotax. Geobot. 3: 102 (1934).

Perennial herbs. Leaves spinulose, decurrent. Capitula globose, homogamous. Involucral bracts linear, spinulose-denticulate. Receptacle densely setose. Florets purple. Achenes glabrous, slightly compressed. Pappus of serrulate bristles. One species, *T. lomonossowii* (Trautv.) Kitag. & Kitam. Mongolia.

Probably a synonyn of *Olgaea* Iljin, as suggested by Bremer (1994). However, corollas of *Olgaea* are zygomorphic, whereas *Takeikadzuchia* was described as having actinomorphic corollas. [Note added in proof: morphological as well as molecular data clearly show that *Takeikadzuchia* is part of *Olgaea* s.l.]

124. *Lamyropappus* Knorring & Tamamsch.

Lamyropappus Knorring & Tamamsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 466 (1954).

Perennial herbs. Leaves elliptic, entire, spinose-dentate, green above, white-woolly beneath; cauline leaves sessile. Capitula long-pedunculate, very large (3–5 cm), solitary. Involucral bracts numerous, small, spiny. Receptacle setose. Florets pink. Corollas very long with linear corolla lobes. Anther filaments glabrous. Achenes obovoid-oblong, glabrous, with longitudinal ridges and marked apical rim. Pappus of long plumose bristles. One species, *L. schakaptaricus* (B. Fedtsch.) Knorring & Tamamsch., central Asia.

III.4. d. Arctium Group

Biennial or perennial herbs, rarely annuals, spiny or less often unarmed. Receptacle with twisted scales. Anther filaments slightly papillose or glabrous. Cypselae streaky (with wavy fringes), very often winged, without nectary. Pappus of free deciduous bristles.

The limits between *Arctium* and *Cousinia* have long been unclear. Most recent work has demonstrated that *Arctium* and *Cousinia* can be segregated by molecular, chromosome and pollen characters. This does not accord with morphology: *Schmalhausenia* and *Hypacanthium*, part of *Arctium* on the basis of the above characters, are morphologically much closer to *Cousinia*. As there is an "Arctioid" group of *Cousinia*, there is a "Cousinioid" group of *Arctium*. Here, the traditional generic division into four genera is followed, transferring subgenus *Cynaroides* of *Cousinia* to *Arctium*. However, it is highly probable that all four genera will have to be broadly redefined.

125. *Arctium* L. Fig. 33

Arctium L., Sp. Pl. 2: 816 (1753); Duistermaat, Gorteria, suppl. 3 (1996), rev.; Susanna et al., Collect. Bot. 26: 101–118 (2003), mol. phylog., gener. delim.
Anura (Juz.) Tschern. (1962).

Unarmed biennial herbs. Leaves very large, broadly ovate, serrulate, rarely entire, sparsely tomentose. Capitula often heterogamous, corymbose or in racemose clusters, dispersed as a unit. Involucral bracts spreading to reflexed, usually apically hooked. Florets purple; outermost often with very long, brightly coloured, "radiant" anther tubes. Achenes dimorphic; outer achenes linear, strongly recurved, unwinged; central ones obovoid-oblong, winged or sulcate, glabrous. Pappus of scabrid bristles. $x = 18$. Circa 27 species (including the "arctioid" species of *Cousinia*); some species probably hybridogenic, temperate Eurasia, introduced elsewhere.

Fig. 33. Compositae-Cardueae. *Arctium lappa*. **A** Habit. **B** Involucral bract. **C** Achene. (Font Quer 1962)

126. *Cousinia* Cass.

Cousinia Cass., Dict. Sci. Nat. 47: 503 (1827); Tscherneva, The *Cousinia* of the SSSR, Leningrad (1988), system.; Susanna et al., Collect. Bot. 26: 101–118 (2003), mol. phylog., gener. delim.
Lipskyella Juz. (1936).
Tiarocarpus Rech. f. (1972).

Perennial, biennial or rarely annual herbs or shrublets. Leaves dentate-spinose to spinose-pinnatisect, often decurrent or semi-amplexicaul. Capitula solitary, corymbose, or variously clustered, homogamous. Involucral bracts scarious, very spiny. Inner bracts often with a large, scarious, coloured appendage of same colour as florets. Florets red, purple, pink, yellow. Achenes obovoid-oblong, often winged, compressed, glabrous, rarely ridged or even wrinkled (*C. dolicholepis* Schrenk), with a very reduced apical rim (sometimes absent). Apical plate extremely small. Pappus of scabrid bristles, rarely absent. $x = 9, 10, 11, 12, 13$. About 600–700 species, central and western Asia, mainly in steppes and semi-deserts.

127. *Schmalhausenia* C. Winkl.

Schmalhausenia C. Winkl., Trudy Imp. S.-Peterburgsk. Bot. Sada 12: 281 (1892).

Spiny perennial herb. Basal leaves pinnatisect, cauline pinnatifid, very spiny, pubescent beneath, subglabrous above. Capitula small, homogamous, few-flowered, clustered in subspherical terminal corymbs or sessile on a very broad (2–3 cm) fistulose stem. Involucral bracts densely covered with white woolly hairs concealing the capitula, ending in long pungent spines. Florets purple. Corolla lobes apically thickened and recurved. Achenes 3- or 4-angled, with a denticulate apical rim. $x = 18$. One species, *S. nidulans* (Regel) Petrak, central Asia.

128. *Hypacanthium* Juz.

Hypacanthium Juz., Trudy Bot. Inst. Akad. Nauk S.S.S.R. ser. 1, 3: 324 (1936).

Spiny perennial herb. Leaves spinose-bipinnatisect, green above, grey-tomentose beneath. Capitula homogamous in lax corymbs, umbilicate. Involucral bracts scarious, spiny; innermost with a scarious, coloured appendage. Florets purple; corolla glandular-punctate. Anther appendages lacerate. Achenes obovoid, compressed, ribbed, without apical rim; apical plate much reduced.

Three species, central Asia. Very closely related to *Schmalhausenia*.

III.4. e. Saussurea Group

Unarmed perennial herbs or subshrubs; only two annual herbs. Leaves entire or pinnatisect, often silver-white below and glabrous above, sometimes hirsute-scabrid. Capitula cylindrical or globose, often paniculate, homogamous. Anther filaments glabrous. Achenes not lignified, soft. Pappus of very long (overtopping involucral bracts), showy, plumose bristles, basally connate in a ring; sometimes with a shorter, pinnulate deciduous pappus connate to a globose nectary. A difficult group because of unclear generic boundaries between *Saussurea* and *Jurinea*, and the high number of small segregates, here included in the two larger genera.

129. *Saussurea* DC.

Saussurea DC., Ann. Mus. Natl Hist. Nat. 7: 156 (1810); Lipschits, Rod *Saussurea* DC., Leningrad (1979), rev.
Hemistepta Bunge (1833).
Aucklandia Falc. (1845).
Cavea W.W. Sm. et Small (1917).

Unarmed perennial herbs, rarely annual. Leaves entire to pinnatisect, decurrent. Capitula solitary, corymbose or paniculate, homogamous. Involucral bracts entire, not spinose. Receptacle with large scales, these apically divided into narrow, twisted segments. Florets purple or pink. Achenes obconical or obpyramidal, costate, ridged, rarely pitted or plicate; usually with an apical rim. Pappus biseriate, outer of short, scabrid, free, deciduous bristles, sometimes absent; inner much longer, deciduous or persistent. $x = 13$. About 300 species, temperate Eurasia, North America, doubtfully native in Australia.

130. *Jurinea* Cass. Fig. 34

Jurinea Cass., Bull. Sci. Soc. Philom. Paris 1821: 140 (1821).
Outreya Jaub. & Spach (1843).
Aegopordon Boiss. (1846).
Jurinella Jaub. & Spach (1847).
Modestia Kharadze & Tamamsch. (1956).
Pilostemon Iljin (1961).
Perplexia Iljin (1962).
Hyalochaete Dittrich & Rech. f. (1979).
Anacantha Soják (1982).
Lipschitziella Kamelin (1993).
Himalaiella Raab-Straube (2003).

Unarmed perennial herbs or shrublets. Leaves entire or dentate to pinnatifid, often white-woolly beneath. Capitula scapose. Florets pink, purple, rarely whitish. Achenes tetrangular, obconical, usually squamulose, verrucate, tuberculate or pitted. Apical plate with a large nectary (reduced or lacking in *J. humilis* DC.), rounded, laterally ribbed. Apical rim patent, usually crenate, rarely toothed or absent (*J. depressa* (Steven) C.A. Mey.). Pappus of scabrid to barbellate or plumose, biseriate bristles, inner basally enlarged and broader, deciduous or rarely persistent. $x = 17, 18$. About 200 species, western and central Asia, Europe, northern Africa. *Diplazoptilon* Ling is probably part of *Jurinea* sensu lato.

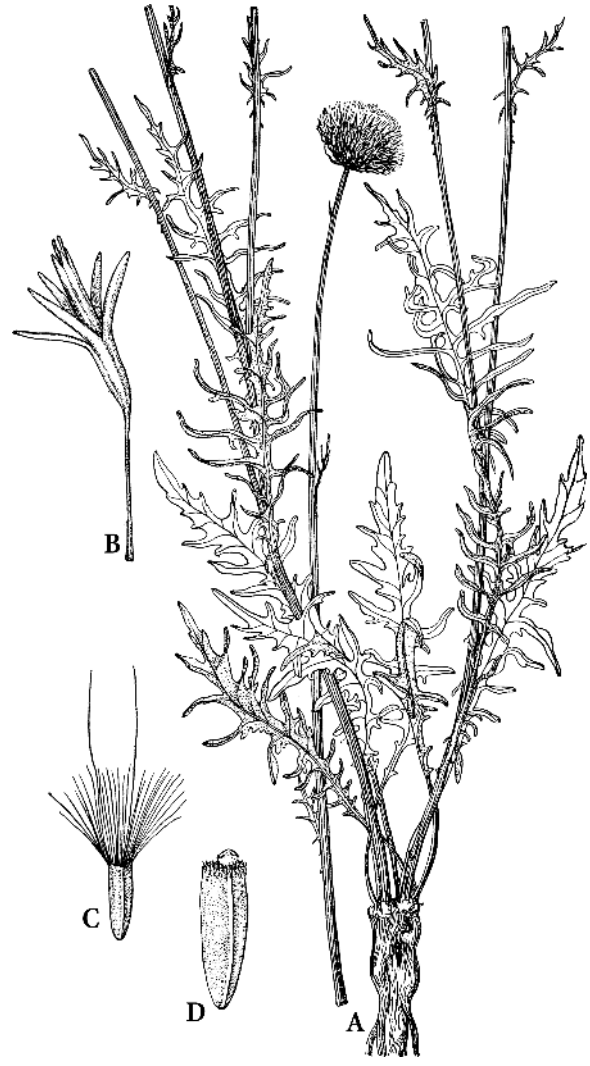

Fig. 34. Compositae-Cardueae. *Jurinea pjatajeviae*. **A** Habit. **B** Floret. **C** Achene with pappus. **D** Achene without pappus, showing nectary. (Iljin 1960)

131. *Dolomiaea* DC.

Dolomiaea DC., Guill. Arch. Bot. 2: 330 (1833).
Bolocephalus Hand.-Mazz. (1938).
Vladimiria Iljin (1939).
Frolovia Lipsch. (1954).

Unarmed perennial herbs, often acaulescent. Leaves in a basal rosette, ovate to lanceolate, often white-woolly beneath. Capitula subscapose. Florets pink or purple, rarely whitish. Achenes tetrangular, obconical, sulcate and ribbed. Apical plate with a large nectary, rounded, laterally ribbed. Apical rim small, toothed. Pappus of scabrid, biseriate bristles, inner basally enlarged and longer, detachable as a single piece. Twelve species, central Asia. Very closely related to *Jurinea*.

132. *Polytaxis* Bunge

Polytaxis Bunge, Del. Sem. Hort. Dorpat.: 8 (1843).

Unarmed annual herbs. Leaves entire, elliptic, fleshy, glandular-villous. Capitula homogamous, solitary or laxly corymbose. Receptacle setose. Involucral bracts few, laxly imbricate. Florets pink. Achenes oblong, sulcate, crenate-papillose in the furrows, sparsely pubescent, with a tuft of hairs at the base of the ridges, with apical rim. Pappus biseriate, persistent; outer bristles smooth, inner plumose, twice as long. Two species, Afghanistan, central Asia. Possibly not generically different from *Saussurea*.

III.5. Subtribe Centaureinae (Cass.) Dumort. (1827).

Perennial, biennial or annual unarmed herbs, shrubs or very rarely treelets, rarely spiny. Capitula often heterogamous with sterile radiant florets, rarely homogamous. Involucral bracts often with a diversely scarious, fimbriate, pectinate, spiny or unarmed appendage; innermost bracts always with a scarious appendage. Achenes with sclerified pericarp. Insertion areole concave, lateral-adaxial, very rarely (*Crupina*) straight, often with an elaiosome. Apical plate straight. Pappus inserted on a parenchymatous ring in the apical plate, double, formed by two rows of differently pinnulate bristles, rarely single by abortion, deciduous or persistent.

Key to the Genera

1. Subshrubs with green virgate branches and small linear leaves 2–3 mm wide, or leafless 2
– Treelets, shrubs, perennial herbs or annuals without green virgate branches, leafy 4
2. Heads heterogamous. Peripheral florets usually large, showy, radiate, with staminodes. Achenes with elaiosome **135. *Psephellus***
– Heads homogamous. Achenes without elaiosome 3
3. Plants leafless. Achenes densely sericeous **149. *Karvandarina***
– Plants basally leafy. Achenes glabrous **158. *Nikitinia***
4. Small pachycaul tree with leaves to 25 cm long clustered in terminal whorls **140. *Centaurodendron***
– Shrubs, shrublets, perennial or annual herbs, not treelets 5
5. Innermost involucral bracts ending in a pinkish, showy, shortly spiny appendage. Achenes with long, oblique insertion areole **141. *Schischkinia***
– Innermost involucral bracts without pinkish spiny appendages. Achenes without long, oblique insertion areole 6
6. Robust unarmed or spinescent annual plant, usually cultivated. Capitula subtended by wide, leaf-like, entire or dentate bracts. Florets orange-saffron or bright yellow **159. *Carthamus***
– Wild plants with capitula not subtended by leaf-like bracts. Florets not saffron 7
7. Receptacle naked, foveolate 8
– Receptacle setose 9
8. Dwarf tragacanthoid shrub or dwarf rosetted perennial. Bracts of the involucre spiny-tipped **153. *Myopordon***
– Annual plant. Bracts of the involucre with a cartilaginous margin **148. *Russowia***
9. Plants usually spiny 10
– Plants unarmed 13
10. Very spiny annual plants. Achenes usually dimorphic **159. *Carthamus***
– Spiny perennials. Achenes all similar 11
11. Florets blue, rarely yellow. Perennial herbs, rarely shrublets **161. *Carduncellus***
– Florets always yellow. Shrubs or subshrubs 12
12. Leaves broadly sheathing, ending in a trifurcate spine. Capitula to 1.5 cm. Pappus of bristles basally connate in a ring, deciduous **162. *Femeniasia***
– Leaves not reduced to a spine. Capitula 2.5–3 cm wide. Pappus persistent **160. *Phonus***
13. Involucral bracts with very wide membranous-scarious, usually lacerate appendage. Achenes ridged or tuberculate, peripheral often dorsiventrally compressed; pappus deciduous (Rhaponticum group) 14
– Involucral bracts with narrow entire hyaline margin, mucronate, spinose, pectinate or filiform. Achenes always laterally compressed, never tuberculate; pappus usually persistent 17
14. Large shrub to 4 m high **155. *Ochrocephala***
– Annual or perennial plants, not shrubby 15
15. Leaves with margins and veins minutely denticulate, very scabrid. Insertion areole two-lipped; lower lip incrassate, white; upper lip with two white recurved costae **151. *Callicephalus***

– Leaves not densely scabrid. Insertion areole inconspicuous 16
16. Small, inconspicuous annuals to 30 cm high. Involucral bracts spinulose **152. *Oligochaeta***
– Perennial herbs with muticous bracts. Achenes subequal or dimorphic **150. *Rhaponticum***
17. Achenes with six translucent costae, outer ones arcuate-falcate, innermost straight **147. *Plagiobasis***
– Achenes without translucent costae, all subequal 18
18. Achenes diversely ridged, ribbed or foveolate, rarely smooth, often sericeous. Insertion areole with a whitish incrassate margin (Volutaria group) 19
– Achenes smooth or sulcate, never foveolate, rarely sericeous. Insertion areole without incrassate margin 23
19. Involucral bracts with very long filiform appendages **146. *Tricholepis***
– Involucral bracts shortly mucronate or muticous 20
20. Robust plants to 150 cm tall 21
– Plants to 80 cm 22
21. Robust annual. Stem deeply striate. Capitula homogamous, small (to 15 mm), clustered in paniculate inflorescences **143. *Goniocaulon***
– Robust perennial to 150 cm tall, rarely smaller biennial or annual. Stem not striate. Capitula heterogamous, to 2 cm, terminal, corymbose or solitary **144. *Mantisalca***
22. Involucral bracts narrowly triangular, with a small appendage, acuminate or shortly spiny **142. *Volutaria***
– Involucral bracts broadly oval, muticous, with only a hyaline margin **145. *Amberboa***
23. Capitula homogamous 24
– Capitula heterogamous 26
24. Outer involucral bracts similar to upper leaves. Achenes markedly 4-angled **161. *Carduncellus***
– Outer involucral bracts not similar to upper leaves. Achenes not 4-angled 25
25. Achenes sulcate; insertion areole almost basal **157. *Klasea***
– Achenes almost smooth; insertion areole markedly lateral **156. *Serratula***
26. Achenes not or only slightly compressed, dark brown with darker band at basis. Insertion areole basal or oblique. Inner row of pappus of 5–10 very short scales **134. *Crupina***
– Achenes compressed, without darker band at basis. Insertion areole lateral. Inner row of pappus of many bristles or scales 27
27. Very scabrid annual herbs. Peripheral sterile florets with large staminodes. Achenes with cream-white, shiny base; insertion areole deeply lateral with a rugulose elaiosome **136. *Stizolophus***
– Annual or perennial herbs or shrubs not very scabrid. Peripheral radiant florets with small staminodes, very often lacking. Base of the achenes not cream-white; elaiosome, if present, smooth 28
28. Shrubs or shrublets, rarely perennial herbs. Achenes without elaiosome. Pappus deciduous 29
– Subshrubs, perennial or annual herbs. Achenes usually with elaiosome. Pappus persistent 30
29. Achenes smooth, slightly falcate, to 4 mm. Insertion areole with five small teeth **137. *Cheirolophus***
– Achenes sulcate, straight, to 8 mm. Insertion areole not toothed **154. *Centaurothamnus***
30. Appendages of bracts long-plumose. Sterile florets flattened. Achenes with three concentric apical ridges **133. *Zoegea***
– Appendages of bracts not long-plumose. Sterile flowers not flattened. Achenes without apical concentric ridges 31
31. Plants with more or less fleshy, densely glandular leaves. Achenes sericeous, outer sterile and oblong **163. *Crocodylium***
– Leaves not fleshy and glandular. Achenes glabrescent or sparsely pilose, outer ones rarely sterile and, if so, then linear-arcuate 32
32. Sterile marginal florets without staminodes **164. *Centaurea***
– Sterile marginal florets with staminodes 33
33. Sterile marginal flowers indistinct. Appendages of bracts usually reduced to cartilaginous margin. Achenes broadly ovate-elliptical, with basal whitish band **139. *Rhaponticoides***
– Sterile marginal florets big and showy. Appendages of bracts well-developed, pectinate or fimbriate. Achenes oblong, without whitish basal band 34
34. Sterile marginal florets with narrow divisions and minute sterile achenes. Achenes arcuate, asymmetrical, ridged. Pappus always present, deciduous **138. *Plectocephalus***
– Sterile marginal florets with wide divisions, without sterile achenes. Achenes symmetrical, smooth. Pappus persistent, often much reduced or absent **135. *Psephellus***

Genera of Centaureinae

Basal Genera

133. *Zoegea* L.

Zoegea L., Mant. pl. 1: 15 (1767).

Unarmed, scabrid annual herbs. Capitula solitary, heterogamous. Involucral bracts purple-stained; outer and median with long palmate-fimbriate appendage; innermost bracts with scarious, lanceolate appendage, yellow above. Outer florets sterile, exceeding the involucre, large, flattened, orange-yellow, pink-purple or white. Corolla tube saccate. Achenes obovoid, strongly compressed, transversely and concentrically sulcate and sparsely sericeous above. Insertion areole with elaiosome. Pappus double; outer of long scabrid bristles in many rows; inner of short scales, apically lacerate. $x = 15$. Three species, Turkey, Middle East, Irano-Turanian region and central Asia.

134. *Crupina* (Pers.) DC.

Crupina (Pers.) DC., Ann. Mus. Natl Hist. Nat. 7: 157 (1810); Couderc-Le Vaillant, Thèse Doctorale, Université de Paris-Sud (1984), rev.

Unarmed annual herbs. Leaves pinnatisect, dentate, with glochidiate hairs and sparse deeply branched hairs. Capitula heterogamous. Involucral bracts unarmed, lanceolate, mucronate. Florets pink-purple, outer sterile. Corolla pilose. Achenes cylindrical or only basally compressed, sparsely sericeous, dark brown or blackish with a basal darker band, and a deep furrow above which forms an apical rim. Insertion areole exactly basal or sublateral. Pappus double, persistent; outer of dark bristles, inner of 5–10 small scales. x = 14, 15, 29. Three species, Mediterranean and Irano-Turanian region reaching eastwards to central Asia, northern Africa, widely naturalized in the western United States (California, Oregon, Idaho and Washington).

135. *Psephellus* Cass.

Psephellus Cass., Dict. Sci. Nat. 43: 488 (1826).
Aetheopappus Cass. (1827).
Phaeopappus Boiss. (1845) pro parte.
Hymenocephalus Jaub. & Spach (1847).

Perennial herbs or dwarf desert shrubs. Leaves usually pinnatisect, sometimes entire-dentate, often silver-white beneath and green above. Capitula long-pedunculate, heterogamous. Involucral bracts with triangular lacerate-fimbriate appendages, silvery or blackish, often scarious and very large, totally covering the bracts, sometimes plicate. Outer florets sterile, with staminodes, radiant, with a broad limb divided into 5–10 subequal lobes. Achenes oblong, compressed, with elaiosome; hilum lateral. Pappus double, sometimes very short or lacking. x = 15. Circa 100 species, western Siberia, Iran, Caucasus, Ukraine, Crimea, Turkey. Some species widely cultivated as ornamentals.

136. *Stizolophus* Cass.

Stizolophus Cass., Dict. Sci. Nat. 44: 36 (1826).

Annual herbs. Leaves entire or lyrate-pinnatifid, scabrid; lobes ending in a short mucro, otherwise unarmed. Capitula solitary or laxly corymbose, heterogamous, globose, markedly contracted above. Involucral bracts very small and many, with ciliate appendages ending in a slender spine. Receptacle setose. Florets yellow; outer sterile with large staminodes, central florets perfect; style very long (3–4 mm). Achenes oblong, faintly ridged, glabrous. Insertion areole very deeply carved, with a rugulose elaiosome. Hilum caudate. Pappus deciduous, double; outer bristles with long pinnules, inner bristles shorter with few pinnules. x = 15. Two species, Turkey, Caucasus and Irano-Turanian region.

137. *Cheirolophus* Cass.

Cheirolophus Cass., Dict. Sci. Nat. 51: 55 (1827); Susanna et al., Pl. Syst. Evol. 214: 147–160 (1999), mol. phylog.
Paleocyanus Dostál (1971).

Shrubs or subshrubs (*Ch. uliginosus* (Brot.) Dostál perennial herb). Leaves entire or pinnatisect, often densely glandular. Capitula indistinctly heterogamous, many-flowered, usually globose. Involucral bracts leaf-like with a small, shortly fimbriate appendage, often tinged red. Flowers usually pink, more rarely whitish or pale yellow. Outer florets sterile, with staminodes, scarcely radiant; central florets perfect. Achenes linear-oblong; detachment scar with five small teeth, without elaiosome; hilum basal. Pappus a single row of easily deciduous bristles. x = 15. Twenty-five species, western Mediterranean region (extending eastwards to Malta), northern Africa and Macaronesia.

138. *Plectocephalus* D. Don

Plectocephalus D. Don in Sweet, Brit. Fl. Gard. 4: 51 (1830); Hind, Curtis's Bot. Mag. 13: 3–7 (1996), rev.
Phalacrachena Iljin (1937).

Unarmed annual or perennial herbs, densely glandular. Leaves with minutely denticulate, cartilaginous margins and veins. Capitula terminal, solitary or laxly corymbose, heterogamous. Involucral bracts membranous, veined, with very large decurrent pectinate-fimbriate appendages, never spiny. Marginal florets long-radiant, with very narrow corolla lobes, sterile, with staminodes. Corolla sometimes sparsely villous and glandular. Achenes obovoid, arcuate, markedly asymmetrical, glabrous, faintly many-ribbed, with a basal narrowing near the areole; insertion areole lateral. Hilum basal. Pappus obscurely double, deciduous. Five species, relict disjoint area: two species in North America, two in South America, two in Russia and Ukraine and one in eastern Africa. One species, *P. americanus* D. Don, cultivated as an ornamental ("basket flower").

139. *Rhaponticoides* Vaill.

Rhaponticoides Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 165 (1754); Agababian, Bot. Inst. Acad. Sci. Armenia, Erevan (1992), rev. ut *Centaurea*.

Centaurea L. (1753) pro minima parte.
Bielzia Schur (1866).

Perennial herbs. Leaves deeply divided, rarely entire, with denticulate lobes, sparsely araneose or glabrous, often somewhat cartilaginous. Capitula terminal, usually solitary, umbilicate-globose, heterogamous. Involucral bracts leaf-like, not appendiculate, with a membranous entire margin, rarely lacerate. Florets pink or yellow. Anther filaments papillose. Achenes broadly oblong, blackish, glabrous, with a cartilaginous and whitish insertion areole and a small elaiosome. Hilum caudate. Pappus double; inner row of shorter and broader bristles. $x = 13?, 15$. Seventeen species, Irano-Turanian and Mediterranean region, eastern Europe.

140. *Centaurodendron* Johow

Centaurodendron Johow, Estud. Fl. Juan Fernández 63 (1896).
Yunquea Skottsb. (1929).

Small pachycaul tree with soft wood. Leaves terminal on the stems, very large (to 30 cm), obovate, with broad (alate) semi-amplexicaul petiole; margins serrate. Capitula comparatively small (to 2 cm), clustered in dense corymbs, heterogamous. Outer bracts with pectinate appendages, innermost with a broad round cucullate appendage. Receptacle setose. Florets purple, outer sterile and radiant. Achenes ovoid, obscurely tetragonous, glabrous. Pappus double, easily deciduous. Two species, Juan Fernández Islands.

141. *Schischkinia* Iljin

Schischkinia Iljin, Repert. Spec. Nov. Regni Veg. 38: 73 (1935).

Annual herb. Leaves linear with palmate spines. Capitula clustered, sessile, heterogamous. Innermost involucral bracts acute, coloured and showy. Florets yellowish; outer sterile with oblong sterile achenes, central with tube 1/10 as long as limb. Achenes oblong, much compressed, glabrous; insertion areole very long, oblique, with rudimentary elaiosome. Pappus double; outer as long as the achene, inner very short, of a solitary, long, broad scale. Pappus of the external sterile achenes reduced to a single long palea. One species, *S. albispina* (Bunge) Iljin, semi-desert steppes of central Asia.

III.5. a. Volutaria Group

Annual or perennial herbs. Capitula heterogamous, very rarely homogamous. Sterile radiant florets usually large and showy, with staminodes. Achenes diversely ribbed, ridged or foveolate, rarely smooth; insertion areole very deep, concave, with incrassate, cartilaginous margin and a small elaiosome. Hilum basal. Pappus of scales, rarely of bristles.

142. *Volutaria* Cass.

Volutaria Cass., Bull. Sci. Soc. Philom. Paris 1816: 200 (1816).
Cyanopsis Cass. (1817).
Volutarella Cass. (1826).

Unarmed annual herbs, rarely subperennial (*V. muricata* (L.) Maire). Leaves entire to dentate-pinnatisect, scabrid. Capitula solitary or laxly corymbose, heterogamous (rarely homogamous). Involucral bracts green, with marked veins, with a mucronate or spinulose linear appendage, often blackish. Outer florets pink, purple or violet, sterile, tubular; central florets of the same colour (in blue-rayed species, rarely yellow). Achenes obovoid-oblong, ribbed, transversely rugulose between the ribs. Insertion areole lateral, with incrassate, cartilaginous margin, with elaiosome. Pappus of linear-oblanceolate persistent scales. $x = 14, 16$. Eighteen species, dry stony places in the Mediterranean and Irano-Turanian region, from Arabia and Iran to Morocco.

143. *Goniocaulon* Cass.

Goniocaulon Cass., Bull. Sci. Soc. Philom. Paris 1817: 33 (1817).

Robust annual herb to 1.5 m high with deeply striate stem. Leaves entire, serrate. Capitula to 15 mm, homogamous, clustered in dense panicles. Involucral bracts with wide scarious margin, apiculate. Receptacle setose. Florets pink. Achenes oblong, longitudinally ridged, glabrous, with a small apical rim. Insertion areole lateral, with incrassate, cartilaginous, white margin and a small elaiosome. Pappus obscurely double with very shortly pinnulate, wide scales. $x = 16$. One species, *G. glabrum* Cass., India, Pakistan, eastern Africa.

144. *Mantisalca* Cass.

Mantisalca Cass., Bull. Sci. Soc. Philom. Paris 1818: 141 (1818).

Microlonchus Cass. (1826).

Unarmed annual, biennial or perennial herb. Leaves dentate-pinnatifid, strongly scabrid. Capitula solitary, pedunculate, heterogamous. Receptacle setose. Involucral bracts coriaceous, with a narrow hyaline margin, apically ending in a triangular, scarious, black, spinescent appendage. Outer florets sterile, with staminodes, purple, longer than the perfect central florets of the same colour. Achenes obovoid, ribbed and transversely rugulose between the ribs, glabrous. Pappus of scales. $x = 11$. One species, *M. salmantica* (L.) Briq. & Cavill. Extremely variable, especially in habit; some species of doubtful value described on the basis of these differences. Dry places, ditches and roadsides in the Mediterranean region, from Turkey to Morocco.

145. *Amberboa* Vaill.

Amberboa Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 182 (1754), nom. cons.; Iljin, Izv. Bot. Sada Akad. Nauk S.S.S.R. 30: 101–116 (1932), part. rev.

Unarmed annual or rarely biennial herbs. Leaves entire to dentate-pinnatisect. Capitula solitary, pedunculate, heterogamous. Outer and middle involucral bracts without appendages or with small brown, scarious, triangular appendage. Outer florets sterile, radiant, with a very expanded 5–8-lobed tubular limb. Florets violet-pink. Corolla lobes apically incrassate, recurved, darker. Achenes obovoid-oblong, densely sericeous, brown, ribbed, transversely rugulose, with a cartilaginous apical rim. Pappus double, persistent, scaly. $x = 16$. Six species, eastern Europe, Caucasus, south-western Asia. One species, *A. moschata* (L.) DC., widely cultivated as an ornamental.

146. *Tricholepis* DC.

Tricholepis DC., Arch. Bot. (Paris) 2: 515 (1833).

Unarmed annual or perennial herbs. Leaves linear, entire or sometimes dentate-pinnatifid. Capitula solitary, pedunculate, terminal, homogamous. Involucral bracts numerous, with a very long subulate-acicular and hair-pointed or spine-tipped appendage. Florets pink, purple, lilac or yellow. Achenes obovoid-oblong, striate or faintly many-ribbed, glabrous. Pappus of two similar rows of wide, pinnulate scales. $x = 16$. Circa 20 species, central Asia, Afghanistan, Myanmar, Nepal, Pakistan and India.

147. *Plagiobasis* Schrenk

Plagiobasis Schrenk, Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 3: 109 (1845).

Unarmed perennial herb. Leaves elliptic-oblong, entire, serrate; cauline leaves sessile. Capitula terminal, globose, homogamous. Involucral bracts orbicular with a wide hyaline margin. Receptacle setose. Florets pink. Achenes dimorphic; peripheral falcate, central linear-oblong, faintly costate, rounded apically. Pappus deciduous, of wide, long pinnulate scales. One species, *P. centauroides* Schrenk, central Asia.

148. *Russowia* C. Winkl.

Russowia C. Winkl., Trudy Imp. S.-Peterburgsk. Bot. Sada 11: 282 (1890).

Unarmed annual herb. Leaves interruptedly pinnatisect with linear-lanceolate lobes. Capitula laxly corymbose. Involucral bracts muticous, with scarious-hyaline margin and three dark, translucent, cartilaginous veins. Receptacle alveolate. Florets pink. Achenes linear-oblong, smooth, sparsely sericeous. Insertion areole lateral, very deep, with spirally incrassate margins, with elaiosome. Pappus obscurely double, of long, narrow, pinnulate bristles. One species, *R. sogdiana* (Bunge) B. Fedtsch., central Asia.

149. *Karvandarina* Rech. f.

Karvandarina Rech. f., Österr. Akad. Wissensch., Math.-Naturwissensch. Kl., Anz. 87: 198 (1950).

Unarmed virgate subshrub. Leaves small, very often totally lacking, entire or dentate, basally hairy, otherwise glabrous. Capitula laxly corymbose, homogamous. Involucral bracts scarious, strongly veined, with a narrow hyaline, decurrent margin and a triangular, red-brown, scarious, not spiny appendage. Florets pink with straight corolla tube. Achenes obovoid-oblong, subcompressed, sericeous-villous, apically truncate, with very narrow apical rim; insertion areole basal-central. Pappus double, outer of scabrid bristles, inner of few, basally wider bristles. One species, *K. aphylla* Rech. f., Aellen & Esfand., Iran, Pakistan.

III.5. b. Rhaponticum Group

Unarmed perennial herbs, rarely annuals. Capitula homogamous. Involucral bracts with very large, unarmed scarious appendages, usually silvery-

white. Achenes often dimorphic, diversely ribbed or papillose, with small insertion areole with a rudimentary elaiosome; hilum basal. Pappus usually deciduous in a ring.

150. *Rhaponticum* Vaill.

Rhaponticum Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 177 (1754); Dittrich, Candollea 39: 45–49 (1984), nomencl.
Leuzea DC. (1815).
Stemmacantha Cass. (1817).
Acroptilon Cass. (1827).

Unarmed perennial herbs. Leaves entire or lobed-pinnatisect, usually snow-white beneath and green above. Capitula large, solitary. Involucral bracts membranous, with an entire or lacerate appendage; inner bracts with a subulate appendage. Florets red-purple, whitish or yellow, with narrow corolla lobes. Achenes obovoid-oblong, more or less ribbed with the ribs ending in 8–10 teeth forming a crenate apical rim, glabrous. Pappus obscurely double; outer of scabrid to shortly plumose, deciduous bristles; inner bristles wider and longer than outer. $x = 12$, 13. Twenty-six species, mountains of Europe, Asia, very doubtfully native in Australia. One species, *Rh. repens* (L.) Hidalgo, is an extremely noxious weed ("Russian knapweed").

151. *Callicephalus* C.A. Mey.

Callicephalus C.A. Mey., Verz. Pfl. Casp. Meer 66 (1831).

Unarmed annual herb. Leaves linear-pinnatisect, scabrid, with denticulate veins. Capitula solitary, terminal, heterogamous. Involucral bracts with a large appendage ending in a short brown mucro. Florets pink-purple, small; outer sterile, very short. Achenes obpyramidal, angled, rugulose, with a denticulate apical rim. Insertion areole two-lipped; lower lip incrassate, white; upper lip with two white recurved costae. Pappus double, outer of scabrid bristles, inner of (4–8) wider, very long, subulate scales. $x = 14$. One species, *C. nitens* (M. Bieb.) C.A. Mey., central and western Asia.

152. *Oligochaeta* (DC.) K. Koch

Oligochaeta (DC.) K. Koch, Linnaea 17: 42 (1843); Wagenitz, Veröff. Geobot. Inst. ETH Stiftung Rübel Zürich 37: 315–329 (1962), rev.

Unarmed annual herbs, minutely glandular. Leaves dentate or dentate-pinnatifid. Capitula solitary, homogamous. Involucral bracts with a triangular, long-decurrent hyaline margin ending in a small, woolly, spinescent appendage. Florets pink-purple or whitish. Style arms very long, rolled outwards. Achenes dimorphic; outer dorsiventrally compressed, often epappose; inner obconical, laterally compressed, smooth or faintly ribbed and rugulose, glabrous, with apical rim. Pappus double, outer of scabrid bristles; inner pappus of 1–5 longer, wider bristles. $x = 14$. Four species, Irano-Turanian region, Caucasus, Afghanistan, India.

153. *Myopordon* Boiss.

Myopordon Boiss., Diagn. Pl. Orient. ser. 1, 6: 107 (1846); Wagenitz, Ber. Deutsch. Bot. Gesell. 71: 271–277 (1958), rev.

Compact, unarmed or spiny subshrubs or perennial herbs, sometimes acaulescent. Leaves entire or pinnatisect. Capitula solitary. Involucral bracts with a wide scarious brown appendage ending in a short thin spine. Receptacle foveolate with short scales. Florets reddish, purple or yellowish. Anther filaments papillose; basal appendages shortly laciniate. Achenes oblong, longitudinally striate, transversely rugose (keeled, plicate or pitted), subcompressed, with apical rim. Pappus of barbellate-smooth bristles. Five species, western Asia.

154. *Centaurothamnus* Wagenitz & Dittrich

Centaurothamnus Wagenitz & Dittrich, Candollea 37: 111 (1982).

Unarmed shrub. Leaves entire, lanceolate, white-lanose with marked veins beneath, tomentose or glabrescent above when old. Capitula solitary, terminal, heterogamous. Involucral bracts scarious, six-veined, with small, dark-brown, woolly appendages. Receptacle setose. Florets rose, outer sterile and radiant. Achenes linear-oblong, ridged, glabrous. Pappus double, persistent. $x = 14$. One species, *C. maximus* (Forssk.) Wagenitz & Dittrich, Yemen.

155. *Ochrocephala* Dittrich

Ochrocephala Dittrich, Bot. Jahrb. Syst. 103: 467–480 (1983).

Tall shrub to 2 m high. Leaves elliptic or ovate, to 18 cm long and 8 cm wide, sparsely floccose. Capitula very large, 45 mm long and to 40 mm wide, heterogamous, corymbose. Involucral bracts with large scarious, whitish, entire or lacerate unarmed appendages, innermost acuminate. Peripheral florets sterile, central florets perfect, with very short

corolla tube. Achenes oblong, costate. Pappus double, inner row with wider bristles. One species, *O. imatongensis* (Philipson) Dittrich, eastern and central Africa, India.

III.5. c. Serratula Group

Unarmed perennial herbs or shrublets. Capitula homogamous, very rarely heterogamous. Appendages of bracts rudimentary. Achenes usually ridged or ribbed. Insertion areole almost basal, small, without elaoisome. Hilum basal. Pappus obscurely double, easily deciduous.

156. *Serratula* L.

Serratula L., Sp. Pl. 2: 816 (1753).

Unarmed perennial herbs. Leaves entire to dentate-lobed or frequently pinnatifid-pinnatisect. Capitula solitary or corymbose, homogamous. Involucral bracts leaf-like, often reddish or pinkish, veined, with an appendage usually reduced to a slender spine; inner bracts scarious, coloured. Receptacle setose. Florets pink or purple. Achenes linear-oblong, glabrous, faintly ribbed. Pappus of pinnulate bristles in two rows; inner bristles basally wider and as long as outer ones. $x = 11$. Two to four species, Eurasia, rare in the south.

157. *Klasea* Cass.

Klasea Cass., Dict. Sci. Nat. 35: 173 (1825).
Schumeria Iljin (1960).

Unarmed perennial herbs. Leaves entire or serrate, sometimes pinnatisect. Capitula homogamous. Involucral bracts leaf-like, veined, with an appendage usually reduced to an apical slender spine, very often reflexed, rarely muticous; rarely appendages well developed, broadly scarious. Florets pink, whitish or yellowish, with narrow corolla lobes. Achenes linear-oblong, sulcate, often apically rugulose between the ridges, glabrous. Insertion areole almost basal. Pappus of barbellate or barbellate-plumose persistent bristles, double; inner row raised above outer. $x = 15$. Sixty-five species, Europe, Mediterranean region, south-western Asia and northern Africa.

158. *Nikitinia* Iljin

Nikitinia Iljin, Bot. Mater Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 356 (1960).

Unarmed, virgate, much-branched subshrub with green branches. Leaves linear, congested at the basis of the stem. Capitula narrowly subcylindrical, terminal, homogamous. Involucral bracts membranous with cartilaginous margin and a very short black mucro. Receptacle subcylindrical, convex, densely setose. Florets pink. Achenes narrowly linear-oblong, 4–5-ribbed, glabrous, with a small apical rim. Pappus double, deciduous; outer of pinnulate bristles, inner of shorter apically lacerate scales. One species, *N. leptoclada* (Bornm. & Sint.) Iljin, Iran, central Asia. Note added in proof: according to Martins and Hellwig, Taxon 54:633–638 (2005), *Nikitinia* should be placed in *Klasea*.

III.5. d. Carthamus Group

Carthamus group; López González, Anales Jard. Bot. Madrid 47: 11–34 (1990), rev.; Vilatersana et al., Pl. Syst. Evol. 221: 89–105 (2000), mol. phylog.

Annual or perennial herbs, rarely shrublets, usually spiny. Leaves pinnatifid, rarely entire. Capitula homogamous. Achenes compressed, very hard, often angulose, glabrous, sometimes dimorphic. Insertion areole very small, without elaiosome. Hilum lateral. Pappus double, persistent, sometimes basally connate in a ring and deciduous.

159. *Carthamus* L.

Carthamus L., Sp. Pl. 2: 830 (1753); Hanelt, Feddes Repert. Spec. Nov. Regni Veg. 67: 41–180 (1963), rev.
Kentrophyllum Neck. ex DC. (1810).

Annual, spiny, rarely unarmed (*C. tinctorius* L.) herbs. Leaves pinnatifid or pinnatisect, usually spiny. Capitula terminal, solitary or laxly corymbose. Involucral bracts foliose, very spiny. Innermost bracts usually without cucullate appendages. Florets yellow or pink, rarely orange. Achenes obpyramidal, markedly dimorphic: outer usually epappose, small, oblong-obconical, rugose; inner pappose, large, oblong-obconical, almost smooth. Pappus double, persistent, formed by two rings of wide scales; inner ring shorter. $x = 10$, 11, 12, 32. Twenty species, Iran, Caucasus, eastern Mediterranean region to central Asia.

Species of sect. *Atractylis* are colonizing weeds very widely distributed in the Mediterranean region and introduced to Australia, California, and Chile. One species, *C. tinctorius* L. (safflower), widely cultivated for oil, dye (substitute of saffron) and as an ornamental.

160. *Phonus* Hill

Phonus Hill, Veg. Syst. 4: 5 (1762).

Very spiny shrubs to 200 cm. Branches covered by remains of leaves. Leaves spinose-dentate or pinnatifid. Capitula terminal, solitary, large, to 3 cm wide, many-flowered. Involucral bracts foliose, green, spiny, innermost without cucullate appendages. Florets yellow. Achenes obconical, angulose, glabrous. Pericarp undifferentiated. Pappus a single row of persistent bristles. $x = 12$. Two species, southern Spain, northern Africa.

161. *Carduncellus* Adans.

Carduncellus Adans., Fam. Pl. 2: 116 (1763).

Perennial or rarely annual herbs, often acaulescent. Leaves pinnatifid or pinnatisect, spiny, rarely unarmed, glabrous or sparsely pubescent. Capitula solitary. Involucral bracts foliose, green, with spiny fimbriate appendages, innermost with cucullate appendages. Florets usually pale or light blue, very seldom yellowish. Achenes obconical, angulose, apically with transversal ridges. Pappus double, sometimes single by abortion of the outer ring, rarely absent, deciduous or rarely persistent. $x = 12$. Twenty-seven species, Iberian Peninsula and northern Africa, one species widely distributed in the Mediterranean region eastwards to Greece.

162. *Femeniasia* Susanna

Femeniasia Susanna, Collect. Bot. (Barcelona) 17: 83 (1987).

Spiny subshrub forming large pulvinules. Stems and leaves fleshy when young. Leaves sheathing, apically transformed into trifid spines. Capitula small, to 1.5 cm wide, terminal. Involucral bracts green, leaf-like, with a short spiny appendage; innermost bracts with a rudimentary appendage. Florets yellow. Achenes broadly obconical or obscurely obpyramidal, very small, blackish, glabrous. Pappus a single row of pinnulate bristles, basally connate, deciduous as a single piece. $x = 12$. One species, *F. balearica* (J.J. Rodr.) Susanna, windy and rocky seashores of Menorca (Balearic Islands).

III.5. e. Crocodylium Group

163. *Crocodylium* Vaill. Fig. 35

Crocodylium Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 163 (1754) ["*Crocodilium*"]; Font et al., Pl. Syst. Evol. 234: 15–26 (2002), mol. phylog., gener. delim.
Aegialophila Boiss. & Heldr. (1849).

Annual or perennial herbs. Leaves interrupted runcinate-pinnatisect, often fleshy, densely glandular. Capitula heterogamous. Involucral bracts oval, with a very large entire or fimbriate-dentate scarious appendage, sometimes spiny. Outer florets sterile, large, radiant, with acheniodes; inner perfect. All florets with many stalked glands, especially on the tube. Achenes oblong-obconical, densely sericeous; insertion areole very small,

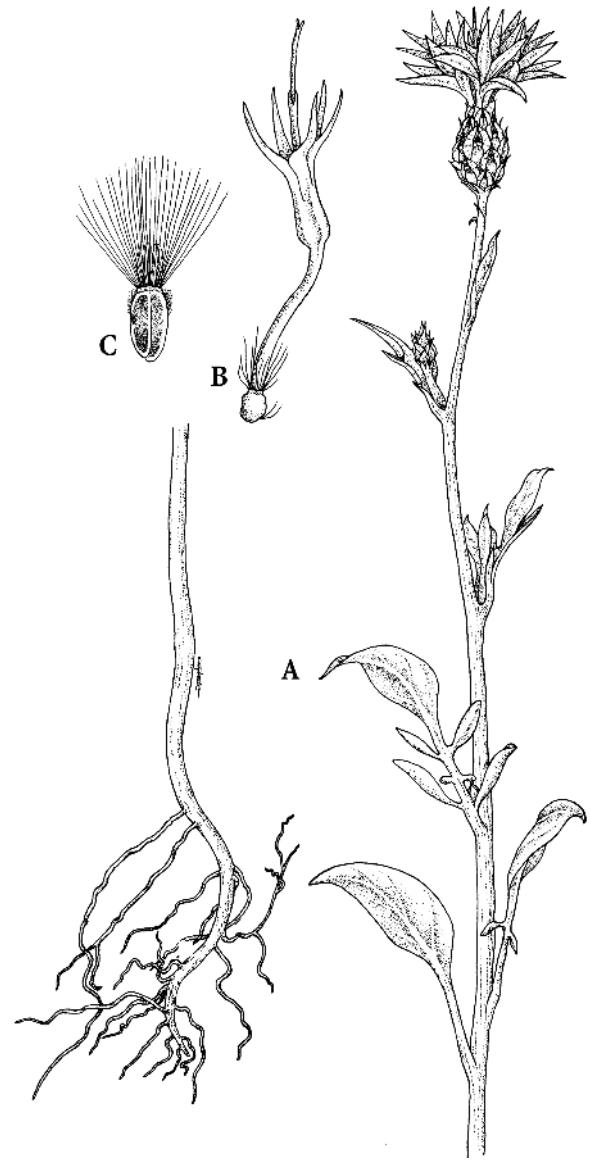

Fig. 35. Compositae-Cardueae. *Crocodylium syriacum*. **A** Habit. **B** Floret. **C** Achene. Drawing by E. Macpherson

sublateral. Pappus double, outer bristles with pinnulae longer than width of bristle, inner row shorter with apically lacerate bristles. $x = 11$. Three species, coastal sands, Greece, Aegean Islands, Turkey, Egypt and Middle East.

III.5. f. Centaurea Group

164. *Centaurea* L. Fig. 36

Centaurea L., Sp. Pl. 2: 909 (1753) pro maxima parte, nom. cons.; Susanna et al. (1995), mol. phylog.; Wagenitz & Hellwig, in Proceedings of the International Compositae Conference, Kew, 1994, Royal Botanic Gardens, Kew: 491–510 (1996), evol.; Garcia-Jacas et al., Pl. Syst. Evol. 185–199 (2000), mol. phylog.
Cnicus L. (1753), nom. cons.
Cyanus Mill. (1754).
Jacea Mill. (1754).
Colymbada Hill (1762).
Acosta Adans. (1763).
Calcitrapa Adans. (1763).
Seridia Juss. (1779).
Melanoloma Cass. (1823).
Chartolepis Cass. (1826).
Tomanthea DC. (1837).
Ptosimopappus Boiss. (1845).
Phaeopappus Boiss. (1846).
Hyalaea Jaub. & Spach (1847).
Cheirolepis Boiss. (1849).
Stephanochilus Coss. & Durieu ex Benth. (1873).
Chrysopappus Takht. (1938).
Grossheimia Sosn. & Takht. (1945).
Wagenitzia Dostál (1973).

Annual, biennial or perennial herbs or shrubs, usually unarmed. Capitula heterogamous, rarely homogamous. Involucral bracts scarious, rarely leaf-like, with a variable apical appendage, spiny or unarmed, membranous, appendage rarely absent. Florets blue, pink, purple, orange or yellow, rarely white. Sterile florets radiant and showy, sometimes very long, rarely reduced. Achenes oblong, compressed, rarely obconical (sect. *Stephanochilus*), brown-blackish, smooth, very rarely ridged (sect. *Cnicus* and *Stephanochilus*), subglabrous or sparsely pilose. Hilum lateral. Insertion areole with elaiosome. Pappus double; outer bristles pinnulate or rarely plumose, inner much shorter, epinnulate, lacerate above; rarely pappus of pinnulate stiff setae (sect. *Cnicus*). $x = 7, 8, 9, 10, 11, 12$. Circa 250 species, Eurasia, especially Irano-Turanian and Mediterranean region.

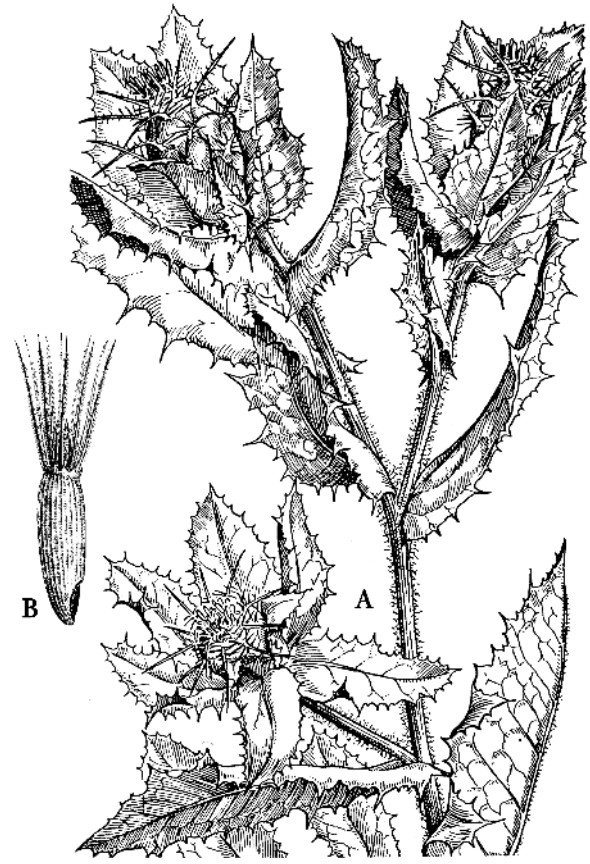

Fig. 36. Compositae-Cardueae. *Centaurea benedicta*. **A** Habit. **B** Achene. (Font Quer 1962)

Some species cultivated as ornamentals (*C. montana* L., *C. ragusina* L.). *Centaurea cyanus* L. is a cosmopolitan weed, associated with cereal cultivation; other species naturalized as noxious weeds in Australia and North America (*C. diffusa* Lam., *C. diluta* Aiton, *C. maculosa* Lam., *C. melitensis* L. and *C. solstitialis* L.).

Carduoid Genera of Uncertain Placement

C. Jeffrey

165. *Cavea* W.W. Sm. & Small

Cavea W.W. Sm. & Small, Trans. Bot. Soc. Edinburgh 27: 119 (1917); Ling & Chen, Acta Phytotax. Sin. 10: 92–102, cum ic. (1965), morph., distrib.

Perennial, sometimes dioecious herb. Leaves alternate, ovate-lanceolate, pubescent. Capitula solitary,

terminal, large, heterogamous and disciform or homogamous and unisexual. Phyllaries few-seriate, imbricate, herbaceous. Receptacle plane, epaleate. Florets all regular; corollas hairy with robust, acute, multicellular hairs, those of pistillate (outer in heterogamous capitula) 3–4-lobed; styles of pistillate florets without articulation, arms spathulate, with marginal, apically confluent stigmatic areas; corollas of functionally staminate (inner in heterogamous capitula) larger, limb campanulate, deeply 5-lobed; anthers shortly calcarate, ecaudate; anther collar poorly developed; endothecial cell wall thickenings inconspicuous or absent; style undivided. Achenes oblong, terete or subquadrangular, densely hirtellous with elongate, multicellular twin hairs. Pappus of numerous, uniseriate, purple, barbellate bristles, of vestigial achenes of staminate florets shorter, with apically slightly expanded bristles. One species, *C. tanguensis* (J.R. Drumm.) W.W. Sm. & Small, north-eastern India, south-western China.

In spite of its strikingly carduoid facies (the species was originally placed in *Saussurea*), *Cavea* may prove to belong elsewhere in Compositae, most likely in or near Inuleae; palynological, carpological and molecular data are lacking.

166. *Dipterocome* Fisch. & Mey.

Dipterocome Fisch. & Mey., Ind. Sem. Hort. Petrop. 1: 26 (1835); Praglowski & Grafstrom, Bot. Notiser 133: 177–188 (1980), palynol.; Reese, Bot. Jahrb. Syst. 110: 325–419 (1989), carpol.

Annual herb, branches prostrate. Leaves alternate, linear, entire, glabrous. Capitula small, sessile, axillary or congested at stem base, few-flowered, heterogamous. Involucre ovoid; phyllaries few, oblong, with hyaline margins, outer smaller. Receptacle epaleate. Marginal florets pistillate, sub-2-seriate; corollas bilabiato-radiate, adaxial lip minute. Inner florets functionally staminate; corolla slender, shortly 5-lobed; filaments connate; anthers ecalcarate, ecaudate; pollen spinulose, ecaveate, with infratectal bacula well developed; style undivided. Achenes terete, outcurving, dorsally spiny, apically bicornute, sometimes dimorphic, with outer less curved and apically echinate. Pappus of a few, flattened, scabrid bristles. One species, *D. pusilla* Fisch. & Mey., Palestine to Afghanistan.

The carduoid pollen and achene features are probably plesiomorphic and this strange genus may, like *Gymnarrhena*, lie at or below the base of Cichorioideae as a relic of a distinct line. Molecular data are lacking.

IV. Tribe Gymnarrheneae Panero & V.A. Funk (2002).

C. Jeffrey

Perennial rosulate, acaulescent, amphicarpic herbs. Leaves forming a dense rosette, sessile, lamina narrowly lanceolate to narrowly ovate, denticulate, acute to attenuate. Capitula of two kinds, subterranean and subaerial. Subterranean capitula homogamous, pistillate, cleistogamous; florets enclosed in the involucral bracts; corolla vestigial. Subaerial capitula (apparently syncalathia) congested in the centre of the leaf rosette, heterogamous, disciform. Involucral bracts imbricate in several series, chartaceous, whitish, acute; receptacle convex, marginally bristly; functionally staminate florets in small groups, loosely connected on very short pedicels, interspersed among the pistillate florets; corollas small, 3–4-lobed, whitish; stamens 3–4, anthers calcarate, ecaudate, without apical appendage; pollen spiny, ecaveate, with massive foot layer, thick columellae and fine net above the columellae; style undivided, truncate, with obtuse hairs apically; ovary vestigial. Pistillate florets solitary, each enclosed in a prominent, stiff, white and green bract; corolla filiform, basally suberized with age; style arms long, with rounded apices. Achenes of subterranean capitula laterally flattened, blackish, sparsely hairy, pappus absent or of short, basally flattened, somewhat scale-like bristles. Achenes of pistillate florets of subaerial capitula ovoid, ciliate, villous with long twin hairs; pappus of long-lanceolate, ciliate, acutely acuminate scales. Achenes of functionally staminate florets vestigial, pappus of a few irregularly lacerate scales or absent. Monotypic.

167. *Gymnarrhena* Desf.

Gymnarrhena Desf., Mem. Mus. Hist. Nat. Paris 4: 1, t. 1 (1818).

Characters of the tribe. $n = 10$. One species, *G. micrantha* Desf., North Africa, Middle East.

Gymnarrhena has usually been included, although sometimes with reservation, in Inuleae. Skvarla et al. (1977) pointed out that the pollen grain structure did not support such a placement

and noted some similarity in wall stratification to certain Cynareae. Bremer (1994) included it in Cichorioideae, without tribal assignment. Panero and Funk (2002), in establishing the tribe Gymnarrheneae, referred it to a new, monotypic subfamily Gymnarrhenoideae because in their cladograms, based on comparative DNA sequence data of several chloroplast DNA genes and markers, totalling some 13.380 bp, *Gymnarrhena* was consistently located by itself below the other cichorioid tribes and above the pertyoid and carduoid clades.

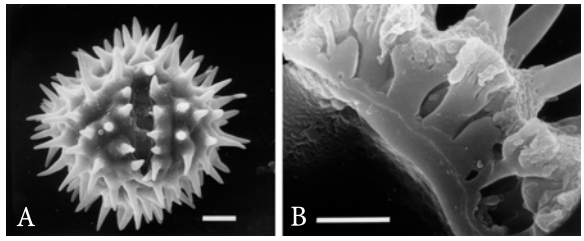

Fig. 37. Compositae-Moquinieae. SEM micrographs of pollen grains. *Pseudostifftia kingii*. **A** Non-lophate tricolporate grain, colpar view, scale bar = 10 µm. **B** Broken grain showing solid bacula positioned irregularly in relation to spines, scale bar = 5 µm

V. Tribe Moquinieae H. Rob. (1994).

Subtribe Pseudostifftiinae H. Rob., R.M. King & F. Bohlmann (1980).

H. Robinson

Monoecious or gynodioecous, moderately branched shrubs or trees; stems not fistulose. Leaves alternate, shortly petiolate, coriaceous, obovate, cuneate, entire, venation pinnate, with glandular dots. Inflorescence terminal, pyramidally thyrsoid; peduncles 1–3 mm long. Heads homogamous; involucre narrowly campanulate, bracts in 4–5 series, gradate, inner bracts deciduous; receptacle epaleaceous. Florets 1–5 per head; corollas regular, lavender to purple, narrowly funnelform, glanduliferous, undivided limb short, lobes 5, linear, smooth; anthers calcarate, shortly tailed; endothecial cells with broad vertical thickened band usually narrowed at each end to one point; apical appendages 3–4 times as long as wide, with cell walls not thickened, anthers aborted in functionally female florets. Pollen spherical, tricolporate, echinate, non-caveate, with strong solid bacula randomly distributed in areas not directly under spines, not grouped or single under spines (Fig. 37). Style base broadly abruptly noduliferous; upper part of style becoming broadened, upper part of shaft and outer surface of arms scabrid, inner surfaces of branches totally stigmatic. Achenes densely setuliferous, 10–17-costate, idioblasts obvious or obscure, raphids obscure, phytomelanin lacking; carpopodia annuliform to stopper-shaped, with subquadrate cells in 3–17 series, the walls thickened; pappus of many capillary bristles, in c. 2 series, outer irregularly somewhat shorter. The presence of triterpenoides and guaianolides has been reported (Bohlmann et al. 1982; Bohlmann and Jakupovic 1990).

Two genera and two species in Brazil.

The tribe consists of two genera originally placed in other tribes – *Moquinia* in Mutisieae (Cabrera 1977) and *Pseudostifftia* in Vernonieae (Robinson 1979). The two were placed together first by Gamerro (1990) in Vernonieae, and a separate tribe was established by Robinson (1994).

Moquinieae differ from Mutiseae s.str. by the smaller and thinner anther appendage and the spinose pollen with simple tectum in the former. Relationship is not considered close. Moquineae are apparently close to Vernonieae, but differ by their thickened scabrid styles similar to those of Arctotideae, rather than these being thin with long sweeping hairs as found in Vernonieae. The pollen also differs by the random positions of the bacula, not directly under the spines as in Vernonieae and Liabeae.

Key to the Genera

1. Inflorescence with strongly racemiform or spiciform branches; heads with 4 or 5 florets; pappus yellow; stems and leaf undersides whitish or pale yellowish-tomentose; plants sometimes gynodioecious
168. *Moquinia*
– Inflorescence with corymbiform branches; heads with 1 floret; pappus white; stems and leaf undersides usually yellowish-lepidote; plants monoecious
169. *Pseudostifftia*

168. *Moquinia* DC. Fig. 38

Moquinia DC., Prodr. 7: 22 (1837), nom. cons., non Spreng. (1828).

Spadonia Less., Syn. Comp. 99 (1832), non Fr. (1829).

Gynodioecious; stem hairs white, arachnoid. Leaf lower surface whitish or pale yellowish-tomentose. Inflorescences with densely racemiform branches. Involucral bracts c. 25, c. 4–5-seriate. Florets 4 or 5.

Achene idioblasts elongate, sometimes in series; carpopodium stopper-shaped, cells in 13–17 series; pappus bristles c. 60, yellowish, with some tips broadened. One species., *M. racemosa* (Spreng.) DC., Bahia and Minas Gerais, Brazil.

169. *Pseudostifftia* H. Rob.

Pseudostifftia H. Rob., Phytologia 44: 444 (1979).

Monoecious; stem and leaf hairs appressed, symmetrically T-shaped, cap-cells broadly fusiform, stalks slender. Inflorescences with corymbiform branches. Involucral bracts c.18, c. 5-seriate. Floret 1. Achene setulae with some intermixed uniseriate hairs, idioblasts obscure; carpopodium annuliform, cells in 5 or fewer series; pappus bristles c. 100, white, tips not broadened. One species, *P. kingii* H. Rob., Bahia, Brazil.

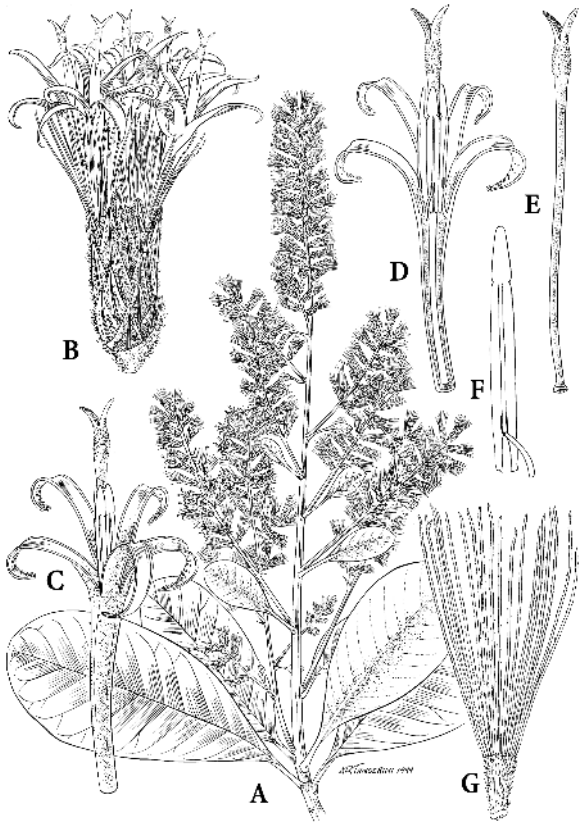

Fig. 38. Compositae-Moquinieae. *Moquinia racemosa*. **A** Habit showing blunt-tipped, abaxially tomentose, alternate leaves. **B** Head; note homogamous condition with regular corollas. **C** Corolla showing tips of anthers and style; note deeply divided lobes. **D** Corolla in long section, one lobe removed, showing anthers and style. **E** Style, showing basal node, swollen upper shaft, showing scabrid surface consisting of short sweeping hairs on upper shaft and backs of lobes, and undivided stigmatic surface inside of branches. **F** Anther showing long calcarate and shortly tailed bases, and apical appendage. **G** Achene with setulae and capillary pappus. (Drawing by A. Tangerini)

VI. Tribe Vernonieae Cass. (1819).

H. Robinson

Annual or perennial herbs, subshrubs, shrubs, scandent shrubs or trees; with simple, T-shaped or stellate hairs. Leaves usually alternate, rarely opposite or ternate; blades usually undivided. Inflorescences cymes, corymbiform with cymose branches, or sometimes spicate; heads homogamous, sessile or pedunculate, with or without foliose bracts at base of involucre; involucral bracts in 3–9 series, usually gradate, rarely subequal or decussate; receptacle usually glabrous, sometimes with pales, spines or partitions. Florets 1–400 in a head, perfect; corollas mostly funnelform with tubes usually broadened above well below filament insertion, less often narrow up to filament insertion, limbs usually actinomorphic with lobes longer than wide, rarely zygomorphic with some lobes longer, lobes usually erect; anther thecae usually calcarate, often tailed, apical appendage flat, thin to somewhat stiffened, with or without glands. Pollen (Fig. 39) spherical; commonly tricolporate and echinate with perforated tectum continuous between colpi, a form obviously derived from lophate forms in at least some subtribes. Many forms are lophate with well-developed muri and variously lacking perforated tectum in lacunae or sometimes over whole grain. Some are lophate with walls crossing colpi or are completely triporate. Polar lacunae are sometimes irregular with lines of colpi completely obscured. Lophate grains are usually echinate but sometimes psilate. Bacula are solid and usually stout, directly under the spines, but are sometimes weak and easily detached from foot-layer. Details of lophate forms are particularly useful in classification. Nectary usually glabrous. Style base with or without sclerified or expanded node, glabrous, upper shaft and outer surfaces of branches with sweeping hairs, hairs with or without septae, branches spreading tangentially, stigmatic papillae covering whole inner surface of branches. Achenes usually prismatic, rarely angled, 3–20-costate, rarely obcompressed in outer row, sometimes inner achenes differing in setulae or pappus, walls usually with resiniferous idioblasts on surface or raphids internally, rarely

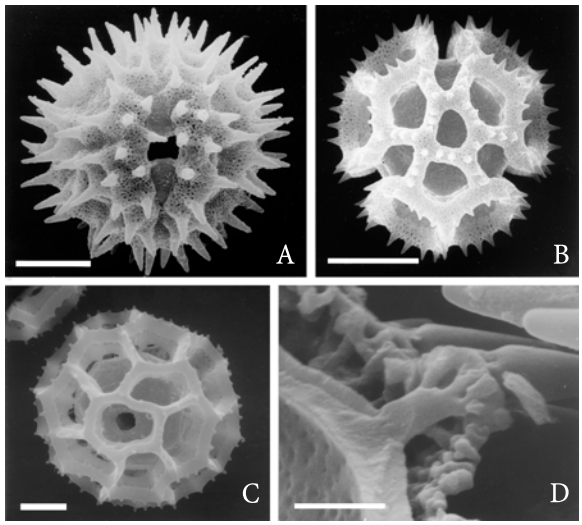

Fig. 39. Compositae-Vernonieae. SEM micrographs of pollen grains. **A** *Vernonanthura fuertesii*. Non-lophate, colpar view. **B** *Lepidaploa salzmannii*. Echinolophate, tricolporate with polar lacuna, polar view. **C** *Phyllocephalum scabridum*. Lophate, triporate, emicropunctate. **D** *Blanchetia heterotricha*. Broken grain showing solid bacula under spine. Scale bars: **A**, **C** = 10 µm, **B** = 13.6 µm, **D** = 2 µm. (**A**, **C**, **D** Robinson and Marticorena 1986; **B** Robinson 1999a)

with phytomelanin; carpopodium stopper-shaped to turbinate, rarely obsolete; pappus usually of long capillary bristles, usually with outer series of shorter bristles or squamellae, rarely coroniform, squamellose without bristles, with flattened or twisted segments, or lacking. Flavones, flavonols, sesquiterpene lactones, nerolidol derivatives, 5-alkylcoumarins, and potentially commercially useful epoxy oils in the seeds have been reported. Sesquiterpenes include glaucolides, hirsutinolides, furoheliangolides and elemanolides (Bohlmann and Jakupovic 1990).

The tribe contains 118 genera and more than 1,000 species, mostly in tropical parts of the world.

Vernonieae are part of subfamily Cichorioideae in the more restricted sense, with closest relationship to Arctotideae, Cichorieae, Liabeae and Moquinieae, all with usually calcarate anther bases and stigmatic papillae across the whole inner surface of the style branches. The tribe differs from Arctotideae and Moquinieae by the narrow styles and long sweeping hairs, from Cichorieae by the usual lack of milky sap and the usually actinomorphic corollas, from Liabeae and Arctotideae-Eremothamneae (included in Arctotideae in this volume) by the usually bluish or reddish flowers and the lack of ray florets, and from Liabeae further by the usually alternate leaves, the solid bacula in the pollen and the often lophate pollen. Moquinieae differ further by the pollen bacula not being directly under single spines. Distinction of Vernonieae pollen from that of Liabeae and a limited SEM survey of Vernonieae pollen types can be seen in Robinson and Marticorena (1986) and Robinson (1999b). Vernonieae are notable for the frequent extreme cymose forms of their inflorescences, involving seriate or scorpioid cymes where each head is produced on a lateral branch below the preceding head. As such, the heads often look sessile and lateral in a straight or arching series. The tribe is more interesting for the truly spicate form of inflorescence in *Pithecoseris* and a species of *Chresta*. The latter is a departure from the basically cymose form found in all other Asteraceae. Vernonieae were one of the original tribes named by Cassini (1819), and they have been consistently recognized in subsequent treatments (Bentham 1873a; Hoffmann 1894; Cronquist 1955; Jones 1977; Bremer 1994). Until Robinson and Brettell (1973c) and Robinson (1977), Vernonieae were usually treated as a close relative of Eupatorieae because of the homogamous rayless heads with bluish to reddish florets, but the latter tribe is a member of subfamily Asteroideae, as detailed in Robinson (1977). The tribe Vernonieae has had a few problems in delimitation, but it is now known to include *Stokesia* with its liguliform corollas (Jones 1977), *Distephanus* with its yellow corollas and trinervate leaves (Robinson and Kahn 1986), and the Hawaiian, mostly apomictic *Hesperomannia* (Kim et al. 1998). Now excluded are two South African genera – *Hoplophyllum*, related to *Eremothamnus* and a member of Arctotideae (Karis 1992; Robinson 1992), and *Corymbium* (Bohlmann and Jakupovic 1990) which is treated as a separate tribe in this volume. Internally, Vernonieae have suffered from an excessively paraphyletic core-genus concept, with *Vernonia* defined only by what it is not. Recent efforts to correct the generic concepts are included in studies by Robinson (1996, 1999b) mostly for the Americas, and Robinson (1999a) for the palaeotropics.

At present, the majority of the American subtribes, including subtribes Vernoniinae, Centratherinae, Chrestinae, Leiboldiinae, Lychnophorinae, Piptocarphinae, Sipolisiinae and Stokesiinae, are considered as comparatively closely related. The single species in Pacourininae is individually distinctive but probably also closely

related. The pantropical Elephantopinae seem closest to the tropical American Rolandrinae. In the western hemisphere, only subtribe Trichospirinae is apparently of remote relationship. In the palaeotropics, subtribe Gymnantheminae has many morphological parallels with the American Piptocarphinae, but has chromosome numbers and some chemistry in common with the other eastern hemisphere subtribes, Erlangeinae and Centrapalinae. The basically palaeotropical Erlangeinae are particularly distinct in the triporate pollen and the presence of 5-alkyl coumarins. The hemispheric geographical separation in the tribe is not complete, with the distinctive *Manyonia* of Vernoniinae found in Africa, and the equally distinctive *Acilepidopsis*, *Mesanthophora* and *Telmatophila* apparently of Erlangeinae found in South America.

Many taxomonic treatments exist for members of Vernonieae in various parts of the world, but most of these do not follow recent generic limits. Many of these treatments are listed in Robinson (1999a, b). An index to American species of Vernonieae, giving present dispositions, is included in Robinson (1999b).

Key to the Subtribes and Unplaced Genera

1. Achenes flattened with pair of widely divergent cornute projections at top **15. Trichospirinae** (p. 174)
– Achenes without a pair of large cornute projections at top 2
2. Corollas liguliform, strongly zygomorphic with deepest sinus towards centre of head 3
– Corollas not or scarcely zygomorphic, without single deepest sinus centred towards centre of head 4
3. Heads separate, on long peduncles **10. Stokesiinae** (p. 165)
– Heads in compound clusters **8. Elephantopinae** (p. 163)
4. Heads compound or sessile in compact glomerules or spikes, not in obvious cymes 5
– Heads separate or on obvious cymose branches 12
5. Florets 4 in each head 6
– Florets not consistently 4 in each head 8
6. Leaves with veins sublongitudinal; heads in axils of broad, imbricated upper leaves **4. Chrestinae** (*Soaresia*)
– Leaves with veins not sublongitudinal; heads subtended by bracts forming secondary involucre 7
7. Pappus biseriate, of bristles and outer broad squamae; achene raphids subquadrate **8. Elephantopinae** (*Caatinganthus*)
– Pappus of a single series of rudimentary awns; achene raphids elongate **12. Erlangeinae** (*Telmatophila*)
8. Branches of inflorescence often with decurrent wings **171. Gorceixia**
– Branches of inflorescence not winged 9
9. African; pappus cupuliform **12. Erlangeinae** (*Muschleria*)
– South American; pappus with bristles, straps, or scales 10
10. Florets 1 in each head of cluster; pappus a short crown or short scales; pollen lophate **9. Rolandrinae** (p. 164)
– Florets usually more than 1 in each head; pappus of elongate segments; pollen lophate or non-lophate 11
11. Pollen usually lophate; raphids often elongate; inflorescences sometimes narrowly spicate with strongly acropetal maturation **4. Chrestinae** (p. 160)
– Pollen non-lophate; raphids always subquadrate; inflorescence not spicate or rarely spicate with large heads **6. Lychnophorinae** (p. 161)
12. Tubes of corollas long and covered with obvious stipitate glands 13
– Corollas without long tubes covered with stipitate glands 14
13. Leaves pinnately divided into linear segments; heads not surrounded at base by many spreading foliose bracts **12. Erlangeinae** (*Rastrophyllum*)
– Leaves not pinnately divided into linear segments; heads surrounded at base by many spreading foliose bracts **5. Centratherinae** (p. 160)
14. Inflorescence never seriately nor scorpioid cymose, heads not borne secundly nor sessile in series of leaf axils; anthers never with glands; mostly palaeotropical or adventive in America 15
– Inflorescence variable, sometimes seriately cymose or scorpioid or heads borne sessile in series of leaf axils; anthers sometimes with glands; almost all American 17
15. Trees or shrubs; inner involucral bracts sometimes deciduous; pollen never triporate **14. Gymnantheminae** (p. 173)
– Herbs, rarely weak trees or shrubs; involucral bracts persistent; pollen sometimes triporate 16
16. Coarse, usually perennial herbs or subshrubs; anther appendages with somewhat thickened cell walls; hairs of stems simple or unevenly T-shaped; achenes c. 10-costate; 5-alkylcoumarins not present **13. Centrapalinae** (p. 171)
– Annual or perennial herbs or weak shrubs or trees; anther appendages thin and usually transparent; hairs of stems simple to symmetrically or asymmetrically T-shaped; pollen triporate to tricolporate; achenes 4–6- or 8–12-costate; 5-alkylcoumarins sometimes present **12. Erlangeinae** (p. 165)
17. Large emergent aquatic herbs; pollen triporate without organized patterns of polar lacunae **11. Pacourininae** (p. 165)
– Not large aquatic herbs; pollen tricolporate or with polar lacunae in regular pattern 18
18. Receptacles with well-developed pales or spines 19
– Receptacles without obvious pales or spines 20
19. Hairs simple; achenes without phytomelanin in the walls; Mexican, Central American **1. Leiboldiinae** (p. 152)
– Hairs stellate or stellate at base, or T-shaped; achenes usually with phytomelanin in the walls; Brazil **7. Sipolisiinae** (p. 162)
20. Pappus bristles not sclerified at base, easily deciduous; heads with more than 100 florets **1. Leiboldiinae** (p. 152)

– Pappus bristles or elements sclerified at base, sometimes fragile; heads usually with 1–75 florets 21
21. Inner involucral bracts deciduous; hairs of stems stellate or lepidote; shrubs, scandent shrubs or trees 22
– Inner involucral bracts persistent; hairs of stems simple or T-shaped; often herbaceous 23
22. Leafy branches often ericoid or with leaf bases imbricated; leaves alternate; heads with 1–75 florets **6. Lychnophorinae** (p. 161)
– Leafy branches not ericoid, leaf bases not imbricated; leaves alternate or opposite; heads with usually fewer than 20 florets **3. Piptocarphinae** (p. 158)
23. Apical anther appendages with thin-walled cells, appendages or connectives sometimes with glands or small hairs; pollen lophate or non-lophate **2. Vernoniinae** (p. 153)
– Apical anther appendages with cell walls thickened at least near margin, without glands or hairs; pollen non-lophate 24
24. Involucral bracts spiniform; pappus of laciniate scales, bearing glands; raphids of achene wall elongate **170. Acanthodesmos** (p. 152)
– Involucral bracts not spiniform; pappus usually of bristles or scales, without glands; raphids of achene wall subquadrate **6. Lychnophorinae** (p. 161)

Unplaced Genera

170. *Acanthodesmos* C.D. Adams & M.C. du Quesnay

Acanthodesmos C.D. Adams & M.C. du Quesnay, Phytologia 21: 405 (1971).

Subshrubs, branchlets distichous, hairs simple. Vestigial spine-like bracts borne opposite lower leaves, leaves white-tomentose below. Heads sessile opposite upper leaves; involucral bracts 15–16, tips mostly setiform; receptacles paleaceous; florets 12–13; anther appendages sclerified; style base conical; sweeping hairs blunt, mostly septate. Achene 10-costate, raphids elongate; pappus laciniate, glanduliferous. Pollen non-lophate. One species, *A. distichus* C.D. Adams & M.C. du Quesnay, Jamaica.

171. *Gorceixia* Baker

Gorceixia Baker, J. Bot. 20: 225 (1882).

Trees; stems partially winged; hairs stellate. Inflorescence corymbiform, of secondary heads containing many sessile heads; secondary involucre of canescent bracts; involucre cylindrical, of 5 or 6 lanceolate subequal bracts. Florets 5; corollas glabrous; anther tails small; style without node; sweeping hairs sharp. Achenes tetragonous, glabrous, raphids elongate; pappus a collar. Pollen non-lophate. One species, *G. decurrens* Baker, eastern Brazil.

VI.1. Subtribe Leiboldiinae H. Rob. (1999).

Herbs or shrubs. Receptacles sometimes paleaceous. Anther appendages sclerified, glabrous. Pappus bristles usually not sclerified at base, easily deciduous. Pollen tricolporate, non-lophate. Characteristic sesquiterpenes: glaucolides.

Key to the Genera

1. Pappus with a single row of long white bristles; style with a distinct basal node; achene with scattered idioblasts 2
– Pappus with more than one row of short coloured deciduous bristles; style base without node; achenes closely covered by idioblasts 3
2. Receptacle with pales; achenes without apical annulus inside pappus bristles **172. *Bolanosa***
– Receptacle without pales; achenes with raised apical annulus inside unsclerified bases of pappus bristles **173. *Leiboldia***
3. Achenes without raised apical annulus inside rows of pappus bristles; involucral bracts with often broadened and ornate tips **174. *Lepidonia***
– Achenes with raised apical annulus inside rows of pappus bristles; involucral bracts with narrow tips **175. *Stramentopappus***

Genera of Leiboldiinae

172. *Bolanosa* A. Gray

Bolanosa A. Gray, Smithsonian Contr. Knowl. 3: 82 (1852).

Perennial rhizomatous herbs; white tomentum of simple hairs. Inflorescences corymbiform. Involucral bracts c. 40, in c. 3 series, outer tomentose, foliiform, inner scarious, reddish-tipped; receptacular pales sheathing. Florets c. 45; anther bases rounded; style with node; sweeping hairs pointed. Achenes 6–7-costate, setuliferous, many idioblasts, raphids elongate; pappus of broad bristles. One species, *B. coulteri* A. Gray, Mexico.

173. *Leiboldia* Schltdl ex Gleason

Leiboldia Schltdl ex Gleason, Bull. New York Bot. Gard. 4: 161 (1906).
Leiboldia Schltdl (1847), nom. nud.
Vernonia sect. *Leiboldia* (Schltdl) Benth. (1873).

Shrubs; hairs simple, contorted. Heads mixed with short bracts, pedunculate; involucral bracts c. 100 in c. 6 series. Florets 100–120; anthers broadly tailed; style with node; sweeping hairs obtuse, often septate. Achenes 4–5-angled, idioblasts sparse, raphids short-oblong; pappus whitish, with callose ring, single capillary series not sclerified

at base, easily deciduous. $n = 19$. One species, *L. serrata* (D. Don) Gleason, Mexico.

174. *Lepidonia* S.F. Blake

Lepidonia S.F. Blake, J. Wash. Acad. Sci. 26: 454 (1936); Turner, Brittonia 33: 401–412 (1981), rev.; Robinson & Funk, Bot. Jahrb. Syst. 108: 212–228 (1987), emend.

Shrubs; hairs simple, multiseptate. Heads single or few in axils of leaves or terminal. Involucral bracts c. 100, tips with appendages; receptacle paleate or glabrous. Florets c. 100; anther bases rounded; style without node; sweeping hairs sharp, septate. Achenes 4–5-ribbed, idioblasts numerous, raphids subquadrate; pappus yellowish, short, multiseriate, unsclerified at base, deciduous. $n = 19$. Seven species, Mexico, Central America.

175. *Stramentopappus* H. Rob. & V.A. Funk

Stramentopappus H. Rob. & V.A. Funk, Bot. Jahrb. Syst. 108: 227 (1987).

Shrubs; hairs simple, multiseptate. Heads few, pedunculate, overtopped by foliose branches; involucral bracts 100–130, in c. 8 series. Florets c. 110; anthers without tails; style without node; sweeping hairs sharp, often septate. Achenes 5-angled, idioblasts dense, raphids subquadrate, apex with callose ring; pappus multiseriate, of short, yellowish, deciduous bristles, unsclerified at base. $n = 19$. One species, *S. pooleae* (B.L. Turner) H. Rob. & V.A. Funk, Mexico (Oaxaca).

VI.2. Subtribe Vernoniinae Cass. ex Dumort. (1829).

Herbs, weak shrubs, or vines. Inflorescence often seriate- or scorpioid-cymose; inner involucral bracts usually persistent. Anther appendages thin-walled, often with glands or hairs. Pollen mostly tricolporate. Characteristic sesquiterpenes: glaucolides.

Key to the Genera

1. Peripheral achenes broadly obcompressed, winged on lateral margins 2
– Achenes not broadly obcompressed nor laterally winged 3
2. Heads sessile in dense scorpioid or seriate cymes; involucral bracts with projecting keel or wing outside; pollen not lophate; corollas zygomorphic **182. *Dipterocypsela***
– Heads pedunculate; involucral bracts acuminate, without a winged keel outside; pollen lophate; corollas actinomorphic **186. *Heterocypsela***
3. Pappus lacking or reduced to a cartilaginous sleeve 4
– Pappus with bristles, straps, or awns 5
4. Shrubs; corollas with 5 lobes; pappus lacking; pollen tricolporate, with three intercolpar-aligned polar lacunae **185. *Harleya***
– Annuals; corollas with 3 or 4 lobes; pappus a cartilaginous sleeve; pollen triporate, with single polar lacuna **195. *Sparganophoros***
5. Pappus of long broadened straps or awns 6
– Pappus with capillary bristles 7
6. Pappus of subulate awns; anther bases long-calcarate; not an aquatic herb **194. *Stilpnopappus***
– Pappus of canaliculate straps; anther without long calcarate bases, with basal spurs shorter than collar; aquatic herb **199. *Xiphochaeta***
7. Receptacle deeply pitted, pits enclosing complete bodies of achenes **176. *Albertinia***
– Receptacles plain to weakly alveolate, not deeply pitted 8
8. Inflorescences densely scorpioid-cymose, with apices usually curved 9
– Inflorescences not truly scorpioid with scorpioid tips, only seriate-cymose to thyrsoid or corymbiform 10
9. Petioles narrowly inserted on stem; older heads deciduous leaving only subtending bracteoles; pappus bristles not clavate distally; anther thecae without sclerified tails; achenes with bulging idioblasts on surface **180. *Cyrtocymura***
– Petioles usually broadly winged to base, broadly inserted; older heads not deciduous, involucral bracts persistent; pappus bristles broadened near tips; anther thecae with sclerified tails; achenes without differentiated idioblasts on surface **184. *Eirmocephala***
10. Plants African; inflorescence seriate-cymose; pollen non-lophate; achenes strongly 5-costate, with very densely disposed subquadrate raphids **189. *Manyonia***
– Plants American; inflorescence variable, simple to complex cymes, thyrsoid, seriate-cymose or with solitary heads; pollen lophate or non-lophate; achenes weakly 5- or 8–10-costate, with subquadrate to elongate raphids mostly in one layer 11
11. Pollen echinate, never lophate; inflorescence a simple cyme or corymbiform, never strongly seriate-cymose 12
– Pollen usually lophate; inflorescence often seriate-cymose or heads in series of leaf axils, sometimes individually pedunculate 17
12. Inflorescence a single spreading cyme; base of plant decumbent, not xylopodial **198. *Vernonia***
– Inflorescence thyrsoid or more complex, with cymose or corymbiform branches; plant bases erect or xylopodial, not decumbent 13
13. Scandent, inflorescence pyramidally thyrsoid, with primary branching at c. 90° angles; secondary branches often racemiform **196. *Trepadonia***
– Erect to subscandent plants; inflorescences thyrsoid with cymose branches, secondary branches not noticeably racemiform 14
14. Corolla lobes much shorter than throat **179. *Cololobus***
– Corolla lobes as long as or longer than throat 15

15. Corollas without hairs inside limb; plants not or rarely subscandent; raphids of achene subquadrate **197. *Vernonanthura***
– Corollas often with hairs inside limb; plants sometimes subscandent; raphids of achenes elongate 16
16. Corollas with whole inside of limb covered with short one-celled hairs **203. *Dasyanthina***
– Corollas often with long, slender, multicellular hairs inside of throat, no hairs on inside of lobes **192. *Quechualia***
17. Corollas slightly zygomorphic with longest lobe centred towards centre of head; basal nodes of inflorescence often with 2 or 3 branches; anther thecae with tails **190. *Mattfeldanthus***
– Corollas actinomorphic; basal nodes bearing heads with at most one branch; anther thecae without tails 18
18. Heads with 4–10 florets 19
– Heads with 10–70 florets 20
19. Hairs of stems T-shaped; pollen with three intercolpar-aligned polar lacunae **191. *Pseudopiptocarpha***
– Hairs of stems simple, often arachnoid; pollen with single lacuna at pole **193. *Stenocephalum***
20. Pollen with colpi reaching poles and with 3 distinct equatorial lacunae across intercolpi; heads often large, mostly 1 cm or more long; style base usually without basal node **188. *Lessingianthus***
– Pollen with or without polar lacunae, intercolpi with only two distinct equatorial lacunae; heads of various sizes, usually less than 1 cm long; style base with or without basal node 21
21. Stems, leaves, peduncles, and involucres loosely sericeous with yellowish hairs 22
– Plants with pubescence variable, never loosely sericeous with yellowish hairs, sometimes stems, leaves, peduncles or involucres sericeous with white hairs 23
22. Anther appendages usually with numerous glands; pollen with muri weakly attached to foot-layer, sometimes easily detached; heads sessile except at ends of seriate-cymose branches **178. *Chrysolaena***
– Anthers without glands; pollen with muri strongly attached to foot-layer by stout baccula; heads often solitary or individually short-pedunculate in clusters **188. *Lessingianthus*** subg. ***Oligocephalus***
23. Heads usually sessile except at ends of cymose branches **187. *Lepidaploa***
– Heads mostly long-pedunculate 24
24. Heads with subinvolucre of foliose bracts; leaves 4–6 cm wide; pollen with 3 intercolpar-aligned lacunae meeting at pole; raphids of achene subquadrate **177. *Aynia***
– Heads without subinvolucre of foliose bracts, with only multiseriate involucre of erect-patent subulate bracts; leaves less than 4 cm wide; pollen with colpi reaching the pole; raphids of achene elongate **183. *Echinocoryne***

Genera of Vernoniinae

176. *Albertinia* Spreng.

Albertinia Spreng., Neue Entdeck. Pflanzenk. 2: 133 (1821) [1820].
Symblomeria Nutt. (1840).

Branching shrubs; hairs T-shaped with multicellular stalks. Inflorescence loosely corymbiform, heads pedunculate; involucral bracts 55–60 in c. 3 series; deep receptacular pits enclosing achenes. Florets 45–50; anther bases rounded; style with node; sweeping hairs broad-acicular. Achene c. 10-costate, raphids subquadrate; pappus capillary, tawny. Pollen non-lophate. One species, *A. brasiliensis* Spreng., eastern Brazil.

177. *Aynia* H. Rob.

Aynia H. Rob., Proc. Biol. Soc. Wash. 101: 959 (1988).

Perennial herbs; hairs simple. Peduncles usually long. Heads subtended by large foliose bracts, involucral bracts c. 100 in 4–5 series, 10–25 mm long. Florets c. 50; anthers tails short, truncate; style with node; sweeping hairs pointed. Achene 10-ribbed, raphids subquadrate; pappus capillary, with squamellae. Pollen echinolophate, with intercolpus-aligned polar lacunae. One species, *A. pseudascaricida* H. Rob., Peru.

178. *Chrysolaena* H. Rob.

Chrysolaena H. Rob., Proc. Biol. Soc. Wash. 101: 956 (1988); Robinson, Proc. Biol. Soc. Wash. 105: 657–663 (1992), key.
Vernonia subsect. *Flexuosae* Cabrera (1944).
Vernonia series *Verbascifoliae* S.B. Jones (1979).

Perennial, usually xylopodial herbs, sericeous or lanate with simple yellowish hairs. Inflorescence seriate-cymose, heads sessile; involucral bracts/florets 1–2/1. Florets 10–65; anther bases obtuse; apical appendage usually with glands; style without prominent node; sweeping hairs broad-acicular. Achenes 5-costate, densely sericeous, with glands, raphids elongate; pappus capillary, with squamellae. Pollen echinolophate, single polar lacunae. n = 10, 17. Nine species, Brazil to Argentina and Peru.

179. *Cololobus* H. Rob.

Cololobus H. Rob., Proc. Biol. Soc. Wash. 107: 557 (1994).

Subshrubs; hairs simple or asymmetrically T-shaped. Inflorescence thyrsoid; involucral bracts, c. 6-seriate, c. 35, in outer 4 series pubescent, inner mostly glabrous. Florets 20–30; corollas glabrous, lobes very short; anther base obtuse; style with node; sweeping hairs blunt, often septate. Achenes 8–10-costate, with setulae and glands, raphids subquadrate; pappus capillary, with squamae. Pollen non-lophate. Three species, eastern Brazil.

180. ***Cyrtocymura*** H. Rob. Fig. 40

Cyrtocymura H. Rob., Proc. Biol. Soc. Wash. 100: 849 (1987).

Perennial herbs; hairs simple. Inflorescences scorpioid-cymose with crowded sessile heads, deciduous with age; involucral bracts 20–30, in c. 3 series. Florets 14–30; corolla lobes sericeous; anther bases rounded; style with node; sweeping hairs broadly acicular. Achenes 10-costate, setuliferous, idioblasts bulging, raphids elongate; pappus capillary, outer squamellae persistent. Pollen non-lophate. $n = 17$. Six species, Mexico, West Indies to Brazil and Argentina.

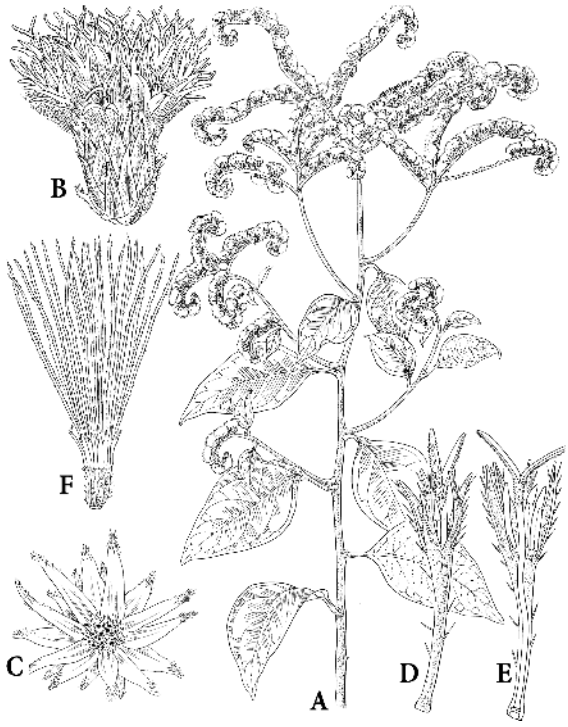

Fig. 40. Compositae-Vernonieae. *Cyrtocymura scorpioides*. **A** Habit showing alternate leaves and scorpioid cymes; note bracts at base of one branch after heads have fallen. **B** Head, note homogamous condition with regular corollas. **C** Spinulose receptacle surface and spreading persistent involucral bracts. **D** Corolla with tips of anthers and style. **E** Corolla in long section, note deeply divided corolla lobes, calcarate anther bases, nectary and node at base of style, sweeping hairs on upper style shaft and backs of style branches, and undivided stigmatic surface inside of style branches. **F** Achene with ribs and setulae, and pappus with capillary inner series and outer series of shorter bristles or squamellae. (Robinson 1999a)

181. ***Dasyanthina*** H. Rob.

Dasyanthina H. Rob., Proc. Biol. Soc. Wash. 106: 778 (1993).

Perennial herbs 2–4 m high; stem hairs T-shaped. Inflorescences rounded-thyrsoid; peduncles slender. Involucral bracts c. 60 in 5–6 series. Florets c. 25; corolla inside with unicellular hairs; anther tails unsclerified, connective with glands; stylar node annular; sweeping hairs pointed. Achenes 8–10-ribbed, setuliferous, raphids elongate; pappus capillary, squamellae persistent. Pollen non-lophate. Two species, eastern Brazil.

182. ***Dipterocypsela*** S.F. Blake

Dipterocypsela S.F. Blake, J. Wash. Acad. Sci. 35: 36 (1945).

Fleshy herbs; hairs symmetrically T-shaped. Seriate cymes with crowded sessile heads. Involucral bracts c. 12 in c. 2 series, subequal, winged. Florets c. 12; corollas zygomorphic, inner lobes longer; anther bases rounded; apical appendage with gland; style with node; sweeping hairs fusiform, septate. Achenes obcompressed, winged, glabrous, raphids subquadrate; pappus bristles short, deciduous. Pollen sublophate. One species, *D. succulenta* S.F. Blake, Colombia.

183. ***Echinocoryne*** H. Rob.

Echinocoryne H. Rob., Proc. Biol. Soc. Wash. 100: 586 (1987).

Perennial herbs; sericeous with straight hairs. Heads pedunculate; involucral bracts c. 110–500 in 6–9 series, linear, straight, pungent. Florets 15–60; anther bases rounded; style with node; sweeping hairs acicular. Achenes 5-costate, sericeous, raphids elongate; pappus capillary, with squamellae. Pollen echinolophate, no polar lacunae. Six species, Brazil.

184. ***Eirmocephala*** H. Rob.

Eirmocephala H. Rob., Proc. Biol. Soc. Wash. 100: 853 (1987).

Perennial herbs; hairs simple. Inflorescence seriate- or densely scorpioid-cymose. Heads sessile, persistent; involucral bracts 24–65, in c. 4 series. Florets 7–35; anthers tailed; apical appendage often glanduliferous; style with node; sweeping hairs acicular. Achenes 10-veined, setuliferous, without idioblasts, raphids elongate; pappus capillary, with squamellae. Pollen non-lophate or

subtriporate with polar lacuna. n = 16, 17. Three species, Central America to central Andes.

185. *Harleya* S.F. Blake

Harleya S.F. Blake, J. Wash. Acad. Sci. 22: 379 (1932).

Shrub, bases decumbent; arachnoid hairs contorted. Leaves discolorous. Inflorescences deflected at nodes, with sessile, axillary clusters of narrow heads; involucral bracts 30–35, in 5 series. Florets 6–8; corollas hairless; anthers without tails; style without node; sweeping hairs acicular. Achenes 5-angled, pustulate, raphids subquadrate; pappus lacking. Pollen echinolophate with intercolpus-aligned polar lacunae. One species, *H. oxylepis* (Benth.) S.F. Blake, Central America.

186. *Heterocypsela* H. Rob.

Heterocypsela H. Rob., Phytologia 44: 442 (1979).

Perennial herbs; hairs symmetrically T-shaped. Peduncles 5–30 mm long; involucral bracts c. 70 in c. 6 series, caudate-acuminate. Florets c. 60–70; anther bases blunt; apical appendages with glands; style with node; sweeping hairs sharp. Outer achenes obcompressed, margins winged, raphids subquadrate, pappus bristles deciduous; inner achenes prismatic, setuliferous, pappus more persistent. Pollen subtriporate. One species, *H. andersonii* H. Rob., eastern Brazil.

187. *Lepidaploa* (Cass.) Cass.

Lepidaploa (Cass.) Cass. in Cuvier, Dict. Sci. Nat. 36: 20 (1825); Robinson, Proc. Biol. Soc. Wash. 103: 464–498 (1990), emend., list; Robinson et al., Phytologia 46: 421–436 (1980), lectotyp.
Vernonia subg. *Lepidaploa* Cass. (1817).
Flustula Rafin. (1838) [1836].

Herbs or shrubs, rarely annual; sericeous or tomentose, hairs simple or T-shaped. Leaves usually alternate. Inflorescences seriately cymose. Heads usually sessile; involucral bracts 20–70, in 3–6 series. Florets (8–)10–35; anther bases obtuse; apical appendages rarely with glands; style with node; sweeping hairs broadly acicular. Achenes 8–10-ribbed, raphids elongate; pappus capillary, with squamellae. Pollen echinolophate, muri weakly attached. n = 17. More than 130 species, tropical America.

188. *Lessingianthus* H. Rob.

Lessingianthus H. Rob., Proc. Biol. Soc. Wash. 101: 939 (1988).

Perennial herbs, sometimes xylopodial; hairs simple. Inflorescences simple or seriate-cymose. Heads sessile or pedunculate; involucral bracts 45–100 in 4–6 series. Florets 15–50; anther bases rounded; style usually without node; sweeping hairs sharp. Achenes 5-costate, without glands, raphids subquadrate or elongate; pappus capillary, with squamellae. Pollen echinolophate, without polar lacunae, with strong bacula. n = 17. More than 102 species, South America, mostly Brazil and Argentina, one or two species north to Colombia and Venezuela.

189. *Manyonia* H. Rob.

Manyonia H. Rob., Proc. Biol. Soc. Wash. 112: 224 (1999).

Perennial herbs; stems hispidulous, hairs simple. Inflorescence seriate-cymose, peduncles 2–3 mm long. Involucral bracts c. 100, outer 3–4 series spreading, subulate. Florets c. 35; anthers without tails; style with node; sweeping hairs acicular. Achenes 5-costate, setulae and idioblasts in furrows, raphids subquadrate; pappus setae fragile, uniseriate, squamellae persistent. Pollen non-lophate. One species, *M. peculiaris* (Verdc.), H. Rob., Tanzania.

190. *Mattfeldanthus* H. Rob. & R.M. King

Mattfeldanthus H. Rob. & R.M. King, Willdenowia 9: 10 (1979).

Shrubs; hairs simple. Inflorescence base pseudotrichotomous, branches seriate-cymose, bracts foliiform. Heads sessile; involucral bracts c. 100, c. 7-seriate. Florets 14–16; outer corollas zygomorphic, innermost lobe longer; anther tails lobed; style with node; sweeping hairs acicular. Achenes c. 10-costate, sericeous, raphids elongate; pappus capillary, with squamellae. Pollen echinolophate, without polar lacunae. Two species, eastern Brazil.

191. *Pseudopiptocarpha* H. Rob.

Pseudopiptocarpha H. Rob., Proc. Biol. Soc. Wash. 107: 561 (1994).

Shrubs or subshrubs; hairs appressed, symmetrically T-shaped. Heads axillary, clustered, sessile; involucral bracts 25–30 in c. 5 series. Florets 8–10; anther tails short; style with node; sweeping hairs

sharp. Achenes weakly 10-costate, setulae, glands, and idioblasts scattered, raphids subquadrate; pappus bristles capillary, with squamellae. Pollen echinolophate, with intercolpus-aligned polar lacunae. Two species, Colombia.

192. *Quechualia* H. Rob.

Quechualia H. Rob., Proc. Biol. Soc. Wash. 106: 780 (1993).

Erect or scrambling shrubs; hairs asymmetrically T-shaped, often proliferated. Inflorescences thyrsoid. Heads pedunculate; involucral bracts 60–90 in 5–6 series. Florets 30–55; corolla limb often with multicellular hairs inside; anther connectives with glands, tails denticulate; style with node; sweeping hairs subacicular. Achenes 8–10-ribbed, setuliferous, raphids elongate; pappus capillary, with squamellae. Pollen non-lophate. $n = 17$. Four species, Peru to Argentina.

193. *Stenocephalum* Sch. Bip.

Stenocephalum Sch. Bip., Jahresber. Pollichia 20/21: 385 (1863); Robinson, Proc. Biol. Soc. Wash. 100: 578–583 (1987), rev.

Perennial herbs; hairs simple, often arachnoid. Leaves pale tomentose below. Heads axillary or in panicles; involucral bracts 15–22 in 3–4 series. Florets 4–7(–10); anther bases rounded; style with node; sweeping hairs short, sharp. Achenes 10-ribbed, setuliferous, without glands, idioblasts, or raphids; pappus capillary, squamellae present. Pollen echinolophate with polar lacuna. $n = 17$. Five species, Central America and tropical South America.

194. *Stilpnopappus* Mart. ex DC.

Stilpnopappus Mart. ex DC., Prodr. 5: 75 (1836).
Strophopappus DC. (1836).

Perennial herbs or shrubs; hairs simple. Inflorescences axillary or seriate-cymose. Heads sessile, 1 to few per node; involucral bracts 20–50 in 3–4 series. Florets 6–50; anther bases obtuse; style with node; sweeping hairs acicular. Achenes 8-costate, projecting rim at top, setuliferous, idioblasts scattered, raphids subquadrate; pappus of lanceolate awns. Pollen non-lophate or lophate with intercolpar-aligned polar lacunae. Twenty species, Brazil, Venezuela.

195. *Sparganophoros* Vaill.

Sparganophoros Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 368 (1754).
Struchium P. Browne (1756).

Decumbent annuals; hairs sparse, simple. Heads axillary, clustered; involucral bracts 20–25 in c. 2 subequal series. Florets 50–70; corolla lobes 3 or 4; anther bases rounded, connective with glands; style with node; sweeping hairs sharp. Achenes 3–5-angled, without setulae, idioblasts numerous, raphids elongate; pappus a cartilaginous sleeve. Pollen subtriporate, with polar lacuna. $n = 16$. One species, *S. sparganophora* (L.) O. Kuntze, pantropical, widely adventive.

196. *Trepadonia* H. Rob.

Trepadonia H. Rob., Proc. Biol. Soc. Wash. 107: 564 (1994).

Vines; hairs mostly symmetrically T-shaped. Leaves alternate or opposite. Inflorescence branching often at 90°, branchlets often subracemose. Involucral bracts c. 25 in c. 5 series. Florets 8–10; corollas glabrous; anther bases obtuse; style with node; sweeping hairs acicular. Achenes 10-costate, setulae scattered, raphids subquadrate; pappus capillary, squamellae persistent. Pollen non-lophate. Two species, Peru.

197. *Vernonanthura* H. Rob.

Vernonanthura H. Rob., Phytologia 73: 66 (1992).

Subshrubs to small trees, sometimes xylopodial; hairs simple or T-shaped. Inflorescences thyrsoid. Heads sessile to long-pedunculate; involucral bracts 6–30(–60) in 4–10 series. Florets 4–30; corollas without hairs; anther bases obtuse or tailed; appendages often with glands or hairs; style with node; sweeping hairs short-acute. Achenes 8–10-costate, setuliferous or with idioblasts; pappus capillary, with squamellae. Pollen non-lophate. $n = 17$. Sixty-five or more species, tropical America.

198. *Vernonia* Schreb.

Vernonia Schreb., Gen. 2: 541 (1791), nom. cons.; Jones & Faust, N. Amer. Fl. 2, 10: 180–195 (1978), reg. rev.
Behen Hill (1762).

Perennial herbs, bases decumbent; hairs simple or symmetrically T-shaped. Inflorescences cymose with branches longer than central axis. Heads usually pedunculate; involucral bracts c.

50 in 5–6 series. Florets 8–120; anthers without tails; appendages often with glands; style with node; sweeping hairs acute, sometimes septate. Achenes 5–10-costate, with setulae, glands and/or idioblasts, raphids subquadrate; pappus capillary, with squamellae. Pollen non-lophate. n = 17. Twenty-two species, south-eastern United States, Bahamas, to central Mexico, 2 distinctive species in South America.

199. *Xiphochaeta* Poepp.

Xiphochaeta Poepp., Nov. Gen. Sp. 3: 44, pl. 250, 8–11 (1842).

Aquatic short-lived herbs; hairs simple, appressed. Heads sessile, 1(–3) in axils; involucral bracts 70–80 in 3–4 series. Florets c. 30; anther bases not calcarate; appendages with glands; style with node; sweeping hairs acicular. Achenes 5-costate, setulae and idioblasts scattered, raphids elongate; pappus segments c. 10, canaliculate, non-costate. Pollen echinolophate. One species, *X. aquatica* Poepp., Amazon and Orinoco basins.

VI.3. Subtribe Piptocarphinae H. Rob., F. Bohlmann & R.M. King (1980).

Woody shrubs, trees or vines; hairs stellate or lepidote. Inner involucral bracts deciduous; anther appendage slightly indurate, glabrous. Achene raphids short or subquadrate. Pollen tricolporate, non-lophate. Characteristic sesquiterpenes: usually glaucolides.

Key to the Genera

1. Pappus a collar, without bristles or scales **205. *Huberopappus***
– Pappus of capillary bristles or scales 2
2. Corollas divided to base of limb, throat lacking, lobes beginning at top of basal tube 3
– Corollas not divided to base of limb, distinct throat present 4
3. Heads with single florets; leaves alternate **202. *Cuatrecasanthus***
– Heads with 9–12 florets; leaves opposite **207. *Joseanthus***
4. Plants lepidote; pappus with laciniate outer collar **204. *Ekmania***
– Plants with mostly stellate hairs or nearly glabrous, sometimes lepidote; pappus without fused outer collar 5
5. Inner pappus of deciduous broadened segments or flattened bristles; style base usually without node 6
– Pappus with many rather persistent capillary bristles; style base with node 8
6. Branchlets of inflorescence without foliose bracts; pubescence not heterotrichous **209. *Piptocoma***
– Branchlets of inflorescence with distinct foliose bracts larger than heads; pubescence heterotrichous or evanescent 7
7. Dark uniseriate hairs prominent among stellate hairs; axis of inflorescence not deflected at nodes; receptacle with thin partitions; pappus with c. 20 deciduous flattened bristles **200. *Blanchetia***
– Dark uniseriate hairs small or evanescent; axis of inflorescence deflected at nodes; receptacle without thin partitions; pappus with only c. 8–10 broad, linear inner segments **206. *Irwinia***
8. Corolla with many hairs inside limb **203. *Dasyandantha***
– Corolla glabrous inside 9
9. Tails of anthers, when present, not sclerified; only inner involucral bracts deciduous; trees or shrubs **201. *Critoniopsis***
– Tails of anthers sclerified, blunt or sharp; most involucral bracts deciduous; erect or scandent shrubs or trees **208. *Piptocarpha***

Genera of Piptocarphinae

200. *Blanchetia* DC.

Blanchetia DC., Prodr. 5: 75 (1836).

Shrubs, with intermixed long dark multicellular hairs and pale stellate hairs. Inflorescences corymbiform with foliose bracts; involucral bracts 25–30 in c. 4 series; receptacle with thin partitions. Florets 8–10; filaments inserted near sinuses; anthers not tailed; style without node; sweeping hairs pointed. Achenes 10-costate, hairless; pappus deciduous, c. 20 flattened bristles. One species, *B. heterotricha* DC., north-eastern Brazil.

201. *Critoniopsis* Sch. Bip.

Critoniopsis Sch. Bip., Jahresber. Pollichia 20/21: 430 (1863); Cuatrecasas, Bot. Jahrb. Syst. 77: 52–84 (1956), reg. rev.; Jones, Brittonia 25: 86–115 (1973), reg. rev.; Robinson, Proc. Biol. Soc. Wash. 106: 606–627 (1993), emend., list.
Turpinia Lex. ex LaLlave & Lex. (1824), nom. illegit.
Monosis DC. sect. *Eremosis* DC. (1836).
Tephrothamnus Sch. Bip. (1863).
Eremosis (DC.) Gleason (1906).

Shrubs or trees; hairs often stellate. Leaves alternate or opposite, petiole often lobed or winged. Inflorescences terminal; involucral bracts 18–25(–35) in 4–6 series. Florets 1–11(–15 or 20); corolla throat present, lobes often recurved, with small glands; anthers often with unsclerified tails; style usually with node; sweeping hairs obtuse. Achenes 5–10-costate; pappus capillary. n = 17. Seventy-six species, Mexico, Central America, Andes to Brazil.

DNA studies (Keeley and Chan, pers. comm.) show that *Tephrothamnus* and *Eremosis* are worthy of separate generic rank.

202. *Cuatrecasanthus* H. Rob.

Cuatrecasanthus H. Rob., Revista Acad. Colomb. Ci. Exact. 17: 209 (1989).

Weak shrubs; hairs with apical cell enlarged at base. Inflorescence terminal; heads sessile in glomerules; involucral bracts c. 15 in 5–6 series. Florets 1; corolla throat lacking; anthers with fimbriate tails; style with node; sweeping hair tips rounded. Achenes 10-costate, glanduliferous and spiculiferous, raphids lacking; pappus capillary, outer setae short. Three species, Ecuador, Peru.

203. *Dasyandantha* H. Rob.

Dasyandantha H. Rob., Proc. Biol. Soc. Wash. 106: 778 (1993).

Small trees; stems sublanate, hairs simple. Leaves to 30 cm long. Inflorescence thyrsoid-paniculate. Heads sessile in glomerules. Involucral bracts c. 30, in c. 4 series. Florets c. 12; corolla throat enlarged, pilosulous inside; anthers with unsclerified tails; style with node; sweeping hairs blunt-tipped. Achenes 8-ribbed, setuliferous; pappus capillary, fragile. One species, *D. cuatrecasasiana* (Aristeg.) H. Rob., Venezuelan Andes.

204. *Ekmania* Gleason

Ekmania Gleason, Bull. Torrey Bot. Club 46: 250 (1919).

Lepidote shrubs. Leaves discolorous below. Inflorescence corymbose; heads with small foliose subinvolucral bract; involucral bracts c. 30 in 4–5 series. Florets c. 12; anther bases rounded; style without node; sweeping hairs acute, often septate. Achenes 10-costate, glanduliferous; outer persistent pappus a laciniate collar, few deciduous flattened bristles inside. One species, *E. lepidota* Griseb., Cuba.

205. *Huberopappus* Pruski

Huberopappus Pruski, Novon 2: 19 (1992).

Shrubs; hairs stellate. Inflorescences of few short-pedunculate heads and small foliiform bracts. Involucral bracts 14–17 in 3–4 series. Florets 19–22; anther bases rounded; style without node; sweeping hairs obtuse, often septate. Achenes 3–5-angled, c. 10-striate, glabrous; pappus collarform, some with single awn. One species, *H. maigualidae* Pruski, Venezuela (Bolivar-Amazonas border).

206. *Irwinia* G.M. Barroso

Irwinia G.M. Barroso, Rodriguesia 32: 11 (1980).

Subscandent shrub; mixed evanescent, small, multicellular and pale stellate hairs. Inflorescence axis deflected at nodes, branches with foliose bracts. Involucral bracts 18–20 in c. 4 series. Florets 5; filaments at sinuses; anther bases rounded; style without node; sweeping hairs obtuse. Achenes 6–7-costate, glabrous; pappus 8–10 deciduous, twisted straps, outer bristles short. One species, *I. coronata* G.M. Barroso, north-eastern Brazil.

207. *Joseanthus* H. Rob.

Joseanthus H. Rob., Revista Acad. Colomb. Ci. Exact. 17: 210 (1989).

Shrubs or trees; hairs sometimes T-formed. Leaves opposite. Inflorescences densely corymbose. Heads shortly pedunculate; involucral bracts 20–30 in c. 4–5 series. Florets 9–12; corolla densely pilosulous, without throat; anthers with fimbriate tails; style with node; sweeping hairs obtuse. Achenes 3–8-costate, with glands and small setulae; pappus capillary, with squamellae. Five species, Colombia, Ecuador.

208. *Piptocarpha* R. Br.

Piptocarpha R. Br., Observ. Comp. 121 (1817) [1818].
Carphobolus Schott in Spreng. (1827).
Vernonia Schreb. sect. *Vanillosma* Less. (1831).
Monanthemum Griseb. (1861), nom. illegit.

Scandent scrambling shrubs or trees; hairs stellate or lepidote. Leaves alternate or opposite. Heads in axillary or terminal clusters; involucral bracts 18–30 in 3–4 series. Florets 3–20; corolla lobes often recurved; anther tails sclerified; style with node; sweeping hairs blunt, often septate. Achenes 3–5-costate, glabrous, with idioblasts, raphids short-oblong; pappus capillary. $n = 17$. Forty-three species, tropical America.

209. *Piptocoma* Cass.

Piptocoma Cass., Bull. Soc. Philom. Paris 1817: 10 (1817); Pruski, Novon 6: 96–102 (1996), emend.
Dialesta Kunth (1818).
Odontoloma Kunth (1818).
Pollalesta Kunth (1818).
Adenocyclus Less. (1829).

Trees and shrubs; hairs stellate to lepidote. Inflorescences corymbiform. Involucral bracts 5–25 in 4–5 series, partly deciduous. Florets 1–12; corolla throat very short; anther bases rounded; style without node; sweeping hairs mostly blunt, often septate. Achenes weakly 7–10-costate, idioblasts present; pappus with deciduous linear segments, persistent outer scales. Eighteen species, Greater Antilles, northern South America.

VI.4. Subtribe Chrestinae H. Rob. (1999).

Inflorescence compound, sometimes spicate, maturing acropetally. Anther appendage thin-walled, usually glabrous; style without node. Pollen tricolporate, lophate. Characteristic sesquiterpenes: glaucolides.

Key to the Genera

1. Leaves deeply lobed; inflorescence a spike of heads without obvious bracts; peduncle swollen and fistulose **211. *Pithecoseris***
– Leaves entire or shallowly dentate; inflorescence not or only slightly spicate; without swollen peduncle 2
2. Clusters of heads borne in axils of large imbricate upper leaves or bracts; leaves broad with many sublongitudinal veins **212. *Soaresia***
– Heads in glomerules or umbels or small spikes, not in axils of series of large leaves or bracts; leaves with pinnate venation or narrow with few longitudinal veins **210. *Chresta***

Genera of Chrestinae

210. *Chresta* Vell. ex DC.

Chresta Vell. ex DC., Prodr. 5: 85 (1836).
Vernonia Schreb. sect. *Pycnocephalum* Less. (1831).
Pycnocephalum (Less.) DC. (1836).
Stachyanthus DC. (1836), nom. rej.
Eremanthus Less. sect. *Pycnocephalum* (Less.) Baker (1873).
Glaziovianthus G.M. Barroso (1947).
Argyrovernonia MacLeish (1984), nom. nov. for *Stachyanthus* DC.

Perennial herbs and subshrubs; hairs symmetrically or asymmetrically T-shaped or forming dense felt. Inflorescences long-peduculate, clusters globose, subumbellate or spicate; involucral bracts 10–20 in 5–6 series. Florets 2–12; corolla tube long; anther bases rounded; appendage sometimes with glands; sweeping hairs fusiform. Achenes 5-angled, raphids short or elongate; pappus capillary, sometimes caducous. Pollen lophate or non-lophate. Eleven species, Brazil, Bolivia.

211. *Pithecoseris* Mart. ex DC.

Pithecoseris Mart. ex DC., Prodr. 5: 84 (1836).

Coarse biennial herbs; hairs symmetrically T-shaped. Leaves deeply pinnatifid. Inflorescence a dense spike, peduncle inflated, fistulose. Involucral bracts c. 8 in c. 3 subequal series. Florets 3–7; anther bases rounded; sweeping hairs fusiform. Achenes 5-costate, setuliferous or glabrous, raphids elongate; capillary pappus caducous, usually with squamellae. Pollen echinolophate, with polar lacuna. One species, *P. pacourinoides* Mart. ex DC., eastern Brazil.

212. *Soaresia* Sch. Bip.

Soaresia Sch. Bip., Jahresber. Pollichia 20/21: 376 (1863), nom. cons., non F. Allem. (1851).
Bipontia S.F. Blake (1937), nom. nov. for *Soaresia* Sch. Bip.

Subshrubs, with xylopodia; stems felted with fusiform hairs. Leaves imbricate, silvery velvety, veins nearly longitudinal. Rows of sessile heads in upper axils. Involucral bracts c. 12 in c. 3 series. Florets 4; corollas sericeous; anthers tailed; sweeping hairs acicular. Achene 5-ribbed, sericeous, raphids elongate; pappus awns c. 15, subulate, basally winged. Pollen echinolophate, with polar lacuna. One species, *S. velutina* Sch. Bip., Brazil (Goias, Minas Gerais).

VI.5. Subtribe Centratherinae H. Rob., F. Bohlmann & R.M. King (1980).

Short-lived herbs. Heads single, terminal, with foliose spreading subinvolucral bracts. Corolla tube slender, densely stipitate-glanduliferous. Style without node. Achene raphids subquadrate. Pollen tricolporate, non-lophate. Characteristic terpenoids: furoheliangolides.

Key to the Genera

1. Perennial herbs or shrubs branching mostly near base, with or without a pappus; achenes glabrous or stiffly setuliferous **213. *Centratherum***
– Weak annual herbs; without a pappus; achenes with small, divergently tipped setulae **214. *Oiospermum***

213. *Centratherum* Cass.

Centratherum Cass., Dict. Sci. Nat. 7: 384 (1817); Kirkman, Rhodora 83: 1–24 (1981), rev.; Robinson, Phytologia 46: 143–145 (1980), emend.
Amphereph is Kunth (1818).
Crantzia Vell. (1827).

Perennial herbs or shrubs branching near base; hairs T-shaped and simple multicellular. Involucral bracts 30–40, in c. 4 series, with distal margins scarious. Florets 40–100+; anthers not tailed; sweeping hairs acicular. Achenes 8–10-ribbed; pappus of short deciduous awns or lacking. n = 16, 32. Three species, tropical America, Philippines, Australia, adventive.

214. *Oiospermum* Less.

Oiospermum Less., Linnaea 4: 339 (1829).

Annual herbs; hairs T-shaped. Leaf blades hairless, glandular-dotted. Involucral bracts c. 45 in c. 4 series. Florets c. 25; anther bases rounded; sweeping hairs short-pointed, few septa. Achenes 10-ribbed, pilosulous, setulae tips flagelliform or hooked; pappus lacking. One species, *O. involucrata* (Spreng.) Less., north-eastern Brazil.

VI.6. Subtribe Lychnophorinae
Benth. & Hook. f. (1873).

Rosettiform herbs to small trees. Heads often compound. Anther appendage indurate, glabrous; style without node. Achene raphids subquadrate. Pollen tricolporate, non-lophate. Characteristic sesquiterpenes: furoheliangolides.

Key to the Genera

1. Acaulescent; peduncles directly from the basal rootstock **222. *Prestelia***
– Leafy stems present 2
2. Pappus with broad, strap-shaped or subulate segments, easily deciduous 3
– Pappus with capillary bristles, persistent 5
3. Leaves with clasping bases; involucral bracts with pungent acuminate tips; heads with c. 80 florets; achenes 10-ribbed **223. *Proteopsis***
– Leaves not clasping at base; involucral bracts not acuminate at tips; heads with 1–23 florets; achenes 4- or 5-angled, sometimes faintly 8–10-ribbed 4
4. Inflorescence with rounded or axillary glomeruli of heads; heads with 1–12 florets **218. *Lychnophora***
– Inflorescence with spiciform cluster of heads; heads with 9–23 florets **219. *Lychnophoriopsis***
5. Herbs with leaves mostly in basal rosette **220. *Minasia***
– Shrubs or trees with cauline leaves 6
6. Ericoid shrubs, often with small densely spirally inserted leaves; heads solitary in axils or on branch tips **221. *Piptolepis***
– Broad-leaved shrubs or trees; heads in corymbiform cymes, axillary clusters, or glomeruli 7
7. Heads terminal, not in clusters, large, with c. 60 florets **215. *Anteremanthus***
– Heads in leaf axils or in dense clusters, with 1–10(–24–26) florets 8
8. Upper leaf surfaces strongly bullate; clusters of heads axillary; corollas with long and narrow tube and throat **216. *Chronopappus***
– Upper leaf surfaces weakly roughened or plane; heads in terminal clusters or glomeruli; corollas short **217. *Eremanthus***

Genera of Lychnophorinae

215. *Anteremanthus* H. Rob.

Anteremanthus H. Rob., Proc. Biol. Soc. Wash. 105: 646 (1992).

Shrubs; hairs mostly T-formed. Inflorescence thyrsoid, with gradate foliaceous bracts. Involucral bracts c. 60 in 5–6 series. Florets c. 60; corolla tube short, lobes with contorted hairs; anther bases rounded; sweeping hairs pointed, often septate. Achene 8–10-ribbed, densely long-setulose; pappus capillary, with squamellae. One species, *A. hatschbachii* H. Rob., Brazil (Minas Gerais).

216. *Chronopappus* DC.

Chronopappus DC., Prodr. 5: 84 (1836).

Shrubs; stem felted with thick-walled fusiform and stellate hairs. Leaves bullate, abaxial tomentum of contorted stellate-based hairs. Heads sessile in upper axils, c. 8 pubescent subinvolucral bracts; involucral bracts c. 8–10, rather deciduous. Florets 8–10; anther bases rounded; sweeping hairs pointed. Achenes 10-angled, glabrous; inner pappus of flattened bristles. One species, *C. bifrons* (DC. ex Pers.) DC., Brazil (Minas Gerais).

217. *Eremanthus* Less.

Eremanthus Less., Linnaea 4: 317 (1829); MacLeish, Ann. Missouri Bot. Gard. 74: 265–290 (1987), rev.
Vanillosmopsis Sch. Bip. (1861).
Sphaerophora Sch. Bip. (1863), nom. illegit.
Paralychnophora MacLeish (1984), nom. nov. for *Sphaerophora* Sch. Bip.

Shrubs and trees; stems felted or woolly or stellate-lepidote. Heads usually in 1 to many dense, globular clusters; involucral bracts 10–40 in 4–7 usually gradate series, innermost deciduous. Florets 1–9, 24–26; corolla tube short; anther bases rounded; sweeping hairs pointed, often septate. Achenes 3–5-angled, or 10(–20)-costate; pappus bristles 3–5-seriate, broadened to filiform. n = 15, 18. Circa 25 species, south-eastern to north-eastern Brazil, eastern Bolivia.

218. *Lychnophora* Mart.

Lychnophora Mart., Denkschr. Königl.-Baier. Bot. Gesell. Regensburg 2: 148 (1822).
Haplostephium Mart. ex DC. (1836).
Lychnocephalus Mart. ex DC. (1836).

Usually candelabriform or rosettiform shrubs or small trees; stem felted with fusiform hairs. Leaves often crowded, with stellate or asymmetrical T-shaped hairs below. Heads sessile in globular or hemispherical clusters. Involucral bracts c. 12–25 in 4–6 series, innermost deciduous. Florets 1–12; corollas glabrous; anther bases rounded; sweeping hairs sharp, mostly septate. Achenes 4–5-angled and 8–10-veined, glabrous; pappus of flattened, usually twisted bristles or straps, often with squamae. n = 17. Circa 30 species, south-eastern to north-eastern Brazil.

219. *Lychnophoriopsis* Sch. Bip.

Lychnophoriopsis Sch. Bip., Jahresber. Pollichia 20/21: 375 (1863); Robinson, Proc. Biol. Soc. Wash. 105: 640–652 (1992), key.
Episcothamnus H. Rob. (1981).

Weakly candelabriform small trees, some hairs long-stalked T-shaped; stems felted with fusiform hairs. Leaves densely spiralled, tomentose below. Axillary heads sessile in elongate clusters. Involucral bracts c. 30–60 in c. 6 series. Florets 9–23; anther tails small; sweeping hairs sharp, often septate. Achenes 8–10-ribbed, 4–5-angled, glabrous; pappus segments strap-shaped or bristle-tipped, with squamellae. n = 17. Four species, south-eastern Brazil.

220. *Minasia* H. Rob.

Minasia H. Rob., Proc. Biol. Soc. Wash. 105: 648 (1992).

Perennial rosettiform silvery herbs; hairs T-shaped. Inflorescences scapose, branched, with crowded or pedunculate heads; involucral bracts 50–60 in c. 5 series, with blunt tomentose tips. Florets 20–30; anther with minute tails; sweeping hairs pointed, septa few. Achene c. 8-veined, at least some setulae; pappus capillary, with squamellae. Five species, Brazil (Minas Gerais).

221. *Piptolepis* Sch. Bip.

Piptolepis Sch. Bip., Jahresber. Pollichia 20/21: 380 (1863), nom. cons.

Ericoid shrubs; hairs appearing granular, stellate, sometimes also thick-walled, straight. Heads single, sessile or pedunculate; involucral bracts 8–18(–25) in 3–4 series. Florets 8–18; anther tails short, lobed; sweeping hairs short-acute. Achenes strongly 10–12-costate, furrows with setulae and glandular dots; pappus bristles flattened, bases often broad, sometimes with shorter setae. Five or six species, south-eastern Brazil.

222. *Prestelia* Sch. Bip.

Prestelia Sch. Bip., Festschr. Naturf. Gesell. Emden 73 (1864).

Perennial acaulous subshrubs, rootstock broad; axils lanulose; hairs stellate-based. Leaves linear. Inflorescences 1 to many pedunculate compound heads, secondary involucre of c. 5 subequal bracts. Individual heads 5–10 in cluster, sessile; involucral bracts c. 12 in c. 2 series. Florets 5–6; anthers not tailed; sweeping hairs acute. Achenes c. 8-costate, scattered setulae, glands and idioblasts; pappus bristles in 2–3 series, no squamellae. One species, *P. eriopus* Sch. Bip., south-eastern Brazil.

223. *Proteopsis* Mart. & Zucc. ex Sch.Bip.

Proteopsis Mart. & Zucc. ex Sch.Bip., Jahresber. Pollichia 20/21: 378 (1863).

Coarse perennial herbs; silvery with appressed elliptic-stellate hairs. Leaves smaller above, bases clasping. Inflorescences a dense cluster of large heads. Involucral bracts c. 60 in c. 6 series, strongly pungent-acuminate. Florets c. 80; anthers with broad tails; sweeping hairs acute. Achenes 10-ribbed, glabrous; pappus of few deciduous awns. One species, *P. argentea* Mart. & Zucc. ex Sch. Bip., south-eastern Brazil.

VI.7. Subtribe Sipolisiinae H. Rob. (1999).

Coarse herbs; hairs mostly stellate or stellate at base. Receptacles paleate or spinose. Anther appendages partly indurate, glabrous; style without node. Achene usually with phytomelanin, raphids usually lacking. Pollen tricolporate, non-lophate. Characteristic terpenoids: furoheliangolides, few eudesmane derivatives.

Key to the Genera

1. Receptacles with deciduous pales; corollas with short basal tube 2
– Receptacles with long spines, without pales; corollas with elongate tube 3

2. Stems and leaves with floccose tomentum; corolla lobes with hairs; pappus of deciduous capillary bristles **224. *Bishopalea***
– Stems and leaves with appressed tomentellum; corolla lobes with spicules, no hairs; pappus of twisted flattened bristles **225. *Heterocoma***
3. Pubescence lepidote; achenes without phytomelanin in walls, with subquadrate raphids **226. *Hololepis***
– Pubescence stellate or with hairs stellately armed near base; achenes with phytomelanin in walls, without raphids 4
4. Large caulescent plants; heads in clusters **227. *Sipolisia***
– Mostly acaulescent plants; heads solitary on long peduncles **228. *Xerxes***

Genera of Sipolisiinae

224. *Bishopalea* H. Rob.

Bishopalea H. Rob., Phytologia 48: 211 (1981).

Erect woolly stems, 1.5–5 m. Heads few, peduncles to 10 mm long, few foliose subinvolucral bracts; involucral bracts 30–35 in c. 4 series; linear pales persistent. Florets c. 20; corolla tubes short, apical hairs on lobes; anther bases pointed; sweeping hairs pointed, septate. Achenes 10-costate, glabrous, with phytomelanin; pappus capillary, deciduous. One species, *B. erecta* H. Rob., Brazil (Bahia).

225. *Heterocoma* DC.

Heterocoma DC., Ann. Mus. Natl Hist. Nat. 16: 190, t. 7 (1810).

Subshrub; hairs appressed; leaves crowded, bases vaginate. Large head in each upper axil; few foliose subinvolucral bracts; involucral bracts c. 100, in c. 4 series; pales linear, persistent. Florets c. 50; corolla tube short; anthers not tailed; sweeping hairs pointed, often septate. Achenes 10-costate, with phytomelanin; pappus elements twisted, strap-shaped, deciduous. One species, *H. albida* (DC.) DC., south-eastern Brazil.

226. *Hololepis* DC.

Hololepis DC., Ann. Mus. Natl Hist. Nat. 16: 155, 189 (1810).

Shrubs or trees; hairs symmetrically T-shaped. Petioles long. Heads axillary, solitary, long-pedunculate; subinvolucral bracts c. 8, foliiform, trinervate; involucral bracts c. 30 in c. 4 series; receptacular spines linear. Florets 25–35; anther tails lobed; sweeping hairs short-pointed to obtuse. Achenes 4-angled, glabrous, raphids subquadrate; pappus of flattened persistent bristles, 2–3-seriate. Three species, south-eastern Brazil.

227. *Sipolisia* Glaz. ex Oliv.

Sipolisia Glaz. ex Oliv., Hooker's Icon. Pl. 23, t. 2281 (1894).

Perennial herbs or shrubs; stems lanate, leaves tomentose. Inflorescence branches bearing leaves only around terminal cluster of 1–6 large sessile heads. Involucral bracts 55–100, lanceolate in c. 6 series; receptacles spinose. Florets 25–50; anther tails broadly lobed; sweeping hairs sharp. Achenes 10-grooved, glabrous, with phytomelanin; pappus bristles deciduous, flattened. One species, *S. lanuginosa* Glaz. ex Oliv., south-eastern Brazil.

228. *Xerxes* J.R. Grant

Xerxes J.R. Grant, Nordic J. Bot. 14: 287 (1994), nom. nov. *Alcantara* Glaz. ex G.M. Barroso (1969), non *Alcantarea* (Morren ex Mez) Harms

Acaulescent perennial herbs; stems lanate, leaves tomentose. Leaf bases clasping. Inflorescences of long, axillary peduncles bearing single heads, with foliose subinvolucral bracts, involucral bracts c. 100 in c. 4 series; receptacle spinose. Florets c. 75; anthers tailed; sweeping hairs acute, septate. Achenes 10-costate, glabrous, with phytomelanin; pappus of deciduous bristles. Two species, south-eastern Brazil.

VI.8. Subtribe Elephantopinae Less. (1830).

Herbs. Involucre decussate with 4, 6 or 8 bracts; florets 4, corollas often zygomorphic, base of anthers sometimes not calcarate; apical appendage thin, glabrous. Achene raphids elongate. Pollen tricolporate to subtriporate, usually lophate. Characteristic terpenoids: dilactones.

Key to the Genera

1. Corollas actinomorphic; plants without basal rosettes **229. *Caatinganthus***
– Corollas zygomorphic, with deepest sinus centred towards centre of head; plants with leaves partly in basal rosette 2
2. Pappus of five contorted bristles; $n = 13$ **232. *Pseudelephantopus***
– Pappus with straight awns or bristles; $n = 11$ 3
3. Pappus with usually 5 strong bristles, rarely many bristles; pollen lophate **230. *Elephantopus***
– Pappus of many capillary bristles; pollen not lophate, with many crowded echinate crests **231. *Orthopappus***

Genera of Elephantopinae

229. *Caatinganthus* H. Rob.

Caatinganthus H. Rob., Smithsonian Contr. Bot. 89: 15 (1999).

Short-lived herbs, tomentum arachnoid. Leaves linear. Branches spiciform, 3–20 adaxial heads, biseriate. Outer involucral bracts 4–6, foliiform distally, inner 4, scariose. Anther bases rounded; style with node; sweeping hairs acicular. Achene 10-ribbed, long-setuliferous, raphids subquadrate; pappus setae c. 10 and scales 10, large. Pollen lophate, single polar lacuna. Two species, northeastern Brazil.

230. *Elephantopus* L.

Elephantopus L., Sp. Pl. 814 (1753).
Elephantosis Less. (1829).

Perennials; pilose, hairs simple, stiff. Leaves mostly basal. Heads in bracteate glomerules; involucral bracts 8. Florets 2–4; corollas zygomorphic, with deep inner sinus; anthers not calcarate, not tailed; style without node; sweeping hairs acicular. Achenes 10-costate, setulose, raphids elongate; pappus bristles 5–15(40–81), straight, basally winged. Pollen triporate, echinolophate. $n = 11$. Twelve or more species, pantropical.

231. *Orthopappus* Gleason

Orthopappus Gleason, Bull. New York Bot. Gard. 4: 237 (1906).

Perennials, hairs simple, stiff, yellow. Leaves mostly basal. Inflorescence a spiciform cluster of narrow heads; involucral bracts 8. Corollas zygomorphic, inner sinus deepest; anthers not long-calcarate; style with node; sweeping hairs acicular. Achenes 5-costate, setuliferous, idioblasts along costae, raphids elongate; pappus bristles 2–3-seriate, inner basally winged. Pollen tricolporate, with crowded echinate ridges. $n = 11$. One species, *O. angustifolius* (Sw.) Gleason, tropical America.

232. *Pseudelephantopus* Rohr

Pseudelephantopus Rohr, Skr. Naturhist.-Selsk. Kjb. 2: 213 (1792), nom. et orth. cons.
Distreptus Cass. (1817).
Matamoria LaLlave & Lex. (1824).
Spirochaeta Turcz. (1851).

Perennial herbs; hairs stiff, simple. Leaves mostly basal. Inflorescences spiciform with clustered sessile heads. Involucral bracts 8. Corollas zygomorphic with deep inner sinus; anther shortly calcarate; style without node; sweeping hairs acicular. Achenes 10-costate, setuliferous, with glands, idioblasts along costae, raphids short-oblong; pappus bristles 5, contorted, base broadened. Pollen triporate, lophate. $n = 13$. Two species, tropical America.

VI.9. Subtribe Rolandrinae Cass. ex Dumort. (1829).

Heads sessile in globose glomerules. Involucral bracts 2–6; florets 1 per head. Achene raphids minute or lacking. Pollen triporate, echinolophate. Characteristic sesquiterpenes: glaucolides.

Key to the Genera

1. Shrubs; corolla lobes glabrous; pappus of short scales; inflorescence with sessile axillary globose clusters of heads, without group of subtending bracts **233. *Rolandra***
– Herbs; corolla lobes with some hairs; pappus of few short bristles; inflorescence a pedunculate globose cluster of heads subtended by foliose bracts **234. *Spiracantha***

233. *Rolandra* Rottb.

Rolandra Rottb., Soc. Med. Havn. Collect. 2: 256 (1775).

Shrubs; hairs simple. Leaves white-tomentose below. Inflorescences axillary, sessile. Involucral bracts 2, awned. Corolla 4-lobed, glabrous; anther bases rounded, with sterile margin; style without node; sweeping hairs acicular. Achenes 5-veined, without setulae, with glands, many poorly differentiated idioblasts; pappus a persistent ring of jagged scales. One species, *R. argentea* Rottb., tropical America.

234. *Spiracantha* Kunth

Spiracantha Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp., folio ed. 4: 22 (1818).

Weak herbs; hairs simple. Leaves white-tomentose below. Inflorescence of pedunculate, 3–4-bracted glomerules; involucral bracts c. 6, inner awned. Corolla with filaments near sinuses, lobes 4 or 5; anther bases obtuse; style without node; sweeping hairs acicular. Achenes fusiform, weakly 5–6-veined, few glands and setulae above; pappus of short bristles. $n = 8$. One species, *S. cornifolia* Kunth, central and northern South America.

VI.10. Subtribe Stokesiinae H. Rob. (1999).

Heads pedunculate in lax cymes; corollas mostly ligulate; anther appendages glabrous; style branches glanduliferous, hairs acicular. Pollen tricolporate with crosswalls in colpi; rhomboidal lacunae. Characteristic sesquiterpenes: elemanolides.

Only one genus:

235. *Stokesia* L'Hér.

Stokesia L'Hér., Sert. Angl. 27 (1789).
Cartesia Cass. (1816).

Perennial herbs; sparsely pilose, hairs simple. Leaves mostly basal. Involucral bracts 40–50 in 3–4 series, outer with long spinose-margined foliiform appendages. Florets 60–70; anther bases rounded; style without node. Achenes with 3–4 sides, glands scattered, raphids few, narrowly rhomboidal; pappus of 4 or 5 awn-like deciduous scales. $n = 7$. One species, *Stokesia laevis* (L.) Greene, south-eastern United States.

VI.11. Subtribe Pacourininae H. Rob. (1999).

Aquatic herbs. Heads axillary, large. Anther appendages sclerified, glabrous; style without node, sweeping hairs acicular. Achenes with corky surface. Pollen triporate, lophate, psilate, emicropunctate.

Only one genus:

236. *Pacourina* Aubl.

Pacourina Aubl., Hist. Pl. Guiane 2: 800, t. 316 (1775).

Hairs simple, small. Leaf bases clasping, margins spinose-toothed. Heads single and sessile in axils; involucral bracts c. 50 in c. 3 series, broad, green, margins whitish. Florets c. 50; corolla lobes sclerified distally; anther tails toothed. Achene c. 10-costate, idioblasts in furrows, raphids none; pappus bristles short, deciduous, squamellae persistent. One species, *P. edulis* Aubl., Central and South America south to Argentina.

VI.12. Subtribe Erlangeinae H. Rob. (1999).

Involucral bracts persistent. Anther appendages thin (sclerified in *Acilepidopsis*), glabrous; sweeping hairs usually acicular. Achene raphids usually elongate. Pollen tricolporate and non-lophate or often triporate, lophate with irregular polar lacunae, sometimes emicropunctate. Chemistry: 5-alkylcoumarins, glaucolides, guaianolides.

Key to the Genera

1. Receptacles with few to many pales 2
– Receptacles without pales 5
2. Pappus of separate or partially united segments; pollen lophate, triporate 3
– Pappus lacking, a crenulated corona or a cupule; pollen non-lophate, tricolporate 4
3. Pales only at periphery of receptacle; stem hairs spreading; leaves opposite or whorled, alternate above; corolla lobes with many hairs; florets c. 15 in a head **239. *Ageratinastrum***
– Receptacle with pales throughout; stem hairs sericeous; leaves spirally inserted; corolla lobes with few hairs; florets c. 80 in a head **247. *Dewildemania***
4. Achenes 10-ribbed, densely glanduliferous; petioles narrow, 1–2 cm long; corolla lobes sericeous with stiff hairs; florets 10–15 in a head; corollas whitish **248. *Diaphractanthus***
– Achenes 5-ribbed, glabrous; petioles short; corolla lobes hairless; florets c. 35 in a head; corollas purple **261. *Omphalopappus***
5. Stem hairs symmetrically T-shaped 6
– Hairs of stems simple or asymmetrical or lacking 13
6. Pappus lacking, coroniform, or of few short prongs or deciduous setae, not with many long bristles 7
– Pappus of many capillary bristles, at least as long as basal tube of the corolla 10
7. Leaves filiform; anther thecae long and narrow, linear, to 3 mm long **264. *Paurolepis***
– Leaves with broadened blades; anther thecae not linear 8
8. Leaves sessile; corolla lobes usually with few to many T-shaped hairs; achenes usually glabrous **251. *Gutenbergia***
– Leaves petiolate; corolla lobes without T-shaped hairs; achene with tips of setulae anchor-shaped or hooked 9
9. Pappus none; corolla lobe tips with strong spreading spines **255. *Iodocephalis***
– Pappus of 4 or 5 short prongs; corolla lobe tips without spines **259. *Msuata***
10. Weak trees or shrubs; achenes 10-ribbed; T-shaped hairs often with long, multiseptate stalks **240. *Ambassa***
– Herbs; achenes 4- or 5-ribbed or terete; T-shaped hairs usually with short stalks 11
11. Annuals or short-lived perennials; pollen lophate, triporate **245. *Cyanthillium***
– Perennials; pollen non-lophate, tricolporate 12
12. Corolla lobes with many symmetrical T-shaped hairs; anthers with short or no tails **253. *Hilliardiella***
– Corolla lobes without symmetrical T-shaped hairs; anthers with basal tails **263. *Orbivestus***
13. Achenes with 4–6 ribs or costae 14
– Achenes with 8–12 angles or ribs, rarely smooth and slightly obcompressed 21
14. Pappus of copious long capillary bristles 15
– Pappus with only a ring of free or united scales, a corona, or absent, with few or no inner caducous bristles, without numerous long bristles 16

15. Annual herbs; hairs asymmetrically T-shaped; anther bases without tails; $n = 9$ **266. *Polydora***
– Perennial herbs; hairs not T-shaped; anther bases with tails **269. *Vernoniastrum***
16. Leaves deeply pinnatifid; achenes densely minutely tuberculate **267. *Rastrophyllum***
– Leaves not deeply pinnatifid; achenes not densely minutely tuberculate 17
17. Outer pappus of partially to totally free scales; inner pappus of short brownish bristles **243. *Brachythrix***
– Pappus absent or with outer pappus a ring or corona and inner pappus white 18
18. Involucral bracts greenish with sclerified pale or reddish margins; leaves alternate or opposite or whorled; achenes with long and broad ribs; pollen tricolporate, lophate or non-lophate **242. *Bothriocline***
– Involucral bracts with margin thinner or less differentiated; leaves alternate; achenes with short or narrow ribs; pollen sometimes triporate 19
19. Corolla glabrous; pappus a high collar or lacking **250. *Ethulia***
– Corolla lobes with hairs; pappus often with caducous bristles 20
20. Heads with 20–100 florets; leaves often broadly sessile (Africa) **249. *Erlangea***
– Heads with 4 florets; leaves narrow (Brazil) **268. *Telmatophila***
21. Pappus short, usually not as long as basal tube of corolla 22
– Pappus of many capillary bristles nearly as long as corolla 26
22. Inflorescence with one or more dense glomeruli of sessile heads; pappus coroniform **260. *Muschleria***
– Inflorescence not densely glomerulate; pappus of scales or short bristles or lacking 23
23. Pappus of short scales; pollen tricolporate, non-lophate; achenes with few setulae **246. *Decastylocarpus***
– Pappus of short bristles or lacking; pollen triporate, lophate; achenes glabrous 24
24. Lower involucral bracts spreading and foliose or with spreading and foliose tips; achenes somewhat obcompressed, strongly rounded at top to a narrow corolla and pappus insertion; raphids subquadrate **265. *Phyllocephalum***
– Lower involucral bracts not spreading and foliose nor with reflexed foliose tips, with only narrow reflexed herbaceous tips; achenes prismatic, not narrowed at top below pappus and corolla; raphids oblong to elongate 25
25. Corolla lobes reflexed when mature; anther thecae partially exserted, pale; style base with distinct node; Africa **256. *Kinghamia***
– Corolla lobes not reflexed; anther thecae strongly exserted, blackish; style base without node; Thailand **257. *Koyamasia***
26. Pappus bristles subplumose **262. *Oocephala***
– Pappus bristles only scabrid or barbellate 27
27. Heads with 4–13 florets; anther thecae with broad or short tails 28
– Heads with 25–100 florets; anther bases without tails 30
28. Leaves mostly in basal rosette, large, tomentose below; involucral bracts with spine-tips **254. *Hystrichophora***
– Leaves mostly cauline; involucral bracts without spine at tip 29
29. Plants with decumbent bases; heads in obvious cymes; stems, leaves, involucral bracts, corollas, and achenes with many yellowish or reddish glandular dots; anther bases with sharp sclerified tails, with sclerified apical appendage; South America **237. *Acilepidopsis***
– Plants erect from xylopodia; heads in clusters at nodes; plants without numerous reddish or yellowish glands; anther tails and appendages not sclerified; Africa **244. *Cabobanthus***
30. Plants glabrous; heads pedunculate from middle of internodes of inflorescence branches; leaves with sessile auriculate bases; South America **258. *Mesanthophora***
– Plants pubescent; heads sessile or peduncles from axils of bracts or leaves; leaves usually petiolate at base; Asia or Africa 31
31. Inflorescences scapiform; stems and bracts with some red stipitate glands with multicellular tips **241. *Bechium***
– Inflorescences with many heads sessile or in panicles; without red stipitate glands with multicellular tips 32
32. Outer pappus of short bristles, not broad scales; hairs of stems not angled, with tips erect; setulae of achenes split to base into unequal halves; Asia **238. *Acilepis***
– Outer pappus of short broad scales or squamellae; hairs of stems L-shaped, transverse cap cells mounted at one end; setulae of achene s not split to base into unequal halves **266. *Polydora***

Genera of Erlangeinae

237. *Acilepidopsis* H. Rob.

Acilepidopsis H. Rob., Phytologia 67: 289 (1989).

Perennial herbs decumbent from thickened rhizome; with numerous glandular dots, hairs forming felt on stems. Inflorescence branches seriately cymose. Heads sessile; involucral bracts c. 30. Florets 8–13, corolla lobes reflexed, sericeo-pilosulous; anther bases and appendages sclerified; style without node. Achene 10-costate; raphids lacking; pappus capillary. Pollen triporate, lophate, emicropunctate. One species, *A. echitifolia* (Mart. ex DC.) H. Rob., Argentina, Bolivia, Brazil, Paraguay.

238. *Acilepis* D. Don.

Acilepis D. Don., Prodr. Fl. Nepal 169 (1825).
Lysistemma Steetz (1864).
Xipholepis Steetz (1864).

Erect perennial herbs, stem hairs multiseptate at base. Heads pedunculate or sessile and single at nodes; involucral bracts 50–200 in 6–12 series. Florets 25–80; corolla lobes gland-dotted; anther base blunt; style with node. Achene 8–10-ribbed, setulae halves very unequal; pappus capillary, pollen tripo-

rate, emicropunctate. Ten or more species, mostly India.

239. *Ageratinastrum* Mattf.

Ageratinastrum Mattf., Notizbl. Bot. Gart. Berlin-Dahlem 11: 412 (1932), nom. nov.
Ageratina O. Hoffm. (1900), non *Ageratina* Spach (1841).

Shrubs or subshrubs; indumentum heterotrichous, hairs rarely symmetrically T-shaped. Leaves mostly opposite or whorled. Inflorescences corymbose. Heads sessile; involucral bracts c. 30 in 3–4 series; pales few. Florets c. 15; corolla with sinuous hairs; anther bases rounded; style with node. Achene 4–5-ribbed; pappus scales united or free, sometimes with 5–7 setae. Pollen triporate, lophate, emicropunctate. Five species, tropical Africa.

240. *Ambassa* Steetz

Ambassa Steetz in Peters, Naturwissensch. Reise Mossambique Bot. 363 (1864).

Weak shrubs or small trees; hairs long-stalked, symmetrically T-shaped. Peduncles 2–10 mm long. Involucral bracts c. 40 in c. 4 series. Florets 20–25; anther bases rounded; style with node. Achene 10-costate, setuliferous, idioblasts numerous; pappus of fragile bristles, narrowed below, persistent squamulae. Pollen triporate, lophate, subpsilate. Two species or more, eastern Africa.

241. *Bechium* DC.

Bechium DC., Prodr. 5: 70 (1836).

Erect or horizontally proliferating herbs; hairs sericeous, red stipitate glands with multicellular tips on stems and bracts. Inflorescences scapiform; heads 1 to many; involucral bracts c. 30 in c. 3 series. Florets 25–50; anther bases rounded, style with node; sweeping hairs pointed, septate. Achenes 10-costate, setulae uneven, many idioblasts; pappus capillary, with squamae. Pollen non-lophate. Two or more species, Madagascar.

242. *Bothriocline* Oliv. ex Benth.

Bothriocline Oliv. ex Benth., Hooker's Icon. Pl. 12: 1133 (1873).
Volkensia O. Hoffm. (1894).

Annual or perennial; hairs simple or asymmetrically T-shaped. Leaves alternate, opposite or ternate. Involucral bracts 25–50 in 3–5 series, margins paler or redder. Florets 3–100; anther base rounded; style with node. Achenes with 4 massive ribs, idioblasts covering furrows, raphids subquadrate; pappus with caducous setae or collarform. Pollen tricolporate, echinolophate, or nonlophate. $n = 20$. Thirty or more species, tropical Africa.

243. *Brachythrix* Wild & Pope

Brachythrix Wild & Pope, Kirkia 11: 25 (1978).

Perennial herbs; hairs simple, multiseptate, sometimes unevenly T-shaped. Heads solitary or in cymose clusters; involucral bracts c. 65 in c. 5 series. Florets c. 40; anther bases with sterile lobe; style with node. Achenes 4–5-angled, raphids subquadrate; pappus bristles short, deciduous, outside with scales or continuous corona. Pollen nonlophate. Six species, Africa.

244. *Cabobanthus* H. Rob.

Cabobanthus H. Rob., Proc. Biol. Soc. Wash. 112: 228 (1999).

Perennial herbs, xylopodial; hairs simple, multiseptate. Heads clustered at upper axils; involucral bracts c. 35 in c. 5 series. Florets c. 10; anthers short-tailed; style with node. Achenes 8–10-costate, with many equal-celled setulae; pappus capillary, with shorter outer bristles. Pollen triporate, lophate, emicropunctate. Two or more species, tropical Africa, Tanzania to Zambia.

245. *Cyanthillium* Blume

Cyanthillium Blume, Bidjr. Fl. Ned. Ind. 889 (1826).
Isonema Cass. (1817), nom. illegit., non R. Br. (1810).
Cyanopsis Blume ex DC. (1836), nom. illegit. et superfl.
Vernonia Schreb. sect. *Tephrodes* DC. (1836).
Seneciodes L. ex T. Post & O. Kuntze (1903).
Triplotaxis Hutch. (1914).

Short-lived herbs; hairs asymmetrically or symmetrically T-shaped. Leaves narrowly petiolate, membranaceous. Heads pedunculate; involucral bracts, c. 30 in 3(–5) series, green. Florets 15–94; corolla with straight hairs; anthers without tails; style with node. Achenes 5-ribbed or terete, with idioblasts; pappus capillary, slender-tipped, squamellae persistent, rarely with callose ring. Pollen triporate, echinolophate. $n = 9, 11, 18$. More than seven species, Indian Ocean, Indonesia, south-eastern and eastern Asia, tropical Africa, widely adventive.

246. *Decastylocarpus* Humb.

Decastylocarpus Humb., Mém. Soc. Linn. Normandie 25: 30, 280 (1923).

Herbs; stem hairs multiseptate or with erect cap cells. Leaves without glands. Heads few, subsessile. Involucral bracts 35 in c. 4–5 series, green. Florets 25–30; corollas with glands, lobes sericeous; anthers without tails; style without node. Achenes 10-costate, no idioblasts, many glands, few setulae, raphids subquadrate; pappus coroniform, dentate. Pollen non-lophate. One species, *D. perrieri* Humbert, Madagscar.

247. *Dewildemania* O. Hoffm.

Dewildemania O. Hoffm. in De Wild., Ann. Mus. Congo sér. 1, Bot. sér. 4, 1: 10 (1903).

Perennial herbs; hairs simple, multiseptate. Heads 1 to many; peduncles bracteiferous; involucral bracts 60–80 in 2–7 series; receptacle paleaceous. Florets c. 80; corollas with stipitate glands; anther untailed; style with node. Achenes 4–5-sided, setuliferous, with idioblasts, raphids subquadrate; 5 or more long pappus scales and alternating broad scales. Pollen triporate, lophate, emicropunctate. Seven species, tropical Africa.

248. *Diaphractanthus* Humb.

Diaphractanthus Humb., Mém. Soc. Linn. Normandie 25: 31, 280 (1923).

Annual herbs; stems sericeous. Petioles narrow, blade with glands. Heads crowded, pedunculate; involucral bracts c. 30, in c. 4 series, green, margins scarious; receptacle paleaceous. Florets 10–15; corollas with glands, lobes sericeous; anthers untailed; style with node. Achenes 10-costate, glands dense, no idioblasts, raphids not visible; pappus 4–5-dentate, coroniform. Pollen non-lophate. One species, *D. homolepis* Humb., Madagascar.

249. *Erlangea* Sch. Bip.

Erlangea Sch. Bip., Flora 36: 34 (1853).
Stephanolepis S. Moore (1900).
Haarera Hutch. & E.A. Bruce (1932).

Short-lived herbs; hairs simple, multicellular. Leaves sessile. Heads pedunculate; involucral bracts 20–200 in 3–7 series. Florets c. 25–100+; corolla tips with hairs and often stalked glands; anther slightly tailed; style with node. Achenes 3–6-angled, mostly glabrous; pappus lacking or with caducous setae. Pollen triporate, lophate, emicropunctate, or tricolporate, non-lophate. $n = 10$. Nine or more species, tropical Africa.

250. *Ethulia* L. f.

Ethulia L. f., Dec. Pl. Horti Upsal. 1 (1762); Gilbert & Jeffrey, Kew Bull. 43: 165–193 (1988), rev.
Hoehnelia Schweinf. (1892).

Short-lived herbs; stem hairs with erect cap cells. Leaves short-petiolate. Inflorescence cymose, heads shortly pedunculate; involucral bracts 15–40 in 2–3 usually subequal series. Florets 3–100; corollas with glands, apices glabrous; anther bases plain; style without node; sweeping hairs short-acute. Achenes 2–6-ribbed, glanduliferous, raphids short-oblong; pappus lacking or coroniform. Pollen non-lophate. Nineteen species, Africa, southern Asia, Indonesia, one species widely adventive.

251. *Gutenbergia* Sch. Bip. ex Walp.

Gutenbergia Sch. Bip. ex Walp., Repert. 2: 703 (1843).
Erlangea Sch. Bip. sect. *Platylepis* S. Moore (1902).

Short-lived herbs; stem hairs symmetrically T-shaped, arms filiform. Leaves opposite, ternate or alternate. Heads pedunculate; involucral bracts 20–40, in 3–5 series. Florets 4–50; corollas usually with T-shaped hairs; anther bases rounded; style scarcely nodular. Achenes 4–5, 8–12-costate, usually glabrous, raphids subquadrate; pappus lacking or short deciduous setae. Pollen triporate, echinolophate. $n = 10$. At least 13 species, Africa.

252. *Herderia* Cass.

Herderia Cass., Ann. Sci. Nat. 17: 421 (1829).

Procumbent annuals; finely sericeous. Leaves small. Heads solitary, terminal; involucral bracts 3–4-seriate, subequal, outer 15–25 more filiform, 25–30 inside. Florets c. 30; corollas 1.5 mm long, minutely stipitate-glanduliferous; anther base blunt; style with node. Achenes 4-ribbed, glabrous, idioblasts reddish; pappus of 5–9 scales and 3–5 short bristles. Pollen triporate, lophate. One species, *H. truncata* Cass., Senegal, Gambia, Ghana, Nigeria, tropical western Africa.

253. *Hilliardiella* H. Rob.

Hilliardiella H. Rob., Proc. Biol. Soc. Wash. 112: 229 (1999).

Perennial herbs; stems with symmetrically T-shaped hairs. Heads pedunculate; involucral bracts

c. 25–40 in 3–4 series, subpersistent. Florets 12–20; corollas with T-shaped hairs; anthers scarcely tailed; style with node. Achenes 4–5-costate, densely setuliferous and idioblastiferous; pappus setae slender, subpersistent, with shorter outer series. Pollen non-lophate. $n = 9, 10$. Eight or more species, mostly southern and eastern Africa.

254. *Hystrichophora* Mattf.

Hystrichophora Mattf., Notizbl. Bot. Gart. Berlin-Dahlem 13: 288 (1936).

Herbs with basal rosette. Leaves to 40 ×25 cm, margins spinulose-toothed, tomentellous below. Inflorescences axillary, appearing terminal, branches often paired, one subsessile, with glomerules of few heads, adaxial branch pedunculate, with globose glomerules of 30–50 narrow heads; involucral bracts 6–7-seriate, spine-tipped. Florets 5–6; corollas glabrous; anther base with sterile margin; style with node (?). Achenes 10-costate, setuliferous, with idioblasts, raphids elongate or lacking; inner pappus squamae c. 12, caducous, 4–5 mm long, squamules persistent. Pollen triporate, lophate. One species, *H. macrophyllum* Mattf., Tanzania (Lindi), Mueraplateau (Rondo).

255. *Iodocephalis* Thorel ex Gagnep.

Iodocephalis Thorel ex Gagnep., Notul. Syst. (Paris) 4: 16, 24 (1920).

Annuals; hairs symmetrically T-shaped. Petioles to 5 mm, blades glandular-dotted. Peduncles 5–10 mm long; involucral bracts c. 20, 3–7-seriate, acuminate, arachnoid-pubescent. Florets 25–70; corolla tips strongly spinose; anther bases obtuse to acuminate; style without node. Achenes 5–7–10-costate, with glands, ribs setuliferous, setulae anchor-shaped or hooked, raphids subquadrate; pappus none. Pollen triporate, lophate. Two species, Laos, Thailand and Vietnam, mostly along banks of Mekong River.

256. *Kinghamia* C. Jeffrey

Kinghamia C. Jeffrey, Kew Bull. 43: 274 (1988); Robinson, Proc. Biol. Soc. Wash. 112: 220–247 (1999), rev.

Perennial herbs; hairs simple, multiseptate. Heads pedunculate; involucral bracts 100–200 in 5–6 series, outer subulate, inner broad, apiculate. Florets 50–80; corolla lobe tips recurved; anthers pale, partially exerted, base obtuse; style with node. Achenes strongly 10-ribbed, glabrous, idioblasts in grooves; pappus with short deciduous setae or none. Pollen triporate, echinolophate. Five species, tropical Africa.

257. *Koyamasia* H. Rob.

Koyamasia H. Rob., Proc. Biol. Soc. Wash. 112: 234 (1999).

Perennial herbs; stem hairs simple, multiseptate. Petioles narrow. Heads solitary, long-pedunculate; involucral bracts c. 90 in 4–5 series, mostly herbaceous and reflexed. Florets c. 90; anther thecae strongly exerted, dark, bases rounded; style without node. Achene 10-costate, glabrous, with idioblasts, raphids minute, oblong; pappus setae short, deciduous. Pollen triporate, lophate, emicropunctate. $2n = 54$. One species, *K. calcarea* (Kitamura) H. Rob., Thailand.

258. *Mesanthophora* H. Rob.

Mesanthophora H. Rob., Novon 2: 172 (1992).

Glabrous perennial herbs. Leaves sessile, shortly decurrent, auriculate, glandular-dotted below. Racemiform leafy cymes with peduncles from middle of internodes; involucral bracts c. 100 in c. 5 series, linear-lanceolate, erect-patent. Florets 90–100; anther bases rounded; style with node. Achenes 8–10-costate, costae scabrid; pappus bristles deciduous, capillary, squamellae persistent. Pollen triporate, lophate, emicropunctate. Two species, Bolivia, Paraguay.

259. *Msuata* O. Hoffm.

Msuata O. Hoffm. in Engler & Prantl, Nat. Pflanzenfam. IV/5: 388 (1894).

Subshrubs; hairs symmetrically T-shaped. Petioles narrow. Heads short-pedunculate; involucral bracts 16–20, 2-seriate. Florets c. 26; corollas glanduliferous; anther bases rounded; style without node; sweeping hairs round-tipped. Achenes 4- or 5-ribbed, sides with glands and idioblasts, setulae beside ribs, with anchor-like points, raphids subquadrate; pappus crown with 4 or 5 short prongs. Pollen non-lophate. One species, *M. buettneri* O. Hoffm., tropical Africa, Congo.

260. *Muschleria* S. Moore

Muschleria S. Moore, J. Bot. 52: 89 (1914).

Rhizomatous shrubs; hairs simple, multiseptate. Leaves linear, tomentose below. Inflorescence ter-

minal, 1 to few glomeruli of sessile heads. Involucral bracts c. 20 in 4–5 series. Florets 4–6; corolla glanduliferous, lobes with multiseriate spines; anther bases sagittate, not tailed; style with node. Achenes 10-costate, glands between costae, idioblasts numerous; pappus coroniform. Pollen non-lophate. $n = 9$. One species, *M. angolensis* S. Moore, Angola, southern tropical Africa.

261. *Omphalopappus* O. Hoffm.

Omphalopappus O. Hoffm. in Engler & Prantl, Nat. Pflanzenfam. IV/5: 234 (1890–1891).
Gossweilera S. Moore (1908).

Perennial herbs; hairs simple, multiseptate. Inflorescences virgately corymbiform. Heads pedunculate, hemispherical; involucral bracts c. 50 in c. 3 series, many subequal; receptacle paleaceous. Florets c. 35; anther thecae reddish, bases plain; style thickened without node. Achenes 5-ribbed, glabrous, without idioblasts, raphids subquadrate; pappus a denticulate corona or cupule. Pollen non-lophate. Two or three species, Angola.

262. *Oocephala* (S.B. Jones) H. Rob.

Oocephala (S.B. Jones) H. Rob., Proc. Biol. Soc. Wash. 112: 281 (1999).
Vernonia Schreb. subsect. *Oocephalae* S.B. Jones (1981).

Shrubs; hairs simple, weakly L-shaped. Inflorescences corymbiform. Heads shortly pedunculate; involucral bracts 35–40 in c. 7 series. Florets c. 15; anther base rounded; style base with ring. Achenes 8-ribbed, setuliferous on ribs; idioblasts in furrows; pappus biseriate, outer shorter, inner setiform, subplumose. Pollen triporate, lophate. Two species, tropical Africa.

263. *Orbivestus* H. Rob.

Orbivestus H. Rob., Proc. Biol. Soc. Wash. 112: 230 (1999).
Vernonia Schreb. subg. *Orbisvestus* S.B. Jones (1981).

Shrubs or subshrubs; hairs T-shaped. Leaf blade sparsely pilose. Inflorescence laxly corymbiform. Heads pedunculate; involucral bracts 25–30 in c. 4 series. Florets 8–16; corollas essentially glabrous; anther bases tailed; style with node. Achenes 4–5-costate, setuliferous, with idioblasts; pappus setae deciduous, with persistent squamae. Pollen non-lophate. $n = 9, 20$. Four or more species, tropical and southern Africa.

264. *Paurolepis* S. Moore

Paurolepis S. Moore, J. Bot. 55: 102 (1917).

Perennial herbs; hairs symmetrically T-shaped. Leaves filiform. Inflorescence diffuse, peduncles elongate. Involucral bracts c. 25, c. 4-seriate. Florets c. 10; corollas sericeous, hairs T-shaped; anther thecae linear, base rounded; style with node. Achenes 4-sided, setulae on ribs, glands in furrows, raphids subquadrate; pappus scales 4, erose, subdeciduous. Pollen triporate, echinolophate. Three species, Africa.

265. *Phyllocephalum* Blume

Phyllocephalum Blume, Bijdr. Fl. Ned. Ind. 888 (1826); Kirkman, Rhodora 83: 1–24 (1981), rev.; Robinson, Proc. Biol. Soc. Wash. 112: 220–247 (1999), emend.
Decaneurum DC. ex Wight (1833), non *Decaneurum* DC. (1833).
Lamprachaenium Benth. in Benth. & Hook. f. (1873).

Short-lived herbs; hairs flagelliform, multicellular. Leaf blades white-tomentose below. Heads 1 to few, pedunculate; with spreading, foliaceous subinvolucre or tips of outer involucral bracts; involucral bracts c. 40, subequal, 2–3-seriate. Florets 75–150; anther bases sharp, diverging; style with node. Achenes obcompressed, oblong, narrowed to corolla, glabrous, 10-costate or smooth and shiny, raphids subquadrate; pappus bristles short, coloured, caducous. Pollen triporate, lophate, emicropunctate. $n = 9$. Circa ten species, India, Java.

266. *Polydora* Fenzl

Polydora Fenzl, Flora 27: 312 (1844).
Crystallopollen Steetz (1863).

Annuals; hairs L-shaped. Inflorescence laxly thyrsoid-paniculate. Heads pedunculate; involucral bracts c. 80, c. 7-seriate, margins scarious, tips black. Florets c. 30; corolla lobes hairless; anthers without tails; style with node. Achenes 5–8–10-ribbed, setuliferous, idioblasts scattered; pappus bristles greenish, yellowish or tawny, rarely white, with squamellae. Pollen triporate, lophate. $n = 9$. Eight species, tropical Africa.

267. *Rastrophyllum* Wild & Pope

Rastrophyllum Wild & Pope, Kirkia 10: 325 (1977).

Annuals; hairs eccentrically T-shaped. Leaves deeply pinnatifid. Heads in corymbiform clusters, peduncles to 5 mm. Involucral bracts 30–40 in

2–5 series. Florets 25–35(?); corolla tubes covered with stipitate glands. Achenes 4-sulcate, surface minutely tuberculate; pappus lacking. Two species, tropical Africa.

268. *Telmatophila* Mart. ex Baker

Telmatophila Mart. ex Baker in Mart., Fl. Brasil. 6, 2: 170 (1873).

Perennials; sericeous with simple hairs. Inflorescences axillary, secondary heads surrounded by foliaceous bracts. Heads cylindrical; subequal involucral bracts and florets 4. Corollas with long hairs distally; style base without node. Achenes oblong-ovoid, c. 8-costate, with idioblasts, long setulae deeply divided, raphids elongate; pappus of c. 8 short, laciniate scales. Pollen triporate. One species, *T. scolymastrum* Mart. ex Baker, northeastern Brazil.

269. *Vernoniastrum* H. Rob.

Vernoniastrum H. Rob., Proc. Biol. Soc. Wash. 112: 233 (1999).
Vernonia Schreb. sect. *Lepidella* Oliv. & Hiern (1877), non *Lepidella* Tiegh. (1911), nec *Lepidella* E.J. Gilbert (1925).

Perennial herbs; hairs simple-multiseptate or slightly uneven at base. Heads single or grouped. Involucral bracts c. 50, c. 3-seriate. Florets c. 50; corolla pilose distally; anther tails short; style with node. Achenes 4–5-angled, with setulae, idioblasts often in transverse bands, raphids elongate; pappus of capillary bristles and squamellae. Pollen triporate, lophate. $n = 10$. Eight species, tropical Africa.

VI.13. Subtribe Centrapalinae H. Rob. (1999).

Coarse herbs. Leaves alternate. Involucral bracts persistent. Anther appendages indurated, glabrous; sweeping hairs pointed. Pollen tricolporate, usually lophate. Characteristic sesquiterpenes: elemanolides.

Key to the Genera

1. Pappus coroniform, of short deciduous bristles or of only small scales, not of long bristles 2
– Pappus of 5-numerous long capillary or flattened bristles 4
2. Receptacle with pales; Australia **278. *Pleurocarpaea***
– Receptacle without pales; Asia 3
3. Hairs of stems simple, multiseptate; pappus none or an annulus or corona **270. *Adenoon***
– Hairs of stems mixed, simple plus T-shaped; pappus a lobate corona or of short deciduous segments **273. *Camchaya***
4. Pappus of flattened bristles; corollas purple to white; style without basal node, with high sheathing nectary 5
– Pappus of capillary bristles; corollas violet or blue; style base with node, nectary short 6
5. Corolla lobes shorter than throat; pappus bristles numerous; pollen lophate; $n = 10$ **272. *Baccharoides***
– Corolla lobes about as long as throat; pappus bristles c. 5; pollen not lophate **277. *Neurolakis***
6. Leaves in basal rosette; West Indies **275. *Lachnorhiza***
– Leaves not restricted to basal rosette; Africa 7
7. Heads surrounded by greatly enlarged foliiform bracts below involucre; leaves often with longitudinal venation **271. *Aedesia***
– Heads not surrounded by greatly enlarged foliiform subinvolucral bracts; venation never longitudinal 8
8. Achenes with weak ribs or costae, without lines of idioblasts along costae; pollen lophate without spurs projecting into colpi; corollas lavender or purple to blue; $n = 9$ **274. *Centrapalus***
– Achenes with strong ribs or costae, usually with lines of idioblasts crowded along sides of costae; pollen lophate with spur walls projecting into colpi; corollas blue; $n = 10$ **276. *Linzia***

Genera of Centrapalinae

270. *Adenoon* Dalzell

Adenoon Dalzell, in Hooker's J. Bot. Kew Gard. Misc. 2: 344 (1850).

Perennials; hairs simple, multiseptate. Inflorescence corymbose. Heads long-pedunculate; involucral bracts c. 50 in 4–5 series; receptacle fimbriate. Florets c. 50; corolla tube pilose; anthers shortly tailed; style without node, nectary long; sweeping hairs acicular. Achene 10-costate, glabrous, raphids elongate; pappus none. Pollen with spur walls, lophate, without polar lacunae. One species, *A. indicum* Dalzell, India.

271. *Aedesia* O. Hoffm.

Aedesia O. Hoffm., in Engler & Prantl, Nat. Pflanzenfam. Nachtr. 1: 321 (1897).

Perennials, glabrous. Solitary terminal heads surrounded by large leaves; involucral bracts c. 50 in 4–5 series, apical margin toothed; receptacle with few pales. Florets c. 50(?); corolla tube long, throat none; anther bases rounded; style without node; sweeping hairs acicular. Achene 10-costate, setulose, raphids subquadrate; pappus capillary, multi-

seriate. Pollen echinolophate. Three species, tropical Africa.

272. *Baccharoides* Moench

Baccharoides Moench, Methodus 528 (1794); Isawumi et al., Grana 35: 205–230 (1996), tax.
Ascaricida Cass. (1817), nom. illegit. superfl.
Candidea Tenore (1839).
Stengelia Sch.Bip. ex Steetz (1864).

Perennials, hairs short-stalked, cap-cells erect. Involucral bracts 25–100, 4–8-seriate, apices often expanded. Florets 25–100; corolla base slender, abruptly expanded into cylindrical limb, throat as long as erect lobes; anther tails small; style without node, nectary tubular; sweeping hairs acicular. Achenes 8–20-ribbed, ribs usually setulose, raphids elongate; pappus pluriseriate, setae flattened, sometimes with squamellae. Pollen echinolophate, with polar lacuna. $n = 10$. Circa 25 species, tropical Africa, southern Asia.

273. *Camchaya* Gagnep.

Camchaya Gagnep., Notul. Syst. (Paris) 4: 14 (1920). Koyama, Acta Phytotax. Geobot. 35: 49–58 (1984), rev.
Thorelia Gagnep. (1920), nom. cons., non *Thorelia* H.F. Hance (1877), nom. rej.
Thoreliella C.Y. Wu (1975), nom. nov. for *Thorelia* Gagnep.

Annuals; hairs T-shaped and simple. Heads few, pedunculate; involucral bracts 20–130, 3–5-seriate, herbaceous and spinose only at tips. Florets 12–130; anther bases rounded; style without node, nectary long; sweeping hairs acicular. Achenes 10-costate, with glands, many idioblasts, raphids short-rhomboid; pappus with corona or short deciduous segments; pollen triporate with cross-walls, echinolophate. Five species, Thailand, China (Yunnan), Laos.

274. *Centrapalus* Cass.

Centrapalus Cass., Bull. Soc. Philom. Paris 1817: 10 (1817).
Vernonella Sonder (1850).

Annuals or perennials, often scapigerous; stem hairs simple, multiseptate. Involucral bracts 125–150, c. 5-seriate, linear, green, often denticulate. Florets c. 100; corollas blue to purplish, lobes sometimes fringed; anther not tailed; style with node; sweeping hairs acute. Achenes weakly 10-costate, setuliferous, raphids oblong; pappus capillary. Pollen lophate or non-lophate. $n = 9$. Nine species or more, Africa.

275. *Lachnorhiza* A. Rich.

Lachnorhiza A. Rich. in Sagra, Hist. Fis. Cuba, Bot. 11: 34 (1850).

Rosettiform perennials; many cells of longest hairs basally spurred. Peduncles long, with 1 or 2 heads. Involucral bracts c. 25, c. 3-seriate. Florets 10–15; corollas glanduliferous; anther bases obtuse; style without node; sweeping hairs acicular. Achenes 10-costate, with glands, raphids oblong; pappus bristles persistent, few spicules. Pollen echinolophate, emicropunctate. One species, *L. piloselloides* A. Rich., Cuba.

276. *Linzia* Sch. Bip. ex Walpers

Linzia Sch. Bip. ex Walpers, Rep. 2: 948 (1843).
Vernonia Schreb. sect. *Azureae* S.B. Jones (1981).

Perennials; hairs simple, multicellular. Involucral bracts 50–150 in 5–6 series, pectinate-denticulate along upper margins. Florets c. 20–50; corollas bluish, lobes apically strigulose; anther base rounded; style base with annulus; sweeping hairs sharp. Achenes strongly 10-costate, setuliferous, costae often bordered with idioblasts, raphids subquadrate; pappus bristles persistent, outer short. Pollen lophate, emicropunctate. $n = 10$. Seven or more species, Africa.

277. *Neurolakis* Mattf.

Neurolakis Mattf., Bot. Jahrb. Syst. 59 Beibl. 133: 12 (1924).

Unbranched perennials; hairs stalked-L-shaped plus simple multiseptate. Heads 1 to few, terminal, large, pedunculate; involucral bracts c. 60, c. 4-seriate, subequal. Florets c. 50; corolla tube filiform, abruptly campanulate above; anther tails broad; style without node; nectary sheathing; sweeping hairs acicular. Achenes 10-ribbed, setuliferous, raphids elongate; pappus bristles c. 5, short, flattened, caducous. Pollen non-lophate. One species, *N. modesta* Mattf., Cameroon, Chad.

278. *Pleurocarpaea* Benth.

Pleurocarpaea Benth., Fl. Austral. 3: 460 (1867).

Perennials; hairs simple, submoniliform, rather L-shaped. Heads few, pedunculate; involucral bracts c. 12, 2–3-seriate; receptacle paleaceous. Florets 8–13; anther bases rounded; style without node; sweeping hairs acute. Achenes 10-grooved, furrows with hairs and glands, raphids lacking; pappus bristles few, short, deciduous, outer fimbriae persis-

tent. Pollen echinolophate, with polar lacuna. One species, *P. denticulata* Benth., northern Australia.

VI.14. Subtribe Gymnantheminae H. Rob. (1999).

Shrubs, vines or trees. Leaves alternate. Inner involucral bracts sometimes deciduous. Corolla lobes sometimes reflexed. Anther appendage indurate, glabrous; sweeping hairs often blunt. Pollen tricolporate, usually non-lophate. Characteristic sesquiterpenes: elemanolides and guaianolides.

Key to the Genera

1. Apomictic, with styles not or scarcely divided at tip, stigmatic tissue lacking; outer surfaces of style only with ends of surface cells protruding (prorulose) or with short spicules, without sweeping hairs; pollen with short spinules (Hawaii) **283. *Hesperomannia***
– Sexually reproducing plants with style branches well-developed; stigmatic tissue on whole inner surface of style branches; long sweeping hairs present; pollen with large spines or lophate with murae in well-developed reticulum 2
2. Pappus of many capillary or flattened bristles which are shorter than or only about as long as the body of the achene 3
– Pappus bristles or awns longer than bodies of achenes 4
3. Receptacles with pales **280. *Centauropsis***
– Receptacles without pales **286. *Oliganthes***
4. Heads with large, rounded, green, outer involucral bracts; pollen lophate with three intercolpar-aligned polar lacunae **285. *Myanmaria***
– Heads without large, rounded, green, outer involucral bracts; pollen often not lophate, without intercolpar-aligned polar lacunae 5
5. Subshrubs; pappus bristles broad and flat, multiseriate; achenes sericeous with long uniseriate hairs **284. *Lampropappus***
– Shrubs, trees or vines; pappus bristles capillary, sometimes slightly flattened, mostly in 1–2 series; achenes usually with short or biseriate setulae 6
6. Inflorescence pinnately branched, frondiform **279. *Brenandendron***
– Inflorescence not pinnate, not frondiform 7
7. Leaves often trinervate; corollas usually yellow; style base with large abrupt node **281. *Distephanus***
– Leaves pinnately veined; corollas not yellow; style base without node or with small gradually enlarged node **282. *Gymnanthemum***

Genera of Gymnantheminae

279. *Brenandendron* H. Rob.

Brenandendron H. Rob., Proc. Biol. Soc. Wash. 112: 244 (1999).

Trees; stems velutinous, hairs fusiform or contorted. Leaves large, sometimes lobed. Inflorescences frondiform, branchlets racemiform or spiciform. Involucral bracts to 110 in 7–9 series, innermost deciduous. Florets 30–50; anther bases long-tailed; style with node; sweeping hairs blunt-tipped. Achenes 8–10-costate, glabrous, with idioblasts, raphids short to moderately elongate; pappus capillary, subpersistent. $n = 9$. Three species, tropical western Africa, Congo, Central African Republic.

280. *Centauropsis* Bojer ex DC.

Centauropsis Bojer ex DC., Prodr. 5: 93 (1836).

Shrubs; stems lepidote or glabrous. Heads 1 to few, subsessile to long-pedunculate; involucral bracts 25–50, in 4–6 series, inner deciduous, sometimes appendaged; receptacle paleaceous. Florets 25–50+; corolla glabrous; anthers with broad tails; style without node; sweeping hairs subacute. Achenes 10- or 20-ribbed, glabrous, raphids elongate; pappus capillary, shorter than achene body. Eight species, Madagascar.

281. *Distephanus* Cass.

Distephanus Cass., Bull. Soc. Philom. Paris 1817: 151 (1817); Robinson & Kahn, Proc. Biol. Soc. Wash. 99: 493–301 (1986), emend., list.
Gongrothamnus Steetz (1862).
Newtonia O. Hoffm. (1892), non *Newtonia* Baill. (1888).
Antunesia O. Hoffm. (1873), nom. nov. for *Newtonia* O. Hoffm.

Shrubs, vines, or trees; hairs arachnoid, contorted, or asymmetrically T-shaped. Leaves often trinervate. Inflorescences terminal; involucral bracts 21–24(–75), 4–6(–7)-seriate. Florets 10–16(–75); corollas usually yellow, mostly glabrous; anther tails often sclerified; style node abruptly enlarged; sweeping hairs obtuse. Achenes (5–)10(–12)-ribbed, raphids elongate; pappus capillary, with squamellae, persistent. Pollen non-lophate or lophate. Forty or more species, Africa, Indian Ocean, India, south-western China.

282. *Gymnanthemum* Cass.

Gymnanthemum Cass., Bull. Soc. Philom. Paris 1817: 10 (1817).
Decaneurum DC. (1833), nom. illegit. superfl.
Monosis DC. in Wight (1834).
Vernonia Schreb. sect. *Strobocalyx* Blume ex DC. (1836).
Plectreca Raf. (1838) ("1836").

Strobocalyx (Blume ex DC.) Spach (1841).
Punduana Steetz (1864).

Shrubs or trees; stems often felted, hairs rarely asymmetrically T-shaped. Inflorescences densely corymbiform; involucral bracts 25–35, 4–5-seriate, inner bracts often deciduous. Florets 1–50; anther base broadly tailed; style usually with node; sweeping hairs pointed or blunt. Achenes 5–10-costate, raphids short, elongate or lacking; pappus bristles persistent, capillary, with squamellae. Pollen non-lophate or lophate. $n = 10, 20$, $2n = 20$, 30. More than 43 species, Africa, southern Asia, Indonesia.

New studies show that *Monosis* DC. in Wight (1834), with c. seven species, is a separate genus with obovate or oblanceolate leaves and lophate pollen. *Strobocalyx* (Bl. ex DC.) Spach should also be resurrected for various Asian and Malaysian species.

283. *Hesperomannia* A. Gray

Hesperomannia A. Gray, Proc. Amer. Acad. Arts 6: 554 (1865).

Mostly apomictic shrubs or trees; hairs matted plus some moniliform. Heads 2–10; involucral bracts c. 50 in 6–7 series. Florets c. 25; corollas yellow; anther tails long, blunt; apical appendages lanceolate; style without node, tip mostly undivided, prorulose. Achenes glabrous, without raphids; pappus capillary, longer than achene. Pollen minutely spiculiferous. Three species, Hawaii.

284. *Lampropappus* (O. Hoffm.) H. Rob.

Lampropappus (O. Hoffm.) H. Rob., Proc. Biol. Soc. Wash. 112: 245 (1999).
Vernonia Schreb. sect. *Lampropappus* O. Hoffm. (1896).
Vernonia Schreb. subsect. *Turbinellae* S.B. Jones (1981).

Subshrubs; stems tomentose, hairs with contorted cells. Leaves tomentose below. Inflorescences corymbiform. Involucral bracts c. 30, c. 4–5-seriate, broad. Florets c. 20; corollas actinomorphic or inner lobe longest; anther bases rounded; style with node; sweeping hairs obtuse. Achenes 5-costate, villous, hairs uniseriate, raphids mostly subquadrate; pappus setae 3-seriate, broad, flat. Three species, Angola, Congo, Malawi, Zambia.

285. *Myanmaria* H. Rob.

Myanmaria H. Rob., Proc. Biol. Soc. Wash. 112: 244 (1999).

Shrubs; hairs simple, multiseptate. Inflorescences corymbiform. Heads pedunculate; outer c. 20 involucral bracts broad, foliiform, 2–3-seriate; inner bracts linear. Florets 35–50; anthers broadly tailed; style without node; sweeping hairs obtuse. Achenes 10-costate, with idioblasts, costae setuliferous, raphids subquadrate; pappus bristles 2–3-seriate, persistent. Pollen echinolophate, with intercolparaligned polar lacunae. One species, *M. calycina* (DC.) H. Rob., Myanmar.

286. *Oliganthes* Cass.

Oliganthes Cass., Bull. Sci. Philom. Paris 1817: 10 (1817).
Vernonia Schreb. sect. *Trianthaea* DC. (1836).
Trianthaea (DC.) Spach (1841).

Shrubs or trees; stem hairs simple, lacking, or T-shaped with contorted cap-cells. Inflorescences corymbiform. Involucral bracts 20–40, 4–6-seriate, sometimes appendaged. Florets 3–150; corolla throat half as long as lobes; anther base plain or short-appendaged; style without node; sweeping hairs acute, few septa. Achenes 10–15-costate, glabrous, raphids subquadrate; pappus bristles flattened, deciduous, fimbriate corona often present. Nine species, Madagascar.

VI.15. Subtribe Trichospirinae Less. (1831).

Creeping herbs. Vegetative leaves alternate, in inflorescence subopposite. Achenes strongly compressed, cuneate, bicornute distally, small awns around corolla base, spiculiferous on surface. Pollen tricolporate, non-lophate.

Only one genus:

287. *Trichospira* Kunth

Trichospira Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Pl., ed. folio 4: 21 (1818).

Perennials; hairs simple, arachnoid. Leaves sessile, tomentose below. Heads axillary, sessile. Involucral bracts c. 12, subequal, receptacle with few pales. Florets c. 10; corollas 4-lobed; anthers with spurs short; style without node; sweeping hairs acute, often septate. Achenes with 2 marginal ribs and 2 or 3 weaker ones on surfaces, raphids lacking. One species, *T. verticillata* (L.) S.F. Blake, tropical America.

VII. Tribe Liabeae (Cass. ex Dumort.) Rydb. (1927).

V.A. Funk, H. Robinson and M.O. Dillon

Mostly perennial herbs or shrubs, sometimes scandent, some annuals or small trees; latex usually present; hairs simple; usually white tomentose on stems and on abaxial surfaces of leaves, sometimes only on tips of involucral bracts, elsewhere sometimes pilose or strigose with stiff hairs. Leaves opposite, sometimes in a rosette, usually petiolate or with a petioliform base, rarely sessile; leaf bases often with pseudostipules or nodal disc, sometimes fused into sheath; leaf blades linear to broadly triangular, ovate, oblanceolate, or elliptical; venation trinervate, pinnate, or palmate. Inflorescences simple or subcymose, sometimes forming a thrysoid panicle (rarely sessile). Heads usually on short to long peduncles; involucre usually subimbricate with bracts in many gradate series; receptacle alveolate, often with projecting crests or points, rarely paleaceous. Ray florets usually present, usually yellow, occasionally reddish to purple or white, 3–c. 320, fertile; limb present, usually linear to elliptic-oblong; style branches elongate, sometimes spiralled. Disc florets usually yellow, rarely red, purple or white, 3–c. 150, perfect, tube or lower throat pilosulous or glandular, lobes elongate, usually linear; anther collars mostly with short-oblong cells; thecae usually pale, blackened in subtribe Munnoziinae; bases calcarate, sometimes tailed and fringed or digitate; apical appendage thin, flat, usually longer than wide, not constricted at base. Pollen spherical, 25–50 µm in diameter in fluid, tricolporate, echinate, spines regularly to somewhat irregularly arranged, never lophate, the bacula tubular or in circle under spines, sometimes reduced and grains caveate (Fig. 41). Style base glabrous, usually enlarged; upper style shaft and backs of branches with sweeping hairs; branches with stigmatic papillae over entire inside surface, with little or no appendage, branches usually shorter than hairy upper style shaft. Cypselae usually prismatic or subterete, with 5–10 ribs, less often 4- or 2-ribbed; variously with biseriate setulae, uniseriate hairs, stipitate glands or glandular dots; pappus usually with numerous long inner capillary bristles and short outer series of squamellae, sometimes with scales or plumose bristles or absent. Chromosome numbers known from 12 genera, base numbers $x = 7, 9, 10, 12, 14, 16$ and 18 (Robinson et al. 1985). A tribal base number of $x = 9$ was most probable from the data cited by Turner et al. (1967), and was proposed by Robinson et al. (1985).

Tribe Liabeae contains approximately 190 species arranged in 16 genera, and is distributed in the montane Neotropics at 50–4,750 m elevation. The greatest generic and species concentration is in western South America; 13 of the 16 genera occur in northern Peru. Most species of Liabeae are found in open areas in mid-elevation forests. A few species in several genera are found in disturbed habitats associated with rivers, roadcuts or treefalls. More rarely, species occupy seasonally dry scrub or desert habitats. A few members are found in essentially alpine habitats well above forested zones, including subparamo, paramo, jalca and puna (> 3,000 m).

Obvious features shared by many but not all members of Liabeae include leaves which are opposite, often strongly trinervate with tomentose undersurfaces, yellow ray and disc florets, and the frequent occurrence of latex. The tribe shares the deeply lobed disc corollas, long-spurred or calcarate anther bases, continuous stigmatic surfaces on the inside of the style branches, and spherical spinose pollen characteristic of members of subfamily Cichorioideae along with Cichorieae, Vernonieae and Arctotideae (Robinson and Funk 1987; Jansen et al. 1991; Bremer 1994). Although

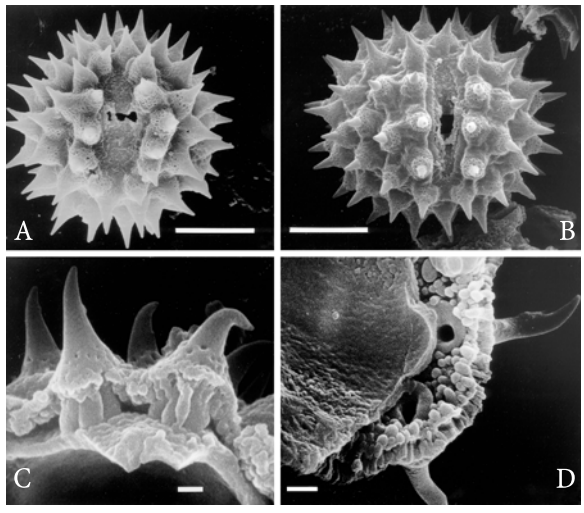

Fig. 41. Compositae-Liabeae. SEM micrographs of pollen grains. **A**, **B** Whole grains. **A** *Microliabum humile*. Form with unevenly disposed spines. **B** *Chrysactinium acaule*. Form with evenly disposed spines. **C**, **D** Broken grains. **C** *Dillandia perfoliata*. Bacula grouped under spines. **D** *Munnozia tenera*. Base of spine fused into cylinder. Scale bars: **A**, **B** = 10 µm, **C**, **D** = 1 µm

monophyly of the subfamily is in doubt, Liabeae, Vernonieae, Cichorieae and Arctotideae appear to form a monophyletic group within the subfamily, and the sister group of Liabeae can be found in one of these tribes (Robinson and Funk 1987; Kim et al. 2003). These four tribes have long sweeping hairs which cover the outer surface of the style branches and the upper style shaft. Latex is found in at least some genera of Cichorieae, Arctotideae and Liabeae, but it is rarely noted for Vernonieae. Cichorieae and Vernonieae have homogamous heads without rays, while presence of rays seems plesiomorphic in Liabeae and Arctotideae. Lophate pollen and bluish florets are common in Cichorieae and Vernonieae, both are lacking in Liabeae and Arctotideae lacks the bluish florets. The history of the classification of Liabeae reflects the difficulty in tribal placement encountered by early workers. Cassini (1823, 1825, 1830), Lessing (1832), de Candolle (1836), Weddell (1855–1857), and Bentham (1873a) all variously treated groups of taxa which are now placed in this tribe as members of Vernonieae, Heliantheae, Helenieae, Senecioneae and Mutisieae. Bentham's classification, which placed most of the taxa in one genus, *Liabum*, in tribe Senecioneae, was essentially adopted by Hoffmann (1894). Rydberg (1927) was the first to propose tribal status for the genera from the North American Flora area. However, despite his work which recognized genera from Mexico, Central America and the West Indies, and isolated works by Blake (1935), Cabrera (1954), and Sandwith (1956), who recognized the affinities of other genera to Liabeae, Bentham's classification was retained more or less intact and accepted by many modern floristic and taxonomic workers (Cronquist 1955; D'Arcy 1975; Carlquist 1976). Nash and Williams (1976) accepted Bentham's concept of a single genus, but they placed the genus in Vernonieae. Robinson and co-workers published a series of papers bringing the genera together into one tribe (Robinson and Brettell 1973a, 1974; Robinson 1983a with included additional references). Nordenstam (1977) followed Robinson's tribal circumscription in a tribe separate from Senecioneae. Robinson (1983a) provided the first modern view of the whole tribe, including a detailed review of previous classification efforts and relevant literature. Since the review of Robinson (1983a), there have been several significant changes in generic limits in the tribe. Two new genera have been described from northern Peru, *Dillandia* (Funk and Robinson 2001) and *Bishopanthus* (Robinson 1983b); *Austroliabum* has been reduced to synonymy under *Microliabum* (Robinson 1990b); and *Liabellum* has been placed into synonymy with *Sinclairia* (Turner 1989) and then resurrected (Robinson 1990a).

Key to the Genera

1. Abaxial surfaces of leaves green, without tomentum; leaves and stems with stiff hairs with enlarged bases 2
– Abaxial surfaces of leaves covered with dense white or grey tomentum; leaves and stems without stiff hairs with enlarged bases 3
2. Coarse perennial herbs, subshrubs, shrubs, or small trees; leaves with 5–9 palmately arranged veins; cypselae 4-sided with 4 ribs **301. *Erato***
– Small erect, decumbent, or creeping herbs; leaves 3-nervate; cypselae compressed with 2 ribs **303. *Philoglossa***
3. Anther thecae dark brown or black 4
– Anther thecae pale yellow or very light brown 5
4. Pappus white; small herbaceous perennials; leaves in a rosette or grouped close together on a short stem **300. *Chrysactinium***
– Pappus sordid or reddish; usually lax subshrubs, sometimes annual or perennial herbs; leaves cauline **302. *Munnozia***
5. Heads sessile, subtended by a rosette of leaves or nearly sessile with peduncles of less than 2 cm long **298. *Paranephelius***
– Heads on peduncles more than 2 cm long 6
6. Leaves pinnately veined 7
– Leaves 3-nervate 10
7. Herbs; heads few; disc florets 10–55; leaves sessile, subperfoliate or perfoliate 8
– Trees, shrubs, or vines; heads many; disc florets 3–34; leaves usually with distinct unwinged to broadly winged petioles 9
8. Adaxial surfaces of leaves rugose to nearly smooth; corollas reddish-orange to red; involucral bracts eximbricate, linear-lanceolate with attenuate tips **299. *Pseudonoseris***
– Adaxial surfaces of leaves bullate; corollas yellow to yellow and purple; involucral bracts subimbricate, lanceolate with acute tips **291. *Dillandia***
9. Trees or shrubs; petioles without wings, bases of petiole pairs fused into a sheath; raphids of cypsela wall elongate **292. *Ferreyranthus***
– Vines or shrubs; petioles with or without wings, sometimes included in perfoliate leaf base but not fused into a sheath; raphids of cypsela wall subquadrate **296. *Oligactis***
10. Pappus lacking **289. *Cacosmia***
– Pappus of bristles, awns and/or squamellae 11
11. Pappus of plumose bristles; disc corollas red **290. *Chionopappus***
– Pappus of capillary bristles, awns and/or squamellae; all corollas yellow 12
12. Heads terminal and solitary on leafy stems; leaf bases fused into a sheath **288. *Bishopanthus***
– Heads few to many but not solitary; leaf bases without a sheath 13

13. Inflorescences with all branches alternate; receptacle scarcely alveolate, without hairs, squamellae or projections; Argentina and Bolivia **295. *Microliabum***
– Inflorescences with at least basal branches opposite; receptacles with hairs, squamellae or projections; Bolivia northwards to Mexico 14
14. Plants without latex; style branches of disc florets longer than hispidulous part of distal style shaft; anther bases digitate; rays 20–120; involucral bracts 50–150 in 5 series; raphids of cypsela walls subquadrate **294. *Liabum***
– Plants with latex; style branches of disc florets shorter than hispidulous part of distal style shaft; anther bases minutely crenulate; rays usually absent or when present 4–25; raphids of cypsela walls elongate 15
15. Herbs; rays always absent; leaf blades shallowly to deeply lobed; petioles winged to base, sometimes perfoliate; disc florets 25–30; inner pappus of 40–50 capillary bristles, outer of 20–40 squamellae **293. *Liabellum***
– Shrubs or vines; rays usually present (absent in a few species); leaf blades entire or serrate; petiole bases simple, not winged and without pseudostipules; disc florets 5–30; inner pappus of 30–40 bristles, outer of 10–15 squamellae **297. *Sinclairia***

VII.1. Subtribe Liabinae Cass. ex Dumort. (1829).

Plants perennial; with or without latex; leaves opposite, stems or leaf undersides always tomentose; anther thecae pale, usually tailed and fringed or digitate at base; florets usually yellow, rarely red or purple; style branches usually shorter than hairy upper shaft; cypselae prismatic or subterete. Pollen spines unevenly grouped.

288. *Bishopanthus* H. Rob.

Bishopanthus H. Rob., Phytologia 54: 64 (1983).

Shrub; with latex. Leaf bases fused into sheath; blades 3-nervate, bullate. Heads solitary, pedunculate, campanulate; involucral bracts c. 25, in 2 subequal series; epaleaceous. Ray florets c. 20; limbs linear. Disc florets c. 25; bases of anther thecae short-tailed, short-fringed. Cypselae with setulae, uniseriate hairs, and glands, raphids subquadrate; pappus bristles c. 35, with short outer bristles. One species, *B. soliceps* H. Rob., Peru.

289. *Cacosmia* Kunth

Cacosmia Kunth in H.B.K., Nov. Gen. et Sp., ed. folio 4: 227 (1818); Nordenstam, Bot. Notiser 130: 279–286 (1977), rev.; Robinson, Fl. Ecuador 190, 2: 1–63 (1978), reg. rev.
Clairvillea DC. (1836).

Shrub; usually with latex; stems densely pubescent. Leaf bases fused into sheath; blades 3–5-nervate, bullate. Inflorescence densely corymbiform; heads cylindrical; involucral bracts 20–25, 5–6-seriate, outer bracts ranked, inner bracts not in ranks; receptacle epaleaceous. Ray florets 5, limbs broad. Disc florets 5–6; bases of anther thecae without tails, minutely digitate. Cypselae 3–5-angled, glabrous, raphids elongate; pappus lacking. $n = 7 + 1$ or 2. Three species in Ecuador, one into Peru.

290. *Chionopappus* Benth.

Chionopappus Benth. in Benth. & Hook. f., Gen. Pl. 2: 485 (1873).

Shrubs; latex not noted; stems arachnoid-tomentose. Leaf bases fused into sheath, blades 3-nervate. Inflorescences simple dichasia; heads campanulate; involucral bracts 50–55, c. 5-seriate; paleae strap-shaped. Ray florets c. 40. Disc florets 75–125; corollas red, glabrous; bases of anther thecae short-tailed. Cypsela 8–10-ribbed, setulae minute, raphids elongate; pappus bristles 8–10, plumose. n = c. 9. One species, *C. benthamii* S.F. Blake, Peru.

291. *Dillandia* V.A. Funk & H. Rob.

Dillandia V.A. Funk & H. Rob., Syst. Bot. 26: 218 (2001).

Moderate-sized to small herbs less than 60 cm tall; latex not noted; stems arachnoid-tomentose. Leaf bases sessile, subpetiolate or perfoliate; surface bullate; blades pinnately veined. Inflorescences of 1–2 heads or, more frequently, a 3–7-headed subumbel; heads campanulate, involucral bracts 25–40, 5–6-seriate; receptacle without chaff. Ray florets 15–40, limbs oblong to narrowly oblong. Disc florets 10–30, corollas yellow to yellow and purple, tubes pilose, anther thecae pale, bases rounded. Cypselae (immature) 7–10-ribbed, densely setulose, with a few subquadrate raphids; pappus bristles 10–30, sometimes shorter outer bristles. Three species, Peru.

292. *Ferreyranthus* H. Rob. & Brettell

Ferreyranthus H. Rob. & Brettell, Phytologia 28: 50 (1974); Dillon & Sagastegui, Arnaldoa 2: 7–23 (1994), rev.; Robinson, Fl. Ecuador 190, 2: 1–63 (1978), reg. rev.

Shrubs or weak trees; without latex; stems arachnoid-tomentose. Leaf bases fused into sheath; blades pinnately veined. Inflorescences densely corymbiform; heads broadly campanulate; involucral bracts 45–55, c. 5-seriate; receptacle squamuliferous. Ray florets 8–12, limbs short.

Disc florets 12–25, corollas glandular-dotted; bases of anther thecae short-tailed, strongly fringed. Cypselae c. 10-ribbed, with setulae and glands, raphids elongate; pappus bristles 10–15, squamellae narrow. n = c. 18. Eight species, Peru, one into Ecuador.

293. *Liabellum* Rydb.

Liabellum Rydb., N. Amer. Fl. 34, 4: 294 (1927).

Small xylopodial herbs; with latex; stems short, arachnoid-tomentose. Leaf bases perfoliate, sessile, blades scarcely to deeply lobed, 3-nervate. Heads terminal, 1–3 on elongate peduncles, broadly campanulate; involucral bracts 20–40, c. 4-seriate; receptacle sometimes puberulous. Rays lacking. Disc florets 25–30; bases of anther thecae scarcely crenulate. Cypsela c. 10-ribbed, setulae long, raphids elongate; pappus bristles 40–50, squamiform setae 20–40. Five species, Mexico.

294. *Liabum* Adans.

Liabum Adans., Fam. 2: 131 (1763); Robinson, Fl. Ecuador 190, 2: 1–63 (1978), reg. rev.
Starkea Willd. (1803).
Andromachia Humb. & Bonpl. (1809).
Allendea La Llave & Lex. (1824).

Perennial herbs; without latex; stems arachnoid-tomentose. Leaf bases connected across node, often forming nodal disc; blades 3-nervate. Inflorescence partly subumbellate; heads broadly campanulate; involucral bracts 50–150, c. 5-seriate; receptacle ridged or bristly. Ray florets 20–120. Disc florets 10–85; style branches long; anther thecae bases digitate. Cypselae c. 10-ribbed, raphids subquadrate; pappus bristles 17–40, squamellae short, narrow. n = c. 12 to 39, many counts are c. 18. Forty-five species, Mexico, Central America, Greater Antilles, and Andes of South America.

295. *Microliabum* Cabrera

Microliabum Cabrera, Bol. Soc. Argent. Bot. 5: 211 (1955), nom. nov. for *Liabellum* Cabrera
Liabellum Cabrera (1954), non *Liabellum* Rydb. (1927).
Angelianthus H. Rob. & Brettell (1974), nom. nov. illegit. superfl. for *Liabellum* Cabrera
Austroliabum H. Rob. & Brettell (1974).

Annual to perennial herbs or subshrubs; with latex; stems white-tomentose and glandular-hairy. Leaf bases broadened or with pseudostipules or nodal discs; blades 3-nervate. Heads solitary or in cymes, broadly campanulate; involucral bracts 30–75, 2–4-seriate, subequal to gradate; receptacle epaleaceous. Rays 10–30; limbs narrowly elliptical to linear. Disc florets 15–175; bases of anther thecae with few or no teeth. Cypselae 8–10-ribbed, setuliferous, raphids elongate; pappus bristles or lamellae 8–16, outer squamellae 8–16. Six species, southern Bolivia, northern Argentina.

296. *Oligactis* (Kunth) Cass.

Oligactis (Kunth) Cass., Dict. Sci. Nat. 36: 16 (1825); Robinson, Fl. Ecuador 190, 2: 1–63 (1978), reg. rev.
Andromachia sect. *Oligactis* Kunth (1818).

Shrubs and vines, without latex. Leaf bases sometimes confluent across nodes; blades pinnately veined. Inflorescence densely corymbiform; heads narrowly to broadly campanulate; involucral bracts 16–55, 4–5-seriate; receptacle ridged and squamuliferous. Ray florets 3–18, limbs short. Disc florets 3–34; style branches rather long; anther thecae bases digitate. Cypselae 5–8-ribbed, with glands and contorted setulae, raphids subquadrate; pappus bristles 20–35, tips often broad, squamellae 7–10. n = 18, 39. Fifteen species, mostly northern Andes, one to Costa Rica.

297. *Sinclairia* Hook. & Arn.

Sinclairia Hook. & Arn., Bot. Beech. Voy. 433 (1841).
Megaliabum Rydb. (1927).
Sinclairiopsis Rydb. (1927).

Subshrubs, shrubs or vines; with latex; stems arachnoid-tomentose. Leaves opposite or ternate, sometimes seasonally deciduous, bases without sheaths or pseudostipules; blades 3-nervate. Inflorescences laxly to densely corymbiform or pyramidal; heads narrowly to broadly campanulate; involucral bracts 18–45, 3–5-seriate; receptacle glabrous, spinulose or puberulous. Ray florets absent or 4–25. Disc florets 5–30; anther thecae bases minutely crenulate. Cypselae c. 8–10-ribbed, glabrous or setuliferous, raphids elongate; pappus bristles 30–40, squamellae 15–20. n = 15 to 18. Thirty species, Mexico, Central America, one to western Colombia.

VII.2. Subtribe Paranepheliinae H. Rob. (1983).

Plants rosettiform or short-stemmed, fibrous-rooted, usually with latex; roots often swollen and fleshy; leaves often pinnately lobed, undersurface

with white tomentum; involucre gradate; ray floret limbs linear; disc corollas funnelform, tubes 2–3 times as long as lobes; thecae pale, base not tailed nor noticeably lobed; style branches longer than scabrid upper style shaft; cypselae prismatic or fusiform, raphids elongate. Pollen spines mostly evenly dispersed.

298. *Paranephelius* Poepp.

Paranephelius Poepp., Nov. Gen. et Sp. 3: 42 (1843); Robinson, Fl. Ecuador 190, 2: 1–63 (1978), reg. rev.
Liabum sect. *Paranephelius* (Poepp.) Benth. in Benth. and Hook. f. (1873).

Acaulescent perennial herbs. Leaf bases not sheathing; blades trinervate to pinnately veined. Heads sessile, broadly campanulate; involucral bracts 40–50, c. 4-seriate; receptacle ridged. Ray florets 20–35; style branches spiralled. Disc florets 20–33. Cypsela c. 10-ribbed, glabrous or with some arachnoid hairs; pappus bristles 45–80, outer series indistinct. n = 9, 14, 15. Seven species, Peru, Bolivia, one to northern Argentina.

299. *Pseudonoseris* H. Rob. & Brettell

Pseudonoseris H. Rob. & Brettell, Phytologia 28: 59 (1974).

Small perennial herbs. Leaf bases sessile, subauriculate; blades pinnately veined. Inflorescence scapose or subscapose; heads pedunculate, broadly campanulate; involucral bracts c. 40, c. 4-seriate; receptacle subglabrous. Ray florets yellow or yellow-orange, 15–20. Disc florets orange-yellow or red, 25–55. Cypselae c. 10-ribbed, with sparse setulae or tomentum; pappus bristles 25–30, squamiform outer series. n = 12(?). Three species, Peru.

VII.3. Subtribe Munnoziinae H. Rob. (1983).

Plants usually with latex; heads often long-pedunculate; ray floret limbs linear; disc corolla throat broadened at base; thecae black, base not tailed nor noticeably lobed; style branches much shorter than hairy upper style shaft, blunt; cypselae prismatic to biconvex, raphids subquadrate. Pollen spines evenly dispersed.

300. *Chrysactinium* (Kunth) Wedd. Fig. 42

Chrysactinium (Kunth) Wedd., Chlor. And. 1: 212 (1857); Robinson, Fl. Ecuador 190, 2: 1–63 (1978), reg. rev.; Funk & Zermoglia, Syst. Bot. 24: 323–338 (1999), rev.
Andromachia sect. *Chrysactinium* Kunth (1818).

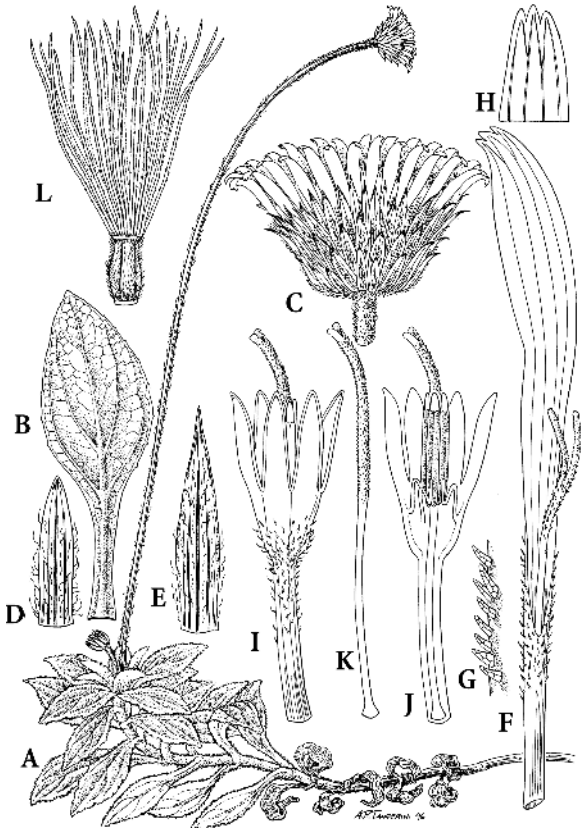

Fig. 42. Compositae-Liabeae. *Chrysactinium wurdackii*. **A** Habit, note opposite leaves. **B** Leaf, note tomentose undersurface. **C** Head, note heterogamous heads. **D** Outer involucral bract. **E** Inner involucral bract. **F** Ray floret corolla and style. **G** Hairs on tube of ray floret. **H** Apex of ray corolla. **I, J** Disc corolla, note continuous stigmatic surface on inside of style branches, calcarate anther bases, and deeply divided corolla. **K** Style of disc floret. **L** Cypsela and pappus. (Drawing by A. Tangerini)

Perennial rhizomatous herbs, rosettiform or short-stemmed; stems evanescent-tomentose. Leaf bases cuneate or petioliform; blade 3-nervate, tomentose. Heads solitary, long-pedunculate, broadly campanulate; involucral bracts 40–60, 4–5-seriate; receptacle squamulose. Ray florets 30–60. Disc florets 30–60; anther collar cells annulate. Cypselae 8–10-ribbed; pappus bristles 30–60, white, no squamellae. n = 12 to 16. Six species, Ecuador, northern Peru.

301. *Erato* DC.

Erato DC., Prodr. 5: 318 (1836); Robinson, Fl. Ecuador 190, 2: 1–63 (1978), reg. rev.
Munnozia subg. *Erato* (DC.) H. Rob. & Brettell (1974).

Coarse perennial herbs; stems and leaves pilose or strigose. Leaves with oblong pseudostipules; blades palmately 5–9-veined, surfaces green. Inflorescence cymose to subumbellate; heads broadly campanulate; involucral bracts 40–100, c. 4-seriate, tips sometimes tomentose; receptacle foveolate and ridged. Ray florets 75–230. Disc florets 20–150. Cypselae 4-ribbed, glabrous or hispidulous; pappus of 25–50 bristles or short awns, no outer series. $n = 9$. Five species, Costa Rica to Peru.

302. *Munnozia* Ruiz & Pav.

Munnozia Ruiz & Pav., Fl. Peru Chil. Prodr. 108 (1794); Robinson, Fl. Ecuador 190, 2: 1–63 (1978), reg. rev.
Alibum Less. (1832).
Prionolepis Poepp. (1845).
Kastnera Sch. Bip. (1853).
Liabum subg. *Chrysastrum* Willd. ex Sch. Bip. (1853).
Munnozia subg. *Kastnera* (Sch. Bip.) H. Rob. & Brettell (1974).

Annual or perennial herbs or subshrubs. Petioles sometimes winged, bases often pseudostipulate; blades 3-nervate to pinnately veined, usually tomentose abaxially. Inflorescence terminal, more or less corymbose; heads broadly campanulate; involucral bracts 17–70, 2–4-seriate, subequal to gradate; receptacle often squamulose. Florets yellow, rarely whitish to lavender. Ray florets 6–70. Disc florets 9–85. Cypselae 6–10-ribbed, setuliferous; pappus bristles sordid to reddish, 5–55, with squamellae. $n = 12$ to 36, most frequently 10, 11 and 12. Forty-six species, mostly from the Andes, few in Costa Rica, Panama.

303. *Philoglossa* DC.

Philoglossa DC., Prodr. 5: 567 (1836); Robinson, Fl. Ecuador 190, 2: 1–63 (1978), reg. rev.

Small erect to creeping herbs; stems and leaves pilose to strigose. Leaf bases with oblong pseudostipules; blades 3-nervate, surfaces green. Involucres broadly campanulate; bracts 20–30, 3–4-seriate, subequal to gradate. Ray florets 21–70. Disc florets 30–60, yellow, rarely deep purple or brown. Cypselae compressed, 2-ribbed, mostly glabrous; pappus deciduous squamellae or awns, or lacking. $n = 18$. Five species, southern Colombia to Bolivia.

VIII. Tribe Cichorieae Lam. & DC. (1806).

Tribe Lactuceae Cass. (1819).

H.W. Lack

Perennial to annual herbs, rarely subshrubs, shrubs or rosette trees, very rarely scandent vines, characterized by ligulate capitula and abundant milky latex. Leaves mostly alternate, entire, lobed to pinnatisect, very rarely spiny. Involucral bracts imbricate in several series or equal and in a single row. Capitula always ligulate and homogamous, solitary or aggregated in synflorescences, sometimes in secondary heads. Involucral bracts various, receptacle mostly epaleate and naked, rarely scaly-bristly or paleate. All florets with a 5-lobed ligule, perfect, of various colours although predominantly yellow. Anthers basally calcarate and caudate, apical appendage elongate and obtuse, filaments smooth. Pollen echinolophate or echinate. Style slender, mostly with long, slender branches, hairs on the shaft and the branches. Achenes and pappus of various forms.

About 86 genera in 12 subtribes, number of species differing widely due to different views on their circumscription, in particular in *Hieracium*, *Pilosella* and *Taraxacum*. Excluding the latter three genera, the tribe contains c. 1,500 species. A predominantly northern hemisphere tribe but found on all continents, with comparatively few strictly tropical species, the latter as a rule in open habitats. Most taxa occur in rather dry to somewhat humid areas, and are almost absent from aquatic habitats. The tribe comprises many widespread, successful and noxious weeds, in particular species of *Chondrilla*, *Crepis*, *Hypochaeris*, *Sonchus*, *Taraxacum* and *Youngia*. In addition, numerous species have become naturalized in areas very far from their native habitats, e.g. European *Sonchus arvensis* on Fiji, and Mediterranean *Crepis pusilla* in southern Australia.

A group notoriously poor in diagnostic characters, with convergent evolution having led to very similar forms in different genera. This applies in particular to the indumentum, with glabrous forms in several groups, the achene, with heteromorphic fruits in a few subtribes, and the pappus, which has been reduced or lost in several groups.

Knowledge of the tribe is extremely unbalanced. Very limited information is available on several genera from central, eastern and south-eastern Asia, whereas the European,

Mediterranean and North American groups have been well studied. Recently described, enigmatic genera include *Faberiopsis*, *Phitosia* and *Spiroseris*. The position of *Thamnoseris*, an endemic of the Desaventuradas Islands off the coast of South America, may be outside the Cichorieae.

Recent molecular studies have brought significant new insights into the systematic relationships of the tribe (e.g. Kim et al. 1999a, b, on Sonchinae), and indicate the need for a completely new view of the group. Certain taxonomic conclusions from these studies have been cautiously integrated into the present treatment, mostly referring to Lactucinae, Sonchinae and the former Dendroseridinae. The recent studies by Chinese workers, in particular on Lactucinae, have also been considered in this account, although they are exclusively based on classical morphology and almost no herbarium material was available to the author for comparison. The circumscription of Lactucinae is still incompletely understood, and is based tentatively on achene characters here.

Very many publications on the taxonomy of Cichorieae are available (Babcock and Stebbins 1943; Stebbins 1953; Carlquist 1960; Jeffrey 1966; Sell 1975; Tomb 1976, 1977; Blackmore 1981, 1982; Voytenko 1989b; Bremer 1993, 1994; Whitton et al. 1995; Blackmore and Persson 1996; Reveal 1997; Tegel 2002; Lee et al. 2003) but no synthetic approach on a global level has been achieved so far. The circumscription of subtribes and genera differs widely in quality and precision, with several genera in Crepidinae and Lactucinae being very vaguely delimited.

Key to the Subtribes[7]

1. Stems winged, resin ducts and latex canals always present **1. *Scolyminae*** (p. 182)
– Stems never winged, only latex canals present 2
2. Florets blue, pappus of minute, irregularly shaped, round to acute scales or absent **2. *Cichoriinae*** (p. 182)
– Florets mostly yellow, sometimes violet, pink or white; if blue, then pappus neither of minute, irregularly shaped, round to acute scales nor absent 3
3. Pappus of very few broad, lanceolate scales, receptacle mostly setose **3. *Catananchinae*** (p. 182)
– Pappus of various forms or absent, but never of only very few broad, lanceolate scales, receptacle very rarely setose 4
4. Pappus in all achenes absent 5
– Pappus at least in central achenes well developed 16
5. Florets white **361. *Atrichoseris***
– Florets of various colours but not white 6
6. Involucral bracts in a single row, basally fused 7
– Involucral bracts almost never in a single row, never basally fused 8
7. Outer achenes with strong hooks or glochids **385. *Koelpinia***
– Outer achenes without strong hooks or glochids **349. *Phalacroseris***
8. Outer achenes stellately patent **381. *Rhagadiolus***
– Outer achenes not stellately patent 9
9. Inner bracts becoming hard and woody in fruit 10
– Inner bracts not becoming hard and woody in fruit 11
10. Inner bracts becoming connate in fruit **309. *Acanthocephalus***
– Inner bracts not becoming connate in fruit **315. *Heteracia epapposa***
11. Achenes deeply furrowed 12
– Achenes not deeply furrowed 13
12. Densely hirsute plant with very long hairs **368. *Hispidella***
– Plants without indumentum **347. *Krigia cespitosa***
13. Branched herbs 14
– Scapose plants 15
14. Achenes apically with two horns **321. *Lapsanastrum***
– Achenes apically without appendages **320. *Lapsana***
15. Perennial plant, rosette of deeply dentate leaves **372. *Aposeris***
– Annual plant, rosette of spathulate leaves **373. *Arnoseris***
16. Inner achenes apically with crown-like structure **374. *Garhadiolus***
– Inner achenes apically different 17
17. At least some pappus setae thick, sometimes with long lateral pinnulae 24
– All pappus setae slender, denticulate or barbellate, but never with long lateral pinnulae 18
18. Pappus comprising very thin, flexible rays **6. Sonchinae** (p. 189)
– Pappus never comprising very thin flexible rays 19
19. Pollen distinctly orange, New World **7. Microseridinae** p.p. (p. 191)
– Pollen never orange, predominantly Old World 20
20. Pappus barbellate or of five rigid awns and slender setae 21
– Pappus not barbellate, always homogenous 22
21. Mostly annual herbs, receptacle paleate or scaly, heads with numerous florets **9. Malacothricinae** p.p. (p. 193)
– Mostly perennial herbs, receptacle naked, heads with few florets **8. Stephanomeriinae** p.p. (p. 192)
22. Achenes basally constricted into a small, smooth annulus, achenes often compressed **5. Lactucinae** (p. 187)

[7] Previous workers (e.g. Stebbins 1953; Jeffrey 1966; Bremer 1993) have refrained from providing a key to the subtribes of Cichorieae, basically for two reasons: (1) the philosophy to place a taxon 'nearest to those genera which it most nearly resembles in respect to the largest number of characteristics' (Stebbins 1953), which has traditionally been applied to Cichorieae, does not easily lead to a clear and workable key; (2) the pappus – 'the most useful single character for subdividing the tribe' (Stebbins 1953) and 'of cardinal value' (Bremer 1994) – has undergone very many transformations, including repeated losses in several subtribes.

– Achenes basally never constricted, rarely compressed 23
23. Plants often with small, soft, branched hairs, pappus setae brittle **10. Hieraciinae** p.p. (p. 194)
– Plants without small, soft, branched hairs, pappus setae non-brittle **4. Crepidinae** p.p. (p. 183)
24. Pappus of bristle-tipped, awn-like scales **348. *Microseris***
– Pappus of setae, the latter barbellate or with long side projections 25
25. Pappus setae truly feather-like or barbellate, New World 26
– Pappus setae mostly with side projections pointing in various directions, Old World 27
26. Mostly perennial herbs, receptacle naked, heads with very few florets **8. Stephanomeriinae** p.p. (p. 192)
– Mostly annual herbs, receptacle paleate or scaly, heads with numerous florets **9. Malacothricinae** p.p. (p. 193)
27. Pappus rays with stiff lateral side projections consisting of a single, giant tubular cell, plant often with coarse indumentum of large hairs **11. Hypochaeridinae** p.p. (p. 195)
– Pappus rays with soft lateral side projections consisting of a row of flattened cells (pappus woolly), plants with soft indumentum of small hairs **12. Scorzonerinae** p.p. (p. 198)

VIII.1. Subtribe Scolyminae Less. (1832).

Very spiny thistle-like herbs with winged stems, resin ducts and latex canals. Exclusively Old World subtribe, comprising a single genus.

304. *Scolymus* L.

Scolymus L., Sp. Pl. 813 (1753); Vazquez, Anales Jard. Bot. Madrid 58: 83–100 (2000), rev.

Annual to perennial herbs, very spiny with winged stems, receptacle paleate, paleae broadly winged and deciduous, enclosing the dorsiventrally compressed achenes, florets yellow, pappus of stiff scabrous bristles or absent. $x = 10$, diploids. Three species, Macaronesia, Mediterranean area.

VIII.2. Subtribe Cichoriinae Cass. ex Dumort. (1829) s. str.

Florets blue, pappus of minute, irregularly shaped, round to acute scales or absent. Exclusively Old World subtribe, comprising a single genus.

305. *Cichorium* L. Fig. 43

Cichorium L., Sp. Pl. 813 (1753); Wagenitz & Bedarff, Davis & Hedge Festschr.: 11–21 (1989), rev.; Kiers et al., Syst. Bot. 24: 645–659 (1999); Kiers, Gorteria suppl. 5: 1–77 (2001), mol. phylog.

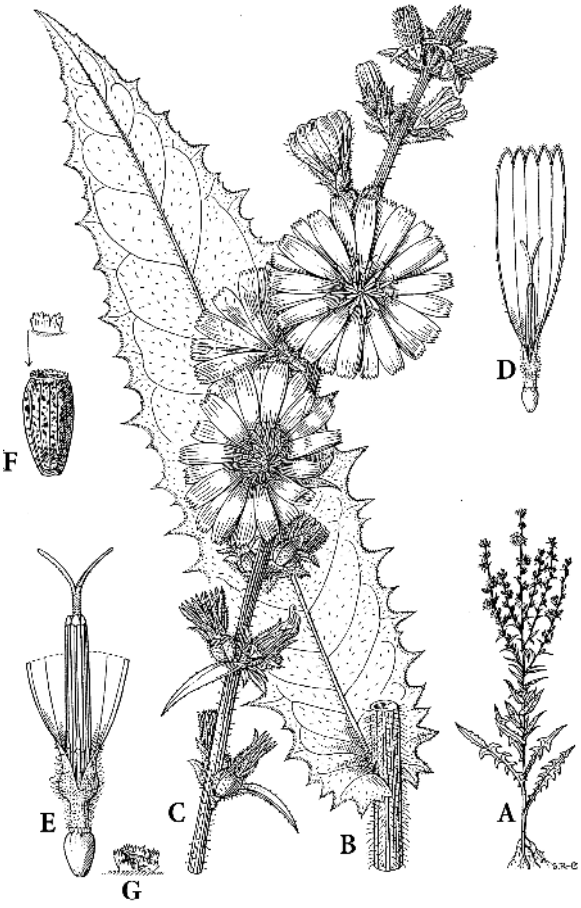

Fig. 43. Compositae-Cichorieae. *Cichorium intybus*. **A** Habit. **B** Middle cauline leaf. **C** Upper part of flowering branch. **D** Floret. **E** Floret, upper part of corolla cut off. **F** Mature achene, part of pappus further enlarged. **G** Part of receptacle. (Ross-Craig 1962)

Annual to perennial herbs, lower part of outer involucral bracts fleshy at flowering time and hard at fruiting time, involucral bracts in two rows, florets few, achenes obovoid to cylindrical. $x = 9$, diploids. Six species, Europe, Mediterranean area, Near East. *Cichorium endivia* L. (endive) and *C. intybus* L. (chicory) cultivated for their edible leaves.

VIII.3. Subtribe Catananchinae K. Bremer (1993).

Perennial to annual herbs, receptacle setose or paleate, achenes without ribs or beak. Pappus of few lanceolate to triangular scales, sometimes prolonged into bristles. Exclusively Old World tribe, comprising three genera.

Key to the Genera

1. Pappus consisting of five triangular, stiff woody bracts, involucral bracts not scarious at margins **308. *Rothmaleria***
– Pappus of lanceolate scales apically prolonged into bristles, involucral scales scarious at margins 2
2. Margins of involucral bracts silvery or shiny, leaves parallel-veined, receptacle bristly **306. *Catananche***
– Margins of involucral bracts neither silvery nor shiny, leaves not parallel-veined, receptacle peripherally paleate **307. *Hymenonema***

Genera of Catananchinae

306. *Catananche* L.

Catananche L., Sp. Pl. 812 (1753).

Annual or perennial herbs, involucral bracts scarious except the midvein, receptacle bristly, bristles persistent, florets blue or yellow, pappus of few lanceolate, apically elongated scales. $x = 9$, 8, diploids and tetraploids. Six species, Mediterranean area.

307. *Hymenonema* Cass.

Hymenonema Cass., Bull. Sci. Soc. Philom. Paris 1817: 34 (1817).

Perennial herbs, involucral bracts with somewhat scarious margins, receptacle paleate on the periphery, paleae persistent, florets yellow, achenes obconical, pilose, pappus of lanceolate, apically elongated scales. $x = 9$, diploids. Two species, endemic to Greece.

308. *Rothmaleria* Font Quer

Rothmaleria Font Quer, Brotéria (Ci. Nat.) 9: 151 (1940); Lack et al., Willdenowia 10: 37–49 (1980), rev.

Perennial scapose herb, involucral bracts with somewhat scarious margins, receptacle paleate, paleae persistent, florets yellow, achenes obconical, pappus consisting of 5(6) triangular, stiff, woody scales. $x = 9$, diploid. Monotypic, *R. granatensis* (Boiss. ex DC.) Font Quer, endemic to the Granada area (Spain).

VIII.4. Subtribe Crepidinae Cass. ex Dumort. (1827).

Involucral bracts usually in two unequal rows, capitula mostly with many flowers, florets mostly yellow, achenes terete to fusiform or obovoid, often ribbed, transversely muricate-tuberculate and beaked, rarely compressed, pappus rays scabrid-barbellate, usually several cells in diameter at base, pappus rarely absent. Old World subtribe, with *Crepis* and *Taraxacum* also in America. The generic limits between *Crepidiastrum*, *Ixeridium*, *Ixeris* and *Youngia* are unclear, and hybrids between them have been reported. *Phitosia* is tentatively included in this subtribe, although it may well belong to another group.

Key to the Genera[8]

1. Achenes all or some muricate with projections, tubercules or scales on upper part below beak; plants with or without deflexed hairs on the stems 2
– Achenes not muricate on upper part below beak, at most hairy or minutely scabrid on the ribs, beaked or unbeaked; plants without deflexed hairs on the stems 7
2. Plants with taproot and many-flowered capitula solitary and terminal on leafless hollow scapes; corolla-tube with tuft of long hairs at the apex; $x = 8$ **325. *Taraxacum***
– Plants not with the above combination of characters; corolla-tube with short, one-celled hairs; $x = 7, 5, 4$ or 3 3
3. Pappus absent or coroniform or only the inner achenes with a pappus of short bristles 4
– Pappus present, of long bristles 5
4. Internal involucral bracts becoming thickened, hardened and finally connate in fruit **309. *Acanthocephalus***
– Internal involucral bracts not becoming thickened, hardened and connate in fruit **315. *Heteracia***
5. Achenes with a corona of 5–6 short, rounded scales below the beak **326. *Willemetia***
– Achenes not as above 6
6. Achenes heteromorphic, outer more or less beakless and clasped at the base by the inner involucral bracts, with deciduous pappus, inner with long beak and persistent pappus **316. *Heteroderis***
– Achenes homomorphic or, if heteromorphic, then not as above **310. *Chondrilla***
7. Pappus of long bristles absent from all achenes 8
– Pappus of long bristles present on at least the central achenes 9
8. Achenes with 20 slender ribs; perennial herbs (Europe) **320. *Lapsana***
– Achenes with 10–13 ribs; annual or biennial scapose herbs (E Asia) **321. *Lapsanastrum***
9. Involucral bracts lax, outer foliaceous, inner blackish; achenes 4-ribbed (Pakistan) **324. *Spiroseris***
– Involucral bracts imbricate, or all of more or less equal length, or in two series with the outer much shorter than the inner; achenes not as above 10
10. Achenes heteromorphic, outer different in form, indumentum or pappus from inner 11
– Achenes homomorphic 12

[8] By C. Jeffrey.

11. Outer achenes prismatic, hairy, with caducous pappus, inner glabrous with persistent pappus (central Asia) **319. *Lagoseriopsis***
– Outer and inner achenes otherwise distinct (widespread) **312. *Crepis***
12. Capitula numerous, aggregated into large synflorescences; dwarf alpine perennial herbs (Sinohimalaya) **323. *Soroseris***
– Capitula few to numerous, but not aggregated into large synflorescences; if dwarf alpine perennial herbs, then capitula few 13
13. Involucral bracts in several series, imbricate or subequal 14
– Involucral bracts in two series, outer much shorter than inner 15
14. Achenes fusiform, involucral bracts imbricate (Sinohimalaya) **314. *Dubyaea***
– Achenes elliptic, smooth, involucral bracts subequal (tropical Africa) **313. *Dianthoseris***
15. Achenes without distinct apical beak, at most gradually narrowed in upper part into a short rostrum or, if with distinct beak, then columnar or fusiform, not compressed 16
– Achenes with distinct apical beak, more or less distinct in colour and/or texture from achene body, more or less compressed 19
16. Achenes narrowed towards the apex 17
– Achenes not narrowed towards the apex, with 10 equal ribs; $x = 5$ **311. *Crepidiastrum***
17. Achenes columnar or fusiform, with more or less equal ribs; plants with indumentum, rarely glabrous 18
– Achenes more or less compressed, with 12–15 slender unequal ribs, the lateral often narrowly wing-like; plants glabrous **327. *Youngia***
18. Plants glabrous; pappus bristles broadened at base; $x = 9$ (Taygetos Mts, Greece) **322. *Phitosia***
– Plants with at least some indumentum; pappus bristles not broadened at base; $x = 8, 7, 6, 5, 4$ or 3 (widespread) **312. *Crepis***
19. Achenes with filiform beak 20
– Achenes with stout beak 21
20. Achenes with 10 narrowly wing-like, smooth ribs **318. *Ixeris***
– Achenes with 9–12 low, shortly more or less spinulose ribs **317. *Ixeridium***
21. Plant creeping, glabrous, leaves deeply palmately divided into 3–5 lobes **318. *Ixeris***
– Plant erect, leaves otherwise; $x = 5$ **311. *Crepidiastrum***

Genera of Crepidinae

309. *Acanthocephalus* Kar. & Kir.

Acanthocephalus Kar. & Kir., Bull. Soc. Imp. Naturalistes Moscou 15: 127 (1842); Voytenko, Bot. Zhurn. (Moscow & Leningrad) 74: 1241–1257 (1989), fruit morph.

Annual herbs, involucral bracts in two rows, inner connate, becoming hard and woody in fruit, florets yellow, achenes at least basally enclosed by woody involucre, pappus absent or of short scabrid-barbellate rays. $x = 3$, hexaploid (?). Two species, Near East, central Asia, China.

310. *Chondrilla* L.

Chondrilla L., Sp. Pl. 796 (1753); Iljin, Bjull. Otd. Kaučukonosov 3: 1–61 (1930), rev.

Biennial or perennial herbs, often with much reduced foliage, heads few-flowered, involucral bracts in two rows, florets yellow, achenes clearly differentiated into main body and beak, main body ribbed, distally tuberculate or with small corona, beak often deciduous with the pappus of long, scabrid-barbellate rays. $x = 7, 5$, diploids, triploids and tetraploids. Circa 25 species, Eurasia, Mediterranean area.

311. *Crepidiastrum* Nakai

Crepidiastrum Nakai, Bot. Mag. (Tokyo) 34: 147 (1920); Pak & Kawano, Mem. Fac. Sci. Kyoto Univ., ser. Biol. 15: 29–61 (1992), rev.
Paraixeris Nakai (1920).

Perennial to annual herbs, occasionally subshrubs, taprooted, 5–19 flowers per capitulum, involucral bracts in two rows, flowers yellow to white, achenes fusiform, somewhat flattened, obtusely 10–20-winged, pappus of scabrid-barbellate, white or brownish, deciduous rays. $x = 5$, diploids. Thirteen species, eastern Asia, Far East.

312. *Crepis* L. Fig. 44

Crepis L., Sp. Pl. 805 (1753); Babcock, Univ. Calif. Publ. Bot. 21: x, 1–197, 22: x, 199–1030 (1947), rev.; Merxmüller, Mitt. Bot. Staatssamml. München 7: 271–275 (1968), rev.; Duvigneaud, Lejeunia n.s. 71: 1–8 (1973), rev.
Zacintha Mill. (1754).

Perennial to annual herbs, involucral bracts in two rows, those of outer row often much shorter than inner, receptacle naked, very occasionally paleate, florets yellow, rarely white or pink, achenes fusiform, not compressed, ribbed, gradually tapering into beak, homomorphic or rarely dimorphic with the inner achenes beaked or outer achenes compressed. Pappus of scabrid-barbellate rays. $x = 8, 7, 6, 5, 4, 3$, diploids, tetraploids, hexaploids, octoploids. About 200 species, all continents except Australia, in America south to northern Mexico.

313. *Dianthoseris* Sch. Bip. ex A. Rich.

Dianthoseris Sch. Bip. ex A. Rich., Tent. Fl. Abyss. 1: 468 (1848).
Nannoseris Hedberg (1957), nom. illegit.

Perennial dwarf acaulescent herb from afro-alpine habitats, capitula sessile, usually broader than long,

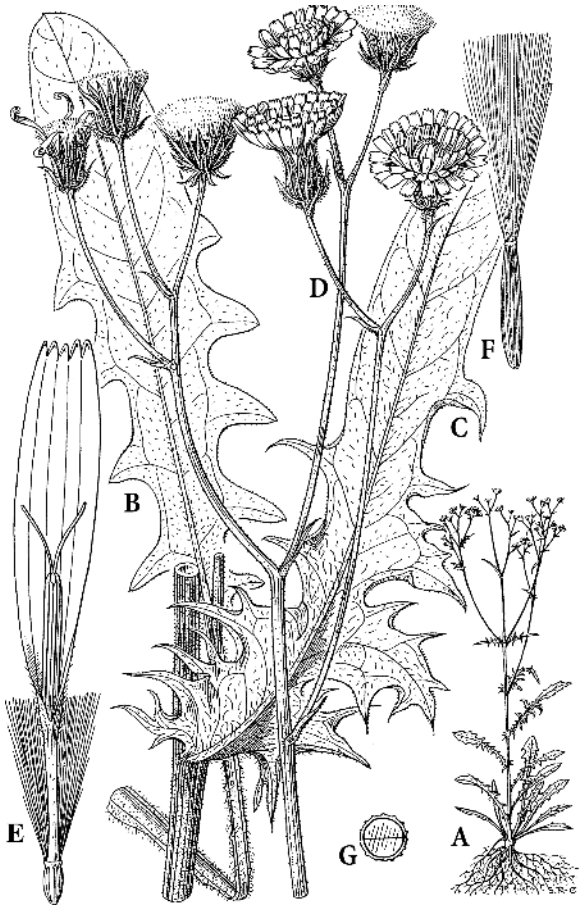

Fig. 44. Compositae-Cichorieae. *Crepis biennis*. **A** Habit. **B** Lower leaf. **C** Middle cauline leaf. **D** Upper part of flowering stem. **E** Floret, part of pappus removed. **F** Achene. **G** Transverse section of achene. (Ross-Craig 1962)

among the rosette of leaves, solitary or few, involucral bracts in several rows, subequal, florets yellow with very short ligule, pappus of scabrid-barbellate rays. $x = 2$, diploid and tetraploid (?). Monotypic, East Africa; *D. schimperi* A. Rich.

314. *Dubyaea* DC.

Dubyaea DC., Prodr. 7:247 (1838); Stebbins, Mem. Torrey Bot. Club 19, 3: 1–76 (1940), rev.; Shih, Acta Phytotax. Sin. 31: 432–450 (1993), rev.

Perennial caulescent or acaulescent herbs, involucral bracts in several rows, receptacle naked, flowers yellow, pink, bluish or purple, achenes fusiform, with 5–10 prominent ribs and 1–6 lesser ones, pappus rays scabrid-barbellate, yellow, white or rufous. $x = 8$, diploids. Fourteen species, Himalayan Mountains, China.

315. *Heteracia* Fisch. & C.A. Mey.

Heteracia Fisch. & C.A. Mey., Index Sem. Hort. Petrop. 1: 29 (1835); Voytenko, Bot. Zhurn. (Moscow & Leningrad) 74: 1241–1257 (1989), fruit morph.

Annual herbs, involucral bracts in two rows, florets yellow, marginal achenes irregularly ribbed, obconical, epappose and persistent, median obpyramidic, beaked, epappose, inner achenes obpyramidic, long-beaked, provided with pappus of fine scabrid-barbellate rays. $x = 4$, diploids. Two species, Crimea, Near East, central Asia, China.

316. *Heteroderis* (Bunge) Boiss.

Heteroderis (Bunge) Boiss., Fl. Orient. 3: 793 (1875); Voytenko, Bot. Zhurn. (Moscow & Leningrad) 74: 1241–1257 (1989), fruit morph.

Annual herb, involucral bracts in 2 rows, florets yellow, achenes dimorphic, outer thickly 5–6-ribbed, unbeaked, pappus absent, enclosed by persistent star-like-arranged involucral bracts, inner achenes caducous, clearly differentiated into main body and long beak, body many-ribbed, distally markedly tuberculate, with pappus of fine scabrid-barbellate rays. $x = 3$, diploid. Possibly monotypic, Near East, central Asia.

317. *Ixeridium* (A. Gray) Tzvelev

Ixeridium (A. Gray) Tzvelev in Kom., Fl. S.S.S.R. 29: 388 (1964); Pak & Kawano, Mem. Fac. Sci. Kyoto Univ., ser. Biol. 15: 29–61 (1992), rev.

Perennial herbs, taprooted, capitula very small, with 5–12 flowers, involucral bracts in 2 rows, receptacle naked, florets yellow, white to purplish, achenes fusiform, beaked, c. 10-ribbed, pappus of yellow to dirty-white scabrid-barbellate rays. $x = 8$, 7, 5, diploids, triploids, tetraploids and hexaploids. Thirteen species, Asia, Malesia to New Guinea.

318. *Ixeris* (Cass.) Cass.

Ixeris (Cass.) Cass. in Cuvier, Dict. Sci. Nat. 25: 623 (1822); Stebbins, J. Bot. (London) 75: 43–51 (1937), rev.; Pak & Kawano, Mem. Fac. Sci. Kyoto Univ., ser. Biol. 15: 29–61 (1992), rev.
Chorisis DC. (1838).

Perennial to annual herbs, stoloniferous or taprooted, involucral bracts in 2 rows, 14–51 flowers per capitulum, receptacle naked, florets yellow, white or purplish, achenes less than 5 mm long, fusiform, slightly compressed, c. 10-winged, pap-

pus of white, persistent scabrid-barbellate rays. x = 9, 8, 7, 6, diploids, triploids, tetraploids, hexaploids. Ten species, Asia, Malesia to New Guinea.

319. *Lagoseriopsis* Kirp.

Lagoseriopsis Kirp. in Kom., Fl. S.S.S.R. 29: 726 (1964); Voytenko, Bot. Zhurn. (Moscow & Leningrad) 74: 1241–1257 (1989), fruit morph.

Annual herb, involucral bracts few, in 2 rows, capitula narrowly cylindrical with 4–6 flowers, receptacle naked, florets yellow, achenes heteromorphic, outer prismatic, hairy, persistent, pappus readily deciduous, inner fusiform apically without tubercles or a crown-like structure, pappus persistent, of scabrid-barbellate rays. Monotypic, central Asia; *L. popovii* (Krasch.) Kirp.

320. *Lapsana* L.

Lapsana L., Sp. Pl. 811 (1753); Pak & Bremer, Taxon 44: 13–21 (1995), rev.

Perennial herbs, heads small, involucral bracts in two rows, receptacle naked, florets yellow, achenes often slightly flattened, beaked, many-ribbed, rounded at apex, pappus absent. x = 7, diploid. Monotypic, Europe; *L. communis* L.

321. *Lapsanastrum* J.-H. Pak & K. Bremer

Lampsanastrum J.-H. Pak & K. Bremer, Taxon 44: 19 (1995); Pak & Bremer, Taxon 44: 13–21 (1995), rev.

Biennial to annual scapose herbs, involucral bracts in two series, florets yellow, achenes oblong, hairy, 10–13-ribbed, ribs unequal, sometimes prolonged into apical hornlike appendages, pappus absent. x = 8, diploid. Four species, eastern Asia.

322. *Phitosia* Kamari & Greuter

Phitosia Kamari & Greuter, Bot. Hron. 13: 14 (2000); Kamari & Greuter, Bot. Hron. 13: 11–36 (2000), rev.

Perennial herb, very similar to *Crepis*, but with a totally deviant chromosome number, lack of indumentum, and basally rather broad pappus rays. x = 9, diploid. Monotypic, endemic to the Taygetos Mountains in Greece; *C. crocifolia* (Boiss. & Heldr.) Kamari & Greuter. Possibly not belonging to Crepidinae.

323. *Soroseris* Stebbins

Soroseris Stebbins, Mem. Torrey Bot. Club 19, 3: 27 (1940); Stebbins, Mem. Torrey Bot. Club 19, 3: 1–76 (1940), rev.; Shih, Acta Phytotax. Sin. 31:432–450 (1993),rev.
Stebbinsia Lipsch. (1956).

Dwarf alpine perennial herbs, stems hollow, capitula on short peduncles, numerous, aggregated into large synflorescences, involucral bracts in 2–3 rows, receptacle naked, 4–25 flowers in each capitulum, florets yellow or white, achenes oblong, apically contracted, pappus rays scabrid-barbellate, yellow, rufous or white. x = 8, diploid. Nine species, Himalayan Mountains, China.

324. *Spiroseris* Rech. f.

Spiroseris Rech. f., Fl. Iran. 122: 338 (1977).

Incompletely known perennial herb, involucral bracts laxly arranged, outer foliaceous, inner blackish, florets yellow, achenes fusiform, 4-ribbed, pappus a single row of scabrid-barbellate, basally connate rays. Monotypic, known only from three collections, endemic to Pakistan; *S. phyllocephala* Rech. f., possibly related to *Dubyaea* DC.

325. *Taraxacum* Weber

Taraxacum Weber in F.H. Wigg., Prim. Fl. Holsat. 56 (1780), nom. cons.; Sterk et al., Biblioth. Koninkl. Ned. Natuurhist. Veren. 42: i–ii, 1–348 (1987), rev.

Perennial scapose herbs with taproot, leaves in basal rosette, scape leafless, hollow, involucral bracts in two unequal series, the outer shorter, often reflexed at tips, receptacle naked, capitula with very many flowers, florets yellow, achenes obovoid, fusiform, ribbed, distally scabrid or warty-tuberculate, with distinct long, slender beak, pappus of many scabrid rays. x = 8, diploids, triploids, tetraploids, pentaploids, hexaploids, septemploids, octoploids, decaploids. Cosmopolitan, but mainly in the northern hemisphere, a single section in southern South America, Australia and New Zealand. Numerous clones described as species.

326. *Willemetia* Neck.

Willemetia Neck., Willemetia 1 (1777–1778); Kirschnerová & Kirschner, Taxon 45: 627–630 (1996), rev.
Calycocorsus F.W. Schmidt (1795).

Perennial herbs with creeping rootstock, scapose or stem branched, involucral bracts in two rows, receptacle naked, flowers yellow, achenes beaked, ribbed, with five squamules forming a distinct apical collar, abruptly narrowing to a fragile, thin ros-

trum, pappus of scabrid bristles. $x = 5$, diploids. Two species, Europe, Caucasus, east to Iran.

327. *Youngia* Cass.

Youngia Cass., Ann. Sci. Nat. (Paris) 23: 88 (1831); Babcock & Stebbins, Publ. Carnegie Inst. Wash. 484:1–106 (1937), rev.

Perennial, biennial to annual herbs, involucral bracts in two rows, usually 8 inner bracts, becoming carinate in fruit, receptacle naked, 5–30 flowers per capitulum, florets yellow, achenes less than 5 mm, unequally many-ribbed, pappus of many scabrid-barbellate rays, white, yellow, fuscous to cinereous. $x = 8, 6, 5$, diploids. Circa 30 species, Asia.

VIII.5. Subtribe Lactucinae Cass. ex Dumort. (1827).

Capitula mostly slender and with few flowers, florets often non-yellow, achenes often compressed and ribbed, often with a beak, carpopodium funnel-shaped, callose, pappus rays fine, at least some basally with very few cells in diameter. Old World tribe, *Lactuca* and *Prenanthes* also in North America.

Key to the Genera[9]

1. Pappus monomorphic, without outer ring of extremely short setae 2
– Pappus dimorphic, with outer ring of extremely short setae 11
2. Capitula sessile, aggregated into compact synflorescences **339. *Syncalathium***
– Capitula sessile or pedunculate, in more or less lax to spiciform inflorescences 3
3. Achenes compressed, with broad, thin, wing-like margins **336. *Pterocypsela***
– Achenes columnar to compressed but without broad, thin, wing-like margins 4
4. Achenes without distinct apical beak, at most gradually narrowed in upper part into a short rostrum 5
– Achenes with distinct apical beak more or less distinct in colour and/or texture from achene body **331. *Lactuca*** p.p.
5. Capitula with more than 7 florets or, if fewer, then plants scandent 6
– Capitula with 5–7 florets 10
6. Achenes more or less cylindrical, at most a little narrowed towards apex, apex truncate 7
– Achenes more or less fusiform, narrowed towards apex 9
7. Achenes with 4–5 ribs or more or less terete; rhizomatous perennials **335. *Prenanthes*** p.p.
– Achenes with 10–12 ribs; rhizomatous perennials or taprooted biennials 8
8. Rhizomatous perennials (E Asia) **331. *Lactuca*** p.p.
– Taprooted biennials (E Asia, North America) **332. *Nabalus***
9. Achenes more or less strongly compressed, ribs on margins often inflated **331. *Lactuca*** p.p.
– Achenes not or little compressed, ribs narrow, equal **334. *Paraprenanthes***
10. Achenes not compressed, with 4–5 ribs **335. *Prenanthes*** p.p.
– Achenes compressed, with 10–20 ribs **333. *Notoseris***
11. Achenes with unequal ribs, margins thickened, often rugose 12
– Achenes with equal ribs, margins not thickened 13
12. Florets 10–40 **329. *Chaetoseris***
– Florets 3–5 **337. *Stenoseris***
13. Achenes compressed, without beak and with 12–18 ribs, or with filiform beak and 4–12 unequal ribs 14
– Achenes little or not compressed, with short to long, stout beak and with 12–18 more or less equal ribs **328. *Cephalorrhynchus***
14. Achenes with filiform beak 15
– Achenes not beaked, with 12–18 ribs **330. *Cicerbita***
15. Achenes with 12 unequal ribs **331. *Lactuca*** p.p.
– Achenes with 4 strongly unequal ribs, the two lateral wing-like, the two facial weak **338. *Steptorhamphus***

[9] By C. Jeffrey.

Genera of Lactucinae

328. *Cephalorrhynchus* Boiss.

Cephalorrhynchus Boiss., Diagn. Pl. Orient. ser. 1, 1(4): 28 (1844).

Perennial to biennial herbs with tuberous rootstocks, involucral bracts in several rows, receptacle naked, florets yellow, white, violet or purple, achenes fusiform, beaked, not compressed, pappus capillary. $x = 9, 8$, diploids. South-eastern Europe to China, 14 species.

329. *Chaetoseris* C. Shih

Chaetoseris C. Shih, Acta Phytotax. Sin. 29: 398 (1991); Shih, Acta Phytotax. Sin. 29: 394–417 (1991), rev.

Perennial to annual herbs, involucral bracts in 3–5 rows, receptacle naked, 10–40 flowers in each capitulum, florets purple to violet, rarely yellow, achenes compressed and beaked, margins thickened and winged, pappus rays capillary. Eastern Asia, 18 species.

330. *Cicerbita* Wallr.

Cicerbita Wallr., Sched. Crit. 433 (1822).

Perennial herbs, rhizomatous or taprooted, leaves clasping the stem, involucral bracts in several rows, receptacle naked, florets blue, lilac or violet,

sometimes yellow, achenes compressed, not beaked, pappus rays capillary. x = 9, 8, diploids. Eurasia, c. 5 species.

331. *Lactuca* L. Fig. 45

Lactuca L., Sp. Pl. 795 (1753); Stebbins, Bull. Jard. Bot. État 14: 333–352 (1937), rev.; Tuisl, Ann. Naturhist. Mus. Wien 72: 587–638 (1968), reg. rev.; Feráková, The genus *Lactuca* L. in Europe (Bratislava, 1975), reg. rev.; Dethier, Bull. Jard. Bot. Belg. 52: 367–382 (1982), reg. rev.; Koopman et al., Amer. J. Bot. 85: 1517–1530 (1998), mol. phylog.
Scariola F.W. Schmidt (1795).
Mulgedium Cass. (1824).
Mycelis Cass. (1824).
Lagedium Soják (1961).
Lactucella Nazarova (1990).
Faberiopsis Shih (1996).

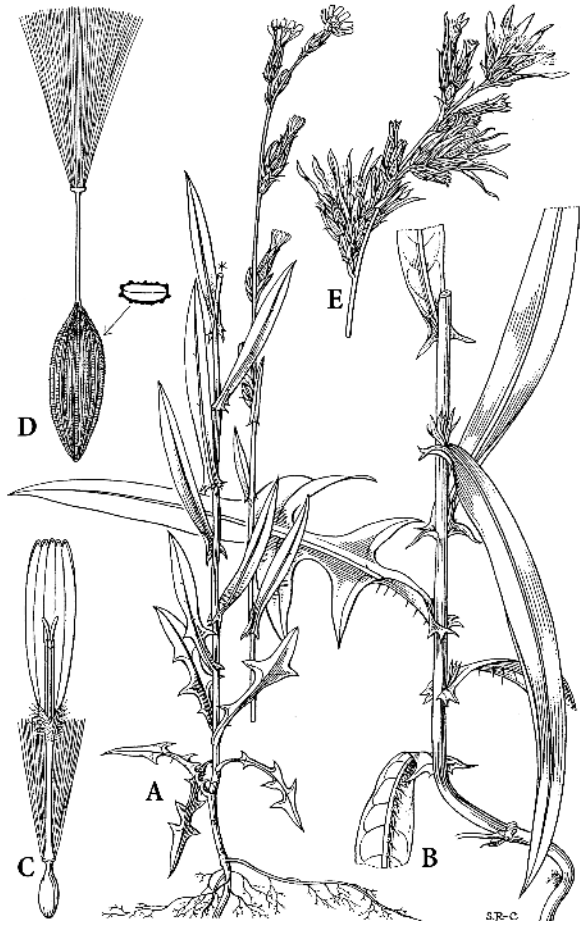

Fig. 45. Compositae-Cichorieae. *Lactuca saligna*. **A** Habit of young plant. **B** Lower part of older plant. **C** Floret, part of pappus removed. **D** Achene and transverse section of achene. **E** Upper part of fruiting stem. (Ross-Craig 1963)

Perennial to annual herbs, rarely scandent or subshrubby, heads often in panicles, involucral bracts in several rows, receptacle naked, florets yellow, bluish, violet or white, achenes compressed, abruptly constricted, beaked, pappus rays capillary, white to yellowish. x = 9 , 8, 6, diploids, triploids and tetraploids. Northern hemisphere, in Asia to New Guinea, in North America to Mexico, in tropical Africa to South Africa, c. 60 species.

Lactuca sativa L. (lettuce) is cultivated for its edible leaves. The single specimen known so far of *Faberiopsis* Shih & Y.L. Chen is characterized by blue florets and is unique in Cichorieae by possessing deeply trisect ligules with a tridentate central and two simple lateral lobes (Shih and Chen 1996). Since this may be an aberrant form, *Faberiopsis* is tentatively regarded here as a synonym of *Lactuca*.

332. *Nabalus* Cass.

Nabalus Cass. in Cuvier, Dict. Sci. Nat. 34: 94 (1825); Milstead, A revision of the North American species of *Prenanthes*, Thesis, Purdue University (1964), reg. rev.; Sennikov, Novosti Sist. Vyssh. Rast. 32:177–181 (2001), rev.

Perennial herbs, involucral bracts 5–15, capitula with 5–38 flowers, receptacle naked, florets blue, lavender, white and yellow, pappus capillary, yellow to red-brown. x = 8, diploids. Eastern Asia, North America, 18 species.

333. *Notoseris* C. Shih

Notoseris C. Shih, Acta Phytotax. Sin. 25: 196 (1987); Shih, Acta Phytotax. Sin. 25: 189–203 (1987), rev.

Perennial herbs, involucral bracts in 3–5 rows, purplish, receptacle naked, 3–5 flowers in each capitulum, florets purple, achenes compressed, purple to reddish-brown, truncate, pappus rays capillary. Eastern Asia, 12 species.

334. *Paraprenanthes* Chang ex C. Shih

Paraprenanthes Chang ex C. Shih, Acta Phytotax. Sin. 26: 418 (1988); Shih, Acta Phytotax. Sin. 26: 382–393, 418–428 (1988), reg. rev.

Perennial to annual herbs, involucral bracts in 2–3 rows, receptacle naked, 7–15 flowers in each capitulum, florets pink or purple, achenes black, beakless, pappus rays capillary. Fifteen species, eastern Asia to Malesia.

335. *Prenanthes* L. s. str.

Prenanthes L., Sp. Pl. 797 (1753); Stebbins, Bull. Jard. Bot. État 14: 333–352 (1937), reg. rev.; Milstead, A revision of the North American species of *Prenanthes*, Thesis, Purdue University (1964), reg. rev.
Faberia Hemsl. (1888).

Perennial herbs, one species scandent, leaves clasping the stem, heads in panicles with up to 5 flowers, nodding, involucral bracts in 2–3 rows, receptacle naked, florets pink, purplish to blue, achenes compressed, not beaked, pappus rays capillary, not thickened at the base. $x = 9$, diploids and tetraploids. Eight species, Eurasia, south to tropical Africa.

336. *Pterocypsela* C. Shih

Pterocypsela C. Shih, Acta Phytotax. Sin. 26: 385 (1988); Shih, Acta Phytotax. Sin. 26: 382–393, 418–428 (1988), reg. rev.

Perennial to annual herbs, involucral bracts in 4–5 rows, receptacle naked, florets yellow, achenes compressed, with two broad wings, pappus rays capillary. Seven species, eastern Asia, China, Malesia to New Guinea. *Pterocypsela indica* (L.) C. Shih (Indian lettuce) is cultivated for its edible leaves.

337. *Stenoseris* C. Shih

Stenoseris C. Shih, Acta Phytotax. Sin. 29: 411 (1991); Shih, Acta Phytotax. Sin. 29: 394–417 (1991), rev.

Perennial herbs, involucral bracts 3, in a single row, receptacle naked, 3(–5) flowers in each capitulum, florets purple to violet, achenes compressed with wings, pappus rays capillary. Six species, eastern Asia.

338. *Steptorhamphus* Bunge

Steptorhamphus Bunge, Mém. Acad. Imp. Sci. Saint-Pétersbourg Divers Savans 7: 381 (1854).

Perennial herbs, mostly tuberous, involucral bracts in several series, receptacle naked, flowers yellow or violet, achenes compressed and winged with long, slender beak, pappus rays capillary. $x = 8$, diploids. Eight species, south-eastern Europe to western Himalaya.

339. *Syncalathium* Lipsch.

Syncalathium Lipsch., Akad. N.S. Sukatschevu 75 Let.: 358 (1956); Ling Yong, Acta Phytotax. Sin. 10: 283–289 (1965), rev.; Shih, Acta Phytotax. Sin. 31: 432–450 (1993), rev.

Perennial to biennial, acaulescent or caulescent herbs, capitula sessile, numerous, aggregated into an often compact synflorescence, involucral bracts 3–5(6) in a single row, pink to pale green, receptacle naked, 3–6 flowers in each capitulum, florets pink or purple, achenes oblong, apically contracted, compressed, pappus rays capillary. Eight species, Himalayas, China.

VIII.6. Subtribe Sonchinae K. Bremer (1993).

Perennial to annual herbs, subshrubs or shrubs. Receptacle naked, achenes ellipsoid-fusiform or oblong-obovoid, mostly without beak, carpopodia never annular-callose. Pappus of setae or dimorphic with setae and cottony hairs, always flexible. Cosmopolitan tribe.

Key to the Genera
(in part based on Kilian 1997)

1. Rosette trees or rosette shrubs of the Juan Fernandez Islands or succulent subshrubs of the Desventuradas Islands 2
– Perennial to annual herbs, rosette subshrubs of Canary Islands 3
2. Rosette trees or rosette shrubs of the Juan Fernandez Islands **341. *Dendroseris***
– Succulent subshrubs of the Desaventuradas Islands **345. *Thamnoseris***
3. Pappus (sub)homomorphic, rays at most gradually differing in thickness from centre towards margin 4
– Pappus dimorphic with few inner setae and numerous outer downy or (rarely) cottony hairs 5
4. Peduncles expanded upwards; marginal achenes always truncate, glabrous and with thick, tuberculose projections; most achenes with 4 main ribs, only the very marginal with 5 main ribs **343. *Reichardia***
– Peduncles never expanded upwards; marginal achenes truncate, cuspidate or rostrate, smooth or transversely wrinkled (but never sculptured as above), glabrous, scabrid or papillose; all or most achenes with 5 main ribs, otherwise marginal achenes pappillose **342. *Launaea*** p.p.
5. All achenes with 4 main ribs and (sub)equal in ornamentation, apex shape, or size; peduncles and involucres often glandular and/or (glabrescent) white tomentose; outer involucral bracts without distinct scarious margin and white tip 6
– Most achenes (except innermost) with 5 main ribs, otherwise marginally (densely) papillose; inner(most) achenes mostly different from marginal in ornamentation, apex shape or size; peduncle and involucre never glandular nor tomentose; outer involucral bracts mostly with distinct (though sometimes thin) scarious margin and/or white, mucronate tip **342. *Launaea*** p.p.

6. Plants (sub)scapose and stoloniferous; all achenes smooth and subcolumnar to slender subfusiform, even marginal little compressed **340. *Aetheorhiza***
– Plants never (sub)scapose and stoloniferous; at least marginal achenes wrinkled and/or distinctly compressed **344. *Sonchus***

Genera of Sonchinae

340. *Aetheorhiza* Cass.

Aetheorhiza Cass. in Cuvier, Dict. Sci. Nat. 48: 425 (1827); Rechinger, Phyton (Horn) 16: 211–220 (1974), rev.

Perennial scapose, stoloniferous herb with tubers along the rhizomes. Flowers yellow, achenes fusiform, apically attenuate, slightly compressed, 4-ribbed, pappus of many setae. $x = 9$, diploid. Monotypic, Europe, Mediterranean area; *Ae. bulbosa* (L.) Cass.

341. *Dendroseris* D. Don

Dendroseris D. Don, Philos. Mag. Ann. Chem. 11: 388 (1832); Carlquist, Brittonia 19: 99–121 (1967), anat.; Sanders et al., Opera Bot. 92: 195–215 (1987), evol.; Crawford et al., Syst. Bot. 17: 676–682 (1992), mol. phylog.; Kim et al., Syst. Bot. 21: 417–432 (1996), mol. phylog.; Kim et al., Pl. Syst. Evol. 215: 85–99 (1999), mol. phylog.; Esselman et al., Amer. J. Bot. 87: 591–596 (2000), mol. phylog.

Rosette trees and shrubs with leaf rosettes at apex of stems, involucral bracts in several rows, receptacle naked or bristly, capitula variously arranged, sometimes solitary, florets whitish or orange-yellow, achenes compressed, rarely winged. $x = 9$, tetraploids. Eleven species, endemic to Juan Fernandez Islands (Chile).

342. *Launaea* Cass.

Launaea Cass. in Cuvier, Dict. Sci. Nat. 25: 321 (1822); Kilian, Englera 17: 1–478 (1997), rev.
Paramicrorhynchus Kirp. (1964).
Hexinia H.L. Yang (1992).

Perennial to annual herbs, small shrubs or subshrubs. Capitula mostly slender and with c. 7–40 flowers, involucral bracts mostly with membranous or translucent margins, florets yellow, pappus of setaceous rays or setaceous and cottony rays. $x = 9$, 8, 7, 6, diploids, tetraploids, hexaploids. Fifty-four species, Old World, one species in Australia.

343. *Reichardia* Roth

Reichardia Roth, Bot. Abh. Beobacht. 35 (1787); Gallego et al., Lagascalia 9:159–217 (1980), rev.

Perennial to annual herbs, leaves marginally somewhat spinulose, peduncles expanded upwards, involucral bracts with scarious margins, capitula with many flowers, florets yellow, marginal achenes truncate, glabrous with thick, tuberculose projections. $x = 9$, 8, 7, diploids. Eight species, Macaronesia, Mediterranean area, Near East, south to tropical Africa.

344. *Sonchus* L. Fig. 46

Sonchus L., Sp. Pl. 793 (1753); Boulos, Bot. Notiser 125: 287–305 (1972), 126: 155–196 (1973), 127: 7–37, 402–451 (1974), rev.; Perez de la Paz, Bot. Macaronés. IV Ci. 1: 51–65

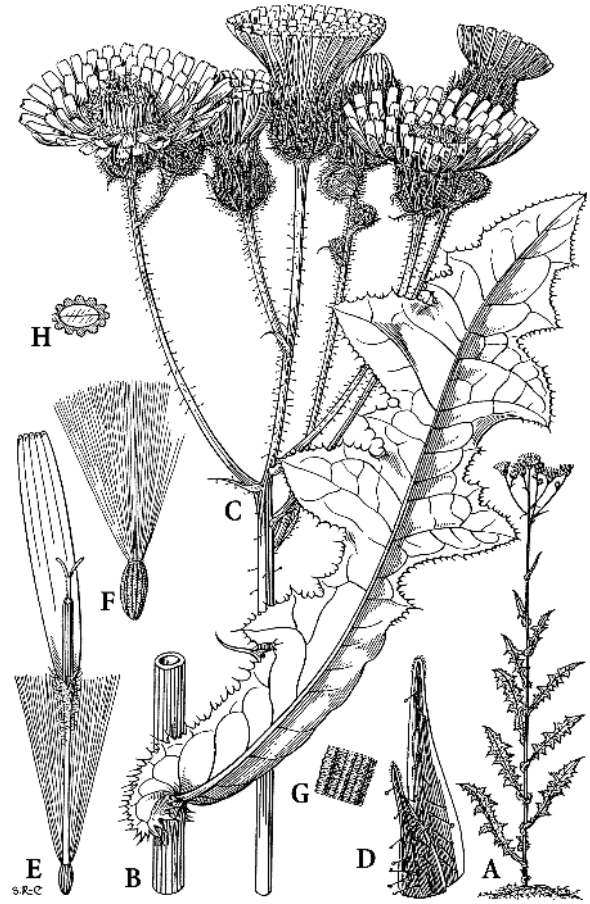

Fig. 46. Compositae-Cichorieae. *Sonchus arvensis*. **A** Habit. **B** Middle cauline leaf. **C** Upper part of flowering stem. **D** Involucral bracts. **E** Floret, part of pappus removed. **F** Achene. **G** Part of achene surface. **H** Transverse section of achene. (Ross-Craig 1963)

(1976), rev.; Aldridge, Bot. Macaronés. IV Ci. 2: 25–58, 81–93 (1976), rev.; Lander, Telopea 1: 129–135 (1976), rev.; Aldridge, Bot. J. Linn. Soc. 76: 249–285 (1978), anat.; Aldridge in Bramwell, Plants and islands: 279–291 (1979), evol.; Kim et al., Syst. Bot. 21: 417–432 (1996), mol. phylog.; Kim et al., Proc. Natl. Acad. Sci. U.S.A. 93: 7743–7748 (1996), mol. phylog.; Kim et al., Pl. Syst. Evol. 215: 85–99 (1999), mol. phylog.; Kim et al., Pl. Syst. Evol. 215:101–118 (1999), mol. phylog.
Atalanthus D. Don (1829).
Sventenia Font Quer (1949).
Kirkianella Allan (1961).
Babcockia Boulos (1965).
Embergeria Boulos (1965).
Taeckholmia Boulos (1967).
Lactucosonchus (Sch. Bip.) Svent. (1969).
Actites Lander (1976).
Wildpretia U. and A. Reiffenberger (1996).

Perennial to annual herbs; on oceanic islands often shrubs to subshrubs with leaves in rosettes at apex of stems. Capitula with many flowers, variously arranged, involucral bracts without translucent margins, receptacle naked, florets yellow, at least marginal achenes wrinkled, pappus of setaceous and downy rays. x = 9, 8, 7, 5, diploids, triploids, tetraploids, hexaploids, octoploids, $2n$ = 90, 126 reported for *Kirkianella novae-zelandiae* (Hook. f.) Allan. Circa 80 species, Old World, with very few species in Australia and New Zealand.

345. *Thamnoseris* Phil.

Thamnoseris Phil., Anales Univ. Chile 1875:191 (1875); Skottsberg, Göteb. Kungl. Vetensk. Samhälles Handl. ser. B, Mat. Naturvetensk. Skr. ser. 5, 5(6): 11–88 (1937), rev.

An incompletely known succulent subshrub with leaf rosette at apex of stems, capitula aggregated into globular synflorescences, the latter on branched terminal shoots, florets yellow (?). Monotypic, Desventuradas Islands; *Th. lacera* (Phil.) Johnst., probably outside Cichorieae.

VIII.7. Subtribe Microseridinae Stebbins (1953).

Pollen distinctly orange, style branches short, blunt, pappus various, rarely absent. An exclusively New World subtribe, except for *Microseris* found also in Australia and New Zealand.

Key to the Genera

1. Pappus absent 2
– Pappus well developed 3
2. Scapose perennial herb **349. *Phalacroseris***
– Branched annual herb **347. *Krigia cespitosa***
3. Basal portion of pappus rays always broad **348. *Microseris***
– Basal portion of pappus rays never broad 4
4. Capitula on leafless scapes **346. *Agoseris***
– Flowering stems branched 5
5. Pappus consisting of long inner bristles and small outer scales **347. *Krigia***
– Pappus different 6
6. Involucral bracts in a single row, native to South America **350. *Picrosia***
– Involucral bracts in several rows, native to North America **351. *Pyrrhopappus***

Genera of Microseridinae

346. *Agoseris* Rafin.

Agoseris Raf., Fl. Ludov. 58 (1817).

Perennial to annual herb, scapose, involucral bracts in 2–4 series, receptacle naked, florets yellow to red-orange, achenes fusiform, tapered to beak, pappus of scabrid-barbellate bristles. x = 9, diploids and tetraploids. Circa 10 species, western North America, Chile and Argentina.

347. *Krigia* Schreb.

Krigia Schreb., Gen. Pl. 532 (1791), nom. cons.; Kim & Turner, Brittonia 44: 173–198 (1992), rev.

Perennial to annual herbs, involucral bracts in 1–2 rows, florets yellow or orange-yellow, pappus double, single or absent, when present of few scales or of few inner bristles surrounded by few outer scales. x = 9, 6, 5, 4, diploids, triploids, tetraploids, hexaploids and dodecaploids. Seven species, North America.

348. *Microseris* D. Don

Microseris D. Don, Philos. Mag. Ann. Chem. 11: 388 (1832); Chambers, Contr. Dudley Herb. 4: 207–312 (1955), rev.; Jansen et al., Amer. J. Bot. 78: 1015–1027 (1991), mol. phylog.; Vijverberg et al., Amer. J. Bot. 86: 1448–1463 (1999), mol. phylog.
Uropappus Nutt. (1841).
Apargidium Torr. & A. Gray (1843).
Nothocalais (A. Gray) Greene (1886).
Stebbinsoseris K.L. Chambers (1991).

Perennial to annual herbs, leaves mostly basal, involucral bracts in 2 to several series, receptacle

naked, florets white to orange, achenes cylindric to fusiform, not beaked, with c. 10 ribs, pappus of 5 to many narrowly lanceolate, bristle-tipped, awn-like scales. $x = 9$, diploids and tetraploids. Fourteen species, North America, Chile, Australia, New Zealand.

349. *Phalacroseris* A. Gray

Phalacroseris A. Gray, Proc. Amer. Acad. Arts 7: 364 (1868).

Perennial scapose herbs, involucral bracts mostly in a single row, basally connate, ligules yellow, fruit 4-angled, smooth, pappus absent. $x = 9$, diploid. Monotypic, California; *Ph. bolanderi* A. Gray.

350. *Picrosia* D. Don

Picrosia D. Don, Trans. Linn. Soc. London 16:183 (1832).

Perennial herbs, involucral bracts in a single series, receptacle naked, flowers white, pink or violet, achenes fusiform, with long beak, pappus of many scabrid bristles. $x = 7$, diploids. Two species, South America.

351. *Pyrrhopappus* DC.

Pyrrhopappus DC., Prodr. 7: 144 (1838), nom. cons.; Northington, Spec. Publ. Mus. Texas Tech. Univ. 6: 1–38 (1974), rev.; Turner & Kim, Amer. J. Bot. 77: 845–850 (1990), rev.

Perennial or biennial herbs, subscapose, involucral bracts in two series, receptacle naked, flowers yellow, achenes subfusiform, long tapering into filiform beak, smooth towards the tip of the body, pappus of thin brownish to reddish rays, surrounded at base by a short villous ring. $x = 6$, diploids and tetraploids. Three species, North America.

VIII.8. Subtribe Stephanomeriinae Stebbins (1953).

Capitula few-flowered, non-yellow flowers, achenes narrowly terete to fusiform, pappus of scabrid or plumose rays. Exclusively New World subtribe.

Key to the Genera

1. Pappus rays plumose 2
– Pappus rays barbellate or pappus of 5 rigid awns and slender bristles 3
2. Achenes mostly beaked, at least 8 mm **357. *Rafinesquia***
– Achenes columnar, mostly 3–6 mm **359. *Stephanomeria***
3. Pappus with 5 rigid awns **352. *Chaetadelpha***
– Pappus without rigid awns 4
4. Shrub 5
– Subshrubs, taprooted perennials or annuals 6
5. Shrub with fleshy, brownish, tomentose stems (San Clemente Island) **355. *Munzothamnus***
– Shrub with succulent leaves (Chichuachuan Desert, Mexico) **354. *Marshalljohnstonia***
6. Subshrubs, branches becoming sharp thorns **356. *Pleiacanthus***
– Perennial or annual herbs, unarmed 7
7. Lower leaves opposite, achenes 8–10-sulcate **358. *Shinnersoseris***
– Lower leaves alternate, achenes variously sculptured, but never 8–10-sulcate **353. *Lygodesmia***

Genera of Stephanomeriinae

352. *Chaetadelpha* A. Gray ex S. Watson

Chaetadelpha A. Gray ex S. Watson, Amer. Naturalist 7: 301 (1873); Tomb, Madroño 21: 459–462 (1972), rev.

Perennial herb, involucral bracts in 2 series, receptacle naked, 5 flowers per head, ligule pale lavender-white, pappus dimorphic with many fine rays and five rigid, thick awns. $x = 9$, diploid. Monotypic, endemic to south-western USA; *Ch. wheeleri* A. Gray.

353. *Lygodesmia* D. Don

Lygodesmia D. Don, Edinburgh New Philos. J. 1829: 311 (1829); Tomb, Brittonia 24: 223–228 (1972), rev.; Tomb, Syst. Bot. Monogr. 1: 1–51 (1980), rev.
Prenanthella Rydb. (1906).

Perennial or annual herbs, rarely subshrubs, capitula few-flowered, involucral bracts in two unequal rows, flowers pink, purplish or white, pappus of distichously barbellate rays. $x = 9, 7$, diploids. Nine species, southern Canada to northern Mexico.

354. *Marshalljohnstonia* Henr.

Marshalljohnstonia Henr., Syst. Bot. 1: 171 (1976); Henrickson, Syst. Bot. 1: 169–180 (1976), rev.

Shrub, leaves fleshy, involucral bracts in several rows, receptacle naked, 10–18 flowers per capitulum, florets pink to purple, cylindric achenes, pappus of slightly flattened, distichously barbellate bristles, pollen echinate. $x = 9$, diploid. Monotypic, endemic to the Chichuachuan Desert in Mexico; *M. gypsophila* Henr.

355. *Munzothamnus* Raven

Munzothamnus Raven, Aliso 5: 345 (1963); Lee et al., Amer. J. Bot. 89: 160–168 (2002), mol. phylog.

Shrub with fleshy, brownish tomentose stems, leaves tufted at branch tips, inflorescences densely stalked-glandular, florets light purple, pappus of non-plumose bristles. $x = 8$, diploid. Monotypic, endemic to San Clemente Island (California); *M. blairii* (Munz & Johnst.) Raven.

356. *Pleiacanthus* (T. Nutall) Rydb.

Pleiacanthus (T. Nutall) Rydb., Fl. Rocky Mount. 1023 (1918); Lee et al., Amer. J. Bot. 89: 160–168 (2002).

Subshrub, woolly at base, branches becoming thick thorns, leaves linear to scale-like, florets 3–5, pink, pappus of non-plumose bristles. $x = 8$, diploid. Monotypic, south-western United States; *P. spinosus* Rydb.

357. *Rafinesquia* Nutt.

Rafinesquia Nutt., Trans. Amer. Philos. Soc. n.s. 7:429 (1841), nom. cons.

Annual herbs, leaves basal and cauline, involucral bracts in 3–4 series, outer series often with membranous margins, receptacle naked, florets white to cream, often rose-tinged, achenes smooth or tubercled, weakly ribbed, tapered to a beak, pappus of stiff distichously plumose rays. $x = 8$, diploids. Two species, California to New Mexico.

358. *Shinnersoseris* Tomb

Shinnersoseris Tomb, Sida 5: 186 (1973); Tomb, Sida 5: 183–189 (1973), rev.

Annual herb, lower leaves opposite, capitula few-flowered, involucral bracts in two unequal rows, ligules violet-pink, c. 1 mm wide, pappus of fine scabrid rays. $x = 6$, diploid. Monotypic, restricted to central North America; *S. rostrata* (A. Gray) Tomb.

359. *Stephanomeria* Nutt.

Stephanomeria Nutt., Trans. Amer. Philos. Soc. n.s. 7:427 (1841), nom. cons.; Gottlieb, Madroño 21: 463–481 (1972), rev.

Subshrubs, perennial to annual herbs, involucral bracts in 2 to several rows, receptacle naked, capitula few-flowered, ligules lavender, pink or whitish, pappus of stiff distichously plumose rays. $x = 8$, diploids and tetraploids. Twenty-two species, British Columbia to Baja California, east to Texas.

VIII.9. Subtribe Malacothricinae K. Bremer (1993).

Perennial to annual herbs, receptacle generally bristly-scaly, rarely paleate, pappus of slender, barbellate or plumose rays, rarely absent. Exclusively New World subtribe.

Key to the Genera

1. Pappus absent — **361. *Atrichoseris***
– Pappus present — 2
2. Pappus plumose — **360. *Anisocoma***
– Pappus various, but not plumose — 3
3. Prostrate herbs — **363. *Glyptopleura***
– Plants different — 4
4. Achenes beaked — 5
– Achenes columnar — **364. *Malacothrix***
5. Perennial herbs, receptacle paleate, pappus brownish — **365. *Pinaropappus***
– Annual herbs, receptacle naked, pappus whitish — **362. *Calycoseris***

Genera of Malacothricinae

360. *Anisocoma* Torr. & A. Gray

Anisocoma Torr. & A. Gray, Boston J. Nat. Hist. 5: 111 (1845).

Annual scapose herb, involucral bracts in several series, with broad papery-transparent margins, receptacle naked, ligules pale yellow, pappus of stiff distichously arranged plumose rays. $x = 9$, diploid. Monotypic, restricted to south-western USA and northern Mexico; *A. acaulis* Torrey & A. Gray.

361. *Atrichoseris* A. Gray

Atrichoseris A. Gray, Syn. Fl. N. Am. 1, 2: 410 (1884).

Annual herb, leaves mostly basal, involucral bracts in 2–4 series, receptacle naked, ligules white, fragrant, achenes with 5 thick, white, corky ribs, pappus absent. $x = 9$, diploid. Monotypic, restricted to south-western USA; *A. platyphylla* A. Gray.

362. *Calycoseris* A. Gray

Calycoseris A. Gray, Smithsonian Contr. Knowl. 5: 104 (1853).

Annual herb, leaves basal and cauline, involucral bracts scarious-margined, in 2 series, receptacle minutely bristly, ligules yellow to white, achenes

tapered to short beak, pappus of slender rays. $x = 9$, diploids. Two species, south-western USA to north-western Mexico.

363. *Glyptopleura* Eaton

Glyptopleura Eaton, Bot. King's Exped. 207 (1871).

Annual herb, forming small tufts, stems semiprostrate, involucral bracts in 2 series, receptacle naked, 7–16 flowers per capitulum, ligules cream to pale yellow, achenes with 5 ribs alternating with 5 rows of pits, abruptly short-beaked, pappus of slender rays. $x = 9$, diploid. Monotypic, restricted to western North America; *G. marginata* Eaton.

364. *Malacothrix* DC.

Malacothrix DC., Prodr. 7: 192 (1838); Williams, Amer. Midl. Naturalist 58: 494–512 (1957), rev.; Davis, Madroño 44: 223–244 (1997), reg. rev.

Perennial to annual herbs, involucral bracts in 3–6 series, receptacle naked or with fragile bristles, ligules yellow or white, achenes fusiform, truncate, pappus of slender rays. $x = 9, 8, 7$, diploids and tetraploids. Twenty-one species, western North America to southern South America.

365. *Pinaropappus* Less.

Pinaropappus Less., Syn. Gen. Comp. 143 (1832); McVaugh, Contr. Univ. Michigan Herb. 9: 359–484 (1972), reg. rev.

Perennial herbs, scapose or with leaves in basal part of stem, receptacle paleaceous, ligules white or pink, achenes fusiform, tapering into short beak, pappus of numerous brownish capillary rays. $x = 9$, 8, diploids and tetraploids. Eight species, southern USA to Guatemala.

VIII.10. Subtribe Hieraciinae Cass. ex Dumort. (1827).

Leaves of various form, never entire and parallel-nerved, mostly with both branched and unbranched hairs. Achenes obovoid-obconical, not compressed, without beak. Pappus bristles scabrid-barbellate, never thick or plumose, rarely absent. Old World subtribe, with *Hieracium* also in America.

Key to the Genera

1. Pappus absent, peduncles swollen in fruit **368. *Hispidella***
– Pappus well developed, peduncles not swollen 2
2. Perennial, stoloniferous herbs 3
– Annual or perennial herbs, never stoloniferous 4
3. Achenes 4-angled, plants nearly glabrous **369. *Hololeion***
– Achenes c. 10-ribbed, plants always densely hairy **370. *Pilosella***
4. Receptacle ciliate with long hairs or scales **366. *Andryala***
– Receptacle naked or shortly fimbriate 6
5. Style branches long **367. *Hieracium***
– Style branches short **371. *Tolpis***

Genera of Hieraciinae

366. *Andryala* L.

Andryala L., Sp. Pl. 808 (1753).
Pietrosia Nyárády ex Sennik. (2000).

Perennial to annual tomentose herbs with branched and unbranched hairs, receptacle ciliate or scaly, florets yellow or orange, style branches long, achenes terete to obconical, glabrous, about 10-ribbed, pappus scabrid to barbellate. $x = 9$, diploids. Circa 25 species, Macaronesia, Mediterranean region.

367. *Hieracium* L. Fig. 47

Hieracium L., Sp. Pl. 799 (1753); Beaman, Syst. Monogr. 29: 1–77 (1990), reg. rev.
Stenotheca Monn. (1829).

Perennial herbs with branched stocks, but without stolons, leaves and stems with branched and unbranched hairs, involucral bracts in several rows, receptacle naked, florets yellow or rarely reddish, style branches long, achenes cylindric, 10-ribbed, ribs apically confluent into an obscure ring, pappus of scabrid-barbellate fragile bristles in two rows. $x = 9$, diploids, triploids, tetraploids, pentaploids. Depending on species concept, c. 90 to more than 1,000 species. Eurasia, North and South America. Numerous clones described as species.

368. *Hispidella* Barnadez ex Lam.

Hispidella Barnadez ex Lam., Encycl. 3: 134 (1789).

Annual herb with branched and unbranched hairs, involucral bracts in a single row, receptacle hairy, peduncles in fruit expanded upwards, florets yellow, inner florets much smaller, brownish, style branches long, achenes 10-ribbed, pappus absent.

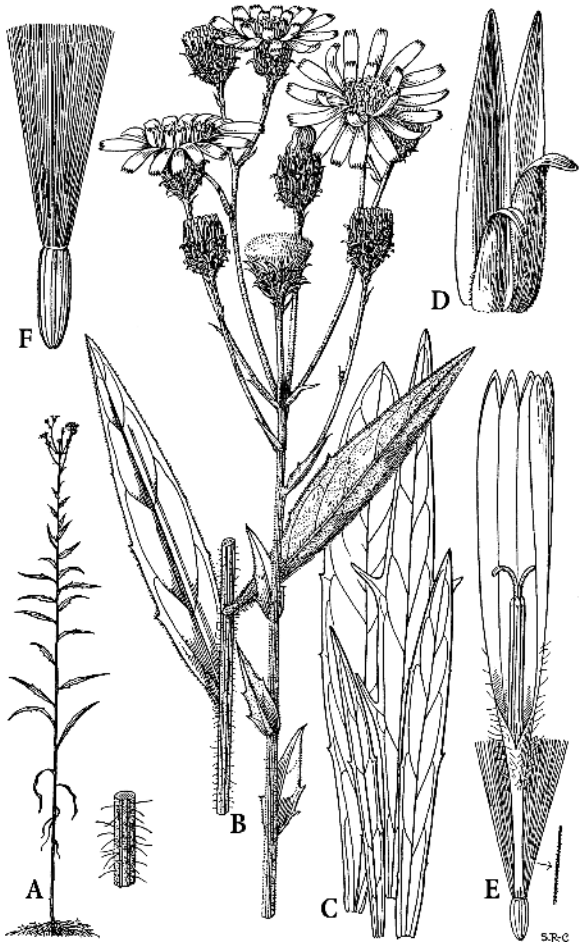

Fig. 47. Compositae-Cichorieae. *Hieracium umbellatum*. **A** Habit. **B** Middle and upper part of plant. **C** Leaf shape variation. **D** Involucral bracts. **E** Floret, part of pappus removed, pappus hair further enlarged. **F** Achene. (Ross-Craig 1963)

$x = 9$, diploid. Monotypic, restricted to Spain and Portugal; *H. hispanica* Barnadez ex Lam.

369. *Hololeion* Kitam.

Hololeion Kitam., Acta Phytotax. Geobot. 10:301 (1941).

Perennial stoloniferous herbs, nearly glabrous, involucral bracts in two rows, receptacle naked, flowers yellow, style branches long, achenes 4-angled, pappus of scabrid-barbellate bristles. $x = 8$, diploids. Three species, eastern Asia.

The stoloniferous growth form is regarded as the main argument against the recent proposal by Sennikov and Illarinova (2001) to include *Hololeion* in *Crepis*, where this character is never found.

370. *Pilosella* Vaill.

Pilosella Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 703 (1754).

Perennial herbs with stolons, with branched and unbranched hairs, capitula on more or less leafless scapes, involucral bracts in several rows, receptacle naked, florets yellow, style branches long, achenes cylindric, 10-ribbed, each rib projecting above to form a finely scalloped apex, pappus of fragile, scabrid-barbellate bristles in a single row. $x = 9$, diploids, triploids, tetraploids, pentaploids, hexaploids, heptaploids, octoploids, nonaploids, decaploids. Depending on species concept, c. 20–80 species. Eurasia, northern Africa. Numerous clones described as species.

371. *Tolpis* Adans.

Tolpis Adans., Fam. Pl. 2: 112 (1763); Mort et al., Taxon 52: 511–518 (2003), mol. phylog.

Perennial to annual herbs, rarely subshrubs, leaves mostly basal, involucral bracts in 2–3 rows, receptacle naked, florets yellow, often becoming green when dry, style branches short, inner florets often much smaller and brownish, achene ribbed, truncate at apex, pappus of scabrid-barbellate bristles or very short scales or both. $x = 9$, diploids, tetraploids, hexaploids. Circa 15 species, Macaronesia, Mediterranean region east to Iran, and south through eastern Africa to southern Africa.

VIII.11. Subtribe Hypochaeridinae Less. (1832).

Leaves of various form, never entire and parallel-veined, mostly hirsute or hispid, never with soft branched hairs. Pappus rays thick, often plumose with many to very few stiff pinnulae orientated in all directions, more rarely scabrid-barbellate, occasionally reduced or absent. Except for *Hypochaeris* (also in South America) and *Picris* (also in Aleutian Islands), an exclusively Old World subtribe (Lack 1979).

Key to the Genera

1. Pappus absent in all achenes 2
– Pappus present at least in central achenes 4
2. Outer achenes stellately patent, inner achenes straight **381. *Rhagadiolus***
– Achenes not stellately patent 3

3. Perennial, rosette of deeply dentate leaves **372. *Aposeris***
– Annual, rosette of spathulate leaves **373. *Arnoseris***
4. Pappus of central achenes often reduced to a crown-like structure **374. *Garhadiolus***
– Pappus of central achenes well developed 5
5. Median and central achenes winged **377. *Hyoseris***
– Median and central achenes not winged 6
6. Pappus of central achenes consisting of setaceous rays with few or no pinnulae **375. *Hedypnois***
– Pappus of central achenes consisting of plumose rays with many pinnulae 7
7. Receptacle paleaceous **378. *Hypochaeris***
– Receptacle naked 8
8. Achene bent, with a diaphragm, involucral bracts in a single row **382. *Urospermum***
– Achene not bent, without a diaphragm, involucral bracts in two or several rows 9
9. Anchor-shaped hairs consistently present 10
– Glabrous or various hair types present, but no anchor-shaped hairs **379. *Leontodon***
10. Outer involucral bracts conspicuously cordate **376. *Helminthotheca***
– Outer involucral bracts inconspicuous, never cordate **380. *Picris***

Genera of Hypochaeridinae

372. *Aposeris* Neck. ex Cass.

Aposeris Neck. ex Cass., Dict. Sci. Nat. 48: 427 (1827).

Perennial scapose herb, leaves pinnate with triangular-subrhombic lobes in basal rosette, involucral bracts in two rows, receptacle naked, ligules yellow, achenes obovoid, pappus absent. $x = 8$, diploid. Monotypic, Europe; *A. foetida* (L.) Less.

373. *Arnoseris* Gaertn.

Arnoseris Gaertn., Fruct. Sem. Pl. 2: 355 (1791).

Annual scapose herb, stems leafless, branched, peduncles expanded upwards, involucral bracts in a single row, receptacle naked, flowers yellow, style branches short, achenes 3–5 angled, pappus absent. $x = 9$, diploid. Monotypic, Europe; *A. minima* (L.) Schweigger & Koerte.

The unconventional placement of this genus in Hypochaeridinae is based on molecular data (Whitton et al. 1995) and on achene characters (Sennikov and Illarionova 2001).

374. *Garhadiolus* Jaub. & Spach

Garhadiolus Jaub. & Spach, Ill. Pl. Orient. 3: 119 (1849).

Annual herbs, involucral bracts in two rows, receptacle naked, florets yellow, achenes dimorphic, outer incurved, subulate, persistent and partly enclosed by the persistent involucral bracts, central incurved, beaked, caducous, apically either with a crown-like structure or with pappus bristles. $x = 5$, diploids. Two species, Caucasus, Near East, central Asia, eastern Asia.

375. *Hedypnois* Mill.

Hedypnois Mill., Gard. Dict. abr. ed. 4 (1754); Nordenstam, Bot. Notiser 124: 483–489 (1971), chrom. nos.

Annual herbs, involucral bracts in two rows, receptacle naked, florets yellow, achenes incurved, ribbed, dimorphic, outer persistent, partly or completely enclosed by the persistent involucral bracts, inner caducous, pappus of central achenes of few coarse bristles, sometimes with few pinnulae, pappus of outer achenes a crown-like structure. $x = 9, 8, 7, 6, 5, 4, 3$, diploids and tetraploids. Three species, Mediterranean region east to Iran.

376. *Helminthotheca* Vaill.

Helminthotheca Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 731 (1754); Holzapfel, Willdenowia 24: 97–218 (1994), reg. rev.

Perennial to annual herbs, with rigid anchor-shaped hairs, involucral bracts in two rows, outer ovate to cordate, inner lanceolate, receptacle naked, florets yellow, achenes somewhat heteromorphic, provided with a long beak, pappus of plumose bristles with stiff pinnulae. $x = 5$, diploids. Four species, Mediterranean region.

377. *Hyoseris* L.

Hyoseris L., Sp. Pl. 808 (1753).

Perennial to annual scapose herbs, involucral bracts in two rows, receptacle naked, florets yellow, outer achenes compressed, median compressed and winged, inner terete and winged, pappus of scales or of scales and scabrid bristles. $x = 8$, diploids. Two species, Mediterranean region.

378. *Hypochaeris* L.

Hypochaeris L., Sp. Pl. 810 (1753); Samuel et al., Amer. J. Bot. 90: 496–507 (2003), mol. phylog.; Weiss-Schneeweiss et al., Pl. Syst. Evol. 241: 171–184 (2003), karyol.
Trommsdorffia Bernh. (1800).
Fabera Sch. Bip. (1845).

Perennial to annual herbs with coarse, multicellular, unbranched hairs, involucral bracts in several

rows, receptacle scaly, florets yellow, white or pink, achenes beaked, sometimes dimorphic, pappus of plumose bristles with stiff pinnulae. $x = 6, 5, 4, 3$, diploids and tetraploids. Circa 50 species, Eurasia, northern Africa, Columbia and western Venezuela to Chile and Argentina.

Testa characters indicate that this genus may not be as homogenous as previously thought (Tegel 2002).

379. *Leontodon* L.

Leontodon L., Sp. Pl. 798 (1753); Widder, Phyton (Horn) 17: 23–29 (1975), rev.

Perennial to annual scapose herbs, rarely tuberous, variously hairy but never with anchor-shaped hairs, leaves usually in basal rosette, involucral bracts in 2 to several rows, receptacle naked, florets yellow, pappus of plumose bristles with stiff pinnulae. $x = 7, 6, 4$, diploids and tetraploids. Circa 40 species, Europe, Mediterranean region to Iran. The genus is probably not monophyletic.

380. *Picris* L. Fig. 48

Picris L., Sp. Pl. 792 (1753); Lack, Diss. Univ. Wien 116: 1–184, cvi (1975), reg. rev.; Holzapfel, Willdenowia 24: 97–218 (1994), reg. rev.

Perennial to annual herbs, with rigid anchor-shaped hairs, stems branched, involucral bracts in 2 to several rows, receptacle naked, ligules yellow, pappus of plumose bristles with stiff pinnulae, rarely reduced to crown-like structures in outer achenes. $x = 5$, diploids, tetraploids and hexaploids. Circa 50 species, Eurasia, Aleutian Islands, south to tropical Africa, east to Australia and New Zealand.

381. *Rhagadiolus* Vaill.

Rhagadiolus Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 737 (1754); Meikle, Taxon 28: 133–141 (1979), rev.; Voytenko, Bot. Zhurn. (Moscow & Leningrad) 74: 1241–1257 (1989), fruit morph.

Annual herbs, involucral bracts in 2 rows, florets yellow, achenes subulate or narrowly fusiform, straight or curved, outer persistent, stellately patent, smooth, completely enclosed by the persistent involucral bracts, inner strongly curved, caducous, often hispidulous, pappus absent. $x = 5$, diploids. Two species, Mediterranean area, Near East.

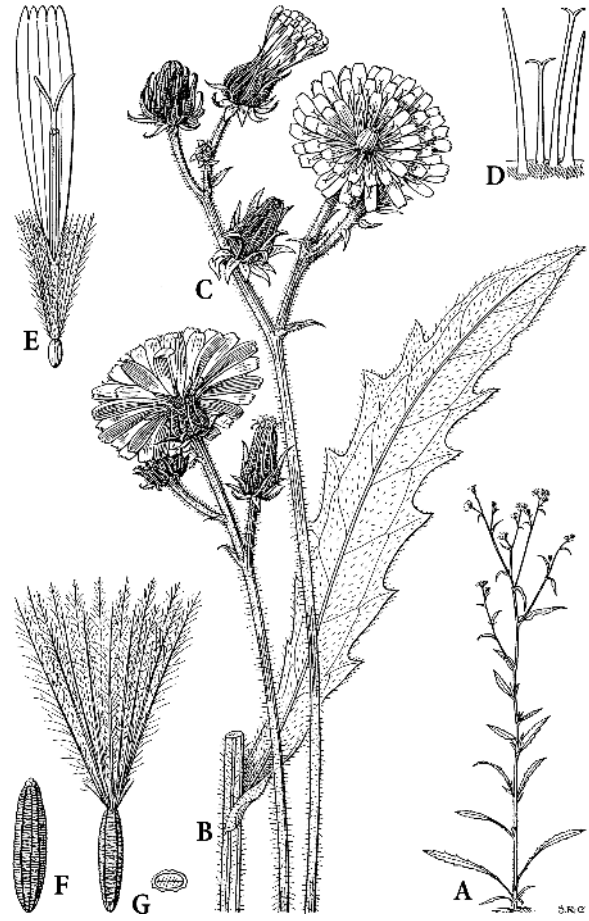

Fig. 48. Compositae-Cichorieae. *Picris hieracioides*. **A** Habit. **B** Middle cauline leaf. **C** Flowering stems. **D** Hairs on leaf margin. **E** Floret, part of pappus removed. **F** Achene with and without pappus. **G** Transverse section of achene. (Ross-Craig 1962)

382. *Urospermum* Scop.

Urospermum Scop., Intr. Hist. Nat. 122 (1777), nom. cons. prop.; Lack & Leuenberger, Pollen Spores 21: 415–425 (1979), pollen.
Tragopogonoides Vaill. (1754), nom. rej. prop.

Perennial or annual herbs, capitula solitary at the end of branches, involucral bracts in a single row, basally connate, receptacle naked, florets pale yellow, achenes with a basally swollen, hollow beak separated by a diaphragm from the proximal, compressed, conspicuously rugose embryo-containing part, pappus of plumose bristles with stiff pinnulae. $x = 7, 5$, diploids. Two species, Macaronesia, Mediterranean region, Near East.

VIII.12. Subtribe Scorzonerinae Cass. ex Dumort. (1827).

Leaves frequently entire, linear-lanceolate and parallel-veined, glabrous or tomentose, never hirsute or hispid. Pappus rays at least in basal part and in central flowers plumose, pinnulae intertwined, cottony, soft; when pappus absent, achenes with many hooked projections. Exclusively Old World subtribe.

Key to the Genera

1. Achenes with hooks or glochids, strongly incurved **385. *Koelpinia***
– Achenes without hooks or glochids, never strongly incurved 2
2. Achenes with distinct wings 3
– Achenes without wings 4
3. Achenes columnar to fusiform, with three broad wings **386. *Pterachaenia***
– Achenes compressed, with two thin wings **388. *Tourneuxia***
4. Involucral bracts in a single row 5
– Involucral bracts in two to several rows 6
5. Pappus of all achenes of many woolly-plumose rays **389. *Tragopogon***
– Pappus of marginal achenes of five scabrid rays, pappus of inner achenes with many woolly-plumose rays **384. *Geropogon***
6. Distal part of achenes densely lanate **383. *Epilasia***
– Achenes completely glabrous or completely hairy **387. *Scorzonera***

Genera of Scorzonerinae

383. *Epilasia* (Bunge) Benth.

Epilasia (Bunge) Benth. in Benth. & Hook. f., Gen. Pl. 2: 532 (1873).

Annual herbs, leaves parallel-veined, involucral bracts in a single row, florets pale yellow or violet-pink, achenes without wings, ribbed, hispid, upper portion of achene hairy, pappus of many plumose bristles, pinnulae intertwined. $x = 6$, diploids. Three species, Caucasus, Near East, central Asia.

384. *Geropogon* L.

Geropogon L., Sp. Pl. ed. 2, 1109 (1763); Díaz de la Guardia & Blanca, Blancoa 9: 31–44 (1986), rev.

Annual herb, leaves parallel-veined, involucral bracts in a single row, basally somewhat connate, florets violet or purple, in outer achenes pappus of five thick scabrous bristles, in inner achenes pappus of plumose bristles, pinnulae intertwined. $x = 7$, diploid. Monotypic, Mediterranean region to Iran; *G. hybridus* (L.) Sch. Bip.

385. *Koelpinia* Pall.

Koelpinia Pall., Reise Russ. Reich 3: 755 (1776); Nazarova, Bot. Zhurn. (Moscow & Leningrad) 66: 1755–1758 (1981), chrom. nos.

Annual herbs, involucral bracts often in a single row, basally somewhat connate, florets yellow, achenes incurved, with hooked projections or glochids, pappus absent. $x = 7, 6$, diploids, hexaploids, octoploids. Five species, Mediterranean region, Near East, central Asia.

386. *Pterachaenia* (Benth.) Lipsch.

Pterachaenia (Benth.) Lipsch., Fragm. Monogr. Roda Scorz. 2: 31 (1939); Lipschitz, Bot. Zhurn. (Moscow & Leningrad) 56: 1150–1152 (1971), rev.; Safavi, Iran. J. Bot. 8: 241–243 (2000), rev.

Annual scapose herbs, florets pale yellow, achenes with three broad whitish wings, spinulose between wings, pappus of plumose bristles, pinnulae intertwined. $x = 6$, diploid. Monotypic, restricted to Iran, Afghanistan and Pakistan; *P. stewartii* (Hook. f.) R.R. Stewart.

387. *Scorzonera* L.

Scorzonera L., Sp. Pl. 790 (1753); Lipschitz, Fragmenty k monografii roda *Scorzonera* L. 1–2 (Moskva 1935, 1939), rev.; Kamelin & Tagaev, Bot. Zhurn. (Moscow & Leningrad) 71:1672–1682 (1986), rev.; Mavrodiev et al., Taxon 53: 699–712 (2004), mol. phylog.
Podospermum DC. (1805).
Gelasia Cass. (1818).
Lasiospora Cass. (1822).
Achyroseris Sch. Bip. (1845).
Avellara Blanca & Díaz de la Guardia (1985).
Takhtajaniantha Nazarova (1990).

Perennial to annual herbs, often with massive rootstock, heads often large, involucral bracts in two or several rows, florets yellow, violet or purple, achenes fusiform, glabrous or hairy, never winged, pappus of plumose bristles, sometimes apically scabrid, pinnulae intertwined. $x = 7, 6$, diploids and tetraploids. Circa 180 species, Eurasia, northern Africa. *Scorzonera hispanica* L. (scorzonera, Spanish salsify) cultivated for edible roots.

388. ***Tourneuxia*** Coss.

Tourneuxia Coss., Bull. Soc. Bot. France 6: 395 (1859).

Annual herb, involucral bracts in two rows, florets yellow, achenes compressed, winged, pappus of plumose bristles, pinnulae intertwined, pappus somewhat laterally positioned. Monotypic, Morocco and Algeria; *T. variifolia* Coss.

389. ***Tragopogon*** L. Fig. 49

Tragopogon L., Sp. Pl. 789 (1753); Mavrodiev et al., Taxon 53:699–712 (2004), mol. phylog.

Perennial to annual herbs, leaves parallel-veined, heads large, involucral bracts in a single row, basally somewhat connate, receptacle naked, ligules yellow, violet or purple, in all achenes pappus with many plumose bristles, sometimes apically scabrid, pinnulae intertwined. $x = 6$, diploids, tetraploids and hexaploids. Circa 110 species, Eurasia, introduced into other parts of the world, there sometimes forming allopolyploids, e.g. *T. mirus* Ownbey of western North America, often precisely datable. *Tragopogon porrifolius* L. (salsify) cultivated for edible roots and for young flowering shoots ('chards').

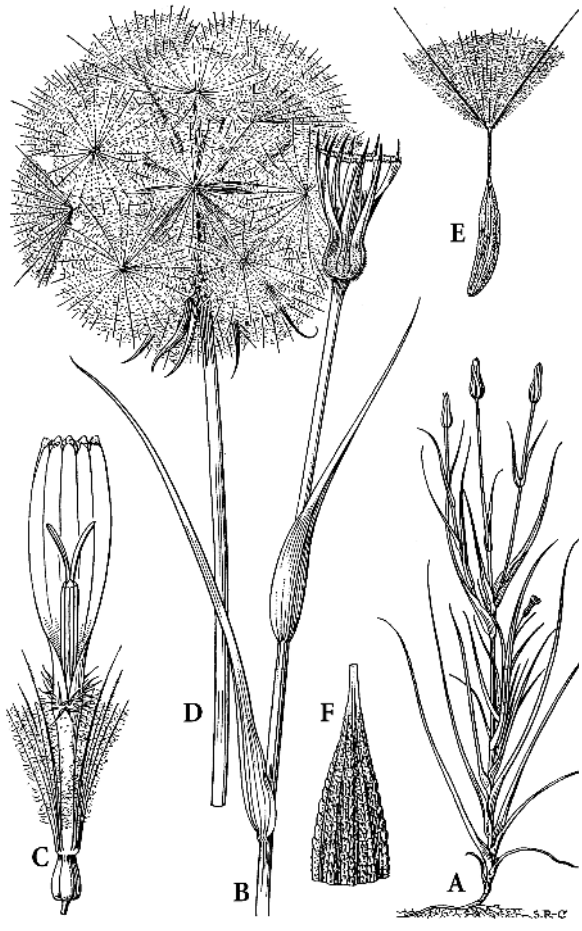

Fig. 49. Compositae-Cichorieae. *Tragopogon pratensis*. **A** Habit. **B** Flowering stem. **C** Floret, part of pappus removed. **D** Fruiting head. **E** Achene. **F** Upper part of achene. (Ross-Craig 1963)

IX. Tribe Gundelieae DC. ex Lecoq & Juillet (1831).

C. Jeffrey

Lacticiferous perennial herbs, shrubs or small trees. Leaves alternate, lamina dentate-lobulate or lobulate-pinnatisect, unarmed or very spiny. Capitula homogamous, discoid, many-flowered, monomorphic and solitary or 1-flowered, dimorphic and aggregated into syncephalia; phyllaries multiseriate, imbricate and free or uniseriate and connate; receptacle epaleaceous. Florets all perfect or perfect and functionally staminate; corolla regular, with broadened, deeply 5-lobed limb, lobes narrow; stamens 5; filaments glabrous; anthers calcarate, basally sagittate, caudate or ecaudate; endothecial cell wall thickenings polarized. Pollen spiny. Style slender, arms short to long, flattened, obtuse to acute, hirtellous or papillose dorsally. Achenes oblong or ovoid, glabrous or sericeous-villous, shed free or enclosed in syncephalium; pappus of multiseriate bristles or coroniform.

Two genera and two species, north-western Africa to central Asia.

The re-establishment of the tribe Gundelieae, its present circumscription, and the clarification of its systematic position have resulted mainly from recent molecular systematic studies (Karis et al. 2001; Funk and Chan 2003). Prior to these, the constituent genera had been variously placed systematically. *Gundelia* had usually been included, albeit with some reservation, in Arctotideae, from which it differs in its vernonioid style and pollen grain structure (Robinson 1994) – liabioid, similar to that of the basal Cichorieae genus *Scolymus* L. *Warionia* has generally been regarded as a member of Mutisieae by, for example, Cabrera (1977) but was excluded from that tribe by Hansen (1991b) on the basis of its rugose, not mutisioid, petal epidermis pattern and vernonioid style. The similarity of its pollen to that of *Hesperomannia* A. Gray of Vernonieae, noted by Marticorena and Parra (1975),

had already suggested its position as a member of Cichorioideae, as did the morphological cladistic study of Karis et al. (1992). The sister-group relationship of *Gundelia* to Cichorieae was demonstrated by Karis et al. (2001) and confirmed by Funk and Chan (2003), who also established the sister-group relationship of *Warionia* to *Gundelia*. The nature of the unique synflorescence of *Gundelia* was established by Claßen-Bockhoff et al. (1989).

Key to the Genera

1. Leaves spiny; perennial herb; capitula 1-flowered, aggregated into syncephalia **391. *Gundelia***
– Leaves not spiny; shrub or small tree; capitula large, solitary **390. *Warionia***

390. *Warionia* Benth. & Coss.

Warionia Benth. & Coss., Bull. Soc. Bot. France 19: 165 (1872); Audissou, Succulentes 21: 30–32 (1998) & Brit. Cact. Succ. J. 17: 124–126 (1999), col. illustr.

Shrub or small tree, aromatic; leaves coarsely dentate-lobulate, unarmed. Capitula solitary, terminal, large, discoid, many-flowered; phyllaries multiseriate, imbricate, lanceolate, acute, free. Florets all perfect. Corolla yellow, tube slender; anthers caudate, tails short, basally slightly fringed; apical appendage rather long, adaxially somewhat keeled. Style base swollen, arms long, slender, acute, dorsally hirtellous with narrow acute hairs extending to below bifurcation. Achenes obovoid, densely sericeous with long twin hairs; pappus of long, multiseriate, scabrid bristles. One species, *W. saharae* Benth. & Coss., North Africa (Sahara).

391. *Gundelia* L.

Gundelia L., Sp. Pl.: 814 (1753); Kamelin, Bot. Zhurn. (Moscow & Leningrad) 72: 974–978 (1987), distrib.; Nersesyan & Mekhakyan, Fl. Rastit. Rast. Arm. S.S.R. 12: 43–45 (1999), palynol.

Robust perennial herb; leaves coarsely lobulate-pinnatisect, very spiny. Capitula 1-flowered, aggregated into 5–7-capitulate syncalathia; floret of central capitulum perfect, florets of the 4–6 outer capitula functionally staminate; syncalathia further aggregated into a large, somewhat elongated terminal head; phyllaries uniseriate, connate, 5 in central capitulum, 2 in outer capitula. Corolla greenish, yellow, white, pink or red-purple, tube short; anthers ecaudate. Pollen with broad columellae, caveate. Styles slender, shaft hirtellous in upper part, arms rather short, thick, rather obtuse, dorsally hirtellous. Achenes oblong, glabrous, each enclosed by the accrescent, lignified, apically spiny phyllaries of the syncalathium, forming a 1-seeded disseminule; pappus a denticulate-fimbriate corona. $n = 9$. One species, *G. tournefortii* L., Middle East and Turkey to central Asia. Other described species are here considered synonymous.

X. Tribe Arctotideae Cass. (1819).

P.O. Karis

Leaves entire or often lobed to pinnatisect, spinulose to spiny or unarmed, commonly with woolly hairs at least beneath, sometimes also with multiseptate, glandular or eglandular hairs, or longitudinally striate hairs. Latex present in Gorteriinae. Capitula frequently radiate and heterogamous, sometimes discoid and homogamous, generally solitary, rarely corymbose or axillary; involucral bracts usually in several rows, imbricate, free or ± connate; ray florets 3- or 4-lobed, fertile, sterile or neuter, sometimes with staminodes, often yellow; disc florets deeply to more shallowly 5-lobed, perfect or sometimes functionally male, generally yellow, lobe veins generally continuous; anthers calcarate, caudate (most Gorteriinae) or ecaudate (Arctotidinae), endothecial tissue with outer periclinal and both anticlinal walls thickened, polarised (some Gorteriinae) or radial (all Arctotidinae) or without such patterns (most Gorteriinae), apical appendage firm (Gorteriinae, *Hoplophyllum*, *Platycarpha*) or soft (Arctotidinae, *Eremothamnus*, *Heterolepis*), usually cordate-ovate and rather short; pollen caveate, echinate, echinolophate or psilolophate; style vernonioid or ± thickened apically, with short or long style branches, often with longer style hairs in a ring well below the bifurcation (arctotoid); cypselae generally ± obovoid, rarely oblong-elliptic, prismatic or obconical, frequently distinctly ribbed, often sericeous-villous with twin hairs, or glabrous. Pappus of scales, rarely of bristles or absent.

Arctotideae comprise 17 genera and about 215 species.

Most recent interpretations of tribal interrelationships of Asteraceae comprise a monophyletic subfamily Cichorioideae s. str., where the two tribes Vernonieae and Liabeae appear as sisters (Bremer

1996; Karis et al. 2001; Panero and Funk 2002; Funk et al. 2004). Apart from the latter grouping, the relations within subfamily Cichorioideae s. str. remain unclear and it is consequently not possible to judge if Arctotideae are sister to Cichorieae, or if any of these tribes are more closely related to Vernonieae plus Liabeae. *Hoplophyllum* and *Eremothamnus* were placed as subfam. Cichorioideae incertae sedis by Bremer (1994). Subsequent studies clearly position *Eremothamnus* (reviewed by Bremer 1996) and its sister group *Hoplophyllum* (Karis et al. 2001; Funk et al. 2004) with Arctotideae. Apart from the strong support by molecular data (Karis et al. 2001), these genera share two unique synapomorphies in their anther endothecial cells with wall thickenings in transverse bands confined to the lower part of each cell, and the 2- to 3-celled sweeping hairs. On the other hand, the thistle-like *Gundelia*, placed by Bremer (1994) in Arctotideae-Gorteriinae, has been shown to be most closely related to Cichorieae (Karis et al. 2001), and it is hence not treated here. *Platycarpha*, another thistle-like plant from South Africa, is tentatively accepted in the tribe, since it shares the scaly pappus, similar pericarp development (Reese 1989) as well as the arctotoid style with Arctotideae. However, molecular data suggest that *Platycarpha* may be closer to the Vernonieae-Liabeae clade (Funk et al. 2004). Styles with a ring of sweeping hairs below the bifurcation are found also in Cynareae. This previously was used as evidence for close relationship between the tribes (Lessing 1832; Bremer 1987). This view was strengthened by the common thistleoid habit. *Heterolepis* has arctotoid disc floret styles, and shares features with both the subtribes recognised here. At this point, it is not evident which features should be regarded as synapomorphies, and the possibility that *Heterolepis* belongs elsewhere in Cichorioideae s. str. must also be considered (Funk et al. 2004). The 3-lobed ray florets (as in subtribe Arctotidinae) possibly are a plesiomorphy, and this is also the case with the rather long, but not markedly soft anther apical appendages. *Heterolepis* has a long filament collar, unlike Arctotidinae, but the cells are inconspicuously reinforced, as in Arctotidinae. The endothecial cells often have no lateral pattern on the walls (on anticlinal walls) or some are polarised (as in Gorteriinae), and the involucral bracts become partly connate (as in Gorteriinae), but are obtuse and apically scarious (as in Arctotidinae). As circumscribed here, Arctotideae do not possess a single morphological synapomorphy, but are diagnosed by a combination of morphological features which are not present in all included genera, as well as partly by molecular data (Karis et al. 2001; Funk et al. 2004). Members of Arctotideae can be recognised as often radiate species with arctotoid disc floret styles, and often with a scaly pappus. *Eremothamnus* and *Hoplophyllum* differ by their bristly pappus and vernonioid disc florets styles, whereas both *Platycarpha* and *Hoplophyllum* have discoid capitula, although those of *Platycarpha* are arranged in secondary heads. *Eremothamnus* and subtribe Arctotidinae share the soft anther apical appendages, but the appendages are longer and less soft in the former. The pollen morphology of Arctotideae has been investigated by several authors (Stix 1960; Leins 1970; Leins and Thyret 1971; Skvarla et al. 1977; Robinson 1994). Interpretations, however, differ (Leins and Thyret 1971; Skvarla et al. 1977), and the significance of pollen characters for infratribal and intratribal relationships are difficult to ascertain (Bremer 1987). For example, the pollen wall is often described as caveate, i.e. the foot layer is separated by cavities (Skvarla et al. 1977), but the cavities in Arctotideae pollen walls may not be homologous with the strictly interapertural cavities prevailing in subfamily Asteroideae (Skvarla et al. 1977; Bremer 1987). It can be noted, however, that at least the conspicuous spine channels occur in *Hoplophyllum* (Robinson 1994), *Eremothamnus* (Leins 1970) as well as in all other Arctotideae taxa investigated by Skvarla et al. (1977).

The basic chromosome number varies to some extent among genera, and at least *Haplocarpha* and *Gazania* contain polyploid species.

All genera occur in Africa, especially in South Africa, except *Cymbonotus* which is native to South Australia. Subtribal division is not entirely clear, although most genera can quite readily be placed in either of the commonly accepted and putatively monophyletic subtribes Arctotidinae and Gorteriinae. With their slightly aberrant morphology, *Eremothamnus*, *Hoplophyllum*, *Platycarpha* and *Heterolepis* are left as Arctotideae incertae sedis. All these taxa need further study in order to elucidate their exact relationships, despite the elaborate molecular study by Funk et al. (2004). Various morphological characters diagnose the two subtribes Arctotidinae and Gorteriinae, and some of these can be assumed to be synapomorphies. Some species of Arctotideae are used as ornamentals. Most common are hybrids originating from *Gazania krebsiana*, *G. linearis* and *G. rigens*, which are cultivated all over the world.

Key to the Subtribes and Unplaced Genera

1. Pappus of barbellate bristles, or of barbellate-subplumose bristle-like, subulate scales 2
– Pappus of scales, never bristle-like, or occasionally pappus absent 4
2. Capitula discoid **394. *Hoplophyllum***
– Capitula radiate 3
3. Capitula sessile; involucral bracts spine-tipped; pappus of scabrid-barbellate bristles **392. *Eremothamnus***
– Capitula pedunculate; involucral bracts unarmed; pappus of barbellate-subplumose bristle-like, subulate scales **393. *Heterolepis***
4. Capitula discoid, in secondary heads ± sessile in a leaf rosette; florets purple **395. *Platycarpha***
– Capitula generally radiate, not in secondary heads; if discoid, then florets yellow 5
5. Involucral bracts free, often obtuse, innermost often apically scarious; ray florets 3-lobed, mostly 4-veined, female (rarely neuter), disc floret lobes generally < 4 times as long as wide, without sclerified margins **1. Subtribe Arctotidinae** (p. 202)
– Involucral bracts more conspicuously connate, acute, sometimes spine-tipped, ray florets 4(–2)-lobed, sterile or neuter, disc floret lobes generally 4–10 times as long as wide, mostly with sclerified margins **2. Subtribe Gorteriinae** (p. 204)

Arctotideae Incertae Sedis

392. *Eremothamnus* O. Hoffm.

Eremothamnus O. Hoffm., Bot. Jahrb. 10: 278 (1889); Karis, Taxon 41: 193–198 (1992), rev.; Karis et al., Taxon 50: 105–114 (2001), phylog.; Funk et al., Taxon 53: 637–655 (2004), phylog.

Small woolly shrub with obovate, entire or apically 3–5-dentate-spiny, spine-tipped, fleshy leaves. Capitula sessile, radiate. Involucral bracts chartaceous, spine-tipped. Ray florets female, fertile, with staminodes, 3-lobed. Anthers caudate, appendage ± soft, endothecial cells with transverse bands in lower half of cells. Style vernonioid, with short 2–3-celled hairs. Cypselae densely sericeous. Pappus of stout, scabrid-barbellate bristles. One species, *E. marlothianus* O. Hoffm., Namibia.

393. *Heterolepis* Cass.

Heterolepis Cass., Bull. Soc. Philom.: 26 (1820), nom. cons.

Shrublets, sometimes scented, with linear-oblong, ericoid, entire or remotely dentate, unarmed leaves. Capitula pedunculate, radiate. Involucral bracts in 2–3 rows, somewhat connate at base, outer lanceolate, foliaceous and acute, inner rounded-truncate, apically scarious and laciniate. Ray florets female, fertile, generally with staminodes, with a filiform lobe ventrally in the sinus of the tube, 3-lobed. Anthers caudate, appendage somewhat soft, endothecium unreinforced laterally or polarised. Style slender, with rather short style branches, apical portion not or only slightly thickened and with short hairs mainly at the border to the shaft. Cypselae densely sericeous. Pappus of stout, subulate, bristle-like, marginally barbellate or subplumose scales in 2 rows. $2n = 20$. Three species, South Africa.

394. *Hoplophyllum* DC.

Hoplophyllum DC., Prodr. 5: 73 (1836); Karis, Taxon 41: 193–198 (1992), rev.; Karis et al., Taxon 50: 105–114 (2001), phylog.; Funk et al., Taxon 53: 637–655 (2004), phylog.

Shrubs with linear, entire, terete or flattened, sparsely dentate-spiny, spine-tipped, longitudinally striate, grooved hard leaves. Capitula sessile, discoid. Involucral bracts chartaceous, spine-tipped. Anthers caudate, endothecial cells with transversal bands in lower half of cells. Styles vernonioid, with short 2–3-celled hairs. Cypselae densely sericeous. Pappus of stout, scabrid-barbellate bristles. $2n = 18$. Two species, South Africa.

395. *Platycarpha* Less.

Platycarpha Less., Linnaea 6: 688 (1831); Funk et al., Taxon 53: 637–655 (2004), phylog.

Perennial herbs with rosulate, entire, obovate-oblanceolate or dentate to pinnatisect, unarmed or spinulose leaves. Capitula crowded in a large, sessile secondary head in the centre of the leaf rosette; each capitulum few-flowered, discoid. Involucral bracts herbaceous to chartaceous, innermost resembling paleae. Florets purple. Anthers often apically emarginate, endothecium polarised or sometimes not reinforced laterally. Style slender, with rather short style branches, apical portion not or only slightly thickened and with short hairs mainly at the border to the shaft. Cypselae oblong, prismatic, transversely rugose, with some apically curled or hooked twin hairs at the base. Pappus of scales in 1–2 rows. Three species, South Africa.

X.1. Subtribe Arctotidinae (Cass.) Dumort. (1819).

Leaves unarmed. Scapes woolly, sometimes also with reddish-septated multiseptate hairs. Capitula radiate. Involucral bracts free, outer with foliaceous

tips, inner obtuse with scarious tips, ray florets 3-lobed, disc florets generally shallowly lobed, styles often markedly thickened apically. Anthers distinctly ecaudate, apical appendages usually obtuse, rounded, soft, ± wrinkled, endothecium radial, collar generally inconspicuous, cells not reinforced. The supposed monophyly of subtribe Arctotidinae is supported by the short, soft and wrinkled anther apical appendages, the rather inconspicuous filament collar, the radial endothecial tissue, as well as by the apically conspicuously thickened disc floret styles. The disc corollas are usually more shallowly lobed than in the taxa outside Arctotidinae, and the lobes are generally slightly less than four times as long as wide. This might be an additional synapomorphy for the subtribe but requires investigation of a larger sample of material. The largest genus *Arctotis* is in need of revision, but it should also be studied in relation to the other genera of the subtribe, where especially the limit against *Arctotheca*, *Cymbonotus*, *Dymondia* and *Haplocarpha* must be considered (McKenzie et al. 2005).

Key to the Genera

1. Ray florets neuter **396. *Arctotheca***
– Ray florets female 2
2. Mat-forming; capitula sessile **399. *Dymondia***
– Not mat-forming; capitula pedunculate or scapose 3
3. Capitula c. 10 mm wide; disc floret lobe venation discontinuous; South Australia **398. *Cymbonotus***
– Capitula >> 10 mm wide; disc floret lobe venation continuous; Africa 4
4. Leaves not conspicuously dentate, cypselae strongly ribbed, often with concavities between three dorsal ribs **397. *Arctotis***
– Leaves conspicuously dentate with broad teeth, cypselae thinly ribbed, without concavities **400. *Haplocarpha***

Genera of Arctotidinae

396. *Arctotheca* Vaill.

Arctotheca Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 604 (1754); Lewin, Feddes Repert. Beih. 11: 1–95 (1922), rev.

Perennial or sometimes annual herbs with rosulate, entire or mostly lobed to pinnatifid leaves. Capitula pedunculate. Ray florets neuter, yellow or pale yellow, sometimes darker towards the base of the lamina; disc floret lobes apically often with an abaxial, thick, deltoid, usually vividly coloured, almost blackish projection. Cypselae rather thinly ribbed mainly dorsally, densely to sparsely villous or glabrous. Pappus of small scales or absent. $2n = 18$. Four species, South Africa, Mozambique.

397. *Arctotis* L. Fig. 50

Arctotis L., Sp. Pl. 922 (1753); Lewin, Feddes Repert. Beih. 11: 1–95 (1922), rev.
Venidium Less. (1831).

Annual or perennial herbs, shrublets or shrubs with entire or lobed to pinnatisect leaves. Capitula pedunculate. Ray florets yellow, orange, cream, white, pink, purple, violet or blue; inner disc florets sometimes female-sterile, lobes sometimes apically with an abaxial, thick, deltoid, usually vividly coloured, almost blackish projection. Cypselae ventrally smooth or rugose and without ribs, dorsally with 3–5 strong ribs or wings sometimes forming 2 dorsal furrows or concavities at maturity, sericeous or pilose or glabrous, often with a basal tuft of long hairs. Pappus of 1–2 rows of large or small scales, sometimes absent. $2n = 18$. Around 60 species, South Africa, Namibia, Angola.

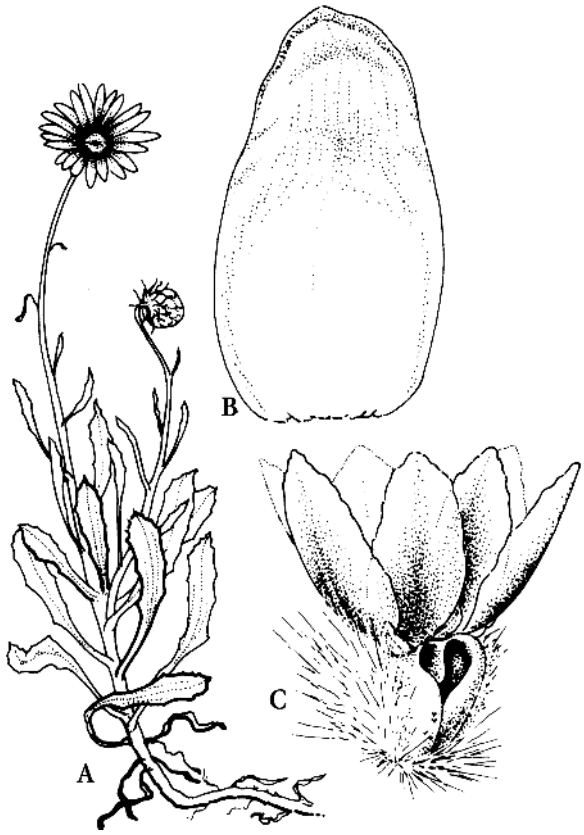

Fig. 50. Compositae-Arctotideae. *Arctotis stoechadifolia*. **A** Habit. **B** Involucral bract. **C** Cypsela. (Walsh and Entwisle 1999)

398. *Cymbonotus* Cass.

Cymbonotus Cass., Dict. Sci. Nat. 35: 397 (1825).

Annual or perennial herbs with rosulate, dentate to lobed or pinnatifid leaves. Capitula pedunculate or scapose, up to c. 10 mm wide. Ray florets with staminodes; disc florets with discontinuous lobe veins. Cypselae with 2 lateral and 2 dorsal ribs, transversely rugose ventrally and between the ribs, glabrous. Pappus absent. Three species, South Australia.

399. *Dymondia* Compton

Dymondia Compton, J. S. African Bot. 19: 110 (1953).

Mat-forming perennial with rosulate, linear-oblanceolate, entire or sinuate-dentate leaves. Capitula sessile. Involucral bracts without scarious appendages. Ray florets sometimes with staminodes; disc floret lobes apically often irregularly 3-lobed. Style branches apically shallowly 3-lobed. Cypselae glabrous. Pappus of 2 rows of ovate-acuminate, laciniate scales. One species, *D. margaretae* Compton, South Africa.

400. *Haplocarpha* Less.

Haplocarpha Less., Linnaea 6: 90 (1831); Lewin, Feddes Repert. Beih. 11: 1–95 (1922), rev.
Landtia Less. (1832).

Tufted or mat-forming perennials with ± rosulate, entire or lobed to pinnatifid, pinnately or sometimes palmately veined leaves; leaf teeth often broad. Capitula scapose. Ray florets dorsally often reddish or greenish; inner disc florets sometimes female-sterile. Cypselae rather thinly ribbed, sometimes transversely rugose, sericeous or glabrous, although mostly with a tuft of long hairs at the base. Pappus of 2 to many rows of subulate-linear, hyaline scales or absent. $2n$ = 10, 12, 18. Eight species, southern and eastern Africa north to Ethiopia.

X.2. Subtribe Gorteriinae Benth. (1873).

Leaves spiny, or unarmed and then often with longitudinally striate hairs; receptacle deeply alveolate, sometimes becoming lignified at anthesis; involucral bracts connate at least at the base (free in *Didelta*), spiny or mucronate, often acute; ray florets sterile or neuter, 4(–2)-lobed, disc corolla lobes generally sclerified marginally along the veins; anthers caudate or ecaudate, apical anther appendages usually acute and firm, endothecium usually without lateral wall thickenings or with some polarised cells, collar conspicuous, with reinforced cells; styles slightly thickened above or not. Subtribe Gorteriinae is most certainly a monophyletic group, as evidenced by the often connate involucral bracts, the deeply alveolate receptacles, the often 4-lobed ray florets, and the sclerified disc floret lobe margins. A comparison of the length/width ratio of the disc corolla lobes reveals that the corollas are more deeply lobed than those of Arctotidinae, but this condition must be considered plesiomorphic. The subtribe comprises two sister groups, a *Berkheya* clade which is supported by molecular data (Funk et al. 2004) and by spiny leaves and mamillate style hairs (Karis 2006). In this clade, *Berkheya* is paraphyletic in relation to *Cullumia*, *Cuspidia*, *Didelta* and *Heterorhachis*. The sister group includes *Gazania*, *Gorteria* and *Hirpicium*, and is supported by molecular data as well as by longitudinally striate leaf/scape hairs, fringed apical anther appendages, "Gazania-type" pollen, and subulate-ensiform style hairs (Karis 2006). *Hirpicium* is paraphyletic in relation to *Gazania* and *Gorteria*.

Key to the Genera

1. Outer part of receptacle with thick-walled cavities, becoming lignified, inner part membranous 2
– Receptacle uniform, becoming entirely lignified or not 3
2. Plants unarmed; leaves entire; outer involucral bracts 3–5, large, broadly ovate to ovate, entire; receptacle breaking into parts each adnate to one outer bract at maturity **404. *Didelta***
– Plants armed; leaves pinnatisect; outer involucral bracts lanceolate to narrowly triangular; receptacle remaining unbroken at maturity **407. *Heterorhachis***
3. Leaves and/or involucral bracts spiny, involucral bracts connate at the base; apical anther appendages with entire margins 4
– Leaves and involucral bracts unarmed, but sometimes hispid and/or mucronate; involucral bracts connate into a lignified cup; apical anther appendages with ± fringed margins 6
4. Annual herb **403. *Cuspidia***
– Perennial herbs, shrublets or shrubs 5
5. Pappus absent or rarely present but very inconspicuous **402. *Cullumia***
– Pappus present **401. *Berkheya***
6. Seeds germinating from within old capitula; cypselae without swollen cells; pappus of minute scales hidden among the twin hairs **406. *Gorteria***
– Seeds not germinating within old capitula; cypselae with longitudinal rows of swollen cells; pappus conspicuous 7

7. Latex not conspicuous; pappus scales in two distinctly unequal rows, outer much longer than inner, overlapping, or sometimes in a single row **408. *Hirpicium***
– Latex often copious; pappus scales in two subequal rows, outer row not overlapping **405. *Gazania***

Genera of Gorteriinae

401. *Berkheya* Ehrh. Fig. 51

Berkheya Ehrh., Beitr. 3: 137 (1788), nom. cons.; Roessler, Mitt. Bot. Staatssamml. München 3: 71–500 (1959), 11: 91–99 (1973), rev.
Carlinoides Vaill. (1754), nom. rej. prop.

Perennial herbs or shrubs with entire or mostly dentate to pinnatisect, spiny or spinulose leaves. Capitula generally radiate, solitary or corymbose, rarely axillary or umbellate. Involucral bracts connate at base, entire or lobed, spiny. Outer periclinal wall of endothecial cells sometimes with large, irregularly rounded pores apically, or periclinal wall rarely ± displaced towards the connective-facing side of the cell. Cypselae more or less distinctly ribbed, densely to sparsely sericeous or glabrous, entirely enclosed in the receptacle. Pappus of subequal or unequal scales generally in 1–2 rows. $2n$ = 14, 16. Around 80 species, southern and tropical Africa north to Nigeria and Ethiopia.

402. *Cullumia* R. Br.

Cullumia R. Br., Ait. Hort. Kew ed. II. 5: 137 (1813); Roessler, Mitt. Bot. Staatssamml. München 3: 71–500 (1959), rev.

Shrublets or shrubs with densely arranged, rigid, entire and often rather small, marginally conspicuously ciliate to spinulose leaves, often with a conspicuous sclerified margin, sometimes decurrent. Capitula sessile, solitary, terminal. Involucral bracts connate at base, outermost foliaceous, inner serrulate, with herbaceous patches at the base. Endothecial cells with thickening on outer periclinal wall, but often ± displaced towards the connective-facing side of the cell. Cypselae oblong-ellipsoid, smooth, glabrous or very rarely minutely pilose, entirely enclosed in the receptacle. Pappus absent or rarely very inconspicuous. Fifteen species, South Africa.

403. *Cuspidia* Gaertn.

Cuspidia Gaertn., Fruct. 2: 454 (1791); Roessler, Mitt. Bot. Staatssamml. München 3: 71–500 (1959), rev.

Annual herb with dentate to lobed, spiny leaves. Capitula mostly sessile. Involucral bracts connate into a crateriform cup, becoming lignified and enclosing the cypselae after anthesis. Cypselae sericeous. Pappus of ciliate to barbellate, subulate scales. One species, *C. cernua* (L. f.) B.L. Burtt, South Africa.

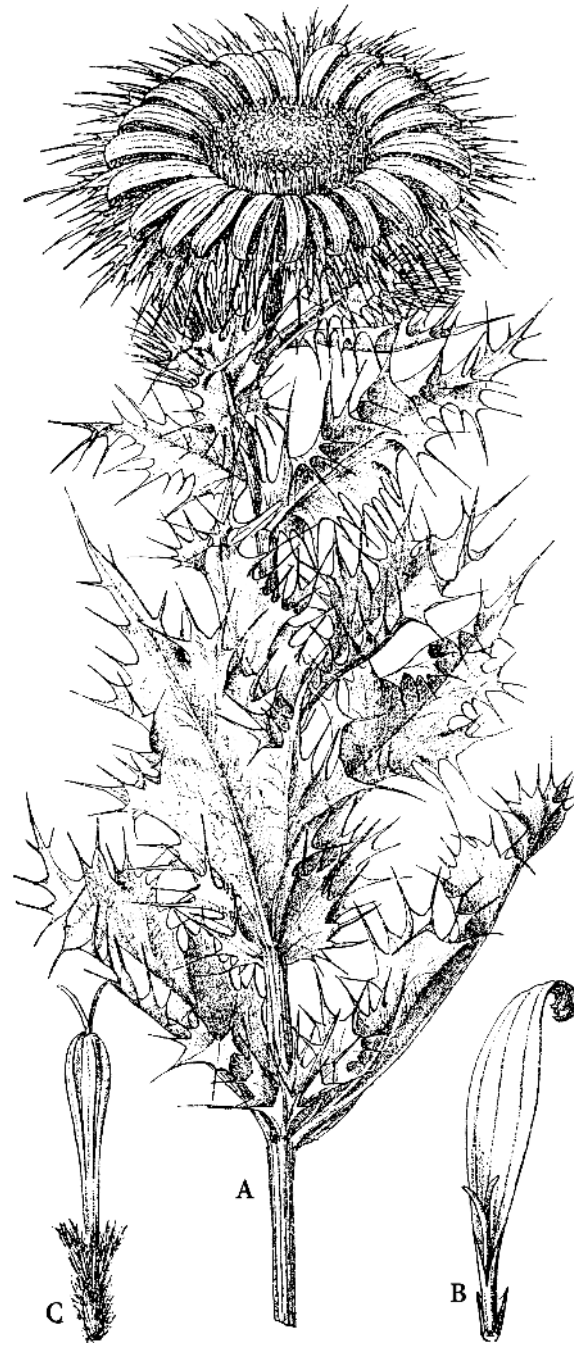

Fig. 51. Compositae-Arctotideae. *Berkheya horrida*. **A** Habit. **B** Ray floret with receptacular bract. **C** Disc floret and cypsela. (Muschler 1911)

404. *Didelta* L'Hér.

Didelta L'Hér., Stirp. Nov.: 55. (1785), nom. cons.; Roessler, Mitt. Bot. Staatssamml. München 3: 71–500 (1959), rev.

Shrublets, shrubs, or rarely small trees with entire, often opposite, mostly unarmed leaves. Capitula sessile or pedunculate. Involucral bracts dimorphic, free, outer row of 3–5 large, broadly ovate-triangular bracts, inner row of several ovate-lanceolate bracts. Receptacle at maturity breaking into 3–5 outer parts and 1 central part enclosing the cypselae, outer parts adnate to 1 of the outer involucral bracts and becoming thickened and lignified, central part membranous. Cypselae sparsely sericeous or glabrous. Pappus of lanceolate-subulate, serrulate to ciliate scales. Two species, South Africa, Namibia.

405. *Gazania* Gaertn.

Gazania Gaertn., Fruct. 2: 451 (1791), nom. cons.; Roessler, Mitt. Bot. Staatssamml. München 3: 71–500 (1959), 11: 91–99 (1973), rev.

Perennial or rarely annual herbs or subshrubs with often rosulate, unarmed, entire to pinnatisect and then often long-petiolate leaves. Leaf hairs small to large, longitudinally striate, often only marginal. Capitula pedunculate or scapose. Scape ± glabrous, rarely with small, longitudinally striate hairs or floccose. Involucral bracts connate into a campanulate-cylindrical cup. Ray florets yellow, orange or reddish with a blackish basal spot and a blackish dorsal stripe. Apical anther appendages ± fringed marginally, endothecial cells with inner anticlinal wall thickened, with no thickenings on outer periclinal wall. Cypselae with longitudinal rows of swollen cells, sericeous, not enclosed in the receptacle. Pappus of linear-subulate, subequal scales in 2 rows. $2n = 10, 12, 14$. Seventeen species, South Africa, Namibia, one species extending into Tanzania and another into Mozambique.

406. *Gorteria* L.

Gorteria L., Syst. ed. 10: 1229 (1759); Roessler, Mitt. Bot. Staatssamml. München 3: 71–500 (1959), 11: 91–99 (1973), rev.

Erect or sprawling annual herbs germinating from within old capitula, with unarmed, entire or dentate to pinnatifid leaves. Stems and leaves with coarse, rigid, longitudinally striate hairs with a multicellular base. Capitula solitary or axillary, pedunculate. Involucral bracts connate into a more or less urceolate cup, becoming lignified and enclosing the cypselae after anthesis. Ray florets yellow or reddish, sometimes with a blackish basal spot (bulging in *G. diffusa* Thunb.) and a blackish dorsal stripe; most disc florets female-sterile, with large or smaller spine-like hairs on the lobes. Apical anther appendages ± fringed marginally, endothecial cells with inner anticlinal wall thickened, with no thickenings on outer periclinal wall. Cypselae apically sericeous. Pappus of minute scales, hidden among the cypsela hairs. Three species, South Africa, Namibia.

407. *Heterorhachis* Sch. Bip. ex Walp.

Heterorhachis Sch. Bip. ex Walp., Rep. 6: 278 (1847); Roessler, Mitt. Bot. Staatssamml. München 3: 71–500 (1959), rev.

Shrub with pinnatisect, spiny leaves. Capitula in terminal racemose clusters. Involucral bracts somewhat connate at the base, in about 3 rows, outer and median foliaceous, median row much longer than outer and inner, ± spreading, innermost ciliate-margined, scarious. Receptacle with the outer parts becoming thickened and lignified at maturity, central part membranous. Outer periclinal wall of endothecial cells sometimes with large, irregularly rounded pores apically. Cypselae obconical, sparsely sericeous or glabrous, entirely enclosed in the receptacle. Pappus of lanceolate-subulate, serrulate to ciliate scales. One species, *H. aculeata* (Burm. f.) Roessler, South Africa.

408. *Hirpicium* Cass.

Hirpicium Cass., Bull. Soc. Philom.: 27 (1820); Roessler, Mitt. Bot. Staatssamml. München 3: 71–500 (1959), 11: 91–99 (1973), rev.
Berkheyopsis O. Hoffm. (1892).

Annual or perennial herbs, subshrubs or shrubs with entire or dentate to pinnatisect, sometimes mucronate leaves. Stems and leaves with coarse, rigid, longitudinally striate hairs with or without a multicellular base. Involucral bracts connate into a cupuliform to broadly campanulate-obconical cup, generally foliaceous, often ciliate-margined. Disc floret lobes sometimes with large or small spine-like hairs. Apical anther appendages ± fringed marginally, endothecial cells with inner anticlinal wall thickened, with no thickenings on outer periclinal wall. Cypselae obconical, more or less ribbed, with longitudinal rows of swollen

cells, sericeous, partly enclosed in the receptacle. Pappus generally of 2 distinct rows of 10+10 broad scales, outer much longer than inner; inner row sometimes absent. $2n = 10$. Twelve species, southern and eastern Africa north to Ethiopia.

XI. Tribe Corymbieae Panero & V.A. Funk (2002).

B. Nordenstam

Scapose perennial herbs with a stout, silky-hairy rhizome. Leaves alternate, mainly rosulate, sessile, entire, linear-lanceolate to narrowly elliptic-oblong, flat or conduplicate, parallel-veined, ± coriaceous, sometimes cartilaginous or herbaceous, acute to acuminate, narrowed to base, glabrous or pubescent, sometimes glandular; cauline leaves gradually smaller. Capitula pedunculate or rarely sessile, several to many in corymbs to panicles terminating a stout erect bracteate scape ('corymbophore'), discoid, single-flowered. Involucre cylindrical, calyculate, involucral bracts 2, enclosing the floret, narrowly oblong to lanceolate, flat or keeled, 3-nerved, glabrous or glandular (viscid when fresh), sometimes scabrid, often with a purplish tinge, apically 2–3-fid or fimbriate; outer (calyculus) bracts 2 or 3, short. Receptacle flat, nude. Floret hermaphrodite; corolla 5-lobed, pink to purplish or white; corolla lobes linear to oblong, spreading, apically cucullate and dorsally papillate. Stamens 5; anthers tetrasporangiate with blackish thecae, shortly sagittate; apical appendage reduced. Pollen grains caveate. Style bifurcate with linear branches; style branches and uppermost part of shaft hairy. Cypselae narrowly oblong, somewhat compressed, densely pubescent. Pappus of basally connate short scales and/or discrete fine bristles. $x = 8$.

Only one genus:

409. *Corymbium* L. Fig. 52

Corymbium L., Sp. Pl.: 928 (1753) & Gen. Pl. ed. 5: 400 (1754); Markötter, Bot. Jahrb. 70: 354–372 (1939), rev.; Weitz, S. African J. Bot. 55: 598–629 (1989), rev.; Weitz, Mitt. Inst. Allg. Bot. Hamburg 23b: 631–642 (1990), rev.

Characters of the tribe. Nine species, Cape region of South Africa.

The singular South African genus *Corymbium* L. has been notoriously difficult to place in any of the traditional tribes in the family. Usually tribe Vernonieae has been suggested, but the genus is aberrant there on account of its strange vegetative and floral morphology, caveate pollen (Bolick 1978) and different phytochemistry. For example, it lacks sesquiterpene lactones typical of Vernonieae but contains diterpenes, not occurring in that tribe (Zdero and Bohlmann 1988; Bohlmann and Jakupovic 1990). Bremer (1994) accepted the genus in subfam. Cichorioideae among genera unassigned to tribe. Molecular evidence suggests a position of *Corymbium* basal to Senecioneae in subfam. Asteroideae or as sister to the subfamily, which led to the proposal of subfam. Corymbioideae Panero & V.A. Funk

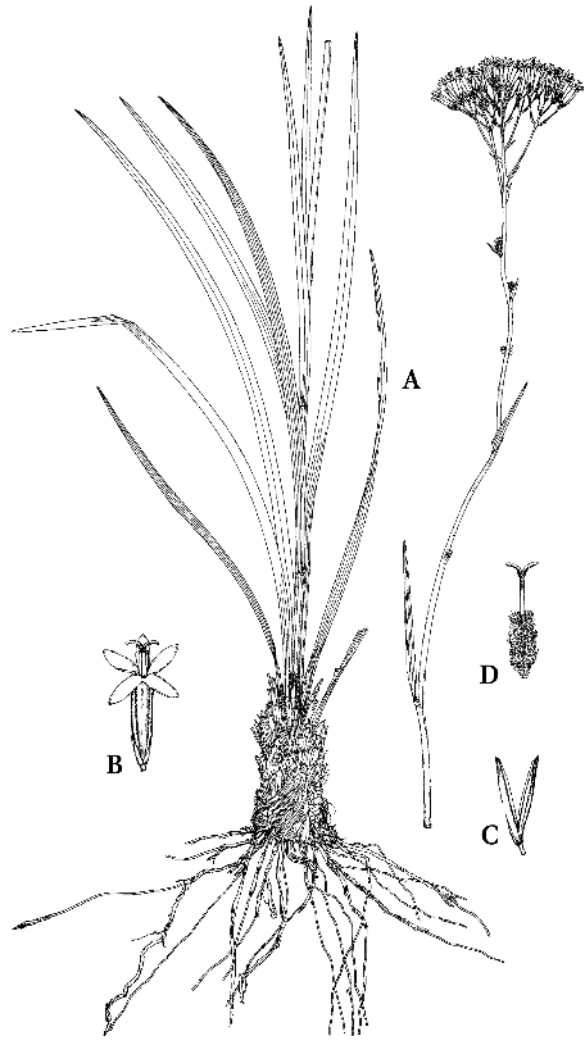

Fig. 52. Compositae-Corymbieae. *Corymbium villosum*. **A** Habit. **B** Single-flowered capitulum. **C** Involucre of two bracts. **D** Ovary and style. (Weitz 1989)

(2002). Many features, such as pollination biology and cytology, are still practically unknown in this unique and isolated group within the family. The flowers produce copious nectar and are frequently visited by bees, beetles, wasps and ants (Weitz 1989). A single report on chromosome number has been published, viz. $2n = 16$ in *C. congestum* E. Mey. ex DC. (Weitz 1989).

XII. Tribe Senecioneae Cass. (1819).

B. Nordenstam

Herbs, shrubs, lianas, epiphytes, treelets or trees. Leaves alternate, cauline or rosulate, more rarely opposite, sessile or petiolate, entire or variously lobed or dissected. Capitula heterogamous or homogamous, radiate, disciform or discoid, often yellow-flowered but sometimes white, orange, pink, purple, red or rarely blue, solitary or corymbose, paniculate or thyrsoid in terminal or lateral synflorescences. Involucre commonly uniseriate, sometimes biseriate or rarely pluriseriate, with or without a calyculus of smaller bracts. Involucral bracts free or connate to various degrees. Receptacle flat or convex to conical, naked or fimbrillate to denticulate with scale-like projections, glabrous or hairy, solid or fistulose. Ray florets female, sometimes sterile or absent, corolla radiate or tubular-filiform; style bifid or simple, fertile or sterile. Disc florets bisexual, perfect or functionally male, rarely female; corolla tubular to funnel-shaped or with a campanulate limb, 4- or 5-lobed. Anthers 4 or 5, tetrasporangiate or rarely bisporangiate (*Gynura*; Pullaiah 1983) with an apical flat appendage, basally obtuse, sagittate or caudate. Endothecial tissue radial or polarized, rarely transitional. Filament collar straight and uniform or basally dilated with larger cells (balusterform). Pollen caveate, in most genera Senecioid (columellae solid) but in some genera Helianthoid (columellae with internal foramina; Skvarla et al. 1977). Style bifid or simple, fertile or sterile, apically truncate or convex, rounded or conical, sometimes with elongate appendage, papillate or hirsute or only apically with short sweeping hairs or minutely papillate, sometimes with a distinct central tuft or pencil of hairs or fused papillae (Fig. 53); stigmatic areas continuous or separated. Cypselae terete, elliptic-oblong or obovoid, sometimes flattened, winged or angled, often ribbed, glabrous or variously pubescent, sometimes heteromorphic; carpopodium ring-like, distinct (up to 12 cell layers or more) or indistinct. Ovary wall crystals often present, often prismatic, plate-like, elongate or isodiametric, sometimes drusiform (Nordenstam 1978; Jeffrey 1986). Pappus of few to many bristles or a single scale or absent, persistent or caducous, uni- to multiseriate, fine and slender to coarse and rigid, barbellate to subplumose, white or sometimes straw-, brick- or red- to purple-coloured.

Senecioneae are one of the largest tribes of Compositae, with 150 genera presently recognized and about 3,500 species, and with a worldwide distribution.

The limits of Senecioneae have become more clear since the 1970s after transfer of several genera to Heliantheae and Helenieae, and the recognition of Liabeae and Corymbieae as distinct tribes (Rydberg 1927; Robinson and Brettell 1973a; Nordenstam 1977; Panero and Funk 2002). The tribe is now reasonably well defined, although the relationships and tribal position of a few

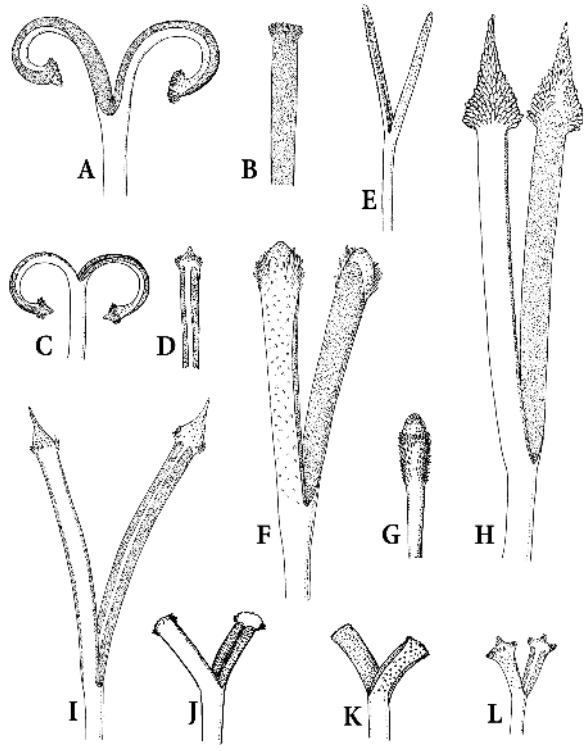

Fig. 53. Compositae-Senecioneae. Style branches from disc florets. **A**, **B** *Dendrosenecio keniensis*. **C**, **D** *Lordhowea insularis*. **E** *Cacaliopsis nardosmia*. **F** *Odontocline tercentenariae*. **G** *Othonna brandbergensis*. **H** *Jacmaia incana*. **I** *Kleinia longiflora*. **J** *Senecio eligulatus*. **K** *Io ambondrombeensis*. **L** *Psednotrichia xyridopsis*. (Drawings by B. Nordenstam)

genera such as *Abrotanella* and *Doronicum* are still problematic or unresolved. A recent addition to the tribe is *Haastia*, which was unassigned as to tribe (Bremer 1994) but fits well in the *Brachyglottis* group (Wagstaff and Breitwieser 2002, 2004). The number of segregates from the core genus *Senecio* has increased dramatically in the last decade. *Senecio* itself (with over 3,000 binomials) will eventually be defined as a monophyletic but still very large genus by continued removal of discordant elements including several sections (e.g. sect. *Jacobaea*). On the tribal level, the phylogeny and relationships within subfamily Asteroideae are not sufficiently known, and it is difficult to discern the closest affinities of Senecioneae among the tribes Astereae, Anthemideae, Calenduleae, Inuleae and Gnaphalieae. Phytochemically, the tribe is rather well characterized by the presence of pyrrolizidine alkaloids in many, but not all genera, and groups of sesquiterpene lactones known as eremophilanes and furanoeremophilanes, and by the absence of polyacetylenes in most genera (Robins 1977). *Doronicum* differs from the rest of the tribe by the presence of acetylenes and in its sesquiterpenoid constituents (Bohlmann et al. 1973).

A number of subtribes have been suggested but the attempts made so far have not been all-inclusive. Subtribes proposed include Blennospermatinae, Abrotanellinae, Tussilagininae, Tephroseridinae, Senecioninae and Adenostylinae (under Eupatorieae). Usually only two subtribes are recognized, viz. Blennospermatinae and Senecioninae, and within the latter a 'senecioid' and a 'tussilaginoid' (initially called 'cacalioid') complex have been loosely characterized ('tussilaginoid' is a better term than 'cacalioid' because of the ambiguity of the rejected name *Cacalia* L.; cf. Jeffrey 1992; Barkley 1999). No formal subtribal classification is proposed here, pending the outcome of an ongoing molecular phylogenetic study of the entire tribe (Pelser, Kadereit, Nordenstam, Breitwieser, Wagstaff, Watson, in progress).

Key to the Genera

1. Disc-florets 4-lobed 2
– Disc-florets 5-lobed 10
2. Dwarf herbs, sometimes tufted. Leaves sessile, linear, up to 5 cm long. Capitula small (3–5 mm broad and long), few-flowered 3
– Herbs, subshrubs or shrubs. Leaves larger, 5–30 cm long, sessile or often petiolate. Capitula larger (7–25 mm broad), many-flowered 4
3. Capitula disciform with tubular marginal florets **410. *Abrotanella***
– Capitula radiate; disc floret style undivided; pappus absent **413. *Ischnea*** p.p.
4. Florets yellow 5
– Florets purple or whitish 8
5. Leaves sessile (Australia, Oceania) **499. *Senecio*** p.p.
– Leaves petiolate (Eurasia) 6
6. Rhizome slender. Capitula solitary or few. Anther base obtuse. Style branches dorsally glabrous **464. *Dolichorrhiza***
– Rhizome thick. Capitula few to many. Anther base caudate or at least sagittate. Style branches dorsally papillate 7
7. Leaves entire, cordate or deltoid to ovate **557. *Caucasalia***
– Leaves lobed or dissected **559. *Iranecio***
8. Leaves ovate or cordate 9
– Leaves lanceolate, cuneate **556. *Pojarkovia***
9. Perennial herbs with rhizome. Calyculus present. Style branches subulate **555. *Adenostyles***
– Shrubs or lianas. Calyculus absent. Style branches linear **543. *Faujasiopsis*** p.p.
10. Plant forming dense cushions; branches and leaves concealed by dense tomentum. Capitula sessile, disciform (New Zealand) **461. *Haastia*** p.p.
– Habit various but not as above 11
11. Involucral bracts pluriseriate to imbricate 12
– Involucral bracts 1–2-seriate 17
12. Capitula radiate, yellow-flowered 13
– Capitula discoid or disciform 14
13. Leaves cauline, entire, woolly beneath (S Africa) **465. *Capelio*** p.p.
– Basal leaves rosulate, dissected, large, glabrous (Peru) **513. *Caxamarca***
14. Plants glabrous or somewhat woolly (mostly on young parts). Capitula few-flowered (3–17 florets) 15
– Plants densely woolly. Capitula many-flowered, discoid 16
15. Leaves sessile, linear or filiform to oblanceolate or reduced to scales. Capitula discoid, yellow-flowered (SW USA, Mexico) **451. *Lepidospartum***
– Leaves petiolate. Capitula disciform with tubular marginal florets, purplish or white to cream-coloured (Indonesia, New Guinea, Australia) **488. *Arrhenechthites***
16. Shrub. Capitula several, medium-sized, corymbose (Cuba) **471. *Shafera***
– Herbs. Capitula large, solitary or few, nodding (South America) **521. *Culcitium***
17. Plants dioecious; capitula radiate or discoid 18
– Plants monoecious or polygamous 23
18. Perennial herbs with rosulate leaves from a rhizome 19
– Shrubs or shrublets, or trees, rarely perennial herbs with cauline leaves and a woody caudex 20
19. Rhizome thin. Leaves present at flowering time. Capitula radiate **417. *Endocellion***
– Rhizome thick. Leaves developing postflorally. Capitula discoid or disciform **418. *Petasites***
20. Leaves crowded at branch ends. Styles undivided in male capitula (Juan Fernandez) **498. *Robinsonia***
– Leaves evenly distributed. Styles bifurcate 21

21. Perennial herbs or shrublets with mostly tomentose leaves; leaf blades up to 5 cm long. Capitula discoid, yellow-flowered **415. *Chersodoma***
– Shrubs with larger glabrous leaves 22
22. Leaves entire. Capitula discoid, pink- to purplish-flowered (Bonin Islands) **422. *Dendrocacalia***
– Leaves serrate. Capitula radiate, yellow-flowered (New Guinea) **467. *Brachionostylum***
23. Indumentum of stellate, T-shaped or pseudo-stellate hairs 24
– Trichomes, if present, not stellate or branched 26
24. Ray florets long, narrowly linear, recurved, reddish **519. *Dresslerothamnus***
– Ray florets oblong, patent, white or yellow 25
25. Ray florets white. Trichomes peltate and stellate. Style branches obtuse or subtruncate **456. *Aequatorium***
– Ray florets yellow. Trichomes substellate and irregularly branched. Style branches acute to acuminate **455. *Nordenstamia***
26. Styles of disc florets undivided (sterile) 27
– Styles of disc florets bilobed (fertile or sterile) 32
27. Aquatic floating herb. Rays white (South Africa) **535. *Cadiscus***
– Terrestrial plants. Rays yellow, pink or purple (seldom white in *Othonna* spp.) 28
28. Small herbs with solitary pedunculate capitula. Pappus absent 29
– Herbs, subshrubs or shrubs. Pappus present, at least in ray florets 30
29. Annual. Leaves alternate, mostly pinnatifid. Cypselae papillate **411. *Blennosperma***
– Perennial herbs. Leaves rosulate, entire or serrate. Cypselae glabrous **413. *Ischnea*** p.p.
30. Herb with postflorally developing, large basal leaves. Ray florets in many series, with linear lamina **419. *Tussilago***
– Leaves and flowers at the same time. Ray florets narrowly oblong to elliptic-oblong 31
31. Perennial herbs, subshrubs or shrubs **531. *Othonna***
– Annual herbs **532. *Gymnodiscus***
32. Filament collar straight, uniform. Endothecial tissue usually polarized. ('Tussilaginoid' genera, usually with uniseriate ecalyculate involucre, florets often non-yellow, stigmatic areas of disc floret styles mostly confluent, disc floret corollas frequently deeply 5-lobed) 33
– Filament collar 'balusterform' or subcylindric with enlarged basal or marginal cells. Endothecial tissue radial (except in *Graphistylis*). ('Senecioid' genera, involucre 1–2-seriate and mostly calyculate, florets often yellow, stigmatic areas of disc floret styles often separated, disc floret corolla lobes mostly triangular-ovate) 96
33. Small annual herb (NW USA) **512. *Crocidium***
– Perennials 34
34. Leaves parallel-veined with 3 or more veins 35
– Leaves pinnately or palmately veined or with a single midrib 38
35. Leaves petiolate, three-veined 36
– Leaves sessile (New Zealand) 37
36. Involucre calyculate, green, with c. 10 phyllaries (China) **424. *Dicercoclados***
– Involucre ecalyculate, yellow, with 5 phyllaries (western USA) **446. *Yermo***
37. Leaves basal and cauline, lanceolate. Capitula pedunculate, radiate **464. *Dolichoglottis***
– Leaves cauline, ovate or obovate. Capitula sessile, disciform **461. *Haastia*** p.p.
38. Petioles, if present, with vaginate sheaths 39
– Petioles, if present, not vaginately sheathing 41
39. Capitula solitary or rarely few, campanulate or hemispherical, nodding, usually ecalyculate **429. *Cremanthodium***
– Capitula several to many in racemose-paniculate or corymbose synflorescences, calyculate 40
40. Leaves rosulate with involute vernation. Cypselae setose **420. *Farfugium*** p.p.
– Leaves cauline or rosulate, not involute in bud. Cypselae glabrous **427. *Ligularia***
41. Leaves pinnately compound, large (Mexico) **443. *Villasenoria***
– Leaves not pinnately compound 42
42. Stem abruptly contracted below synflorescence 43
– Stems and branches gradually tapering 45
43. Leaves palmately veined, often deciduous before anthesis. Resiniferous subsucculent shrubs **444. *Pittocaulon***
– Leaves pinnately veined, persistent at anthesis 44
44. Epiphytes or lax suffrutescent herbs. Endothecium polarized **441. *Nelsonianthus***
– Trees, shrubs or shrublets. Endothecium radial **442. *Telanthophora***
45. Capitula discoid or disciform 46
– Capitula radiate 76
46. Leaves 3-nerved, elliptic-ovate or lanceolate 47
– Leaves pinnately or palmately veined or just midribbed 48
47. Capitula axillary, solitary or in pairs, calyculate. Involucral bracts c. 10, green (China) **424. *Dicercoclados***
– Capitula corymbose, ecalyculate. Involucral bracts 5, yellow (western USA) **446. *Yermo***
48. Leaves sessile or subsessile 49
– Leaves petiolate 52
49. Shrubs or small trees. Leaf venation pinnate-reticulate from a prominent midrib. Capitula disciform or sometimes discoid; florets white or cream to pink or purplish (New Guinea) **466. *Papuacalia*** p.p.
– Shrubs, shrublets or herbs. Leaves pinnately to nearly parallel-veined or one-nerved, sometimes forming spines. Capitula discoid, bright or creamy yellow (western USA) 50
50. Shrubs or shrublets. Leaves small (0.5–5 cm long), often fascicled, or transformed into spines **450. *Tetradymia***
– Herbs or subshrubs. Leaves usually larger, elliptic-ovate to lanceolate, not fascicled 51
51. Leaves mostly basal and 15–35 cm long, glabrous. Capitula in elongate thyrsoid-racemiform synflorescence **447. *Rainiera***
– Leaves cauline, 4–12 cm long, white-tomentose beneath. Capitula in short corymbose synflorescence **449. *Luina***
52. Subshrub with white cortex on old stems. Involucral bracts 5 in 2 series (Namibia) **554. *Dauresia***
– Herbs or shrubs, not with white cortex. Involucral bracts uniseriate 53
53. Florets yellow or orange-coloured 54

– Florets white to cream or pink to purplish 60
54. Shrubs with opposite leaves 55
– Herbs with alternate or rosulate leaves 56
55. Scandent shrub. Involucre ecalyculate (Hispaniola) **474. *Herodotia***
– Erect shrub or shrublet. Involucre calyculate (Colombia, Venezuela) **470. *Scrobicaria***
56. Leaves pinnately veined, with broadly winged and amplexicaul petiole. Synflorescence elongate, spike-like (China) **428. *Ligulariopsis***
– Leaves palmately veined, at least basally; petiole winged or not 57
57. Capitula thyrsoid-racemose in elongate synflorescence; involucre ecalyculate (Eurasia) **423. *Parasenecio*** p.p.
– Capitula corymbose-paniculate or racemose; involucre calyculate 58
58. Villous herb with few, palmately lobed leaves. Capitula racemose. Style branches attenuate, papillate (Japan) **421. *Miricacalia***
– Plants glabrous or sparsely pubescent to floccose-tomentose. Capitula corymbose-paniculate 59
59. Leaves mostly basal, tomentose beneath, palmately lobed. Capitula campanulate. Style branches attenuate, obtuse to rounded. Endothecium polarized (western USA) **448. *Cacaliopsis***
– Leaves cauline, glabrous or pubescent, entire or variously lobed. Capitula cylindrical to narrowly campanulate. Style branches linear, ± truncate. Endothecium radial (SW USA, Central America) **440. *Roldana*** p.p.
60. Shrubs or trees 61
– Perennial herbs 67
61. Capitula disciform; marginal florets with reduced ligules (New Guinea) **466. *Papuacalia*** p.p.
– Capitula discoid 62
62. Scandent shrublets (Bolivia, Peru) **452. *Paracalia***
– Erect shrubs or trees 63
63. Plants densely tomentose especially on lower leaf surface 64
– Plants glabrous or thinly tomentose in parts 65
64. Leaves linear to lanceolate (or narrowly ovate); young stems and leaves glandular (Australia) **462. *Bedfordia***
– Leaves elliptic-oblong to obovate, not distinctly glandular (New Zealand) **458. *Brachyglottis*** p.p.
65. Glutinous shrub with scattered leaves 5–8 cm long (New Zealand) **463. *Traversia***
– Trees with large leaves crowded towards branch ends 66
66. Divaricately much-branched tree. Synflorescences lateral, axillary, pendulous (St. Helena) **469. *Lachanodes***
– Unbranched or little-branched trees or treelets. Synflorescences terminal, erect (Venezuela, Colombia) **453. *Paragynoxys***
67. Leaves pinnately veined. Plant pubescent in most parts (southern USA) **437. *Rugelia***
– Leaves palmately veined 68
68. Leaves peltate 69
– Leaves with marginal petiole attachment 71
69. Leaves few, cauline, palmatisect (E Asia) **426. *Syneilesis***
– Leaves several to many, entire or lobed 70
70. Scapigerous herbs with rosulate leaves. Involucre calyculate. Corolla shortly lobed (Central America) **433. *Psacaliopsis*** p.p.
– Leaves basal and cauline. Involucre ecalyculate with 5 phyllaries and 5 florets. Corolla deeply lobed (E & SE USA) **438. *Arnoglossum***
71. Capitula disciform 72
– Capitula discoid 73
72. Capitula solitary on a long scape, disciform with purple (rarely white) shortly ligulate marginal florets (Europe) **416. *Homogyne***
– Capitula corymbose. Floret colour various but not purple (Central America) **440. *Roldana*** p.p.
73. Leaves rosulate or subrosulate. Corollas deeply lobed **434. *Psacalium***
– Leaves cauline, alternate 74
74. Corollas deeply lobed. Endothecium polarized (Mexico) **436. *Digitacalia***
– Corollas lobed to about the middle of the limb 75
75. Capitula in elongate thyrsoid-racemose synflorescence. Endothecium polarized (Eurasia) **423. *Parasenecio*** p.p.
– Capitula corymbose-paniculate. Endothecium radial (SW USA, Central America) **440. *Roldana*** p.p.
76. Rays yellow 77
– Rays white or cream 83
77. Trees or shrubs 78
– Herbs 86
78. Leaves opposite, tomentose beneath 79
– Leaves alternate or rosulate 80
79. Erect trees or shrubs. Leaves entire. Capitula campanulate or cup-shaped, many-flowered (South America) **454. *Gynoxys***
– Scandent shrubs or shrublets. Leaves serrate. Capitula turbinate-obconical, few-flowered (Hispaniola) **473. *Ekmaniopappus*** p.p.
80. Leaves linear to lanceolate, sessile or subsessile, clustered terminally on branches 81
– Leaves elliptic-oblong to obovate, usually petiolate 82
81. Leaves linear, single-veined, with glossy exudates (Tasmania) **459. *Centropappus***
– Leaves linear-lanceolate to lanceolate, pinnately veined (SW USA, Central America) **445. *Barkleyanthus***
82. Leaves elliptic-ovate or obovate, entire with denticulate margins, ± herbaceous (Chile) **457. *Acrisione***
– Leaves elliptic-oblong, entire or serrate-lobed, coriaceous (New Zealand) **458. *Brachyglottis*** p.p.
83. Ray florets reduced, cream (New Guinea) **466. *Papuacalia*** p.p.
– Capitula distinctly radiate with white ligules 84
84. Leaves ± tomentose below (New Zealand) **458. *Brachyglottis*** p.p.
– Leaves glabrous or glabrescent 85
85. Leaves up to 40 cm long. Ray florets short, c. 0.5 cm. Anthers ecaudate (St. Helena) **468. *Pladaroxylon***
– Leaves up to 10 cm long. Ray florets 1–2 cm long. Anthers conspicuously caudate **460. *Urostemon***
86. Leaves peltate, petiolate, with hairy base **433. *Psacaliopsis*** p.p.
– Leaves not peltate 87
87. Leaves pinnatisect, cauline (China, Taiwan, Japan) **430. *Nemosenecio***
– Leaves entire or dentate-lobate 88
88. Involucre biseriate 89
– Involucre uniseriate 90

89. Stout and somewhat suffrutescent herbs. Leaves densely woolly beneath **465. *Capelio*** p.p.
– Glabrous or sparsely pubescent herbs **414. *Doronicum***
90. Leaves basal and cauline, tapering to the base like a winged petiole 91
– Leaves rosulate or cauline, distinctly petiolate, at least the basal ones 92
91. Involucre ecalyculate **432. *Tephroseris***
– Involucre calyculate (Mexico, Guatemala) **439. *Robinsonecio***
92. Rhizome thick or roots tuberous 93
– Rhizome thin or roots fibrous 94
93. Leaves rosulate with involute vernation. Cypselae hairy **420. *Farfugium*** p.p.
– Leaves cauline; vernation not involute. Cypselae glabrous **425. *Sinacalia***
94. Leaves palmately laciniate. Capitula large, showy. Pappus absent (Mexico) **435. *Pippenalia***
– Leaves entire to lobed. Capitula small or medium-sized. Pappus usually present 95
95. Leaves rosulate and/or cauline, palmately veined (China, Korea, Myanmar) **431. *Sinosenecio***
– Leaves rosulate, entire, pinnately veined (New Zealand) **458. *Brachyglottis*** p.p.
96. Involucral bracts connate (to various extents) 97
– Involucral bracts free 111
97. Annual herbs (often delicate, glabrous) 98
– Perennial herbs, subshrubs or shrubs 105
98. Leaves rosulate 99
– Leaves cauline 100
99. Leaves linear-filiform (Angola) **540. *Psednotrichia***
– Leaves pinnatipartite (South Africa) **530. *Euryops annuus***
100. Capitula discoid or disciform 101
– Capitula radiate 102
101. Leaves sessile. Capitula discoid. Cypselae ellipsoid (W Africa) **539. *Bafutia***
– Leaves petiolate, auriculate. Capitula disciform. Cypselae compressed (S Africa) **494. *Stilpnogyne***
102. Pappus absent 103
– Pappus present 104
103. Ray florets yellow (S Africa) **538. *Steirodiscus***
– Ray florets white or pink (tropical Africa) **536. *Stenops***
104. Leaves amplexicaul, serrulate. Pappus of few short caducous bristles (South Africa) **537. *Oligothrix***
– Leaves not amplexicaul, entire. Pappus of many persistent bristles (Australia) **499. *Senecio gregorii*, *S. calcicola***
105. Compact low perennials, forming mats, cushions or rosettes. Leaves densely set, entire or apically lobed. Ray florets mostly white (yellow in 2 species of *Werneria*) (South America) 106
– Perennial herbs, subshrubs or shrubs. Ray florets (if present) yellow 108
106. Mat- or cushion-forming plants. Leaves very closely set, those covering rhizomes brown, blackish or whitish; angular-terete, entire or apically few-lobed **524. *Xenophyllum***
– Rosette-forming or solitary small perennials. Leaves assembled near rhizome tips and below capitula, green 107
107. Plants glabrous. Style branch tips papillate or glabrous **525. *Werneria***
– Plants densely strigose. Style branch tips with elongated hair tuft **523. *Misbrookea***
108. Leaves succulent, entire or with serrate margins. Style branches of disc floret papillate-hairy 109
– Leaves coriaceous or herbaceous, entire or variously lobed. Style branches of disc floret truncate to obtuse with apical papillae, otherwise glabrous 110
109. Capitula discoid, florets white or pink to purplish. Style branches with a long papillate appendage **534. *Lopholaena***
– Capitula radiate or disciform, yellow-flowered. Style branches papillate-hairy outside **533. *Hertia***
110. Capitula borne on unbranched axillary or pseudoterminal naked peduncles (Africa, SW Arabia) **530. *Euryops***
– Capitula many in terminal bracteate corymbs. Leaves large, herbaceous, pinnatilobate (Cuba) **481. *Oldfeltia***
111. Style branches of disc floret apically acute, conical or acuminate, with an appendage, tuft or pencil of fused hairs or papillae 112
– Style of disc floret apically truncate or rounded-obtuse 134
112. Capitula discoid or disciform 113
– Capitula radiate 122
113. Capitula disciform; marginal female florets numerous, filiform **503. *Erechtites***
– Capitula discoid, homogamous 114
114. Style appendage triangular-conical or elongate, made up of cellular tissue, papillate 115
– Style appendage a central tuft or pencil of fused hairs or papillae 117
115. Truly succulent herbs or shrubs **501. *Kleinia*** p.p.
– Plants herbaceous, at most subsucculent, or shrubs with coriaceous leaves 116
116. Herbs or subshrubs. Capitula corymbose-paniculate or solitary, calyculate **502. *Gynura*** p.p.
– Shrublet with small coriaceous leaves. Capitula ecalyculate, solitary on long peduncles **527. *Lamprocephalus***
117. Involucre ecalyculate **541. *Emilia***
– Involucre calyculate 118
118. Florets pure yellow **500. *Solanecio*** p.p.
– Floret colour various but not pure yellow 119
119. Leaves distinctly petiolate. Capitula nodding **517. *Aetheolaena***
– Leaves subsessile or shortly petiolate. Capitula erect or nodding 120
120. Leaves imbricate with revolute margins, tomentose beneath **516. *Lasiocephalus***
– Leaves not imbricate, flat 121
121. Leaves herbaceous, entire or lobed to dissected. Florets white, yellowish, red, blue, etc. Involucre cylindrical (Africa to Yemen) **506. *Crassocephalum*** p.p.
– Leaves coriaceous, entire, serrate. Florets greenish yellow. Involucre campanulate (Colombia) **518. *Arbelaezaster***
122. Herbs 123
– Shrubs or subshrubs 128
123. Leaves rosulate, pinnatipartite or laciniate. Involucre calyculate or conspicuously calyculate (Peru, Ecuador) **496. *Dorobaea***
– Leaves not rosulate. Involucre calyculate or ecalyculate 124
124. Rays white (Chile, Argentina) **504. *Iocenes***

– Rays variously coloured but not white (except in *Graphistylis organensis* f. *albiflora* from Brazil) 125
125. Leaves distinctly petiolate 126
– Leaves subsessile or shortly petiolate 127
126. Petiole conspicuously auriculate and amplexicaul. Leaves strongly nerved **515. *Garcibarrigoa***
– Petiole without or with small auricles. Leaves normally veined **514. *Pseudogynoxys*** p.p.
127. Coarse herbs (or subshrubs). Leaves elliptic-lanceolate, serrate, subcoriaceous. Capitula many; involucre campanulate or cup-shaped (Brazil) **511. *Graphistylis***
– Soft herbs. Leaves entire or lobed, herbaceous. Capitula few to several; involucre cylindrical (tropical Africa, Yemen) **506. *Crassocephalum*** p.p.
128. Scandent subshrubs or shrubs. Rays conspicuous, red or orange to yellow, fragrant (Central & South America) **514. *Pseudogynoxys*** p.p.
– Erect shrubs or small trees 129
129. Leaves linear-lanceolate, < 3 cm wide. Receptacle naked (Costa Rica) **522. *Charadranaetes***
– Leaves elliptic-lanceolate to oblong-ovate, > 3 cm wide. Receptacle denticulate (i.e. with tooth-like processes) 130
130. Leaves ± hairy. Ray florets numerous (8–21), lamina distinctly longer than tube, yellow or orange (South & Central America) **512. *Talamancalia***
– Leaves glabrous at least when mature. Ray florets few (2–8 or rarely more in *Lundinia*), short; lamina about equalling the tube in length 131
131. Low shrubs. Leaf-blades up to 4 cm long. Rays narrow, pale yellow (Lord Howe Island) **487. *Lordhowea***
– Tall shrubs or small trees. Leaves larger. Rays bright yellow 132
132. Style branches apically with an acuminate papillate appendage; stigmatic areas continuous (Jamaica) **484. *Jacmaia***
– Style branches with apical hair tuft; stigmatic areas separated 133
133. Style branches apically rounded with hair pencil. Anthers ecaudate (Costa Rica) **486. *Jessea***
– Style branches truncate with minute hair tuft. Anthers caudate (Cuba, Hispaniola) **483. *Lundinia***
134. Leaves opposite, sessile or subsessile, entire with dentate or denticulate margins 135
– Leaves alternate or rosulate 136
135. Erect subshrub with radiate capitula (Madagascar) **505. *Io***
– Scandent shrubs with discoid or radiate capitula (Colombia) **520. *Cabreriella***
136. Anthers distinctly caudate ('Synotoids' a.o.) 137
– Anthers basally obtuse to sagittate 153
137. Erect shrubs or shrublets with narrowly linear or acicular leaves 138
– Herbs or shrubs, sometimes scandent. Leaves flat, pinnately or sometimes palmately veined 139
138. Leaves closely set, patent. Capitula several, pedunculate **548. *Parafaujasia***
– Leaves imbricate, appressed. Capitula solitary, sessile **545. *Eriotrix***
139. Pappus bristles few, rigid, basally flattened **544. *Faujasia***
– Pappus bristles numerous, soft or slender, terete 140
140. Scandent herbs or subshrubs 141
– Erect shrubs or sometimes subshrubs 149
141. Leaves pinnately veined 142
– Leaves palmately veined 144
142. Florets white or pink to lilac (Mascarene Islands) **543. *Faujasiopsis*** p.p.
– Florets yellow 143
143. Style branches truncate (Madagascar) **546. *Hubertia faujasioides***
– Style branches obtuse-rounded (Jamaica) **482. *Odontocline*** p.p.
144. Leaves not auriculate 145
– Leaves auriculate 147
145. Petioles not prehensile (Madagascar, La Réunion) **547. *Humbertacalia*** p.p.
– Petioles prehensile 146
146. Capitula radiate or discoid (Indomalesia) **552. *Cissampelopsis***
– Capitula disciform (Africa) **550. *Mikaniopsis***
147. Florets whitish. Petioles not prehensile (Madagascar, La Réunion) **547. *Humbertacalia*** p.p.
– Florets yellow. Petioles prehensile 148
148. Plant subsucculent. Capitula discoid (South Africa) **551. *Delairea***
– Plant herbaceous. Capitula radiate (tropical Africa) **553. *Austrosynotis***
149. Capitula small, with 1–2 ray florets and 4–5 disc florets, ecalyculate (Canary Isl.) **489. *Bethencourtia***
– Capitula > 5-flowered, calyculate 150
150. Styles with clearly separated stigmatic areas 151
– Style with continuous or barely separated stigmatic areas 152
151. Diffuse subshrubs or shrubs with leaves often caulirosulate (S & SE Asia) **549. *Synotis***
– Leaves evenly distributed (Cuba, Hispaniola) **483. *Lundinia***
152. Style branch apex blunt with only very short papillae (Madagascar, La Réunion) **546. *Hubertia***
– Style branch apex rounded-conical with 1–2 lateral bunches of sweeping hairs (Jamaica) **482. *Odontocline*** p.p.
153. Cypselae compressed. Herbs or subshrubs. Leaves mostly lobed to dissected, palmately veined 154
– Cypselae not compressed. Leaves mostly pinnately veined, or linear, midveined 155
154. Florets yellow. Cypselae distinctly compressed with thickened margins (Africa & Madagascar) **491. *Cineraria***
– Florets non-yellow (white, pink, purple, etc.). Cypselae not much compressed, margins not thickened (Macaronesian islands) **490. *Pericallis***
155. Ray florets bilabiate with a short limb and two small ventral lobes. Scandent shrub with three-nerved leaves (Hispaniola) **472. *Mattfeldia***
– Ray florets ligulate or absent. Non-scandent plants 156
156. Capitula ecalyculate 157
– Capitula calyculate (sometimes with a single calyculus bract) 162
157. Shrubs or subshrubs 158
– Herbs 160
158. Capitula borne singly on unbranched terminal or axillary peduncles 159
– Capitula several, corymbose **499. *Senecio*** p.p.
159. Peduncles terminal, scapose, bracteate. Ray florets white or cream. Cypselae dimorphic: in ray florets

glabrous with caducous pappus, in disc florets with myxogenic hairs and persistent pappus **528. *Phaneroglossa***
– Peduncles axillary, naked. Ray florets yellow. Cypselae homomorphic **530. *Euryops*** spp.
160. Pappus a single scale or absent. Capitula few-flowered, pink to purplish **542. *Emiliella***
– Pappus of slender bristles. Florets several to many, colour various 161
161. Cypselae dimorphic: outer adaxially midribbed and glabrous, inner smooth and hairy. Capitula radiate, yellow **492. *Bolandia***
– Cypselae homomorphic. Capitula discoid or sometimes radiate; floret colour various **541. *Emilia*** p.p.
162. Style branches of disc florets short, erect, apically dilated, dorsally papillate-hairy. Capitula disciform with purplish-creamy white florets (Indonesia, New Guinea, Australia) **488. *Arrhenechthites*** p.p.
– Style branches of disc florets linear or oblong, spreading 163
163. Pachycaul trees or tree-like suffrutescent herbs ('dendrophorbs') with large leaves assembled terminally on stems and branches 164
– Herbs, shrubs or small trees with more slender stems and more evenly distributed (or rosulate) leaves 165
164. Megaphytic rosette-trees. Styles of disc florets with continuous stigmatic areas. Cypselae 5-ribbed or 5-angled (tropical African mountains) **529. *Dendrosenecio***
– Subshrubs, shrubs or treelets. Styles of disc florets with separated stigmatic areas. Cypselae 8–10-ribbed (South America) **510. *Dendrophorbium***
165. Herbs 166
– Subshrubs, shrubs or shrublets, or small trees 172
166. Annual herbs 167
– Perennial herbs 168
167. Involucral bracts c. biseriate; inner with 2 dark resin ducts. Cypselae subtriquetrous, black, papillose-hairy apically and basally and along three longitudinal lines (southern Africa) **493. *Mesogramma***
– Involucral bracts ± uniseriate, without dark stripes. Cypselae ± terete **499. *Senecio*** p.p.
168. Roots fibrous (rhizome present in some Old World and South American spp.) 169
– Rhizomatous herbs with most leaves basal, often rosulate or nearly so 171
169. Styles of disc florets with separate stigmatic areas, apically ± truncate and with sweeping hairs 170
– Styles with continuous stigmatic areas, apically obtuse and without distinct sweeping hairs. Capitula discoid, orange-flowered (Hispaniola) **585. *Ignurbia***
170. Cypselae dimorphic: outer 4-winged, glabrous; inner 6-ribbed, with mucilaginous hairs **526. *Oresbia***
– Cypselae homomorphic **499. *Senecio*** p.p.
171. Capitula campanulate to cup-shaped, radiate or rarely discoid; florets yellow, orange or red. Corolla lobes deltoid-ovate **495. *Packera***
– Capitula cylindrical-turbinate, discoid; florets white or pink. Corolla lobes lanceolate **497. *Hasteola***
172. Scandent shrubs or shrublets 173
– Erect subshrubs, shrubs or small trees 176
173. Styles of disc florets with continuous stigmatic areas (Cuba, Hispaniola) 174
– Styles of disc florets with separated stigmatic areas 175
174. Leaves 3-nerved from the base, glabrous **475. *Leonis***
– Leaves pinnately veined, tomentose beneath **476. *Nesampelos***
175. Leaves tomentose beneath. Cypselae 8–10-ribbed (Hispaniola) **479. *Elekmania*** p.p.
– Leaves glabrous or variously pubescent. Cypselae 5-ribbed or 5-angled (South & Central America) **508. *Pentacalia*** p.p.
176. Styles of disc florets apically rounded and subglabrous, dorsally puberulous. Capitula discoid, few-flowered (Brazil) **507. *Hoehneophytum***
– Style of disc florets truncate or obtuse, penicillate. Capitula radiate or discoid, usually many-flowered 177
177. Cypselae 5-ribbed or 5-angled (South & Central America) 178
– Cypselae 8–10-ribbed 179
178. Erect shrubs or shrublets. Leaves closely set, subsessile or shortly petiolate, often small, ericoid to lanceolate or elliptic-ovate **509. *Monticalia***
– Epiphytic shrubs. Leaves more laxly distributed, petiolate **508. *Pentacalia*** p.p.
179. Styles of disc florets with continuous stigmatic areas (Cuba) 180
– Styles of disc florets with separated stigmatic areas 181
180. Involucral bracts biseriate. Style branches with stigmatic areas extending to the adaxial side, which is papillate in the middle **480. *Herreranthus***
– Involucral bracts uniseriate. Style branches stigmatic inside, glabrous outside **478. *Antillanthus*** p.p.
181. Style of disc florets obtuse, with short and few sweeping hairs (Caribbean) 182
– Style of disc florets ± truncate with distinct sweeping hairs. Capitula yellow-flowered 183
182. Capitula radiate, white-flowered (Jamaica) **477. *Zemisia***
– Capitula radiate or discoid, yellow-flowered (Hispaniola) **479. *Elekmania*** p.p.
183. Ovary wall crystals prismatic, plate- or needle-like. Capitula radiate or sometimes discoid or disciform **499. *Senecio*** p.p.
– Ovary wall crystals drusiform. Capitula always discoid (Africa, Madagascar, Yemen) **500. *Solanecio*** p.p.

Genera of Senecioneae

410. *Abrotanella* Cass. Fig. 54

Abrotanella Cass., Dict. Sci. Nat. 36: 27 (1825); Swenson, Pl. Syst. Evol. 197: 149–193 (1995), rev.; Swenson & Bremer, Syst. Bot. 22: 493–508 (1997), biogeogr.; Heads, Biol. J. Linn. Soc. 67: 39–432 (1999), biogeogr.

Dwarf or prostrate perennial herbs, often forming mats or cushions. Leaves alternate, sessile with sheathing base, entire, coriaceous or subcarnose, glabrous with sunken glands. Capitula mostly sessile, small, disciform; florets few, whitish, greenish-yellow or red to purplish. Marginal florets female, tubular. Disc florets perfect or functionally male, 4-lobed; corolla lobes with central vascular strand and without lateral strands.

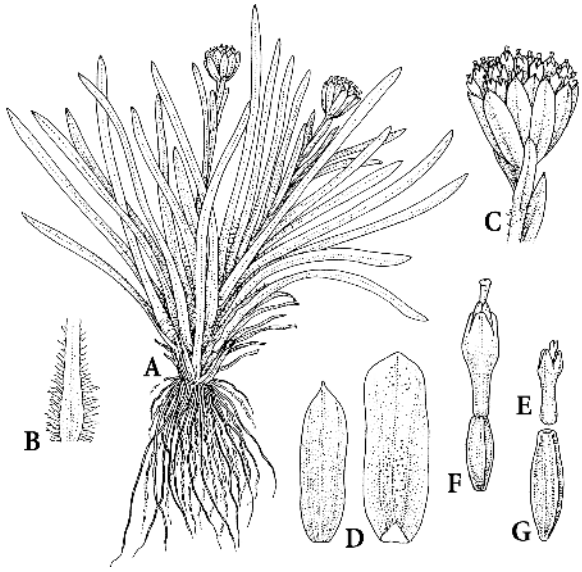

Fig. 54. Compositae-Senecioneae. *Abrotanella linearis*. **A** Habit. **B** Leaf base. **C** Capitulum. **D** Involucral bracts. **E** Outer floret. **F** Central floret. **G** Mature cypsela. (Swenson 1995)

Anthers shortly caudate; endothecium polarized. Style simple or shortly bilobed, truncate-obtuse, papillose. Cypselae oblong-obovoid, glabrous or papillose-puberulous with twin hairs, without pappus, but sometimes with an apical rim of small teeth. n = 9, 18. Twenty species, Australasia, southern South America.

411. *Blennosperma* Less.

Blennosperma Less., Syn. Gen. Comp.: 267 (1832); Ornduff, Brittonia 16: 289–295 (1964), rev.; Swenson, Doct. Diss. Uppsala Univ.: 10–12 (1995).

Small annual herbs. Leaves alternate, sessile, mostly pinnatifid. Capitula solitary on naked peduncles, radiate, yellow- or purplish-flowered. Receptacle conical. Ray florets female, tube reduced. Disc florets 5-lobed, functionally male. Anthers ecaudate; endothecium polarized. Style simple, sterile, apically enlarged. Cypsela obovoid, with short myxogenic twin hairs. Pappus absent. n = 7, 8, 9, 16. Three species, Chile, California.

412. *Crocidium* Hook.

Crocidium Hook., Fl. Bor.-Am. 1: 335, t. 112 (1834); St. John, Torreya 28: 73–77 (1928), rev.; Morton, N. Amer. Fl. ser. 2, 10: 147 (1978), rev.

Small annual herb. Leaves basal, rosulate, and cauline and clasping, entire or somewhat dentate to lobed. Capitula solitary, radiate, yellow-flowered. Receptacle conical. Ray florets female, with distinct tube, with or without pappus bristles. Disc florets perfect. Anther base obtuse, ecaudate; endothecium polarized. Style branches with conical hair tip; stigmatic areas separated. Cypselae obovoid, with short myxogenic twin hairs. Pappus bristles slender, densely barbellate, caducous. n = 9. One species, *C. multicaule* Hook., north-western USA.

413. *Ischnea* F. Muell.

Ischnea F. Muell., Trans. Roy. Soc. Victoria 1, 2: 13 (1889); Koster, Blumea 22: 207–217 (1975), rev.; Royen, Alpine Fl. New Guinea 4: 3352–3363 (1983), rev.; Swenson, Pl. Syst. Evol. 191: 247–263 (1994), rev.

Small perennial herbs, subrosulate, tufted or solitary. Leaves linear-oblanceolate, entire or sparsely dentate. Capitula solitary, small and few-flowered, shortly radiate, yellow- or purplish-flowered. Involucral bracts biseriate. Receptacle slightly convex, naked. Ray florets with ± reduced tube. Disc florets functionally male; corolla 4- or 5-lobed. Anthers ecaudate; endothecium polarized. Style simple, sterile. Cypselae elliptic-oblong, glabrous, without pappus. n = 9. Four species, New Guinea.

414. *Doronicum* L.

Doronicum L., Sp. Pl.: 855 (1753) & Gen. Pl. ed. 5: 377 (1754); Cavillier, Ann. Cons. Jard. Bot. Genève 13: 195–367 (1911), rev.; Gorshkova, Fl. U.S.S.R. 26: 669–682 (1961), reg. rev.; Edmondson, Fl. Turkey 5: 137–145 (1975), reg. rev.; Ferguson, Fl. Eur. 4: 190–191 (1976), reg. rev.; Edmondson, Notes Roy. Bot. Gard. Edinburgh 37: 67–74 (1978), reg. rev.; Rechinger, Fl. Iran. 164: 44–48 (1989), reg. rev.; Chen, Fl. Reip. Pop. Sin. 77, 1: 4–13 (1999), reg. rev.; Alvarez Fernandez, Ann. Missouri Bot. Gard. 90: 319–389 (2003), rev.

Perennial herbs. Leaves basal and cauline, rounded-cordate or ovate-oblong; basal leaves petiolate; cauline leaves sessile, often amplexicaul. Capitula solitary or few to several, corymbose, large, radiate, yellow-flowered. Involucral bracts biseriate. Anther base obtuse or auriculate; endothecium polarized. Style branches obtuse with few sweeping hairs; stigmatic areas continuous. Cypselae oblong, ribbed, glabrous or pubescent. Pappus bristles numerous, often lacking in ray florets, slender, sometimes dimorphic. Pollen helianthoid. n = 15, 20, 30, 45, 60. Circa 40 species, Eurasia, northern Africa.

415. *Chersodoma* Phil.

Chersodoma Phil., Anales Mus. Nac. Chile 1891: 33 (1891); Cabrera, Revista Mus. La Plata, Bot. 6: 343–355 (1946), re-establ., rev.; Nordenstam, Opera Bot. 44: 22–23 (1978), notes, subg. nov.; Dillon & Sagástegui, Brittonia 48: 582–604 (1997), rev.

Dioecious shrubs, subshrubs or perennial herbs. Leaves petiolate or subsessile, often tomentose beneath, entire; margins sometimes dentate, often revolute. Capitula solitary, pedunculate, or few and laxly paniculate, homogamous; florets either pistillate with aborted anthers or functionally male with sterile ovary. Anthers caudate; endothecial tissue polarized; filament collar cylindrical, uniform. Style branches apically rounded to subtruncate without sweeping hairs, dorsally puberulous-papillose; stigmatic areas separated at least in the basal half. Cypselae oblong, ribbed, glabrous or hairy. Pappus bristles slender, white or purplish-brown, persistent. n = 10. Nine species, Andean South America from Argentina to Peru.

416. *Homogyne* Cass.

Homogyne Cass., Bull. Soc. Philom. Paris 1816: 198 (1816); Vierhapper, Oesterr. Bot. Z. 1923(6–8): 150–164 (1923), syst. position; Tutin, Fl. Eur. 4: 188–189 (1976), rev.

Perennial herbs. Leaves mostly basal, petiolate, rounded to cordate, entire with dentate to lobulate margins, palmately veined; cauline leaves smaller, few. Capitula solitary on long peduncles, disciform, purple- or white-flowered. Marginal florets female, tubular and very shortly radiate. Disc florets perfect. Anthers exserted, ecaudate. Style branches truncate, penicillate. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender, white or dirty white. n = c. 28, 29, 30, 60, 65, 65–70, 70, 80. Three species, central and southern Europe.

417. *Endocellion* Turcz. ex Herder

Endocellion Turcz. ex Herder, Bull. Soc. Imp. Naturalistes Moscou 38: 345 (1865); Toman, Folia Geobot. Phytotax. (Prague) 7: 381–406 (1972), rev.

Perennial dioecious herbs with a slender rhizome. Leaves rosulate, developing after anthesis, petiolate, ± ovate, palmately veined; cauline leaves sessile, scale-like. Capitula solitary or rarely few together, yellow-flowered, calyculate. Male capitula discoid or disciform with functionally male disc florets. Female capitula radiate, lacking disc florets; florets radiate. Cypselae oblong, glabrous. Pappus bristles numerous, slender. n = 28, 29, 30, c. 50+, 56. Two species, Siberia, eastern Asia.

418. *Petasites* Mill.

Petasites Mill., Gard. Dict. abr. ed.: 4 (1754); Toman, Folia Geobot. Phytotax. (Prague) 7: 381–406 (1972), rev.; Cherniawski & Bayer, Canad. J. Bot. 76: 2061–2075 (1999), reg. rev.; Chen, Fl. Reip. Pop. Sin. 77, 1: 94–101 (1999), reg. rev.; Kupriyanova, Flora U.S.S.R. 26: 645–654 (1961), reg. rev. (sub *Nardosmia*).
Nardosmia Cass. (1825).

Perennial dioecious or subdioecious herbs with a thick rhizome. Leaves rosulate, developing after anthesis, petiolate, rounded-cordate or triangular, entire to palmately lobed, palmately veined. Cauline leaves scale-like. Capitula several, paniculate-racemose, large, calyculate, radiate, disciform or discoid; 'male' capitula with or without marginal florets and with numerous tubular functionally male florets. Female capitula with sterile tubular or shortly radiate florets and numerous filiform female florets. Styles apically clavate to cylindrical, shortly bilobed. Cypselae cylindric-oblong, glabrous, ribbed. n = 10, 14, 16, 26, 28, 29, 30, 40, c. 44, 45, 60. Circa 20 species, Eurasia, North America.

419. *Tussilago* L.

Tussilago L., Sp. Pl.: 865 (1753) & Gen. Pl. ed. 5: 372 (1754).

Perennial rhizomatous herb. Leaves rosulate, petiolate, large, developing after anthesis, rounded-cordate, entire with dentate margins. Capitula solitary on a bracteate scapiform stem, radiate, yellow. Ray florets numerous, female, with narrow rays. Disc florets functionally male, tubular. Anthers sagittate. Style branches apically clavate, sterile. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender, persistent. n = 30, 36. One species, *T. farfara* L., Eurasia.

420. *Farfugium* Lindl.

Farfugium Lindl., Gard. Chron. 1857: 4 (1857); Kitamura, Acta Phytotax. Geobot. 8: 77–89 (1939), rev.; Koyama, Mem. Fac. Sci. Kyoto Univ. ser. Biol. 2: 38 (1968), reg. rev.

Perennial herbs with a thick rhizome. Leaves rosulate, petiolate, with involute vernation, ovate-cordate or reniform, entire with dentate margins, palmately veined. Capitula few to several, corym-

bose, radiate, calyculate, yellow-flowered. Disc florets perfect. Anthers caudate. Style branches tapering towards the obtuse apex, papillate throughout. Cypselae oblong, hairy. Pappus bristles numerous, slender. n = 30, 31. Three species, Japan, southeastern China, Korea, Taiwan.

421. *Miricacalia* Kitam.

Miricacalia Kitam., Acta Phytotax. Geobot. 5: 214 (1936); Koyama, Mem. Fac. Sci. Kyoto Univ. ser. Biol. 2: 163 (1969), rev.; Robinson & Brettell, Phytologia 27: 265–276 (1973), notes.

Perennial villous herb. Leaves few, petiolate, palmately lobed and veined. Capitula several, racemose, discoid, calyculate, yellow-flowered. Anthers ecaudate, auriculate. Style branches long, papillate, apically truncate, penicillate. Cypselae narrowly elliptic-oblong, glabrous, beaked and with a long carpopodium. Pappus bristles numerous, slender. n = 26, 27, 30. One species, *M. makineana* (Yatabe) Kitam., Japan.

422. *Dendrocacalia* (Nakai) Nakai ex Tuyama

Dendrocacalia (Nakai) Nakai ex Tuyama, Bot. Mag. (Tokyo) 50: 129 (1936); Koyama, Mem. Fac. Sci. Kyoto Univ. ser. Biol. 2: 157–158 (1969), rev.; Kato & Nagamasu, J. Pl. Res. 108: 443–450 (1995), morph.

Erect branched dioecious shrub with soft wood. Leaves ovate to oblanceolate, entire, glabrous, pinnately veined. Capitula several, corymbose, discoid, calyculate, pink to purplish-flowered. Florets 5, female or functionally male. Anther base obtuse. Style branches papillate, apically truncate, penicillate; stigmatic areas continuous. Cypselae oblong, pubescent. Pappus bristles numerous, slender. n = 30. One species, *D. crepidifolia* (Nakai) Nakai ex Tuyama, Bonin Island.

423. *Parasenecio* W.W. Smith & Small

Parasenecio W.W. Smith & Small, Trans. Proc. Bot. Soc. Edinburgh 28: 93 (1923); Chen, Fl. Reip. Pop. Sin. 77, 1: 19–87 (1999), reg. rev.; sub *Cacalia* auct. non L.: Pojarkova, Fl. U.S.S.R. 26: 683–697 (1961), reg. rev.; Koyama, Mem. Fac. Sci. Kyoto Univ. ser. Biol. 2: 163–181 (1969), reg. rev.; Koyama, Acta Phytotax. Geobot. 29: 65–84, 171–178 (1978) & 30: 65–84 (1979), reg. rev.
Koyamacalia H. Robins. & Brettell (1973).

Perennial herbs. Leaves basal and cauline, petiolate, or cauline leaves sometimes sessile, rounded-cordate to deltoid or ovate, entire or palmately lobed, usually palmately veined; margins usually denticulate to serrate. Capitula numerous, discoid, paniculate-racemose or in spike-like synflorescences, small, ecalyculate, white-, cream- or yellow-flowered. Anthers sagittate to shortly caudate. Style branches with continuous stigmatic areas, apically obtuse, papillate. Cypselae elliptic-oblong, glabrous, with distinct carpopodium. Pappus bristles numerous, slender, white or tawny to reddish. n = 20, 26, 29, 30, 31, 45, 60. Circa 70 species, Eurasia from Russia eastwards with the majority in eastern Asia, one species reaching the Aleutian Isl.

424. *Dicercoclados* C. Jeffrey & Y.L. Chen

Dicercoclados C. Jeffrey & Y.L. Chen, Kew Bull. 39: 213 (1984).

Perennial rhizomatous herb. Leaves cauline, petiolate, entire, lanceolate, three-veined; margins sparsely denticulate. Capitula solitary or few together, axillary, pedunculate, discoid, calyculate, yellow-flowered. Anthers caudate with long firm tails. Style branches with continuous stigmatic areas, apically with two hair tufts. Cypselae narrowly oblong, glabrous. Pappus bristles numerous, slender. One species, *D. triplinervis* C. Jeffrey & Y.L. Chen, China.

425. *Sinacalia* H. Rob. & Brettell

Sinacalia H. Rob. & Brettell, Phytologia 27: 274 (1973); Nordenstam, Opera Bot. 44: 15 (1978), syst., nomencl.; Jeffrey & Chen, Kew Bull. 39: 215–222 (1984), rev.; Chen, Fl. Reip. Pop. Sin. 77, 1: 13–18 (1999), rev.

Perennial herbs with an underground tuber. Leaves cauline, petiolate, ovate to rounded-cordate or deltoid, entire or palmately lobed, palmately veined or nearly so. Capitula several to many, rarely solitary, thyrsoid or paniculate-corymbose, narrow, radiate, ecalyculate, yellow-flowered. Anthers auriculate or sagittate, apical appendage dark-coloured, midlined. Style branches ± truncate, apically papillate, stigmatic areas continuous but basally discrete. Cypselae oblong, ribbed, glabrous, with distinct cylindrical carpopodium. Pappus bristles numerous, slender. n = 30. Four species, China.

426. *Syneilesis* Maxim.

Syneilesis Maxim., Prim. Fl. Amur.: 165 (1859); Koyama, Mem. Fac. Sci. Kyoto Univ. ser. Biol. 2: 159–162 (1969), rev.; Robinson & Brettell, Phytologia 27: 265–276 (1973), notes; Chen, Fl. Reip. Pop. Sin. 77, 1: 89–93 (1999), reg. rev.

Perennial rhizomatous herbs. Seedling with a single cotyledon. Leaves cauline, few, petiolate, peltate, palmately lobed or dissected and palmately veined. Capitula several to many, racemose-paniculate or corymbose, discoid, calyculate, white-flowered. Anthers caudate. Style branches elongate, papillate, apically truncate and penicillate. Cypselae narrowly elliptic to oblong, glabrous. Pappus bristles numerous, slender. $n = 26, 39$. Seven species, eastern Asia.

427. *Ligularia* Cass.

Ligularia Cass., Bull. Soc. Philom. Paris 1816: 198 (1816), nom. cons.; Handel-Mazzetti, Bot. Jahrb. 69: 95–142 (1938), reg. rev.; Pojarkova, Notul. Syst. Herb. Inst. Bot. Komarov. Acad. Sci. U.R.S.S. 12: 293–318 (1950), syst.; Pojarkova, Fl. U.S.S.R. 26: 788–857 (1961), reg. rev.; Koyama, Mem. Fac. Sci. Kyoto Univ. ser. Biol. 2: 39–52 (1968), reg. rev.; Liu, Fl. Reip. Pop. Sin. 77, 2: 4–115 (1989), reg. rev.; Rechinger, Fl. Iran. 164: 48–51 (1989), reg. rev.

Perennial herbs with a creeping rhizome. Leaves basal and cauline, petiolate with strongly sheathing leaf base, oblong to oblanceolate or cordate, entire with often serrate-dentate margins. Capitula several to many, racemose-paniculate, radiate or sometimes discoid, yellow-flowered. Involucre narrowly cup-shaped to cylindrical, calyculate. Anthers auriculate to shortly caudate. Style branches subtruncate to obtuse with short lateral sweeping hairs, papillate apically or throughout. Cypselae narrowly oblong to elliptic-oblong, ribbed, glabrous. Pappus bristles numerous, slender, white or tawny to rufous. $n = 15–16, 16, 24, 25–26, 27, 29, 30, 31$. Circa 125 or more species, Eurasia. Genus under revision (I. Illarionova).

428. *Ligulariopsis* Y.L. Chen

Ligulariopsis Y.L. Chen, Acta Phytotax. Sin. 34: 631 (1996); Chen, Fl. Reip. Pop. Sin. 77, 1: 87–89 (1999), rev.

Perennial herb. Leaves cauline, petiolate, ovate, pinnately veined; petiole winged and with amplexicaul base. Capitula numerous in elongated spike-like thyrsoid-paniculate synflorescence, discoid, few-flowered. Disc florets perfect, yellow. Anther base obtuse, ecaudate. Style branches obtuse, penicillate, papillate to below bifurcation. Cypselae cylindrical-oblong, ribbed, glabrous. Pappus bristles numerous, slender, purplish-brown. $n = 29$. One species, *L. shichuana* Y.L. Chen, China.

429. *Cremanthodium* Benth.

Cremanthodium Benth., Hooker's Icon. Pl. 12: 37, t. 1141 (1873); d'O. Good, J. Linn. Soc., Bot. 48: 259–316 (1929), rev.; Koyama, Mem. Fac. Sci. Kyoto Univ. ser. Biol. 2: 52–60 (1968), reg. rev.; Liu, Fl. Reip. Pop. Sin. 77, 2: 115–171 (1989), reg. rev.

Perennial herbs. Leaves rosulate, sometimes also a few cauline, petiolate, ovate-cordate to reniform or elliptic-oblong to lanceolate, rarely pinnatifid; leaf base sheathing. Capitula solitary or few, racemose, broad, nodding, radiate or discoid, ecalyculate. Involucre broadly cup-shaped or campanulate. Florets white, pink, purple, yellow or orange-coloured. Anthers ecaudate. Style branches obtuse, penicillate, dorsally papillate. Cypselae elliptic-oblong, glabrous. Pappus bristles numerous, slender, white or reddish. $n = 29$. Circa 75 species, China, Tibet and Himalaya.

430. *Nemosenecio* (Kitam.) B. Nord. Fig. 55

Nemosenecio (Kitam.) B. Nord., Opera Bot. 44: 45 (1978), 45–46, new comb., new sp.; Jeffrey & Chen, Kew Bull. 39: 262–266 (1984), reg. rev.; Chen, Fl. Reip. Pop. Sin. 77, 1: 161–166 (1999), reg. rev.
Senecio sect. *Nemosenecio* Kitam. (1937).

Perennial herbs. Leaves cauline, shortly petiolate, pinnately lobed or dissected. Capitula several, corymbose, radiate, yellow-flowered, ecalyculate. Anthers short, ecaudate, with narrow apical appendage; endothecium transitional. Style branches truncate, stigmatic areas partly confluent but discrete at least basally. Cypselae narrowly oblong, glabrous or sparsely pubescent. Pappus bristles numerous, slender, persistent. $n = 5, 10, 20, 24$. Six species, Japan, China.

431. *Sinosenecio* B. Nord.

Sinosenecio B. Nord., Opera Bot. 44: 48 (1978), 48–51, new comb.; Jeffrey & Chen, Kew Bull. 39: 222–261 (1984), rev.; Chen, Fl. Reip. Pop. Sin. 77, 1: 101–141 (1999), rev.

Perennial herbs with fibrous roots or a rhizome. Leaves rosulate and/or cauline, petiolate, rounded to cordate, reniform or triangular-ovate, entire or margins dentate or sinuate-lobate. Capitula solitary or several, corymbose-paniculate, radiate, yellow-flowered, ecalyculate. Anthers ecaudate; endothecium polarized. Style branches apically truncate to obtuse with short or long sweeping hairs, dorsally papillate, stigmatic areas confluent or narrowly separated. Cypselae elliptic-oblong, ribbed, glabrous or pubescent, sometimes heteromorphic

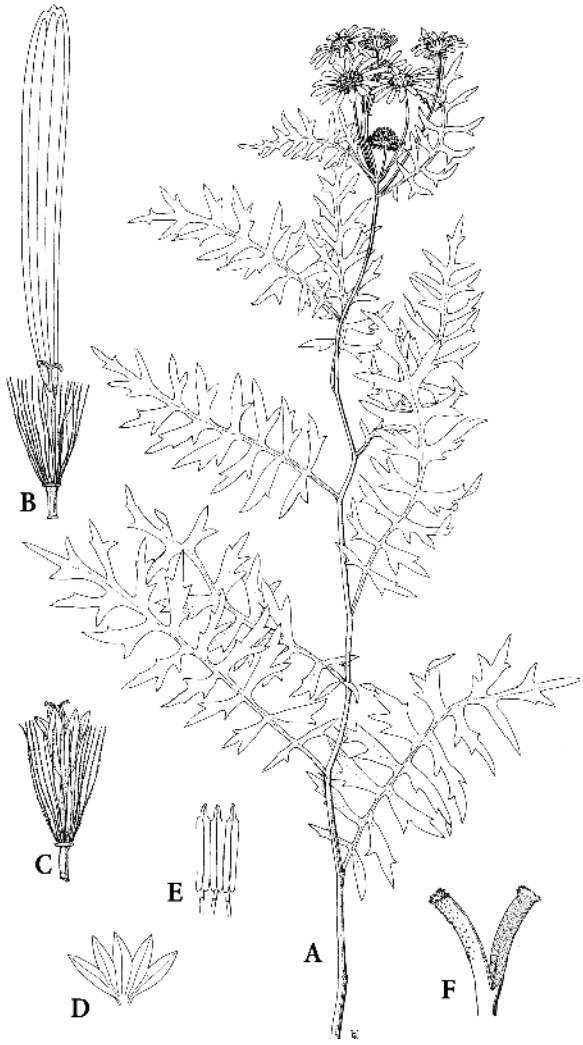

Fig. 55. Compositae-Senecioneae. *Nemosenecio yunnanensis*. **A** Habit. **B** Ray floret. **C** Disc floret. **D** Corolla of disc floret, opened. **E** Stamens. **F** Style branches of disc floret. (Drawing by B. Nordenstam)

(glabrous and epappose in ray florets, hairy and pappose in disc florets). Pappus bristles numerous, slender, persistent or caducous, sometimes absent in ray florets. n = 23, 24. Circa 40 species, south-eastern Asia, mainly China, one species in Canada (prob. not congeneric).

432. *Tephroseris* (Reichenb.) Reichenb.

Tephroseris (Reichenb.) Reichenb., Deutsche Bot. Fl. Sax.: 146 (1842); Cufodontis, Feddes Repert. Beih. 70: 1–266 (1933), rev.; Nordenstam, Opera Bot. 44: 43–45 (1978), new comb.; Jeffrey & Chen, Kew Bull. 39: 267–285 (1984), reg. rev.; Chen, Fl. Reip. Pop. Sin. 77, 1: 141–161 (1999), reg. rev.

Perennial or biennial herbs. Leaves radical and cauline, sessile with often petioliform base, entire with often serrate or dentate margins, pinnately veined. Capitula few or several, rarely solitary, radiate or occasionally discoid, ecalyculate, yellow-, orange- or red-flowered. Anthers with radial endothecium, filament collar cylindrical. Style branches truncate to obtuse, with continuous stigmatic areas. Cypselae oblong, ribbed, glabrous or pubescent. Pappus bristles numerous, slender. n = 9, 13, 14, 17, 18, 19(?), 20, 22, 23, 24, 25, 32, 36, 40, c. 40, 48, 45–52. Circa 50 species, northern Eurasia, one species in North America.

433. *Psacaliopsis* H. Rob. & Brettell

Psacaliopsis H. Rob. & Brettell, Phytologia 27: 408 (1974).

Perennial scapigerous herbs. Leaves rosulate, petiolate, peltate, entire or lobed, palmately veined, with hairy leaf base. Capitula solitary or few, radiate, yellow-flowered, or discoid and reddish-flowered, calyculate. Disc floret corolla shortly lobed, with resin canals. Anthers with radial endothecium; filament collar cylindrical. Style branches with continuous stigmatic areas. Cypselae oblong, glabrous. Pappus bristles numerous, slender, caducous. n = 30. Circa 6 species, Mexico, Guatemala.

434. *Psacalium* Cass.

Psacalium Cass., Dict. Sci. Nat. 43: 461 (1826); Rydberg, Bull. Torrey Bot. Club 51: 370–376 (1924), reg. rev.; Pippen, Contr. U.S. Natl Herb. 34: 415–436 (1968), 384–410 (1968), rev. (sub *Odontotricho*); Robinson & Brettell, Phytologia 27: 254–264 (1973), rev.
Odontotrichum Zucc. (1832).

Scapigerous perennial herbs. Leaves rosulate or at least mainly basal, petiolate, peltate or with marginal petiole, rounded-ovate, entire or dentate-lobate to pinnatisect; leaf bases hairy; cauline leaves reduced. Capitula several to many, paniculate to corymbose or racemose, discoid, calyculate. Corolla white or yellowish or purplish, deeply lobed. Anthers ecaudate; endothecium radial. Style branches with continuous stigmatic areas. Cypselae elliptic-obovoid, somewhat compressed, ribbed, glabrous or pubescent. Pappus bristles numerous, slender, or absent. n = c. 25, c. 29, 30. Circa 40 species, south-western USA (Arizona), Mexico, Guatemala.

435. *Pippenalia* McVaugh

Pippenalia McVaugh, Contr. Univ. Michigan Herb. 9: 470 (1972).

Perennial scapigerous herb. Leaves rosulate, long-petiolate, peltate, laciniate, palmately veined; leaf base hairy. Capitula solitary, long-pedunculate, radiate, yellow, ecalyculate. Corolla lobes of disc floret short. Anther base ecaudate, obtuse. Style branches apically obtuse, shortly penicillate, dorsally papillate. Cypselae oblong-obovoid, ribbed, glabrous. Pappus absent. n = 15, 30. One species, *P. delphinifolia* (Rydb.) McVaugh, Mexico.

436. *Digitacalia* Pippen

Digitacalia Pippen, Contr. U.S. Natl Herb. 34: 378 (1968), 378–383, rev.; Robinson & Brettell, Phytologia 27: 407 (1974), notes; Turner, Phytologia 69: 150–159 (1990), rev.

Erect perennial herbs. Leaves evenly distributed on stem, petiolate, ± palmately lobed and veined. Capitula several, corymbose, discoid, calyculate. Corolla white, cream or purplish, deeply lobed. Anthers ecaudate; endothecium polarized. Style branches truncate to obtuse with continuous stigmatic areas. Cypselae narrowly cylindrical, oblong, ribbed, glabrous or pubescent. Pappus bristles numerous, slender. n = 30. Five species, Mexico.

437. *Rugelia* Shuttlew. ex Chapm.

Rugelia Shuttlew. ex Chapm., Fl. South. U.S.: 246 (1860); Pippen, N. Amer. Fl. ser. 2, 10: 153–154 (1978), rev. (as *Cacalia rugelia*).

Perennial rhizomatous herb, pubescent in most parts. Radical leaves large, petiolate, ovate, denticulate, pinnately veined; cauline leaves smaller, subsessile, entire, elliptic-ovate, palmately veined. Capitula few to several, long-pedunculate, cymose, many-flowered, discoid, calyculate; florets white or ochroleucous. Anthers ecaudate, basally obtuse. Style branches apically truncate and penicillate. Cypselae narrowly cylindrical-oblong, striate, glabrous. Pappus bristles numerous, rather rigid, scabrid. n = 28. One species, *R. nudicaulis* Shuttlew. ex Chapm., southern USA.

438. *Arnoglossum* Raf.

Arnoglossum Raf., Fl. Ludov.: 64 (1817); Vuilleumier, J. Arnold Arbor. 50: 104–123 (1969), rev., notes; Robinson, Phytologia 28: 294–295 (1974), rev.; Pippen, N. Amer. Fl. ser. 2, 10: 151–159 (1978), rev. (sub *Cacalia*).
Mesadenia Raf. (1832).

Perennial herbs. Leaves basal and cauline, petiolate, entire or somewhat lobed, ovate-cordate to elliptic, palmately veined. Capitula few, small and few-flowered, corymbose, discoid, ecalyculate. Receptacle conical. Corolla deeply lobed, white to yellowish or pink. Anthers with radial endothecium. Style branches truncate, penicillate, with continuous stigmatic areas. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender. n = 25, 26, 27, 28, 55. Eight species, central, eastern and south-eastern USA.

439. *Robinsonecio* T.M. Barkley & J.P. Janovec

Robinsonecio T.M. Barkley & J.P. Janovec, Sida 17: 77–81 (1996).

Perennial herbs with a thick rhizome. Stem subscapose. Leaves rosulate, petiolate, ovate-lanceolate or spathulate, entire with denticulate margins. Capitula solitary or up to 8, corymbose, radiate, yellow-flowered. Involucral bracts biseriate, with a distinct or reduced calyculus. Disc florets perfect. Anther collars cylindrical. Style branches with continuous stigmatic areas. Cypselae elliptic-oblong, glabrous or appressed-hirsute. Pappus bristles numerous, slender. Pollen helianthoid. n = 30. Two species, Mexico, Guatemala.

440. *Roldana* La Llave & Lex.

Roldana La Llave & Lex., Nov. Veg. Descr. 2: 10 (1825); Robinson & Brettell, Phytologia 27: 408–424 (1974), review; Turner, Phytologia 80: 276–279 (1996), new taxa; Panero & Villaseñor, Brittonia 48: 79–90 (1996), new taxa; Rydberg, Bull. Torrey Bot. Club 51: 376–377 (1924), rev. (sub *Pericalia*); Pippen, Contr. U.S. Natl Herb. 34: 410–415 (1968), rev. (sub *Pericalia*). Revision ongoing (A.M. Funston).
Pericalia Cass. (1827).

Herbs, subshrubs or treelets, mostly with a hairy tuberous caudex and fleshy roots; stems with large pith. Leaves alternate, petiolate, often peltate, palmately or sometimes pinnately veined, rounded-ovate, entire and dentate to lobate or pinnatisect. Capitula several to numerous, paniculate to corymbose, radiate, disciform or discoid, yellow-, white- or greenish-flowered. Involucre cylindrical to narrowly campanulate, calyculate. Anthers with transitional endothecium; filament collars cylindrical. Style branches with continuous stigmatic areas. Cypselae elliptic-obovoid, ribbed, glabrous or pubescent. Pappus bristles numerous,

slender. $n = 30, 60$. Circa 65 species, south-western USA (Arizona), Mexico to Panama.

441. *Nelsonianthus* H. Rob. & Brettell

Nelsonianthus H. Rob. & Brettell, Phytologia 27: 54 (1973).

Epiphytes or lax suffrutescent herbs. Stems abruptly contracted below synflorescence. Leaves clustered towards stem ends, petiolate, 3–5-veined from the base, entire with serrulate margins. Capitula few to several, radiate or discoid, yellow-flowered, calyculate. Anthers sagittate to shortly caudate; endothecium polarized. Style branches obtuse; stigmatic areas continuous except basally. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender. Two or three species, Mexico, Guatemala.

442. *Telanthophora* H. Rob. & Brettell

Telanthophora H. Rob. & Brettell, Phytologia 27: 424 (1974).

Treelets, shrubs or shrublets. Leaves alternate, mostly terminal on abruptly contracted stem ends, petiolate, persistent, entire or dentate-lobed, pinnately veined. Capitula several or numerous, small, paniculate-corymbose, radiate or discoid, ± distinctly calyculate, yellow-flowered. Anthers with radial endothecium; filament collar cylindrical. Style branches obtuse with continuous stigmatic areas. Cypselae elliptic-oblong, ribbed, mostly glabrous. Pappus bristles numerous, slender. Pollen helianthoid. $n = 30$, c. 38, c. 65. Twelve to 14 species, Panama to Mexico.

443. *Villasenoria* B.L. Clark

Villasenoria B.L. Clark, Sida 18: 631–634 (1999).

Tall perennial suffruticose herb. Stem simple, erect, tapering to synflorescence. Leaves cauline, petiolate, large, pinnately compound. Capitula numerous in elongate paniculate-racemose clusters, radiate, yellow-flowered. Involucre cylindrical or narrowly campanulate, biseriate, calyculate. Anthers with radial endothecium, filament collar basally somewhat enlarged. Style branches apically truncate or subconical with short sweeping hairs, stigmatic areas continuous. Cypselae oblong-cylindrical, glabrous. Pappus bristles numerous, slender. One species, *V. orcuttii* (Greenm.) B.L. Clark, Mexico.

444. *Pittocaulon* H. Rob. & Brettell

Pittocaulon H. Rob. & Brettell, Phytologia 26: 451 (1973).

Erect shrubs or small trees, resiniferous, subsucculent. Leaves cauline, mostly assembled terminally at branch ends, petiolate, often deciduous before anthesis, palmately lobed and veined. Capitula several, corymbose, radiate, yellow-flowered, calyculate. Anthers with radial endothecium; filament collar uniformly cylindrical. Style branches with continuous stigmatic areas. Cypselae elliptic-oblong, ribbed, glabrous. Pappus bristles numerous, slender. $n = 30$. Six species, Mexico.

445. *Barkleyanthus* H. Rob. & Brettell

Barkleyanthus H. Rob. & Brettell, Phytologia 27: 407 (1974).

Erect branching glabrous shrub, with a weak taproot and many lateral roots; stems with chambered pith. Leaves cauline, assembled terminally on branches, subsessile, entire, lanceolate or linear-lanceolate, pinnately veined. Capitula several, corymbose, radiate, yellow-flowered, ecalyculate. Anthers with radial endothecium. Style branches with continuous stigmatic areas. Cypselae narrowly elliptic-oblong, ribbed, sparsely pubescent. $n = 30$. One species, *B. salicifolius* (Kunth) H. Rob. & Brettell, south-western USA, Mexico, Central America.

446. *Yermo* R.D. Dorn

Yermo R.D. Dorn, Madroño 38: 199 (1991).

Perennial herb with a thick taproot. Leaves basal and cauline, entire, petiolate, lanceolate to elliptic-obovate, 3-nerved. Capitula numerous, corymbosely crowded, discoid. Involucre with 5 phyllaries, yellow, ecalyculate. Corolla deeply lobed, yellow. Anthers auriculate. Style branches obtuse to truncate, penicillate, with continuous stigmatic areas. Cypselae elliptic-oblong, c. 10-veined, mostly puberulous. Pappus bristles numerous, slender, caducous. One species, *Y. xanthocephalus* R.D. Dorn, western USA.

447. *Rainiera* Greene

Rainiera Greene, Pittonia 3: 291 (1898); Strother, N. Amer. Fl. ser. 2, 10: 162–163 (1978), rev.

Perennial herb with a short rhizome. Leaves basal and cauline, sessile but tapering into a petioliform base, entire, broadly oblanceolate, upper leaves gradually smaller, pinnately veined. Capitula several in elongated thyrsoid panicles, narrow and few-flowered, discoid. Corolla lobes lanceolate, pale yellowish. Anther base obtuse or minutely

sagittate. Style branches truncate, papillate. Cypselae cylindrical-oblong, many-nerved, glabrous. Pappus bristles numerous, slender. One species, *R. stricta* (Greene) Greene, north-western USA.

448. *Cacaliopsis* A. Gray

Cacaliopsis A. Gray, Proc. Amer. Acad. Arts 19: 50 (1883); Nordenstam, Opera Bot. 44: 21–22 (1978), notes; Strother, N. Amer. Fl. ser. 2, 10: 160–161 (1978), rev.

Perennial rhizomatous herb. Leaves mostly basal, petiolate, palmately lobed and veined. Capitula solitary or few, corymbose to racemose or subumbellate, discoid, yellow- to orange-flowered, calyculate. Corolla lobes short. Anthers ecaudate. Style branches apically obtuse to rounded to subconical, dorsally papillate, stigmatic areas discrete but apically confluent. Cypselae cylindrical-oblong, many-nerved, glabrous. Pappus bristles numerous, slender. n = 30. One species, *C. nardosmia* (A. Gray) A. Gray, western North America.

449. *Luina* Benth.

Luina Benth., Hooker's Icon. Pl. 12: 36, t. 1139 (1873); Nordenstam, Opera Bot. 44: 21–22 (1978), notes; Strother, N. Amer. Fl. ser. 2, 10: 161–162 (1978), rev.

Perennial tomentose or lanate herbs or subshrubs. Leaves cauline, sessile or petiolate, entire, lanceolate or oblanceolate to elliptic-ovate. Capitula several, corymbose to racemose, discoid, yellow- or cream-flowered. Anthers shortly caudate; filament collar narrow, elongate. Style branches obtuse or subtruncate, dorsally finely papillate, stigmatic areas discrete except towards the apex. Cypselae narrowly oblong to fusiform, nerved, glabrous or pubescent. Pappus bristles numerous, slender. n = 30. Two species, western North America.

450. *Tetradymia* DC.

Tetradymia DC., Prodr. 6: 440 (1838); Strother, Brittonia 26: 177–202 (1974), rev.; N. Amer. Fl. ser. 2, 10: 163–170 (1978), rev.

Shrubs, spinescent or unarmed, often canescent. Leaves cauline, sessile, alternate, sometimes fascicled, small and narrow, filiform or linear-lanceolate to oblanceolate (some transformed into spines). Capitula solitary or few together, axillary or corymbose, small and few-flowered, discoid, ecalyculate, cream- or yellow-flowered. Anthers sagittate, ecaudate. Style branches truncate to obtusely conical, papillate-puberulous. Cypselae oblong to narrowly elliptic-obovate or turbinate, with glandular ribs, otherwise glabrous or pubescent. Pappus bristles numerous, slender or scale-like, sometimes lacking. n = 30, 31, 45, 60, 62, 90. Ten species, western North America.

451. *Lepidospartum* (A. Gray) A. Gray

Lepidospartum (A. Gray) A. Gray, Proc. Amer. Acad. Arts 19: 50 (1883); Strother, N. Amer. Fl. ser. 2, 10: 171–173 (1978), reg. rev.

Broom-like shrubs or treelets. Leaves sessile, linear-oblanceolate to filiform or scale-like, entire. Capitula solitary to several or many, racemose, axillary or terminal, discoid, small and mostly few-flowered, yellow-flowered. Involucral bracts pluriseriate. Anthers sagittate or caudate. Style branches slender, papillate-puberulous, apically with a conical penicillate appendage. Cypselae narrowly elliptic-oblong or fusiform, glabrous or pubescent. Pappus bristles numerous, slender. n = 30, c. 45. Three species, south-western USA, Mexico.

452. *Paracalia* Cuatrec.

Paracalia Cuatrec., Brittonia 12: 183 (1960).

Scandent shrublets. Leaves cauline, petiolate, elliptic-ovate, entire. Capitula several, corymbose, small and few-flowered, discoid, ecalyculate. Corolla white, deeply lobed. Anther base acute; endothecium polarized. Style branches apically with a pointed tuft of hairs; stylopodium distinct. Cypselae oblong, glabrous. Pappus bristles numerous, slender. Two species, Bolivia, Peru.

453. *Paragynoxys* (Cuatrec.) Cuatrec.

Paragynoxys (Cuatrec.) Cuatrec., Brittonia 8: 153 (1955); Correa, Brittonia 55: 157–168 (2003), rev.

Erect single-stemmed or little-branched trees or treelets. Leaves alternate, crowded towards branch ends, petiolate, large, entire, elliptic-ovate or obovate, coriaceous. Capitula numerous, few-flowered, paniculate, discoid, calyculate. Corolla white, deeply lobed. Anthers sagittate or shortly caudate. Style branches apically obtuse-conical, papillate. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender. n = c. 40. Twelve species, Andes of Colombia and Venezuela.

454. *Gynoxys* Cass.

Gynoxys Cass., Dict. Sci. Nat. 48: 455 (1827).

Shrubs or trees. Leaves opposite, petiolate or subsessile, entire, elliptic-oblong to ovate or obovate, coriaceous, densely tomentose beneath. Capitula few to many, corymbose-paniculate, radiate or discoid, yellow-flowered. Anthers ecaudate. Style branches with an apical conical-pointed hair pencil, stigmatic areas confluent. Cypselae elliptic-oblong, ribbed, glabrous or pubescent. Pappus bristles numerous, slender. n = c. 12, c. 36, c. 40, 40. Circa 120 species, Andes from Argentina and Bolivia to Venezuela.

455. *Nordenstamia* Lundin

Nordenstamia Lundin, Comp. Newslett. 44: 15 (2006); Nordenstam, Comp. Newslett. 44: 19–23 (2006); new comb. *Senecio* L. sect. *Praegynoxys* Cuatrec. (1951).
Gynoxys Cass. sect. *Praegynoxys* (Cuatrec.) Cuatrec. (1955).
Aequatorium B. Nord. subg. *Praegynoxys* (Cuatrec.) B. Nord. (1997).

Shrubs or trees (up to 18 m tall), pubescent with branching, globular-echinate or substellate trichomes especially on leaves and young parts. Leaves alternate (rarely opposite). Capitula several, paniculate-corymbose, radiate, yellow-flowered, calyculate. Ray florets few (2–5). Anthers sagittate or shortly caudate. Style branches with an apical pointed appendage; stigmatic areas continuous or barely separated. Cypselae elliptic-oblong, 8–10-ribbed, glabrous or glandular-puberulous. Pappus bristles numerous, slender but often dilated apically, white to fulvous. Circa 20 species, Argentina, Bolivia, Peru, southern Ecuador.

456. *Aequatorium* B. Nord. Fig. 56

Aequatorium B. Nord., Opera Bot. 44: 59 (1978); Díaz-Piedrahita & Cuatrecasas, Revista Acad. Colomb. Ci. 17, 67: 659–666 (1990), reg. rev.; Díaz-Piedrahita & Cuatrecasas, Revista Acad. Colomb. Ci. 19, 73: 247–252 (1994), new taxa, key; Nordenstam, Comp. Newslett. 31: 1–16 (1997), reg. rev.

Erect shrubs or trees, stellate-tomentose in young parts. Leaves alternate, petiolate, entire, lanceolate to elliptic-ovate, with margins often dentate or denticulate, coriaceous; tomentum mainly on lower side, in two layers; a white or greyish inner layer overlain by a scurfy rusty-brownish looser layer peeling off in patches; trichomes peltate-stellate. Capitula several to numerous, paniculate-corymbose, radiate, calyculate. Ray florets white or cream. Disc florets perfect; corolla deeply lobed, white or pale yellowish. Anthers ecaudate; endothecium polarized; filament collar cylindrical. Style branches obtuse or subtruncate, apically and dorsally papillate, stigmatic areas continuous. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, somewhat coarse, persistent, white or brownish to fulvous. Circa 12 species, Ecuador, Colombia, south Venezuela.

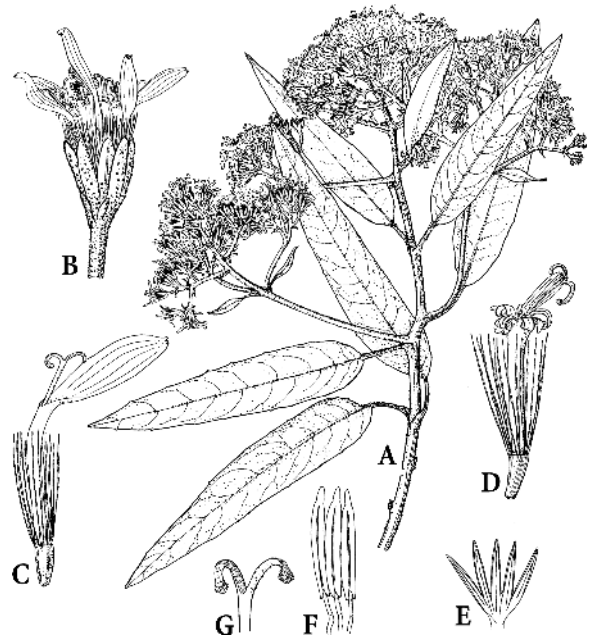

Fig. 56. Compositae-Senecioneae. *Aequatorium jamesonii*. **A** Habit. **B** Capitulum. **C** Ray floret. **D** Disc floret. **E** Corolla of disc floret, opened. **F** Stamens. **G** Style branches of disc floret. (Drawing by B. Nordenstam)

457. *Acrisione* B. Nord.

Acrisione B. Nord., Bot. Jahrb. Syst. 107: 582 (1985).

Shrubs or small trees with large soft pith. Leaves alternate, cauline, petiolate, entire with denticulate margins, elliptic-ovate to obovate. Capitula several to many, corymbose, radiate, ecalyculate, yellow-flowered. Anthers sagittate, becoming exserted. Style branches of disc florets with ± continuous stigmatic areas, apically obtuse, papillate. Cypselae elliptic-oblong, ribbed, puberulous. Pappus bristles numerous, slender. Two species, Chile.

458. *Brachyglottis* J.R. Forst. & G. Forst.

Brachyglottis J.R. Forst. & G. Forst., Char. Gen. Pl.: 91 (1776); Allan, Fl. N. Z. 1: 736–758 (1961), rev. (mostly as

Senecio); Drury, N. Z. J. Bot. 11: 731–784 (1977), key, rev. (as *Senecio*); Nordenstam, Opera Bot. 44: 25–31 (1978), emend., new comb.; Webb, N. Z. J. Bot. 25: 148–152 (1987), notes; Wagstaff & Breitwieser, Syst. Bot. 29: 1003–1010 (2004), phylog.

Shrubs or trees or perennial herbs with a ± thick rhizome. Leaves cauline or rosulate, sessile or petiolate, entire or dentate to lobed, pinnately veined. Capitula solitary and scapose, or several and corymbose, radiate or disciform, yellow-, cream- or white-flowered. Anthers caudate or sagittate. Style branches with ± continuous stigmatic areas, basally somewhat discrete. Cypselae oblong, ribbed, glabrous or pubescent. Pappus bristles numerous, slender, usually persistent, white. $n = 30$. Circa 30 species, New Zealand.

459. *Centropappus* Hook. f.

Centropappus Hook. f., London J. Bot. (Hooker) 6: 124 (1847).

Glabrous shrub or small tree. Leaves alternate, bunched terminally, sessile, linear, one-nerved, entire, obtuse, with glossy exudate. Capitula in short terminal corymbs, radiate, yellow-flowered. Involucral bracts uniseriate. Corolla lobes of disc florets deeply lobed, without midvein. Anthers basally rounded, ecaudate. Style branches apically truncate, papillate; stigmatic areas continuous. Cypselae oblong, glabrous, smooth. Pappus bristles apically subplumose. One species, *C. brunonis* Hook. f., Tasmania.

460. *Urostemon* B. Nord.

Urostemon B. Nord., Opera Bot. 44: 31 (1978); Drury, N. Z. J. Bot. 13: 769–780 (1975, as *Senecio*), morph.

Shrub or treelet, sometimes epiphytic, glabrous except for glands and T-shaped trichomes on young parts. Leaves cauline, petiolate, somewhat sinuate-dentate to subentire. Capitula several, laxly corymbose, radiate, ecalyculate. Ray florets white. Disc florets perfect; corolla yellow, deeply lobed. Anthers caudate with long papillate tails. Style branches apically obtuse to convex, papillate also dorsally, stigmatic areas continuous. Cypselae narrowly oblong, glabrous, striate with 10 veins and 10 resin canals. Pappus bristles numerous, stiff and rather coarse, dirty white, persistent. $n = 30$. One species, *U. kirkii* (Hook. f. ex Kirk) B. Nord., New Zealand (North Island).

461. *Haastia* Hook. f.

Haastia Hook. f., Handb. N. Z. Flora: 156 (1864); Allan, Fl. N. Z. 1: 675–676 (1961), rev.; Bailes, Q. Bull. Alp. Gard. Soc. 55: 118–122 (1987), notes.

Compact shrub forming dense cushions or mats, or procumbent to suberect subshrubs. Leaves densely imbricate, spathulate, apically crenulated, covered with long hairs, or alternate, patent to recurved, oblong-obovate, tomentose. Capitula solitary, sessile, terminal, heterogamous and disciform. Involucral bracts subuniseriate to biseriate, glabrous or hairy. Marginal florets pistillate with exserted style branches. Disc florets hermaphroditic, tubular, white. Anthers ecaudate. Style branches linear with apical conical tuft of obtuse hairs, or slender and dorsally papillate-hairy; stigmatic areas separated or continuous. Cypselae linear-oblong, compressed or subterete, glabrous. Pappus bristles numerous, coarse and basally flattened, or slender throughout, persistent. $n = 30$. Three species, New Zealand (not monophyletic, perhaps better treated as two separate genera).

462. *Bedfordia* DC.

Bedfordia DC. in Guill., Arch. Bot. (Paris) 2: 332 (1833); Gray, Muelleria 3: 64–66 (1974), rev.; Orchard, Muelleria 19: 81–94 (2004), rev.

Erect shrubs or treelets. Leaves sessile, alternate, entire, linear-lanceolate to elliptic, margins serrulate to denticulate, lower side tomentose. Capitula solitary and axillary or several and corymbose, discoid, ecalyculate, yellow-flowered. Corolla deeply lobed with lanceolate lobes. Anther base shortly auriculate; filament collar short. Style branches obtuse, dorsally papillose. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender. $n = 30$. Two species, south-eastern Australia, Tasmania.

463. *Traversia* Hook. f.

Traversia Hook. f., Handb. N. Z. Fl.: 163 (1864); Allan, Fl. N. Z. 1: 758 (1961), rev.

Erect branching glutinous shrub. Leaves cauline, sessile, elliptic to obovate, entire with serrate margins, pinnately to reticulately veined. Capitula few to several, corymbose, discoid, calyculate. Corolla white, deeply lobed. Anther base ecaudate, auriculate. Style branches apically truncate and papillose. Cypselae elliptic-oblong, ribbed, glabrous. Pappus bristles coarse and rigid, basally connate, scabrid,

unequal, off-white, persistent. $n = 30$. One species, *T. baccharoides* Hook. f., New Zealand.

464. *Dolichoglottis* B. Nord.

Dolichoglottis B. Nord., Opera Bot. 44: 33 (1978); Allan, Fl. N. Z. 1: 741–742 (1961, as *Senecio*), rev.

Perennial herbs with a thick woolly caudex. Stem erect, silky-woolly and glandular. Leaves basal and cauline, sessile, lanceolate or linear-lanceolate, parallel-veined, entire with margins sometimes toothed. Capitula few to several, corymbose, radiate. Involucral bracts biseriate. Ray florets yellow, white or pinkish. Disc florets perfect, yellow, 5-, occasionally 4-lobed. Anthers ecaudate. Style branches obtuse or subtruncate, stigmatic areas continuous or only basally discrete. Cypselae oblong, ribbed, with mucilaginous twin hairs. Pappus bristles stiff and rather coarse, persistent. $n = 30$. Two species, New Zealand.

465. *Capelio* B. Nord.

Capelio B. Nord., Comp. Newslett. 38: 72 (2002), 71–78, rev., key, new sp.; Comp. Newslett. 39: 48–51 (2003), nomencl.
Celmisia Cass. (1817), nom. rej., non Cass. (1825), nom. cons.
Alciope DC. in Lindley (1836) & DC. (1836), nom. illegit.

Perennial woolly herbs. Leaves cauline, petiolate, elliptic-ovate, entire, densely woolly beneath. Capitula solitary or few to several, corymbose, long-pedunculate, radiate, yellow-flowered. Involucre bi- to triseriate, ecalyculate. Anthers ecaudate; endothecium polarized with few thickenings. Style branches apically obtuse, papillate; stigmatic areas continuous. Cypselae oblong, pubescent. Pappus bristles numerous, slender. Three species, southern Africa.

466. *Papuacalia* Veldk.

Papuacalia Veldk., Blumea 36: 168 (1991).

Erect shrubs or trees, often pubescent and glandular. Leaves sessile or petiolate, entire, linear-lanceolate to elliptic-oblong. Capitula several to numerous in lateral synflorescences, disciform or discoid, with creamy-white or pinkish-purple florets. Ray florets, if present, with reduced ray. Disc florets perfect or functionally male. Anthers ecaudate with polarized endothecium. Style branches truncate-obtuse, apically papillate, sometimes also dorsally. Cypselae oblong, glabrous or pubescent. Pappus bristles numerous, slender but apically clavate. $n = 36$. Fourteen species, New Guinea.

467. *Brachionostylum* Mattf.

Brachionostylum Mattf., Nova Guinea 14: 527 (1932).

Dioecious shrub. Leaves alternate, petiolate, elliptic-ovate, entire with serrulate or denticulate margins. Capitula several, axillary, corymbosely paniculate, radiate, calyculate. Ray florets female or sterile, yellow; disc florets functionally male. Stamens with cylindrical uniform filament collar. Style branches apically rounded, glabrous. Cypselae narrowly oblong, ribbed, glabrous. Pappus bristles numerous, slender, caducous. One species, *B. pullei* Mattf., New Guinea.

468. *Pladaroxylon* (Endl.) Hook. f.

Pladaroxylon (Endl.) Hook. f., Hooker's Icon. Pl. 11: 47, t. 1055 (1870); Mabberley, Kew Bull. 30: 413–420 (1975, as *Senecio*), morph., notes; Drury, N. Z. J. Bot. 13: 769–780 (1975, as *Senecio*), morph.; Nordenstam, Opera Bot. 44: 36–38 (1978), re-establ.

Erect tree to 5 m tall, upwards branching dichotomously or trichotomously. Leaves shortly petiolate, assembled towards branch ends, elliptic-obovate, entire with somewhat dentate margins. Capitula numerous, corymbose in terminal synflorescences, radiate, narrowly campanulate, calyculate, white-flowered. Disc florets perfect; corolla deeply lobed, slightly zygomorphic. Anthers ecaudate, with subcylindrical filament collar. Style branches linear, with narrowly separated stigmatic areas, apically truncate, papillate. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender, persistent. One species, *P. leucadendron* (G. Forst.) Hook. f., St. Helena.

469. *Lachanodes* DC.

Lachanodes DC. in Guill., Arch. Bot. (Paris) 2: 332 (1833); Mabberley, Kew Bull. 30: 413–420 (1975, as *Senecio*), morph., notes; Drury, N. Z. J. Bot. 13: 769–780 (1975, as *Senecio*), morph.; Nordenstam, Opera Bot. 44: 36–38 (1978), re-establ., nomencl.

Branching tree to 5 m tall. Leaves cauline, large, petiolate, oblong-obovate to elliptic-ovate, entire with denticulate margins, pinnately veined. Capitula several, paniculate in lateral pendulous synflorescences, discoid, few-flowered. Corolla white, deeply lobed. Stamens with narrowly cylindrical filament collar. Style branches long

and much exserted, apically obtuse, papillate also dorsally towards the apex, with mostly continuous stigmatic areas. Cypselae oblong, glabrous, ribbed. Pappus bristles pluriseriate, slender, persistent. One species, *L. arborea* (Roxb.) B. Nord., St. Helena.

470. *Scrobicaria* Cass.

Scrobicaria Cass., Dict. Sci. Nat. 48: 456 (1827); Nordenstam, Opera Bot. 44: 63–64 (1978), re-establ.

Small erect shrubs. Leaves cauline, opposite, shortly petiolate or subsessile, entire with dentate margins. Capitula few to several, rather densely corymbose, discoid, calyculate, yellow-flowered. Involucre ± biseriate. Anthers caudate; endothecial tissue transitional; filament collar subcylindrical or slightly balusterform. Style branches apically obtuse to conical, papillate; stigmatic areas continuous. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender, white. Two species, Colombia, Venezuela.

471. *Shafera* Greenm.

Shafera Greenm., Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 327 (1912).

Erect or somewhat scandent tomentose shrub or subshrub. Leaves cauline, petiolate, entire, elliptic-ovate. Capitula several, corymbose, discoid, yellow-flowered, calyculate. Involucre pluriseriate with imbricate phyllaries. Anthers sagittate. Style branches apically obtuse. Cypselae elliptic-oblong, pubescent with twin hairs; carpopodium distinct, annular. Pappus bristles numerous, slender. One species, *S. platyphylla* Greenm., Cuba.

472. *Mattfeldia* Urb.

Mattfeldia Urb., Ark. Bot. 23, A(11): 90 (1931).

Scandent shrub. Leaves cauline, petiolate, entire, elliptic-ovate, three-nerved. Capitula few or several, paniculately corymbose, small and few-flowered, radiate, yellow-flowered. Ray florets bilabiate with a short lamina and two small ventral lobes. Disc florets perfect. Style branches truncate, penicillate. Cypselae narrowly elliptic-oblong, glabrous. Pappus bristles numerous, slender. One species, *M. triplinervis* Urb., Hispaniola.

473. *Ekmaniopappus* A. Borhidi

Ekmaniopappus A. Borhidi, Acta Bot. Hung. 37: 109 (1992).

Scandent shrubs or shrublets. Leaves opposite or alternate, petiolate, ± ovate with serrate to dentate margins, tomentose beneath. Capitula several to many, paniculate in axillary and terminal synflorescences, small and few-flowered, radiate, yellow-flowered. Involucre cylindrical, calyculate. Anthers sagittate or auriculate. Style branches apically truncate and shortly penicillate. Cypselae elliptic-oblong, 8-ribbed, glabrous. Pappus bristles numerous, slender. Two species, Hispaniola.

474. *Herodotia* Urb. & Ekm.

Herodotia Urb. & Ekm., Ark. Bot. 20 A, 5: 63 (1926).

Scandent shrub. Leaves opposite, petiolate, entire, elliptic-ovate, glabrous, with sinuate-lobulate margins. Capitula several, paniculately corymbose, discoid, 2–3-flowered, yellow. Involucre biseriate with 8 phyllaries, ecalyculate. Anthers ecaudate with obtuse base. Style branches dorsally papillate, apically truncate, penicillate. Cypselae elliptic-oblong, subglabrous with scattered small hairs, with thick carpopodium. Pappus bristles numerous, slender. One species, *H. haitiensis* Urb. & Ekm., Hispaniola.

475. *Leonis* B. Nord.

Leonis B. Nord., Comp. Newslett. 44: 55 (2006).

Almost glabrous scandent shrublet (vine). Leaves alternate, ovate to elliptic, entire or shallowly trilobate, 3-nerved, petiolate. Capitula in short axillary corymbs along the stems and branches, radiate, calyculate. Involucral bracts uniseriate. Resin ducts present in involucre, corollas, styles etc. Anthers sagittate. Style branches of disc florets obtuse with few short sweeping hairs; stigmatic areas continuous. Cypselae glabrous or sparsely setose or papillate, 10-ribbed. Pappus bristles pluriseriate, basally connate, persistent. One species, *L. trineura* (Griseb.) B. Nord., Cuba, Hispaniola.

476. *Nesampelos* B. Nord.

Nesampelos B. Nord., Comp. Newslett. 44: 58 (2006).

Lianas with tomentose glabrescent stems. Leaves alternate, petiolate, elliptic-ovate, entire with dentate to denticulate margins, coriaceous, upper side glabrescent and glossy, lower side brownish-tomentose. Capitula in terminal or axillary lateral corymbs, radiate, calyculate. Involucre tomentose. Ray florets yellow, creamy or white. Anthers basally obtuse, ecaudate. Style branches apically subtruncate with short sweeping hairs; stigmatic

areas separated. Cypselae 10-striate, ciliate in upper half. Pappus bristles pluriseriate, basally connate, persistent. Three species, Hispaniola.

477. *Zemisia* B. Nord.

Zemisia B. Nord., Comp. Newslett. 44: 71 (2006).

Erect, diffuse or divaricate shrub, tomentose throughout, but leaves glabrescent adaxially. Leaves alternate, petiolate, ovate to lanceolate, with denticulate to subentire margins, midribbed and pinnately veined. Capitula numerous in terminal corymbose synflorescence, radiate, calyculate. Involucral bracts uniseriate, 8–13. Receptacle alveolate. Ray florets 3–6, white. Disc florets hermaphrodite; corolla cream; lobes distinctly midlined, apically thickened. Anthers distinctly caudate. Style branches subtruncate with few short pili abaxially; stigmatic areas separated. Cypsela 8-nerved, villous-papillate with white obtuse mucilaginous hairs; carpopodium distinct. Pappus bristles numerous, c. biseriate, persistent. One species, *Z. discolor* (Sw.) B. Nord., Jamaica.

478. *Antillanthus* B. Nord.

Antillanthus B. Nord., Comp. Newslett. 44: 51 (2006).

Erect or scandent shrubs. Leaves cauline, linear or lanceolate to oblong-ovate, entire, glabrous or pubescent. Capitula few to several, corymbose or paniculate, radiate or discoid, white-, cream- or yellow-flowered. Receptacle alveolate. Resin canals often present in corolla and style. Anthers sagittate or caudate. Style branches obtuse with rather few and short sweeping hairs; stigmatic areas continuous. Cypselae elliptic-oblong, 10-ribbed, glabrous or pubescent. Pappus bristles numerous, slender, basally connate. Seventeen species, Cuba.

479. *Elekmania* B. Nord.

Elekmania B. Nord., Comp. Newslett. 44: 66 (2006).

Erect or scandent shrubs or subshrubs, sometimes strongly resiniferous. Leaves alternate, petiolate, entire or with dentate-lobulate margins, usually tomentose below, glabrous above. Capitula several to numerous in lateral or terminal corymbose or cymose synflorescences, radiate or sometimes discoid, yellow-flowered. Corolla lobes midveined, apically papillate. Anthers ecaudate or shortly caudate; apical appendage lanceolate. Style branches truncate or somewhat obtuse with short sweeping hairs; stigmatic areas separated. Cypselae glabrous or hirsute, 8–10-ribbed. Pappus bristles numerous, slender. Circa ten species, Hispaniola.

480. *Herreranthus* B. Nord.

Herreranthus B. Nord., Comp. Newslett. 44: 62 (2006).

Shrub or treelet; stem with large pith; young branches tomentose, ± glabrescent. Leaves alternate, petiolate, entire, elliptic-oblong to lanceolate or oblanceolate, glabrous above, densely tomentose beneath, midribbed. Capitula terminal, cymose or corymbose, discoid. Involucral bracts biseriate. Anthers shortly or distinctly caudate. Style branches apically shortly papillate; stigmatic areas continuous and extending to the dorsal side. Cypselae 10-ribbed, hairy. Pappus bristles pluriseriate, persistent. One species, *H. rivalis* (Greenm.) B. Nord., Cuba.

481. *Oldfeltia* B. Nord. & Lundin

Oldfeltia B. Nord. & Lundin, Comp. Newslett. 38: 66 (2002).

Erect glabrous shrub. Leaves cauline, shortly petiolate, elliptic-lanceolate, large, entire with serrate to denticulate margins. Capitula numerous, corymbosely paniculate, discoid, yellow-flowered. Involucre cylindrical, with 5 connate bracts, pale yellowish-green, calyculus bracts few. Receptacle convex, nude. Anthers basally sagittate to shortly caudate. Style branches apically triangular-conical with many short clavate sweeping hairs; stigmatic areas discrete. Cypselae oblong, glabrous. Pappus bristles numerous, slender. One species, *O. polyphlebia* (Griseb.) B. Nord. & Lundin, Cuba.

482. *Odontocline* B. Nord.

Odontocline B. Nord., Opera Bot. 44: 23 (1978).

Erect or scandent shrubs. Leaves alternate, petiolate, entire or pinnatifid, margins sometimes serrate. Capitula several to many, corymbose, radiate, yellow- or orange-flowered, fragrant. Involucre narrowly campanulate to subcylindrical, uniseriate, minutely calyculate. Receptacle denticulate. Anthers caudate. Style branches apically rounded-obtuse with subterminal sweeping hairs; stigmatic areas continuous. Cypselae oblong, ribbed, glabrous or pubescent. Pappus bristles numerous, slender, persistent. $n = 30$. Six species, Jamaica.

483. *Lundinia* B. Nord.

Lundinia B. Nord., Comp. Newslett. 44: 64 (2006).

Erect shrub or small tree. Leaves petiolate, lanceolate or oblong-lanceolate, entire with ± denticulate margins. Capitula several, corymbose, radiate, yellow-flowered. Receptacle denticulate. Anthers caudate. Style branches apically truncate, often with a minute short hair tuft; stigmatic areas separated. Cypselae elliptic-oblong, pubescent. Pappus bristles numerous, slender, short. One species, *L. plumbea* (Griseb.) B. Nord., Cuba, Hispaniola.

484. *Jacmaia* B. Nord.

Jacmaia B. Nord., Opera Bot. 44: 64 (1978).

Erect shrub. Leaves sessile or subsessile, lanceolate or oblanceolate, with sinuate-dentate margins, pinnatilobate towards the base. Capitula numerous, corymbose, radiate, yellow-flowered. Involucre cylindrical or narrowly campanulate, tomentose, basally incrassate, uniseriate, calyculate. Receptacle denticulate. Ray florets few and short. Disc florets hermaphrodite; corolla tubular and widening above, slightly zygomorphic. Anthers shortly caudate; endothecial tissue transitional. Style branches apically with an acuminate distinct papillate appendage; stigmatic areas continuous. Cypselae narrowly oblong, ribbed, setose apically, with distinct carpopodium. Pappus bristles numerous, very slender and almost smooth, persistent. One species, *J. incana* (Sw.) B. Nord., Jamaica.

485. *Ignurbia* B. Nord.

Ignurbia B. Nord., Willdenowia spec. vol. 31, 1: 464 (2006).

Erect perennial herb, shortly hairy or glandular on stems, leaves and peduncles. Leaves alternate, herbaceous, irregularly incised-lobed, petiolate. Capitula numerous in terminal corymbs, discoid, calyculate, orange-flowered. Corolla tubular, gradually widening above. Anthers ecaudate; apical appendage narrow; endothecial tissue radial with short ± isodiametric cells; filament collar long, uniformly wide, with larger cells along the margins. Pollen grains minutely spinulose. Style branches apically obtuse, papillate, without distinct sweeping hairs; stigmatic areas continuous. Cypselae 10-ribbed, glabrous. Pappus bristles pluriseriate, basally connate, persistent. Two species, Hispaniola.

486. *Jessea* H. Rob. & Cuatrec.

Jessea H. Rob. & Cuatrec., Novon 4: 49 (1994); Nordenstam, Bot. Jahrb. Syst. 118: 147–152 (1996), rev.

Erect shrubs or subshrubs, with large pith. Leaves sessile or petiolate, large, oblong-ovate or elliptic-lanceolate, entire or lobed to laciniate, with dentate margins, closely arcuately pinnativeined; leaf base ± clasping. Capitula numerous, densely corymbosely paniculate, radiate, yellow-flowered. Involucre uniseriate, cylindrical or narrowly cup-shaped, calyculate. Receptacle with scale-like projections. Corolla of disc florets with lanceolate to narrowly ovate lobes. Anthers ecaudate. Style branches apically rounded-obtuse with a central hair tuft; stigmatic areas separated. Cypselae oblong, ribbed, glabrous or pubescent. Pappus bristles numerous, slender, caducous. n = c. 50. Four species, Costa Rica, Panama.

487. *Lordhowea* B. Nord.

Lordhowea B. Nord., Opera Bot. 44: 38 (1978); Drury, N. Z. J. Bot. 13: 769–780 (1975, as *Senecio*), morph.

Erect glabrous shrub. Leaves cauline, alternate, petiolate, elliptic-ovate, coarsely dentate or lobate. Capitula many, corymbose, overtopped by leaves, radiate with few and short pale yellow ray florets, paucicalyculate. Receptacle denticulate. Disc florets hermaphrodite, corolla lobes lanceolate. Anthers ecaudate. Style branches apically conical and acute, dorsally papillate especially towards the apex, stigmatic areas separated. Cypselae narrowly oblong, 10-ribbed, glabrous. Pappus bristles numerous, slender, persistent. n = 19. One species, *L. insularis* (Benth.) B. Nord., Lord Howe Isl.

488. *Arrhenechthites* Mattf.

Arrhenechthites Mattf., Bot. Jahrb. Syst. 69: 288 (1938); Belcher, Ann. Missouri Bot. Gard. 43: 1–85 (1956), rev.

Shrubs or robust perennial herbs. Leaves cauline, petiolate, elliptic-ovate, entire with dentate to serrate margins. Capitula numerous, in terminal cymose synflorescences, disciform. Involucre cylindrical, biseriate to pluriseriate, paucicalyculate. Marginal florets few, female, tubular, purplish. Disc florets few, perfect or functionally male, white or cream-coloured, sometimes with purplish tube, deeply lobed. Anthers with broadly balusterform collars. Style branches short, apically dilated and truncate, papillate. Cypselae oblong, glabrous, with distinct carpopodium. Pappus

bristles numerous, slender. n = c. 50. Six species, Indonesia, New Guinea, south-eastern Australia.

489. *Bethencourtia* Choisy

Bethencourtia Choisy in Buch, Phys. Beschr. Canar. Ins.: 148 (1825); Nordentstam, Comp. Newslett. 44: 24–31 (2006), rev. (as *Canariothamnus*)
Canariothamnus B. Nord. (2006).
Senecio sect. *Bethencourtii* DC. (1838).

Glabrous shrublets. Leaves alternate, sessile, linear-oblanceolate, entire, few-toothed or lobed. Capitula small, corymbose, ecalyculate, yellow-flowered. Involucral bracts 4–7. Ray florets 1–3, short. Disc florets 3–5. Anthers caudate; endothecium radial; filament collar balusterform. Style branches apically obtuse, with short papilliform sweeping hairs; stigmatic areas confluent or barely discrete. Cypselae oblong, shortly hirsute. Pappus semi-persistent. n = 10. Three species, Canary Islands.

490. *Pericallis* D. Don in Sweet

Pericallis D. Don in Sweet, Brit. Fl. Gard. ser. 2: pl. 228 (1834); Nordenstam, Opera Bot. 44: 15–21 (1978), re-establ., new comb.; Swenson & Manns, Taxon 52: 533–546 (2003), phylog.; Swenson, Svensk Bot. Tidskr. 98: 193–206 (2004), popular review.

Perennial herbs or subshrubs. Leaves cauline, petiolate, cordate to reniform or ovate, entire or dentate to lobed, palmately veined. Capitula several or rarely solitary, or many, corymbose, radiate, ecalyculate. Florets white, pink, purple or blue. Anthers ecaudate; filament collar much dilated basally. Style branches truncate to obtuse, stigmatic areas discrete. Cypselae terete or somewhat compressed, elliptic-oblong, ribbed, glabrous. Pappus bristles numerous, sometimes absent in ray florets, caducous. Pollen helianthoid. n = 30. Fifteen species, Canary Islands, Madeira, Azores (*P. hybrida* B. Nord., the florists' so-called Cineraria, is widely used in horticulture).

491. *Cineraria* L.

Cineraria L., Sp. Pl. ed. 2: 1242 (1763) & Gen. Pl. ed. 6: 426 (1764); Hilliard, Compositae in Natal: 372–387 (1977), reg. rev. Genus under revision (G. Cron).

Perennial herbs or subshrubs. Leaves cauline or radical, petiolate, cordate or rounded to ovate, entire or dentate, lobed or pinnatilobate or pinnatisect, glabrous or tomentose, palmately veined. Capitula few or several to many, corymbose, radiate or rarely discoid, paucicalyculate, yellow-flowered. Disc florets perfect or rarely functionally male. Anthers slightly sagittate; filament collar balusterform. Style branches truncate to obtuse with short sweeping hairs; stigmatic areas separated. Cypselae compressed with winged or thickened margins, brown or blackish. Pappus bristles numerous, slender, caducous. n = 10, 20. Circa 35 species, Africa, Madagascar, Arabia.

492. *Bolandia* Cron

Bolandia Cron, Novon 16:224 (2006).

Annual or perennial herbs. Leaves alternate, petiolate, entire or lobed to dissected, araneose or tomentose, glabrescent. Capitula solitary on bracteate peduncles, radiate, ecalyculate, yellow-flowered. Involucral bracts uniseriate. Anthers minutely sagittate. Style branches apically with a central hair pencil; stigmatic areas separated. Cypselae dimorphic: outer abaxially convex and white-villous, adaxially midribbed and glabrous; inner weakly ribbed, uniformly hairy. Pappus bristles pluriseriate, caducous. Two species, South Africa, Lesotho.

493. *Mesogramma* DC.

Mesogramma DC., Prodr. 6: 304 (1838); Nordenstam & Pelser, Comp. Newslett. 42: 74–88 (2005), re-establ.

Glabrous annual herb. Leaves alternate, petiolate, ovate-lanceolate, grossly dentate or lobate. Capitula solitary or few to several, laxly corymbose, radiate, yellow-flowered, minutely calyculate. Involucral bracts biseriate, inner phyllaries with two distinct dark resin ducts. Corolla of disc florets black-veined. Anthers sagittate. Style branches truncate; stigmatic areas separated. Cypselae subtriquetrous, black, with white papilliform hairs apically and basally and in three longitudinal lines. Pappus bristles white, persistent. One species, *M. apiifolium* DC., southern Africa.

494. *Stilpnogyne* DC.

Stilpnogyne DC., Prodr. 6: 293 (1838).

Small annual glabrous herb. Leaves alternate, petiolate, ovate-cordate, entire with distally dentate or lobulate margins. Capitula few to several, corymbose, disciform, yellow-flowered. Involucral bracts uniseriate, basally connate, ecalyculate. Marginal florets usually 3, female, tubular or with a short limb. Disc florets few, hermaphrodite. Anthers

ecaudate with rounded base. Style branches apically subtruncate to somewhat convex, penicillate. Cypselae oblong-obovate, compressed, puberulous. Pappus bristles uniseriate, slender, lacking in marginal florets. One species, *S. bellidioides* DC., southern Africa.

495. *Packera* A. Löve & D. Löve

Packera A. Löve & D. Löve, Bot. Notiser 128: 520 (1976); Barkley, Trans. Kansas Acad. Sci. 65: 318–408 (1962, as *Senecio*), rev.; Freeman & Barkley, Sida Contr. Bot. 16: 699–709 (1995), reg. syn.; Trock, Sida Contr. Bot. 20: 1023–1041 (2003), reg. rev.

Perennial herbs with a creeping rhizome and fibrous roots. Leaves basal, often rosulate, and cauline, reduced upwards. Capitula solitary to many, corymbose, radiate or sometimes discoid, yellow- or orange- to red-flowered. Corolla lobes deltoid to triangular-ovate. Anthers ecaudate. Style branches truncate, apically penicillate. Cypselae oblong, ribbed, glabrous or sometimes pubescent. Pappus bristles numerous, slender. Pollen helianthoid. n = mostly 22 and 23; also reported: 20 (doubtful), 24, c. 30, 35, 40, 46, 60, 69. Circa 75 species, North America, Mexico, Siberia.

496. *Dorobaea* Cass.

Dorobaea Cass., Dict. Sci. Nat. 48: 453 (1827); Nordenstam, Opera Bot. 44: 51–53 (1978), re-establ.; Nordenstam & Pruski, Comp. Newslett. 27: 31–42 (1995), reg. rev.

Perennial glabrous herbs with fibrous roots. Leaves rosulate, petiolate, lanceolate to ovate, pinnatipartite or laciniate. Capitula solitary on long, bracteate peduncles, large, radiate, conspicuously calyculate, yellow- or orange-flowered. Corolla lobes lanceolate with a median resin duct. Anthers ecaudate with radial endothecium and balusterform filament collar. Style branches apically convex to conical, stigmatic areas separated. Cypselae oblong, ribbed, glabrous or shortly hirsute. Pappus bristles numerous, slender. n = c. 50. Three species, Peru, Ecuador.

497. *Hasteola* Raf.

Hasteola Raf., New Fl. 4: 79 (1837).
Synosma Raf. ex Britton & A. Br. (1898).

Tall perennial herb with rhizome. Leaves basal, long-petiolate, hastate, deltoid with serrate margins; cauline leaves progressively smaller. Capitula numerous, corymbose, cylindrical or turbinate, discoid, distinctly calyculate. Corolla white or pinkish, with narrow lobes. Anthers ecaudate. Style branches obtuse. Cypselae narrowly oblong, ribbed, glabrous. Pappus bristles numerous, slender. n = 18, 20. One species, *H. suaveolens* (Raf.) Pojark., eastern USA.

498. *Robinsonia* DC.

Robinsonia DC. in Guill., Arch. Bot. (Paris) 2: 333 (1833), nom. cons.; Sanders et al., Opera Bot. 92: 195–215 (1987), biogeogr., evol.; Sang et al., Syst. Bot. 20: 55–64 (1995), phylog.
Rhetinodendron Meisn. (1839).
Symphyochaeta (DC.) Skottsb. (1951).

Dioecious trees or tall shrubs. Leaves cauline, sessile, entire, narrowly elliptic to elliptic-ovate, mostly assembled towards branch ends. Capitula many, corymbose, radiate or discoid, calyculate. Florets yellow to greenish or purplish. Anthers aborted in female heads. Styles undivided in male heads. Cypselae elliptic-oblong, ribbed, glabrous or pubescent. Pappus bristles numerous, often connate basally. n = 20. Seven species, Juan Fernandez Islands.

499. *Senecio* L. Fig. 57

Senecio L., Sp. Pl.: 866 (1753) & Gen. Pl. ed. 5: 373 (1754); Hooker, Fl. Brit. India 3: 338–356 (1881), reg. rev.; Greenman, Bot. Jahrb. 32: 1–33 (1902), reg. rev.; Ann. Missouri Bot. Gard. 25: 795–822 (1938), reg. rev.; Cabrera, Lilloa 5: 65–120 (1939), reg. rev.; Lilloa 15: 27–501 (1949), reg. rev.; Brittonia 7, 2: 53–74 (1950), reg. rev.; Arquiv. Jard. Bot. Rio de Janeiro 15: 163–269 (1957), reg. rev.; Schischkin, Fl. U.S.S.R. 26: 699–788 (1961), reg. rev.; Cabrera, Fl. Prov. Buenos Aires 4, 6: 282–319 (1963), reg. rev.; Humbert, Fl. Madag. 189: 677–804 (1963), reg. rev.; Aristeguieta, Fl. Venez. 10: 765–815 (1964), reg. rev.; Merxmüller, Prodr. Fl. Südwestafr. 139: 162–173 (1967), reg. rev.; Cabrera, Fl. Patagonica 7: 176–275 (1971), reg. rev.; Cabrera, Fl. Ilustr. Entre Ríos Argent. 6: 433–451(1974), reg. rev.; Cabrera & Klein, Fl. Ilustr. Catarinense, Compostas: 135–217 (1975), reg. rev.; Matthews, Fl. Turkey 5: 145–168 (1975), reg. rev.; Chater & Walters, Fl. Eur. 4: 191–205 (1976), reg. rev.; Hilliard, Compositae in Natal: 387–502 (1977), reg. rev.; Barkley, N. Amer. Fl. ser. 2, 10: 50–139 (1978), reg. rev.; Cabrera, Fl. Prov. De Jujuy 10: 489–586 (1978), reg. rev.; Cabrera & Zardini, Darwiniana 22: 427–492 (1980), reg. syn., key; Jeffrey & Chen, Kew Bull. 39: 351–432 (1984), reg. rev.; Cabrera, Darwiniana 26: 79–217 (1985), reg. rev.; Jeffrey, Kew Bull. 41: 879–904 (1986), reg. rev.; Nordenstam, Fl. Iran. 164: 59–95, pl. 38–63 (1989), reg. rev.; Chen, Fl.

Reip. Pop. Sin. 77, 1: 225–304 (1999), reg. rev.; Thompson, Muelleria 19: 101–214 (2004), part. reg. rev.
Madaractis DC. (1838).
Crociseris (Reichenb.) Fourr. (1868).
Curio P.V. Heath (1999).

Annual or perennial herbs, subshrubs or shrubs. Leaves alternate, cauline or rosulate, sessile or petiolate, rarely peltate, entire or variously lobed or dissected. Capitula solitary or few to numerous, corymbose, radiate, disciform or discoid, usually calyculate. Florets often yellow, sometimes pink to purple, rarely blue or white. Anthers usually ecaudate; filament collar balusterform. Style branches truncate with short sweeping hairs; stigmatic areas separated. Cypselae elliptic-ovate to narrowly oblong, often 8–12-ribbed, glabrous or pubescent. Pappus bristles numerous, slender, persistent or caducous. n = mostly 10 or 20 but also reported are 9, 16, 18, 19, 21, 22, 30, 32, 35, 40, c. 45, 46, 49, 50, 52, 60, c. 70, c. 80, 90, c. 91. Circa 1,250 species, cosmopolitan, many in South America and southern Africa.

Several discordant elements have recently been segregated (Nordenstam 2006c, e, f; Nordenstam & Pelser 2005) and some more need to be removed from *Senecio* in order to achieve monophyly. One of these segregates is the Eurasian genus *Jacobaea* Mill. (1754) with c. 35 species (Nordenstam 2006a; Pelser et al. 2006).

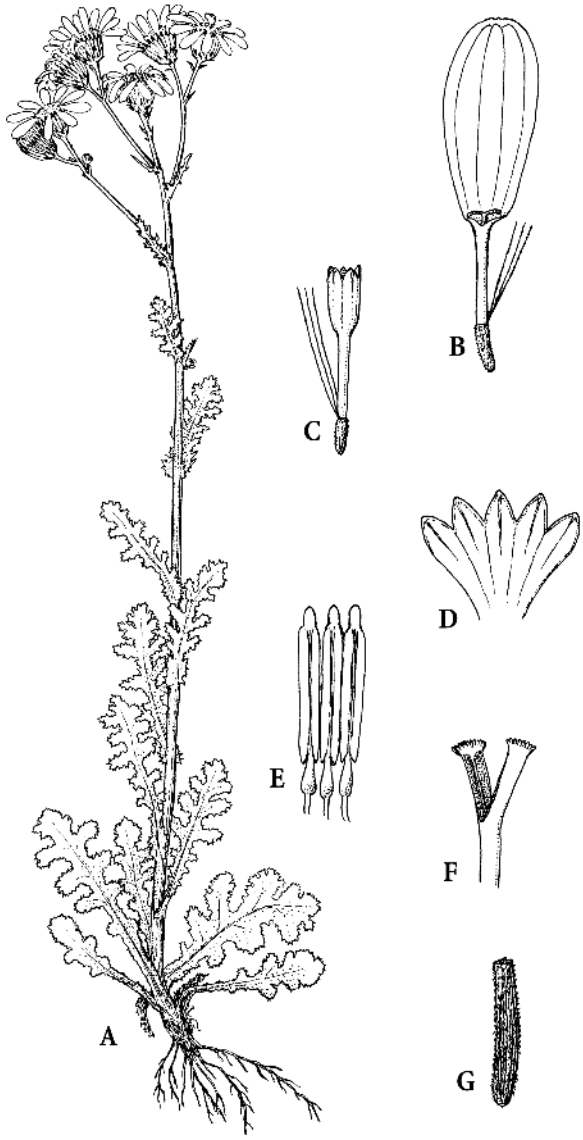

Fig. 57. Compositae-Senecioneae. *Senecio vernalis*. **A** Habit. **B** Ray floret. **C** Disc floret. **D** Corolla of disc floret, opened. **E** Stamens. **F** Style branches of disc floret. **G** Cypsela (pappus removed). (Drawing by B. Nordenstam)

500. *Solanecio* (Sch. Bip.) Walp.

Solanecio (Sch. Bip.) Walp., Rep. 6: 273 (1846); Jeffrey, Kew Bull. 41: 920–923 (1986), rev.

Perennial herbs, shrubs or small trees. Leaves cauline, sessile or petiolate, entire to serrate or lobed to laciniate. Capitula few to many, corymbose, discoid, calyculate, yellow-flowered. Anthers ecaudate. Style branches truncate, occasionally with a central hair tuft. Cypselae oblong, ribbed, glabrous or pubescent; carpopodium distinct, annular. Ovary wall crystals drusiform. Pappus bristles numerous, slender. n = 10, c. 90. Sixteen species, tropical Africa, Madagascar, Yemen.

501. *Kleinia* Mill.

Kleinia Mill., Gard. Dict. abr. ed.: 4 (1754); Halliday, Kew Bull. 39: 817–827 (1984), reg. rev.; Jeffrey, Kew Bull. 41: 923–929 (1986), reg. rev.; Halliday, Hooker's Icon. Pl. 39, 4: t. 3876–3900 (1988), part. rev.; Thulin, Nordic J. Bot. 22: 419–426 (2003), new spp.
Notonia DC. (1833).
Notoniopsis B. Nord. (1978).

Succulent herbs or shrubs. Leaves cauline, sessile or shortly petiolate, entire to incised-lobed, sometimes reduced to scales or absent. Capitula solitary or few to numerous, corymbose, discoid, with or without calyculus. Florets white, yellow, greenish, orange, red or purplish; corolla tubular, gradually widened upwards. Anthers ecaudate, with long, slightly balusterform filament collar. Style branches linear, apically with a convex or conical to long-

acuminate, papillose-hairy appendage; stigmatic areas separated. Cypselae oblong, ribbed, glabrous. Ovary wall crystals drusiform. Pappus bristles numerous, slender, persistent. n = 9, 10, 20, c. 50. Circa 50 species, Africa, Madagascar, Canary Islands, Arabia, east to India and Sri Lanka.

502. *Gynura* Cass.

Gynura Cass., Dict. Sci. Nat. 34: 392 (1825), nom. cons.; Davies, Kew Bull. 33: 335–342 (1978), Kew Bull. 33: 629–640 (1979), Kew Bull. 35: 363–367 (1980), Kew Bull. 35: 711–734 (1981), rev.; Jeffrey, Kew Bull. 41: 929–930 (1986), reg. rev.; Chen, Fl. Reip. Pop. Sin. 77, 1: 309–322 (1999), reg. rev.

Perennial herbs or subshrubs, erect or scrambling or climbing, sometimes subsucculent; roots fibrous or tuberous. Leaves cauline, sessile or petiolate, entire or lobed to pinnatifid. Capitula solitary or few to several, corymbosely paniculate, discoid. Involucre cylindrical or campanulate, calyculate. Florets white, greenish, yellow, orange, red or purplish. Anthers ecaudate, basally obtuse or sometimes auriculate. Style branches apically with elongate vascularized papillate appendage. Cypselae oblong, ribbed, glabrous or pubescent; carpopodium annular or indistinct. Ovary wall crystals drusiform. Pappus bristles numerous, slender. n = 5, 10, 11, 17, 20. Circa 40 species, Palaeotropics.

503. *Erechtites* Raf.

Erechtites Raf., Fl. Ludov.: 65 (1817); Belcher, Ann. Missouri Bot. Gard. 43: 1–85 (1956), rev.; Barkley & Cronquist, N. Amer. Fl. ser. 2, 10: 139–142 (1978), reg. rev.

Annual or perennial herbs. Leaves cauline, sessile, pinnatilobate or entire with serrate margins. Capitula several, corymbose, disciform. Involucre cylindrical, calyculate. Marginal florets female, filiform. Disc florets perfect, white to yellowish. Style branches with apical appendage of fused hairs. Cypselae oblong, ribbed; carpopodium indistinct. Pappus bristles numerous, slender. n = 20. Five species, North and South America, West Indies.

504. *Iocenes* B. Nord.

Iocenes B. Nord., Opera Bot. 44: 58 (1978).

Erect perennial herb with a short rhizome. Leaves basal and cauline, lower leaves petiolate, lyrato-pinnatifid or incised-lobed, upper leaves sessile, half-clasping. Capitula several, corymbose, radiate, paucicalyculate. Ray florets white. Disc florets perfect, yellow. Anthers ecaudate. Style branches apically with an elongated hair pencil. Cypselae oblong, 10-ribbed, glabrous; carpopodium distinct. Pappus bristles numerous, slender, persistent. n = 20. One species, *I. acanthifolius* (Hombr. & Jacq.) B. Nord., with two subspecies, Argentina, Chile.

505. *Io* B. Nord.

Io B. Nord., Comp. Newslett. 40: 47 (2003).

Glabrous half-shrub. Leaves opposite, subsessile, ovate-lanceolate, entire with denticulate margins. Capitula laxly corymbose, radiate, yellow-flowered, calyculate. Anthers sagittate. Style branches apically truncate without sweeping hairs, dorsally papillate; stigmatic areas continuous. Cypselae oblong, glabrous. Pappus bristles uniseriate, slender. One species, *I. ambondrombeensis* (Humb.) B. Nord., Madagascar.

506. *Crassocephalum* Moench

Crassocephalum Moench, Methodus: 516 (1794); Humbert, Fl. Madag. 189: 829–843 (1963), reg. rev.; Jeffrey, Kew Bull. 41: 904–908 (1986), reg. rev.

Perennial herbs. Leaves cauline, sessile or petiolate, sometimes amplexicaul, entire or lobed, margins often serrate. Capitula few or several, corymbose, radiate or discoid, cylindrical, calyculate. Florets creamy white or yellow, orange, pink to red or mauve, purple or blue. Anthers ecaudate; filament collar narrow, elongate. Style branches apically rounded and shortly appendiculate, dorsally papillate. Cypselae oblong, ribbed, glabrous or with thickened twin hairs; carpopodium indistinct. Pappus bristles numerous, slender. n = 5, 10, 12, 16, 20, 24, c. 45. Twenty-four species, tropical Africa, Madagascar, Yemen (two weedy species introduced in many tropical countries).

507. *Hoehneophytum* Cabrera

Hoehneophytum Cabrera ('*Hoehnephytum*'), Brittonia 7: 53 (1950); Hind, Kew Bull. 48: 257–259 (1993), notes; Hind, Kew Bull. 54: 897–904 (1999, publ. 2000), notes.

Suffrutescent herbs or shrubs. Leaves cauline, petiolate, elliptic, entire. Capitula several, corymbose, discoid, few-flowered, yellow, calyculate. Anther base obtuse. Style branches apically rounded with short sweeping hairs, dorsally puberulous; stigmatic areas separated. Cypselae oblong, ribbed, pubescent. Pappus bristles numerous, slender. Three species, Brazil.

508. *Pentacalia* Cass.

Pentacalia Cass., Dict. Sci. Nat. 48: 461 (1827); Robinson & Cuatrecasas, Phytologia 40: 37–50 (1978), reg. rev.; Cuatrecasas, Phytologia 49: 241–260 (1981), reg. rev.; Díaz-Piedrahita & Cuatrecasas, Asteraceas de la Flora de Colombia, Senecioneae-I: 25–174 (1999), reg. rev.

Scandent shrubs or epiphytes, glabrous or pubescent with simple hairs. Leaves petiolate, oblong to elliptic-ovate, entire with margins often dentate to serrate, often coriaceous. Capitula several to many, corymbosely paniculate in terminal or lateral synflorescences, radiate or disciform, yellow- or rarely white-flowered. Anthers sagittate to caudate. Style branches truncate or obtuse, with separated stigmatic areas. Cypselae elliptic-oblong, 5-angled or -ribbed, glabrous or sometimes pubescent. Pappus bristles numerous, slender, white or pink to rufous. n = 20, c. 40, 45–50, 50, c. 51. Circa 200 species, Andes of South America, Central America north to Mexico.

509. *Monticalia* C. Jeffrey

Monticalia C. Jeffrey, Kew Bull. 47: 69 (1992), 69–74, notes, new comb.; Robinson & Cuatrecasas, Phytologia 40: 37–50 (1978, as *Pentacalia* subg. *Microchaete*), reg. rev.; Díaz-Piedrahita & Cuatrecasas, Asteraceas de la Flora de Colombia, Senecioneae-I: 175–345 (1999, as *Pentacalia* subg. *Microchaete*), reg. rev.
Microchaete Benth. (1845), nom. illegit. rej., non Thuret ex Bornat & Flahault (1886), nom. cons.

Erect shrubs or shrublets. Leaves closely set, shortly petiolate to subsessile, often small, ericoid or linear-lanceolate to elliptic-ovate. Capitula several to numerous, corymbose, radiate or discoid, mostly yellow-flowered. Anthers sagittate to shortly caudate. Style branches truncate to obtuse with discrete stigmatic areas, papillate apically and sometimes dorsally. Cypselae 5-angled or -ribbed, with distinct carpopodium. Pappus bristles numerous, slender, white. n = c. 10, 20, c. 40. Circa 70 species, Andes of South America, Central America north to Costa Rica.

510. *Dendrophorbium* (Cuatrec.) C. Jeffrey

Dendrophorbium (Cuatrec.) C. Jeffrey, Kew Bull. 47: 65 (1992), 65–69, notes, new comb.; Díaz-Piedrahita & Cuatrecasas, Asteraceas de la Flora de Colombia, Senecioneae-I: 8–25 (1999), reg. rev.
Senecio L. sect. *Dendrophorbium* Cuatrec. (1951).

Erect suffrutescent herbs ('dendrophorbs'), shrubs or trees. Leaves large, cauline, often assembled apically on branches, entire, petiolate, margins dentate or denticulate. Capitula numerous in ± dense terminal corymbose or paniculate synflorescences. Anther base ecaudate or rarely caudate, rounded-obtuse or minutely auriculate. Style branches apically truncate to obtusely convex; stigmatic areas narrowly separated. Cypselae elliptic-oblong, 5-ribbed; carpopodium distinct. Pappus bristles numerous, slender. n = c. 40, 49–50, c. 50. Circa 75 species, Andes of South America from Bolivia to Venezuela, Argentina, Brazil, Paraguay.

511. *Graphistylis* B. Nord.

Graphistylis B. Nord., Opera Bot. 44: 56 (1978); Hind, Kew Bull. 48: 285 (1993), notes; Nordenstam, Comp. Newslett. 24: 51 (1994), new comb.

Erect subshrubs or somewhat lignescent herbs, usually pubescent and glabrescent. Leaves shortly petiolate or subsessile, entire, elliptic to lanceolate, with serrate or denticulate margins. Capitula several to numerous, corymbose-paniculate, radiate, yellow- or rarely white-flowered, calyculate. Disc florets perfect, corolla lobes triangular-ovate with a median resin duct. Anther base obtuse, auriculate; endothecial tissue mainly polarized. Style branches apically with an elongated hair pencil and lateral shorter hair tufts; stigmatic areas narrowly separated. Cypselae narrowly oblong, ribbed, glabrous. Pappus bristles numerous, slender, persistent. n = 50. Eight species, Brazil.

512. *Talamancalia* H. Rob. & Cuatrec.

Talamancalia H. Rob. & Cuatrec., Novon 4: 50 (1994); Nordenstam & Pruski, Comp. Newslett. 27: 31–42 (1995), key, new comb.

Herbs, subshrubs or shrubs, erect or ascending, hirsute or lanate, glabrescent. Leaves cauline, petiolate with a ± winged petiole and half-clasping base, pinnatilobate at least proximally, otherwise entire with serrate margins. Capitula few to several, laxly corymbose, radiate, orange- or yellow-flowered; involucre broadly campanulate, calyculate. Receptacle naked. Disc florets numerous; corolla lobes narrowly oblong. Anthers ecaudate. Style branches apically rounded with a short central hair tuft; stigmatic areas separated. Cypselae 10-ribbed, with short mucilaginous hairs. Pappus bristles pluriseriate, slender, caducous. Four species, Peru, Ecuador, Panama, Costa Rica.

513. *Caxamarca* Dillon & Sagástegui

Caxamarca Dillon & Sagástegui, Novon 9: 156–161 (1999).

Perennial herb with foetid tuberous fasciculate roots and unbranched erect stem. Basal leaves rosulate, large, dissected; cauline leaves smaller, sessile, entire with serrate to dentate margins, with decurrent base forming wings. Capitula several, corymbose-cymose, radiate, yellow-flowered. Involucre hemispherical, basally swollen, pluriseriate, calyculate. Disc florets numerous, with deeply lobed corolla. Anthers ecaudate. Style branches apically with a conical hair tuft; stigmatic areas separated. Cypselae 10-ribbed, pilose. Pappus bristles biseriate, slender, persistent. One species, *C. sanchezii* Dillon & Sagástegui, Peru.

514. *Pseudogynoxys* (Greenm.) Cabrera

Pseudogynoxys (Greenm.) Cabrera, Brittonia 7: 54 (1950); Robinson & Cuatrecasas, Phytologia 36: 177–192 (1977), rev.; Pruski, Syst. Bot. 21: 101–105 (1996), new sp.

Scandent herbs or subshrubs. Leaves petiolate, entire or rarely lobate, margins often serrate. Capitula few to several, occasionally solitary, corymbose, radiate, orange-red- or orange- to yellow-flowered, fragrant, calyculate. Anther base obtuse to sagittate, ecaudate. Style branches apically with an elongate acuminate appendage of fused hairs. Cypselae oblong, ribbed, glabrous or puberulous to hirsute; carpopodium indistinct. Pappus bristles numerous, slender. $n = 10$ (questionable), 45, 47–48. Fourteen species, South America from Bolivia and Brazil to Central America and Mexico. *Pseudogynoxys chenopodioides* (Kunth) Cabrera is cultivated as an ornamental and occurs as a garden escapee.

515. *Garcibarrigoa* Cuatrec.

Garcibarrigoa Cuatrec., Caldasia 15: 6 (1986).

Perennial herbs. Leaves petiolate, entire with serrulate margins, elliptic-lanceolate, basally auriculate and stem-clasping, strongly pinnately veined. Capitula solitary or few, corymbose, radiate, orange- or yellow-flowered. Anthers ecaudate. Style branches apically with a triangular-acuminate hair tuft. Cypselae oblong, ribbed, glabrous; carpopodium indistinct. Pappus bristles numerous, slender. Two species, Ecuador, Colombia.

516. *Lasiocephalus* Schlecht.

Lasiocephalus Schlecht., Gesell. Naturf. Freunde Berlin Mag. Neusten Entdeck. Gesamt. Naturk. 8: 308 (1818); Nordenstam, Opera Bot. 44: 53–56 (1978, under *Aetheolaena*).

Erect or ascending little-branched shrublets. Leaves small and closely set, subsessile, entire, elliptic or obovate to lanceolate, tomentose, margins revolute. Capitula solitary or few together, nodding, discoid, yellow-flowered, calyculate. Anther base ecaudate, obtuse. Style branches apically obtuse or truncate with a median hair pencil. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender. Two or three species, Andes of Peru, Ecuador, Colombia.

517. *Aetheolaena* Cass.

Aetheolaena Cass., Dict. Sci. Nat. 48: 453 (1827); Nordenstam, Opera Bot. 44: 53–56 (1978), re-establ., new comb.; Cuatrecasas, Phytologia 40: 307–312 (1978), rev. (sub *Lasiocephalo*).
Lasiocephalus sensu auct. plur., non Schlecht. (1818).

Scandent or ascending half-shrubs. Leaves scattered, petiolate but upper cauline leaves often sessile, triangular-ovate, entire, often dentate or serrulate. Capitula few to many, corymbose-paniculate, discoid, nodding, calyculate; florets dirty white to greenish-yellow. Anther base ecaudate, obtuse. Style branches apically convex or conical with a central elongate hair pencil and shorter lateral hairs or papillae; stigmatic areas separated. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender, caducous. $n = 20$. Circa 15 species, Andes of South America from Bolivia to Venezuela.

518. *Arbelaezaster* Cuatrec.

Arbelaezaster Cuatrec., Caldasia 15: 1 (1986).

Erect perennial herb with rhizome. Leaves cauline, shortly petiolate, ovate, entire with denticulate or serrate margins. Capitula several, paniculate-corymbose, discoid with greenish-yellow florets, calyculate. Anthers sagittate. Style branches with an apical tuft of fused long hairs; stigmatic areas separated. Cypselae oblong, glabrous, ribbed. Pappus bristles numerous, slender. One species, *A. ellesworthii* (Cuatrec.) Cuatrec., Colombia.

519. *Dresslerothamnus* H. Rob.

Dresslerothamnus H. Rob., Phytologia 40: 493 (1978); Robinson, Syst. Bot. 14: 380–388 (1989), rev.

Scandent shrubs with T-shaped or substellate trichomes. Leaves cauline, petiolate, elliptic-ovate, entire. Capitula several, corymbose-paniculate, radiate, calyculate. Rays flagelliform, twisted and recurved, reddish. Disc florets perfect, yellow. Anthers caudate with long and often papillose tails. Style branches apically truncate, papillate and with a short median hair tuft; stigmatic areas separated. Cypselae oblong, ribbed or angled, glabrous. Pappus bristles numerous, slender with enlarged tips, caducous. Four or five species, Colombia, Panama, Costa Rica.

520. *Cabreriella* Cuatrec.

Cabreriella Cuatrec., Bol. Soc. Argent. Bot. 119: 15 (1980).

Scandent glabrous shrubs. Leaves opposite, sessile or subsessile, ovate-cordate, entire with dentate margins. Capitula several, corymbose, radiate or discoid, yellow-flowered, calyculate. Disc florets perfect. Anthers basally sagittate or shortly caudate. Style branches of disc florets apically truncate or obtuse, papillate; stigmatic areas separated. Cypselae elliptic-oblong, 5-ribbed, glabrous. Pappus bristles numerous, slender. Two species, Colombia.

521. *Culcitium* Humb. & Bonpl.

Culcitium Humb. & Bonpl., Pl. Aequin. 2: 1 (1808); Cuatrecasas, Fieldiana Bot. 27: 40–51 (1950), rev.

Perennial herbs, densely tomentose. Leaves rosulate, lanceolate to elliptic, entire, margins sometimes serrulate. Capitula large, solitary or few, corymbose, nodding, discoid, many-flowered, yellow- or cream-flowered. Involucre pluriseriate, calyculate. Anthers ecaudate. Style branches truncate to obtuse. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, very slender. Circa 15 species, Andes of South America, from Chile to Venezuela.

522. *Charadranaetes* J. Janovec & H. Rob.

Charadranaetes J. Janovec & H. Rob., Novon 7: 162–168 (1997).

Semi-woody glabrous shrub. Leaves cauline, petiolate, entire with serrate margins, foetid when crushed. Capitula 2 or 3, radiate, narrow; involucre uniseriate, calyculate. Ray florets yellow or orange-coloured. Disc florets perfect, yellow; corolla lobes linear-lanceolate with resin ducts. Anther base ecaudate, obtuse or slightly sagittate. Style branches apically rounded with subterminal short sweeping hairs. Achenes oblong, ribbed, glabrous. Pappus bristles many, slender, caducous. One species, *C. durandii* (Klatt) J. Janovec & H. Rob., Costa Rica.

523. *Misbrookea* V.A. Funk

Misbrookea V.A. Funk, Brittonia 49: 111 (1997).

Perennial rhizomatous herb forming mats or growing solitary, densely hairy with long strigose trichomes. Leaves closely set and appressed, sessile, oblong-obovate, greyish-green. Capitula solitary, sessile or subsessile, radiate, ecalyculate. Involucral bracts connate. Ray florets white. Disc florets perfect, yellow. Anthers shortly sagittate. Style branches apically obtuse, papillate and centrally penicillate; stigmatic areas separated. Cypselae oblong, ribbed, hairy. Pappus bristles numerous, slender, persistent. n = c. 58, c. 58 + 2B. One species, *M. strigosissima* (A. Gray) V.A. Funk, high Andes of Bolivia and Peru.

524. *Xenophyllum* V.A. Funk

Xenophyllum V.A. Funk, Novon 7: 235 (1997); Funk, Estudios sobre diversidad y ecologia de plantas, Univ. Catol. Quito: 25–35 (1997), reg. rev., key.

Perennial herbs forming hummocks or mats; rhizomes covered with leaves or leaf bases. Leaves closely spirally set, entire and ± thick or small with lobed tips, bright green at least distally, becoming brown or blackish. Capitula solitary, sessile, ecalyculate, radiate. Involucral bracts connate at least basally. Ray florets white or purplish. Disc florets perfect, white or yellow. Style branches apically truncate to rounded, papillate. Cypselae obovate, ribbed, glabrous. Pappus bristles numerous, slender. n = 52, c. 54. Twenty-one species, high Andes from Argentina and Chile to Colombia.

525. *Werneria* Kunth

Werneria Kunth in HBK., Nov. Gen. Sp. Pl. ed. folio 4: 148 (1818); Rockhausen, Bot. Jahrb. Syst. 70: 273–342 (1940), rev.; Cabrera, Not. Mus. La Plata 13 Bot. 60: 49–61 (1948), reg. rev.; Funk, Estudios sobre diversidad y ecologia de plantas, Univ. Catol. Quito: 25–35 (1997), reg. rev., key.

Perennial rosulate herbs growing solitary or in small clumps. Leaves sessile, closely set at rhizome tips or below capitula, entire, glabrous. Capitula solitary, sessile or pedunculate, ecalyculate. In-

volucral bracts connate to various degrees. Ray florets white or rarely yellow. Disc florets perfect, white or yellow. Anthers sagittate. Style branches apically obtuse, papillate. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender. n = c. 21, c. 48, 50, c. 58, c. 75, c. 77, c. 103, 111. Twenty-five to 30 species, high Andes of South America.

526. *Oresbia* Cron & B. Nord.

Oresbia Cron & B. Nord., Novon 16:216 (2006).

Perennial tomentose-araneose herb. Leaves alternate, sessile, elliptic-ovate or spathulate with denticulate to serrate margins, glabrescent above, base half-clasping. Capitula few to several, laxly corymbose, rarely solitary on long peduncle, radiate, yellow-flowered, calyculate. Anthers sagittate or shortly caudate. Style branches apically truncate, papillate. Cypselae dimorphic: outer 4-winged, glabrous; inner 6-ribbed with mucilaginous hairs. Pappus bristles white, caducous. One species, *O. heterocarpa* Cron & B. Nord., South Africa.

527. *Lamprocephalus* B. Nord.

Lamprocephalus B. Nord., Bot. Notiser 125: 323 (1976).

Shrublet. Leaves cauline, sessile, linear, coriaceous. Capitula solitary on long, bracteate peduncles, discoid, red-flowered. Involucre uniseriate, ecalyculate. Corolla tubular, shortly lobed. Anthers slightly sagittate. Style branches apically with large oblong-triangular obtuse appendage, glabrous but minutely papillate; stigmatic areas continuous. Cypselae oblong, 5-angular, with short myxogenic twin hairs. Pappus bristles copious, pluriseriate, slender, persistent. One species, *L. montanus* B. Nord., South Africa.

528. *Phaneroglossa* B. Nord.

Phaneroglossa B. Nord., Opera Bot. 44: 66 (1978).

Ascending subshrub, glabrous except for woolly leaf-axils. Leaves cauline, sessile, closely set, linear-lanceolate or oblanceolate, entire, midribbed, basally half-clasping; margins denticulate and somewhat revolute. Capitula solitary, long-pedunculate, radiate, ecalyculate, white- or cream-flowered. Involucral bracts uniseriate, basally connate. Tube of ray florets shortly hirsute. Disc florets perfect. Anther base auriculate. Style branches apically conical; stigmatic areas continuous. Cypselae dimorphic, oblong with wing-like ridges: those of ray florets glabrous, brown to black; those of disc florets hirsute on the curved ridges with mucilaginous twin hairs, brown. Pappus bristles numerous, pluriseriate, slender, caducous in ray florets, persistent in disc florets. One species, *P. bolusii* (Oliv.) B. Nord., South Africa.

529. *Dendrosenecio* (Hauman ex Hedberg) B. Nord.

Dendrosenecio (Hauman ex Hedberg) B. Nord., Opera Bot. 44: 40 (1978); Mabberley, Kew Bull. 28: 61–96 (1973, as *Senecio* subg. *Dendrosenecio*), morph.; Jeffrey, Kew Bull. 41: 887–892 (1986, as *Senecio* ser. *Arborei*), rev.; Mabberley in Vuilleumier & Monasterio (eds) High altitude tropical biogeography: 81–102 (1986), morph.; Knox, Contr. Univ. Michigan Herb. 19: 241–257 (1993), rev.; Knox & Palmer, Amer. J. Bot. 82: 1567–1573 (1995), phylog.

Pachycaul trees or tree-like herbs ('dendrophorbs'). Leaves very large, assembled towards ends of stem and branches, sessile or petiolate, ovate-elliptic or panduriform, pinnately and reticulately veined. Capitula numerous in terminal panicles, large, nodding, radiate or discoid, yellow-flowered. Involucre ± biseriate, calyculate. Anther base auriculate; filament collar somewhat balusterform to almost straight. Style branches truncate and shortly penicillate, with continuous stigmatic areas. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender. n = 10, c. 40, 50. Eleven species, mountains of tropical Africa.

530. *Euryops* (Cass.) Cass.

Euryops (Cass.) Cass., Dict. Sci. Nat. 16: 49 (1820), nom. cons. prop.; Nordenstam, Opera Bot. 20: 1–409 (1968), rev.; Nordenstam, Bot. Notiser 121: 209–232 (1968), cyt., morph.; Nordenstam, Opera Bot. 23: 1–77 (1969), biogeogr.
Jacobaeastrum Vaill. (1754), nom. rej. prop.
Gamolepis sensu auct. plur., non Less. (1832).
Ruckeria DC. (1838).
Lasiocoma Bol. (1906).
Thodaya Compt. (1931).
Lysichlamys Compt. (1943).

Shrubs or shrublets or perennial (one annual) herbs. Leaves cauline or rarely subrosulate, sessile, entire to variously lobed or pinnatisect. Capitula axillary on naked peduncles, often numerous, or pseudo-terminal and solitary, radiate or rarely discoid, yellow-flowered. Involucre uniseriate, ecalyculate; bracts connate or rarely free. Disc florets

perfect or rarely functionally male; corolla lobes deltoid-ovate. Anthers ecaudate. Style branches truncate-obtuse, with discrete stigmatic areas. Cypselae elliptic-oblong, glabrous or pubescent with often myxogenic twin hairs. Pappus bristles uniseriate, flexuous, caducous, or absent. n = 10, 20, 30. One hundred species, Africa, Arabia, Socotra.

531. *Othonna* L.

Othonna L., Sp. Pl.: 924 (1753) & Gen. Pl. ed. 5: 396 (1754); Merxmüller, Prodr. Fl. Südwestafr. 139: 129–135 (1967), reg. rev.; Rowley, The succulent Compositae (1994), horticult. review.

Perennial succulent shrubs or herbs with underground tubers or corms. Leaves cauline or rosulate, sessile or shortly petiolate, entire or dentate to serrate or lobed, terete to flat, mostly glabrous. Capitula solitary and pedunculate to many and corymbose, radiate or discoid, ecalyculate. Involucral bracts uniseriate, connate at least basally. Florets yellow, white, pink or purple. Anthers ecaudate. Style branches of disc florets simple, sterile, apically conical or obtuse. Cypselae elliptic-oblong, glabrous or pubescent. Pappus bristles numerous, slender, persistent or caducous, white, straw-coloured or pink to rufous or purplish. n = 10, 20, 30, c. 40. Circa 120 species, southern Africa north to Angola and Zimbabwe. Genus biphyletic and under revision (B. Nordenstam).

532. *Gymnodiscus* Less.

Gymnodiscus Less., Linnaea 6: 95 (1831).

Annual glabrous herbs. Leaves rosulate or some cauline, pinnately lobed or dissected. Capitula few to several, corymbose, small and few-flowered, radiate, yellow-flowered, ecalyculate. Involucral bracts connate. Disc florets functionally male with a simple sterile style. Anthers ecaudate. Cypselae oblong-ovoid, glabrous. Pappus bristles numerous, slender, lacking in disc florets. n = 9. Two species, southern Africa.

533. *Hertia* Less.

Hertia Less., Syn. Gen. Comp.: 88 (1832).
Othonnopsis Jaub. & Spach (1852).

Shrubs or subshrubs or perennial herbs with a thick rhizome. Leaves cauline, sessile, entire with margins sometimes serrate, linear to lanceolate or obovate, glabrous, ± succulent. Capitula solitary, axillary or terminal, or several paniculate-corymbose, radiate or disciform, yellow-flowered. Involucral bracts uniseriate, often connate at least basally. Receptacle flat, naked. Disc florets functionally male. Anthers ecaudate. Style branches obtuse, dorsally hirsute or papillate. Cypselae elliptic-oblong, ribbed, glabrous or pubescent. Pappus bristles numerous, slender, persistent. n = 10. Circa 10 species, southern and northern Africa, south-western Asia east to Iran.

534. *Lopholaena* DC.

Lopholaena DC., Prodr. 6: 335 (1838); Phillips & Smith, Trans. Roy. Soc. S. Afr. 21: 221–238 (1934), rev.; Jeffrey, Kew Bull. 41: 932 (1986), reg. rev.

Perennial herbs, subshrubs or shrubs, with a thick rhizome. Leaves cauline, sessile, entire, fleshy or coriaceous, margins often serrate. Capitula solitary or several, paniculate-corymbose, discoid, ecalyculate. Involucral bracts ± connate, dorsally keeled. Florets white or pink to purple. Style branches with elongate subulate appendage. Cypselae elliptic-oblong, glabrous or pubescent. Pappus bristles numerous, slender. Eighteen species, southern Africa.

535. *Cadiscus* E. Mey. ex DC.

Cadiscus E. Mey. ex DC., Prodr. 7: 254 (1838).

Aquatic herb. Leaves floating, alternate, linear, amplexicaul. Capitula solitary, axillary, radiate, ecalyculate. Involucral bracts uniseriate, connate. Ray florets white. Disc florets functionally male, yellow; style simple, sterile. Cypselae oblong, hirsute. Pappus bristles few, coarse, subpaleaceous. n = 10. One species, *C. aquaticus* E. Mey. ex DC., South Africa.

536. *Stenops* B. Nord.

Stenops B. Nord., Opera Bot. 44: 73 (1978); Nordenstam, Comp. Newslett. 23: 1–2 (1993), syn., new comb.
Pseudocadiscus Lisowski (1987).

Glabrous annual subcarnose sub-aquatic herbs. Leaves cauline, sessile, simple, linear to narrowly elliptic-oblong, margins slightly denticulate. Capitula few, corymbose-paniculate, radiate, ecalyculate. Involucral bracts uniseriate, connate to about the middle. Receptacle conical. Ray florets white or pink to mauve. Disc florets perfect, yellow. Anthers ecaudate; filament collar much dilated basally. Style branches apically truncate with

short sweeping hairs; stigmatic areas separated. Cypselae 5-angled, glabrous. Pappus absent. Two species, Tanzania, Zambia.

537. *Oligothrix* DC.

Oligothrix DC., Prodr. 6: 293 (1838).

Small annual herb. Leaves cauline, sessile and amplexicaul, entire with somewhat serrate margins. Capitula few, laxly corymbose, small and few-flowered, radiate. Involucral bracts connate. Ray florets short, white or yellow. Disc florets perfect, yellow. Anthers ecaudate; filament collar basally much enlarged. Style branches truncate, penicillate. Cypselae elliptic-oblong, ribbed, puberulous. Pappus bristles few, slender, caducous. One species, *O. gracilis* DC., South Africa.

538. *Steirodiscus* Less.

Steirodiscus Less., Syn. Gen. Comp.: 251 (1832).
Gamolepis Less. (1832).
Psilothonna E. Mey. ex DC. (1838).

Small annual glabrous herbs. Leaves cauline, sessile, entire and linear or pinnately lobed. Capitula solitary or few, corymbose, radiate, yellow-flowered, ecalyculate. Involucral bracts uniseriate, connate at least basally. Receptacle convex. Disc florets perfect or functionally male. Anthers ecaudate with rounded base. Style branches truncate to conical-obtuse, penicillate. Cypselae oblong-ovate, glabrous or puberulous. Pappus absent. $n = 8, 10$. Five species, southern Africa.

539. *Bafutia* C.D. Adams

Bafutia C.D. Adams, Kew Bull. 15: 439 (1962).

Annual herb. Leaves cauline, sessile, oblanceolate, entire with sometimes serrulate margins. Capitula few, corymbose, small, discoid, ecalyculate. Involucral bracts uniseriate, connate. Florets hermaphrodite, pink to purplish; corolla lobes oblong-ovate. Anthers ecaudate. Style branches short, apically obtuse-clavate, penicillate. Cypselae oblong, glabrous. Pappus bristles few, short, caducous. One species, *B. tenuicaulis* C.D. Adams, Cameroun Mts., western tropical Africa.

540. *Psednotrichia* Hiern

Psednotrichia Hiern, J. Bot. 36: 289 (1898); Anderberg & Karis, Nordic J. Bot. 15: 375–379 (1995), re-establ.
Xyridopsis B. Nord. (1978).

Small annual herbs, ± glabrous. Leaves mostly basal, entire, linear-filiform. Capitula solitary on slender naked peduncles, small, discoid, yellow-flowered, ecalyculate. Involucral bracts uniseriate, connate to about the middle. Corolla lobes unequal, narrowly ovate, with a median resin duct. Anthers ecaudate; filament collar gradually widening towards the base. Style branches apically with a short conical hair tuft, dorsally minutely papillate; stigmatic areas separated. Cypselae elliptic-oblong, shortly hirsute with obtuse mucilaginous twin hairs. Pappus bristles several, flexuous, distinctly barbellate, caducous. Two species, Angola.

541. *Emilia* (Cass.) Cass.

Emilia (Cass.) Cass., Dict. Sci. Nat. 34: 393 (1825); Humbert, Fl. Madag. 189: 804–823 (1963), reg. rev.; Barkley & Cronquist, N. Amer. Fl. ser. 2, 10: 147–150 (1978), reg. rev.; Nicolson, Syst. Bot. 5: 391–407 (1980), reg. rev.; Jeffrey, Kew Bull. 41: 908–920 (1986), reg. rev.
Pithosillum Cass. (1826).
Pseudactis S. Moore (1919).

Annual or perennial herbs with fibrous roots, mostly glabrous. Leaves cauline, sessile or petiolate, sometimes amplexicaul. Capitula solitary or few to several, corymbose, radiate or discoid, ecalyculate. Florets white, pink, red, purple, orange or yellow. Involucral bracts uniseriate. Style branches apically truncate or obtuse, minutely papillate, sometimes with a small central hair tuft. Cypselae elliptic-oblong; carpopodium indistinct. Pappus bristles numerous, slender, persistent. $n = 5, 8, 10, 11, 15, 20$. Circa 100 species, tropical regions, mostly in Africa (some tropical weeds).

542. *Emiliella* S. Moore

Emiliella S. Moore, J. Bot. 56: 225 (1918); Torre, Garcia de Orta, sér. Bot. 2: 85–88 (1975), rev.

Annual herbs, mostly glabrous. Leaves cauline, petiolate or sessile, entire or lobed, sometimes basally auriculate and/or amplexicaul. Capitula solitary or few, corymbose, discoid. Involucre cylindrical, ecalyculate. Florets few, pink to purplish blue. Style branches truncate. Cypselae narrowly oblong, ribbed, glabrous. Pappus a single scale or absent. Five species, Angola, Zaire, Zambia.

543. ***Faujasiopsis*** C. Jeffrey

Faujasiopsis C. Jeffrey, Kew Bull. 47: 77 (1992), rev.; Jeffrey, Fl. Mascar. 109: 134–139 (1993), rev.

Scandent or erect shrubs. Leaves cauline, entire, broad, glabrous. Capitula several, corymbose, disciform or discoid, white- or lilac-flowered, ecalyculate. Female florets tubular-campanulate, 4- or 5-lobed. Anthers caudate; filament collar short. Style branches apically obtuse. Cypselae oblong, glabrous; carpopodium distinct. Pappus bristles numerous, slender. $n = 10$. Three species, Mauritius, La Réunion.

544. ***Faujasia*** Cass.

Faujasia Cass., Bull. Soc. Philom. Paris 1819: 20 (1819); Jeffrey, Kew Bull. 47: 78 (1992), rev.; Jeffrey, Fl. Mascar. 109: 139–142 (1993), rev.

Erect shrubs or shrublets. Leaves cauline, sessile, linear to ovate, entire with often serrate or dentate margins. Capitula many in terminal corymbiform cymes, radiate or discoid, yellow- or cream- to white-flowered, calyculate; peduncles stiff, bracteolate. Anthers caudate. Style branches apically obtuse. Cypselae oblong, ribbed, glabrous; carpopodium indistinct, annular. Pappus bristles numerous, basally flattened. Four species, La Réunion.

545. ***Eriotrix*** Cass.

Eriotrix Cass., Bull. Soc. Philom. Paris 1817: 32 (1817); Jeffrey, Fl. Mascar. 109: 142–144 (1993), rev.

Erect glabrous shrublets. Leaves cauline, small, closely appressed, narrowly linear-filiform or subulate. Capitula solitary, sessile or some subsessile, disciform, white- or yellowish-flowered. Marginal florets female, tubular. Disc florets perfect. Anthers sagittate. Style branches truncate or obtuse, penicillate. Cypselae oblong, ribbed, glabrous. Pappus bristles several or numerous, flexuous and entangled. Two species, La Réunion.

546. ***Hubertia*** Bory

Hubertia Bory, Voy. Iles Afrique 1: 334, t. 14 (1804); Jeffrey, Kew Bull. 47: 79–81 (1992), emend., new comb.; Jeffrey, Fl. Mascar. 109: 147–150 (1993), reg. rev.

Shrubs or suffrutescent herbs, erect or rarely scandent. Leaves cauline, sessile or petiolate, unlobed or lobed with margins often serrate to dentate. Capitula several to many, corymbose, radiate, disciform or discoid, yellow- or cream-flowered, calyculate. Anthers caudate; filament collars cylindrical or only slightly balusterform. Style branches apically obtuse or rounded; stigmatic areas separated or partly confluent. Cypselae oblong, glabrous or sometimes pubescent; carpopodium distinct. Pappus bristles numerous, slender. Circa 25 species, Madagascar, La Réunion, Comores.

547. ***Humbertacalia*** C. Jeffrey

Humbertacalia C. Jeffrey, Kew Bull. 47: 82 (1992), 82–83, rev.; Jeffrey, Fl. Mascar. 109: 132–134 (1993), rev.

Scandent subshrubs. Leaves cauline, petiolate, pinnately or palmately veined, unlobed with margins often serrate or dentate. Capitula numerous in axillary or terminal synflorescences, discoid, few-flowered, calyculate; florets white or sometimes greenish-yellowish. Anthers caudate. Style branches apically obtuse or rounded, sometimes with a pointed hair tuft. Cypselae oblong, glabrous or pubescent; carpopodium distinct. Pappus bristles numerous, slender. Eight species, Madagascar, La Réunion.

548. ***Parafaujasia*** C. Jeffrey

Parafaujasia C. Jeffrey, Kew Bull. 47: 79 (1992); Jeffrey, Fl. Mascar. 109: 146 (1993), rev.

Erect shrubs. Leaves cauline, closely set, sessile, spreading, linear, one-nerved. Capitula numerous in terminal pyramidal thyrsoid synflorescences, discoid, yellow-flowered. Anthers caudate. Style branches apically truncate with short papillae. Cypselae oblong, glabrous; carpopodium indistinct. Pappus bristles ± thick, straight, scabrid, free from the base. Two species, Mauritius, La Réunion.

549. ***Synotis*** (C.B. Clarke) C. Jeffrey & Y.L. Chen

Synotis (C.B. Clarke) C. Jeffrey & Y.L. Chen, Kew Bull. 39: 285 (1984); 211, 285–339, reg. rev.; Chen, Fl. Reip. Pop. Sin. 77, 1: 167–217 (1999), reg. rev.

Erect or scrambling herbs or subshrubs with woody rhizome. Leaves cauline, often assembled on branch ends, petiolate or sometimes sessile, pinnately veined, entire or somewhat lobed, rarely pinnatisect, lanceolate to elliptic-oblong or ovate, sometimes cordate; margins usually dentate or serrate. Capitula several to numerous, corymbose or racemose, radiate, disciform or discoid, yellow- or cream-flowered, calyculate.

Disc florets perfect; corolla lobes short. Anthers caudate. Style branches truncate to obtuse, penicillate, sometimes with a tuft of longer papillae. Cypselae narrowly cylindrical-oblong, glabrous or sometimes pubescent. Pappus bristles numerous, slender, white or fulvous to rufous. n = 10, 18, 20. Circa 55 species, eastern Asia, especially Sinohimalayan region.

550. *Mikaniopsis* Milne-Redh.

Mikaniopsis Milne-Redh. in Exell, suppl. Cat. Vasc. Pl. S. Thomé: 27 (1956); Jeffrey, Kew Bull. 41: 878–879 (1986), reg. rev.; Lisowski, Fragm. Flor. Geobot. 35: 43–53 (1991), reg. rev.

Scandent perennial herbs or subshrubs. Leaves cauline, with prehensile petioles, exauriculate, ovate-cordate, palmately veined. Capitula several, paniculate-corymbose, disciform, yellow- or white-flowered, calyculate. Marginal florets female with tubular-campanulate corolla. Disc florets perfect. Anthers caudate. Style branches apically obtuse and appendiculate with a central hair tuft. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender. Fifteen species, tropical and subtropical Africa.

551. *Delairea* Lem.

Delairea Lem., Ann. Sci. Nat. Bot. sér. 3, 1: 329 (1844).

Scandent-climbing succulent herb. Leaves petiolate, ovate-cordate, palmately veined; petioles auriculate at base. Capitula several, corymbose, discoid, yellow-flowered, calyculate. Anthers caudate. Style branches obtuse, penicillate. Cypselae oblong, ribbed, glabrous; carpopodium distinct. Pappus bristles numerous, slender. n = 10. One species, *D. odorata* Lem., South Africa.

552. *Cissampelopsis* (DC.) Miq.

Cissampelopsis (DC.) Miq., Fl. Ned. Ind. 2: 102 (1856); Jeffrey & Chen, Kew Bull. 39: 339–351 (1984), reg. rev.; Koyama, Acta Phytotax. Geobot. 39: 151–163 (1988), reg. rev.; Chen, Fl. Reip. Pop. Sin. 77, 1: 217–225 (1999), reg. rev.

Scandent perennial herbs or subshrubs. Leaves cauline, with prehensile petioles, exauriculate, ovate or cordate to deltoid, palmately veined. Capitula many, corymbose-paniculate, discoid or radiate, calyculate. Ray florets yellow. Disc florets perfect, white to pink or yellow; corolla lobes lanceolate. Anthers caudate. Style branches truncate or obtuse, penicillate. Cypselae narrowly oblong, ribbed, glabrous. Pappus bristles numerous, slender, white or rufescent. Ten species, eastern and south-eastern Asia (Indomalesia).

553. *Austrosynotis* C. Jeffrey

Austrosynotis C. Jeffrey, Kew Bull. 41: 828 (1986).

Scandent perennial herb. Leaves cauline, petiolate with prehensile petioles, auriculate, ovate-cordate, palmately veined. Capitula several, paniculate-corymbose, radiate, yellow-flowered, calyculate. Anthers caudate. Style branches truncate, penicillate. Cypselae oblong, glabrous. Pappus bristles numerus, slender. One species, *A. rectirama* (Bak.) C. Jeffrey, Tanzania, Malawi.

554. *Dauresia* B. Nord. & Pelser

Dauresia B. Nord. & Pelser, Comp. Newslett. 42: 76 (2005).

Glabrous subshrubs with white cortex. Leaves alternate, petiolate, rounded-cordate, dentate, palmately veined. Capitula densely corymbose, discoid, white- or yellow-flowered, ecalyculate. Involucral bracts 5, biseriate. Corolla deeply 5-lobed. Anthers shortly caudate; endothecial tissue polarized. Style branches apically obtuse with hair tufts. Cypselae papillate-hirsute on ribs, mucilaginous when soaked. Pappus bristles numerous, white. Two species, Namibia.

555. *Adenostyles* Cass.

Adenostyles Cass., Dict. Sci. Nat. 1, suppl. 59 (1816); Vierhapper, Oesterr. Bot. Z. 1923 (6–8): 150–164 (1928), syst. position; Toman et al., Preslia (Praha) 40: 122–132 (1968), syst. position; Tutin, Fl. Eur. 4: 189 (1976), rev.; Wagenitz, Phyton (Horn) 23: 141–159 (1983), rev.
Cacalia L. (1753 & 1754), nom. rej.

Perennial rhizomatous herbs. Leaves basal and cauline, petiolate, upper cauline leaves sometimes sessile and half-clasping, rounded-cordate, entire with dentate margins, pinnately veined. Capitula numerous, corymbose, narrow, discoid, calyculate. Florets 4-lobed, white or purplish. Anther base ecaudate, obtuse. Style branches elongate, subulate, papillose; stigmatic areas largely continuous. Cypselae oblong, ribbed, glabrous. Pappus bristles numerous, slender, persistent. n = 19. Three species, central and southern Europe.

556. *Pojarkovia* Askerova

Pojarkovia Askerova, Nov. Syst. Vyssh. Rast. 21: 186 (1984); Nordenstam, Pl. Syst. Evol. 206: 19–32 (1997), syst.

Perennial herb with short thick rhizome. Leaves cauline, shortly petiolate, lanceolate, entire, cuneate. Capitula numerous, corymbose, narrow, discoid, calyculate. Corolla deeply 4-lobed, whitish. Anther base ecaudate, auriculate; endothecium transitional (partly polarized). Style branches long, linear, puberulous, apically truncate, penicillate; stigmatic areas separated. Cypselae oblong, glabrous. Pappus bristles numerous, slender, persistent. n = 20. One species, *P. stenocephala* (Boiss.) Askerova, Caucasus.

557. *Caucasalia* B. Nord.

Caucasalia B. Nord., Pl. Syst. Evol. 206: 22 (1997), 19–32, rev.

Perennial rhizomatous herbs, glabrous or glandular-puberulous. Leaves cauline, petiolate, cordate or oblong-ovate, with dentate or denticulate margins. Capitula several, corymbose, radiate or discoid, yellow-flowered, shortly calyculate. Disc floret corolla 4-lobed. Anthers with radial endothecium, filament collar basally dilated. Style branches obtuse to truncate with short sweeping hairs, stigmatic areas confluent or barely separated. Cypselae oblong, glabrous, ribbed. Pappus bristles numerous, persistent. n = 19, 38. Four species, Caucasus, south-western Asia.

558. *Dolichorrhiza* (Pojark.) Galushko

Dolichorrhiza (Pojark.) Galushko, Nov. Sist. Vyssh. Rast. 6: 210 (1970); Nordenstam, Fl. Iran. 164: 51–53 (1989), reg. rev.; Nordenstam, Pl. Syst. Evol. 206: 19–32 (1997), syst.

Perennial herbs with a long thin rhizome. Leaves mostly basal and some cauline, petiolate, rounded-cordate or reniform, palmately veined; margins dentate or lobulate. Capitula solitary or several, corymbose, radiate or discoid, yellow-flowered, calyculate. Disc florets 4-lobed. Anther base ecaudate, obtuse. Style branches apically truncate and penicillate, otherwise glabrous; stigmatic areas separated at least basally. Cypselae oblong, ribbed, glabrous; carpopodium distinct. Pappus bristles numerous, slender, caducous. n = 15–16, 20, 22. Four species, Caucasus, Iran.

559. *Iranecio* B. Nord.

Iranecio B. Nord., in Rech. f. (ed.) Fl. Iran. 164: 53 (1989), 53–59, reg. rev.; Jeffrey, Kew Bull. 47: 102–103 (1992), emend., new comb.

Perennial herbs with a short stout rhizome. Leaves alternate, petiolate, entire to pinnatisect. Capitula few to several, corymbose-paniculate, broadly campanulate to hemispherical, radiate, yellow-flowered. Disc floret corollas 4-lobed. Anthers caudate. Style branches with continuous or partially separated stigmatic areas, apically truncate to obtuse and papillate. Cypselae oblong, glabrous or shortly villous, ribbed, with a distinct carpopodium. Pappus bristles numerous, slender, white to sordid or straw-coloured, persistent. n = 12, 15–17, 20. Sixteen species, south-western Asia.

XIII. Tribe Calenduleae Cass. (1819).

B. Nordenstam

Herbs, subshrubs, shrubs or small trees; unarmed or sometimes spinescent. Leaves alternate or opposite, sessile or petiolate, entire or variously lobed or dissected. Capitula solitary or corymbose, pedunculate or rarely sessile, heterogamous, radiate. Involucre 1–3-seriate or imbricate; receptacle naked. Ray florets female, fertile or sterile, rarely neuter, yellow to orange or white, pink to purple or blue. Disc florets hermaphrodite, perfect or functionally male, 5-lobed, yellow to orange or reddish. Anthers caudate; apical appendage triangular-ovate, flat; endothecial tissue polarized. Pollen grains spinulose, exine without bacula (Praglowski and Grafström 1980). Style fertile or sterile, entire or shortly bilobed to bifurcate; stigmatic areas divided at least basally; sweeping hairs in a subapical collar or extending down the style-branches (*Garuleum*). Cypselae homomorphic to polymorphic, terete, triquetrous or flattened, winged or wingless, straight or curved, sometimes rostrate, glabrous, in some taxa with a fleshy coloured or whitish exocarp (Fig. 58). Pappus absent. Chromosome number known from seven genera, with x = 7, 8, 9, 10, 11 or 15. *Calendula* has the most complex karyology, with all basic numbers represented except 10.

This small tribe currently comprises 12 genera and about 120 species.

Taxonomically, the tribe is fairly well understood at the species level, based on a lifelong study by Norlindh (e.g. 1943, 1960, 1977) and ongoing work by Nordenstam and colleagues (Nordenstam 1994a, b, 1996, 2004, 2006d; Nordenstam et al. 2006). The generic delimitation still poses problems, however, the most problematic

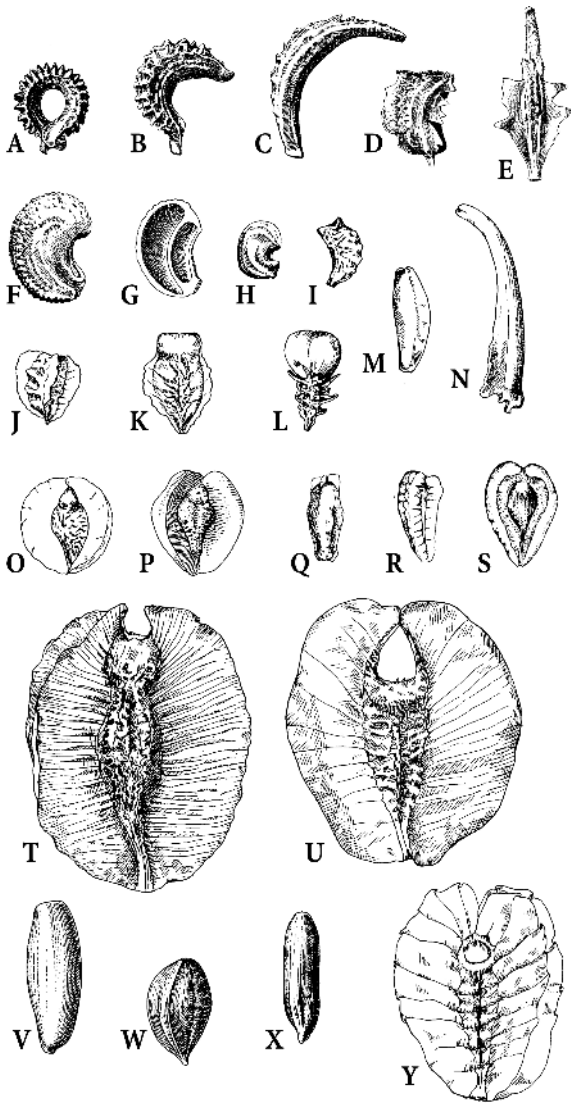

Fig. 58. Compositae-Calenduleae. Cypsela morphology. **A** *Calendula arvensis*. Annulate cypsela. **B–E** *Calendula maderensis*. **B** Falcate, **C** rostrate, **D** trialate, **E** alate-rostrate cypsela. **F, G** *Nephrotheca ilicifolia*. **F** Radial side. **G** Longitudinal section, showing cavities. **H** *Gibbaria scabra*. Reniform cypsela, radial side. **I–N** *Oligocarpus calendulaceus*. **I** Wingless, **J, K** trialate, **L** aculeate with enclosed apical cavity, **M** subterete, **N** rostrate cypsela. **O** *Norlindhia amplectens*. Cypsela trialate with efenestrate small cavity. **P** *Norlindhia breviradiata*. Cypsela trialate with efenestrate small cavity. **Q** *Norlindhia aptera*. Exalate cypsela. **R, S** *Garuleum bipinnatum*. **R** Triangular-obpyramidate ray cypsela. **S** Outer disc cypsela, 2-winged with thickened margin. **T** *Inuloides tomentosa*. Cypsela trialate with large efenestrate apical cavity. **U** *Tripteris nervosa*. Cypsela trialate trifenestrate. **V** *Osteospermum grandidentatum*. Cypsela cylindrical. **W** *Osteospermum herbaceum*. Cypsela ellipsoid triangulate. **X** *Osteospermum ciliatum*. Cypsela cylindrical, basally sulcate. **Y** *Monoculus monstrosus*. Cypsela trialate unifenestrate. (**A–H** Norlindh 1962, **I–P, T–Y** Norlindh 1943, **Q** original, **R, S** Norlindh 1977)

genus being *Osteospermum*. Although some of its elements have been recently transferred to other genera, it remains heterogeneous and further taxonomic changes can be forseen. *Osteospermum* sect. *Homocarpa* is closely related to the genus *Chrysanthemoides*, which is defined by a single character, the drupaceous fruits. A thin fleshy and sometimes coloured exocarp is found on the cypselae of members of sect. *Homocarpa* and sect. *Coriacea* as well, and future changes in generic taxonomy are inevitable. Pending further studies, a conservative view on the limits of *Osteospermum* and *Chrysanthemoides* is taken here (cf. Wood and Nordenstam 2004). Secondary compounds found in only Calenduleae include two fatty acids, viz. calendic acid in one group of genera (*Calendula*, *Chrysanthemoides*, *Osteospermum*) and dimorphecolic acid in another (*Dimorphotheca*) (Smith et al. 1960; Barclay and Earle 1965). Cyanoglycosides, mainly linamarin, also serve to characterize the genus *Dimorphotheca* in its present circumscription, i.e. including *Castalis* and *Osteospermum* sect. *Blaxium* (Valadon 1977). Calenduleae are also noteworthy for the high occurrence of diterpenes with a pimarane skeleton (Alvarenga et al. 2005). The centre of the tribe is clearly southern Africa, where all genera but one occur. Of these, *Osteospermum* and *Tripteris* extend into the northern hemisphere. *Calendula* is confined to the northern hemisphere, with a mainly Mediterranean distribution range extending eastwards as far as Iran.

The habitats of many Calenduleae are the South African fynbos and karoo vegetation types, also mountains and deserts. Some of the annuals, such as *Dimorphotheca pluvialis*, contribute to the spectacular spring flower displays after good rains in South Africa. In horticulture, plants of the tribe are well known since ancient times, such as the common marigold (*Calendula*), and more recently several cultivars of *Dimorphotheca* are becoming increasingly popular. The tribe is traditionally regarded as related to Senecioneae (Bremer 1987) but molecular evidence also indicates affinities to Astereae, Anthemideae and Gnaphalieae (Panero and Funk 2002).

Key to the Genera

1. Ray florets female-sterile or neuter **569. *Dimorphotheca***
– Ray florets female, fertile 2
2. Cypselae polymorphic, some curved and/or rostrate 3

– Cypselae homo- or dimorphic, seldom rostrate 4
3. Outer cypselae cymbiform, straight or curved, inner strongly curved and sometimes annular. Style undivided **560. *Calendula***
– Cypselae straight or slightly curved, but not annular, winged or wingless or 6-angled, some rostrate, surface smooth or rugose to aculeate. Style bifid **561. *Oligocarpus***
4. Style of disc florets deeply bifurcate and papillate-hairy outside **570. *Garuleum***
– Style of disc florets shallowly bifid with a subapical collar of sweeping hairs 5
5. Cypselae drupaceous with a distinct black-blue or orange-red fleshy layer **567. *Chrysanthemoides***
– Cypselae dry or rarely with a thin whitish or blue-blackish fleshy layer 6
6. Disc florets perfect, with flattened cypselae **569. *Dimorphotheca***
– Disc florets functionally male, with cypselae undeveloped and not flattened 7
7. Cypselae reniform with a ventral cavity 8
– Cypselae straight or slightly curved without ventral cavity 9
8. Leaves linear-subulate. Involucral bracts imbricate. Rays white or cream **568. *Gibbaria***
– Leaves ovate-oblong with dentate margins. Involucral bracts subuniseriate. Rays yellow **568a.*Nephrotheca***
9. Rays white, pink or purple **569. *Dimorphotheca***
– Rays yellow-orange 10
10. Cypselae 3-winged (rarely wings reduced) with apical cavity 11
– Cypselae winged or not, without apical cavity **566. *Osteospermum***
11. Disc corolla lobes with sclerenchymatic strands. Cypselae fenestrate 12
– Disc corolla without sclerenchymatic strands. Cypselae not fenestrate 13
12. Cypselae 3-winged and 3-fenestrate **564. *Tripteris***
– Cypselae 3-winged, unifenestrate **563. *Monoculus***
13. Perennial herb with entire tomentose leaves **565. *Inuloides***
– Annual herbs, glandular-pubescent, leaves lobate to dentate **562. *Norlindhia***

Genera of Calenduleae

560. *Calendula* L.

Calendula L., Sp. Pl.: 921 (1753); Lanza, Atti R. Accad. Sci. Palermo 11: 1–166 (1919), rev.; Meusel & Ohle, Oesterr. Bot. Z. 113: 191–210 (1966), part. rev.; Heyn et al., Israel J. Bot. 23: 169–201 (1974), part. rev.; Ohle, Feddes Repert. 85: 245–283 (1974), reg. rev.; Ohle, Feddes Repert. 86: 1–17 (1975), reg. rev.

Herbs or subshrubs, often glandular and aromatic. Leaves alternate, sessile, entire or dentate. Capitula pedunculate, radiate. Involucre 1–2-seriate. Ray florets female-fertile, yellow to orange. Disc florets functionally male with undivided style. Cypselae polymorphic, some curved, rostrate, winged or annular. $2n$ = 14, 16, 18, 22, 28, 30, 32, 36, 42, 44, 46, 54, c. 85. About 15 species (or 10–25, depending on taxonomic opinion), Macaronesia, northern Africa, Mediterranean region, southern and central Europe, Anatolia, Yemen, Iraq to Iran.

561. *Oligocarpus* Less.

Oligocarpus Less., Syn. Gen. Comp.: 90 (1832); Norlindh, Studies in the Calenduleae I: 346–352 (1943), rev. (as *Osteospermum* sect. *Oligocarpus*); Nordenstam, Comp. Newslett. 44: 45 (2006).

Annual herbs, glandular-puberulous. Leaves alternate, entire or dentate to lobate. Capitula solitary, small, radiate. Involucre ± uniseriate. Ray florets female-fertile, short, yellow. Cypselae polymorphic, curved or straight, winged or wingless, some rostrate, surface smooth or aculeate. Disc florets functionally male, yellow. Style shortly bilobed. Two species, South Africa, St. Helena.

562. *Norlindhia* B. Nord.

Norlindhia B. Nord., Comp. Newslett. 44: 41 (2006).

Annual herbs, glandular-pubescent with black-tipped glands. Leaves alternate, petiolate or sessile, sinuato-dentate or denticulate, base half-clasping. Capitula corymbose, radiate. Involucral bracts uniseriate or nearly so. Ray florets female, fertile, yellow to orange. Cypselae homo- or dimorphic with apical cavity (sometimes small or absent), without fenestra, 3-winged or wingless, some often rostrate. Disc florets functionally male, yellow; corolla without sclerenchymatic strands. Style apex minutely bifid. Three species, northwestern Cape Province in South Africa, southern Namibia.

563. *Monoculus* B. Nord.

Monoculus B. Nord., Comp. Newslett. 44: 39 (2006).

Annual herbs, glandular-pubescent. Leaves alternate, dentate or sinuately lobed. Capitula corymbose, radiate. Involucral bracts biseriate with broad scarious margins. Ray florets female, fertile, yellow or orange. Cypselae 3-winged with a unifenestrate apical cavity. Disc florets functionally male with blackish-purplish corolla lobes. Style shortly bifid. $2n$ = 16. Two species, western Cape Province in South Africa, southern Namibia.

564. *Tripteris* Less.

Tripteris Less., Linnaea 6: 95 (1831), nom. cons.; Norlindh, Studies in the Calenduleae I: 263–346 (1943), rev. (as *Osteospermum* subg. *Tripteris*).

Annual or perennial herbs, subshrubs or shrubs. Leaves alternate or opposite, entire or variously lobed. Capitula solitary or corymbose, radiate. Involucre biseriate to subuniseriate. Ray florets female-fertile, yellow to orange. Cypselae 3-winged with an apical trifenestrate cavity, homomorphic. Disc florets functionally male. Style shortly bifid. $2n$ = 18, 32. About 20 species, southern and tropical Africa north to Egypt, Arabia and Jordan.

565. *Inuloides* B. Nord.

Inuloides B. Nord., Comp. Newslett. 44: 44 (2006).

Tomentose shrublet or small subshrub. Leaves mainly rosulate, petiolate, spathulate-orbiculate, entire. Capitula solitary, scapose, radiate. Involucral bracts subuniseriate, inner ones with scarious-fimbriate margins. Ray florets female-fertile, yellow but turning blue upon drying. Cypselae 3-winged, with apical cavity but lacking fenestra, rugose between the wings and apically glandular-hairy. Disc florets functionally male, yellow. Style bilobed. Anther appendage margined, blackish. One species, *I. tomentosa* (L. fil.) B. Nord., south-western Cape Province in South Africa.

566. *Osteospermum* L. Fig. 59

Osteospermum L., Sp. Pl.: 923 (1753); Norlindh, Studies in the Calenduleae I: 98–263 (1943), rev.

Annual or perennial herbs, subshrubs or shrubs. Leaves alternate or opposite, entire or divided. Capitula radiate. Involucre 1–3-seriate. Ray florets female-fertile, yellow or orange. Cypselae homo- or heteromorphic, straight or slightly curved, terete or triquetrous, sometimes winged, with or without apical cavities. Disc florets functionally male. Style minutely bifid. $2n$ = 16, 18, 36. About 45 species, southern and tropical Africa, Somalia and south-western Arabia.

567. *Chrysanthemoides* Fabr.

Chrysanthemoides Fabr., Enum.: 79 (1759); Norlindh, Studies in the Calenduleae I: 367–403 (1943), rev.; Griffoen, M.Sc. Thesis, Univ. Cape Town (1995), rev.

Shrubs or small trees. Leaves alternate, shortly petiolate, glabrous (pubescent when young), entire or dentate. Capitula solitary or corymbose, radiate, shortly pedunculate. Ray florets female-fertile, yellow. Cypsela drupaceous with a fleshy red, orange, blue, purple or black exocarp, globose to ovoid. Disc florets functionally male. Style minutely bifid. $2n$ = 18, 20, 36. Two, or perhaps up to six species, southern and eastern tropical Africa, introduced in St. Helena, Australia, etc.

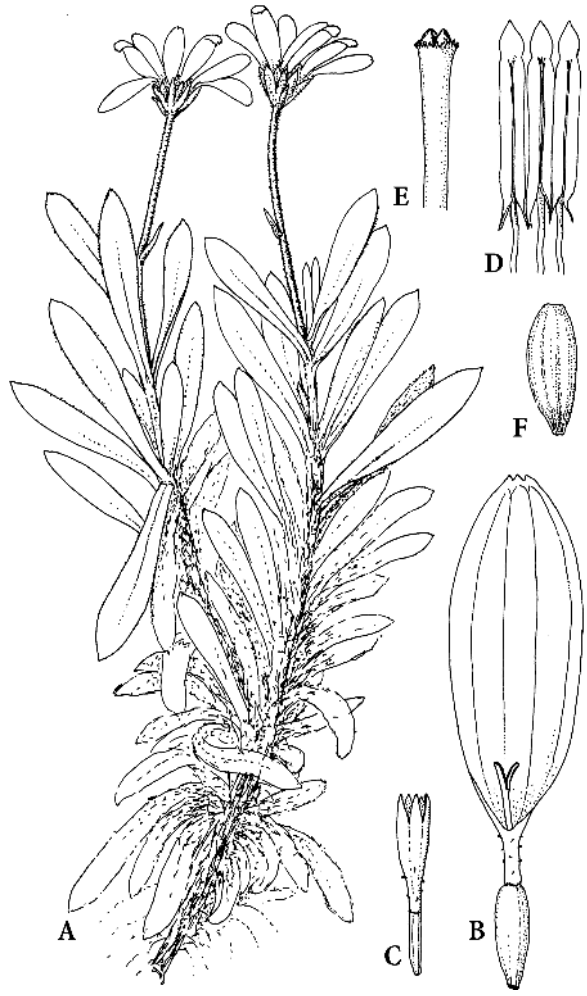

Fig. 59. Compositae-Calenduleae. *Osteospermum burttianum*. **A** Habit. **B** Ray floret. **C** Disc floret. **D** Stamens. **E** Style of disc floret. **F** Cypsela. (Drawing by B. Nordenstam)

568. *Gibbaria* Cass.

Gibbaria Cass., Bull. Sci. Soc. Philom. Paris 1817: 139 (1817); Norlindh, Studies in the Calenduleae I: 358–366 (1943), rev.

Erect shrublet. Leaves alternate, linear-subulate, entire, scabrid. Capitula terminal, 1–3, pedunculate, radiate. Involucre 2–3-seriate. Ray florets

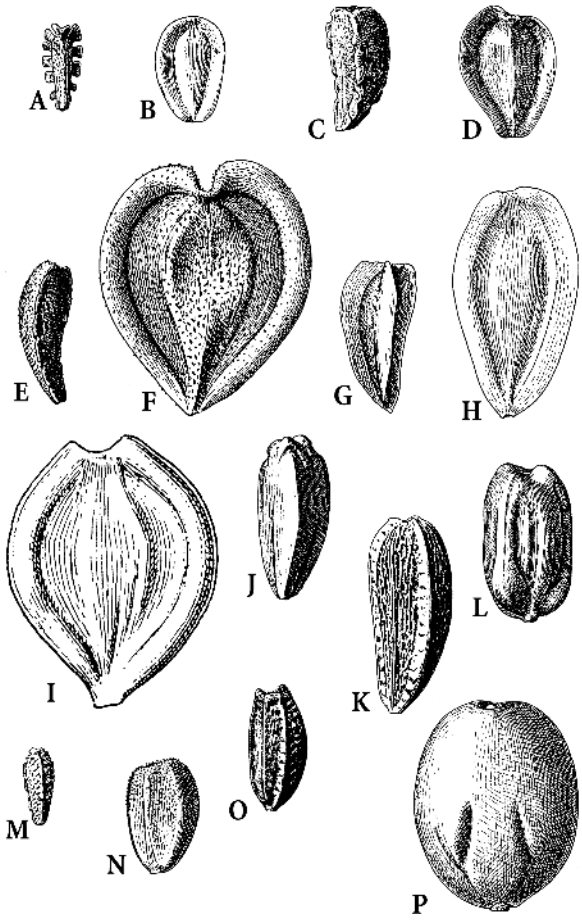

Fig. 60. Compositae-Calenduleae. Cypsela forms in *Dimorphotheca*. **A**, **B** *Dimorphotheca polyptera*. **A** Ray cypsela. **B** Disc cypsela. **C**, **D** *D. zeyheri*. **C** Ray cypsela. **D** Disc cypsela. **E**, **F** *D. cuneata*. **E** Ray cypsela. **F** Disc cypsela. **G**, **H** *D. montana*. **G** Ray cypsela. **H** Disc cypsela. **I** *D. nudicaulis* var. *graminifolia*. Disc cypsela suborbicular, flattened with thickened margins. **J** *D. fruticosa*. Cypsela triquetrous. **K** *D. ecklonis*. Cypsela acutely triangulate. **L** *D. scabra*. Cypsela triquetrous with incrassate angles. **M** *D. dregei*. Cypsela triangulate tuberculate. **N** *D. caulescens*. Cypsela obtusely 5–6-angled. **O** *D. jucunda*. Cypsela acutely triangulate with additional weak rib(s). **P** *D. walliana*. Cypsela globose and basally sulcate. (Norlindh 1943)

female-fertile, white or cream with yellow to orange reverse. Cypselae homomorphic, reniform with a ventral cavity, glabrous. Disc florets functionally male, yellow or orange. Style shortly bilobed. One species, *G. scabra* (Thunb.) T. Norl., southern Cape Province in South Africa.

568a. *Nephrotheca* B. Nord. & Källersjö

Nephrotheca B. Nord. & Källersjö, Comp. Newslett. 44: 33 (2006).

Glandular smelly shrub or shrublet. Leaves alternate, ovate-oblong, flat; margins dentate, scabrid. Capitula terminal, solitary, shortly pedunculate. Involucre subuniseriate. Ray florets female-fertile, yellow, sometimes reddish-purple beneath, obliquely laterally attached to the ovary. Cypselae homomorphic, reniform, with ventral cavity. Disc florets functionally male, yellow. Style minutely bilobed. $2n = 20$. One species, *N. ilicifolia* (L.) B. Nord. & Källersjö, south-western Cape Province in South Africa.

569. *Dimorphotheca* Vaill. Fig. 60

Dimorphotheca Vaill., Königl. Akad. Wissensch. Paris Phys. Abh. 5: 547 (1754), nom. cons.; Norlindh, Studies in the Calenduleae I: 38–76 (1943), rev.
Blaxium Cass. (1824).
Castalis Cass. (1824).
Xenismia DC. (1836).
Acanthotheca DC. (1838).
Osteospermum sect. *Blaxium* (Cass.) T. Norl. (1943).

Annual or perennial herbs, subshrubs or shrubs. Leaves alternate, entire or divided. Capitula solitary or corymbose, pedunculate, radiate. Involucre uniseriate. Ray florets female-fertile or female-sterile or neuter, yellow or orange, purple or white. Ray floret cypsela (when present) triquetrous or subterete, sometimes winged or tuberculate. Disc florets perfect or functionally male. Style shortly bilobed. Disc floret cypsela (when present) flattened with thickened margin. $2n = 18, 20$. Twenty species, southern Africa, Zimbabwe, Angola.

570. *Garuleum* Cass.

Garuleum Cass., Bull. Sci. Soc. Philom. Paris 1819: 172 (1819); Norlindh, Bot. Notiser 130: 377–380 (1977), part. rev.

Perennial herbs or shrubs. Leaves alternate, sessile, dentate to pinnatisect. Capitula solitary or corymbose, pedunculate, radiate. Involucre 2–3-seriate, ± imbricate. Ray florets female-fertile, blue or purple to mauve or white or yellow. Cypselae straight, triquetrous or angular, glabrous. Disc florets perfect or functionally male, yellow. Style deeply bifurcate with linear papillate-hirsute branches. Cypselae (when present) flattened, winged with a thickened rim, glabrous. Eight species, South Africa, Namibia.

XIV. Tribe Gnaphalieae (Cass.) Lecoq & Juillet (1831).

R.J. Bayer, I. Breitwieser, J. Ward and C. Puttock

Herbs, subshrubs or shrubs (Fig. 61), generally unarmed. Stems generally with fibres in phloem, without resin canals. Leaves alternate, rarely opposite, generally entire, and generally tomentose at least on the lower surface. Capitula heterogamous disciform or homogamous discoid, rarely heterogamous radiate, solitary or variously grouped, sometimes forming dense secondary heads. Involucral bracts (Figs. 62, 63) generally papery, generally brightly coloured or hyaline and with a thickened, cartilaginous basal portion (stereome) composed of compact sclerenchyma. Receptacles generally epaleate. Female outer florets generally filiform or often absent. Central florets generally perfect, sometimes functionally male. Anthers ecalcarate, with tails (Fig. 62); endothecial tissue almost always polarised. Pollen (Fig. 62) with two-layered ectexine comprising an outer columellate layer and an irregularly interlaced basal layer ('gnaphalioid' type). Style branches (Fig. 62) with hairs apically, sometimes apically and dorsally, or rarely dorsally only; stigmatic rows generally separated (Fig. 62). Cypselae (Fig. 63) generally small and oblong to obovoid, usually hairy; pericarp generally with 2–3 or 5 vascular bundles. Pappus (Fig. 63) generally of plumose or barbellate to scabrid capillary bristles, occasionally of bristles and scales, only scales, or absent. Base chromosome number variable but often $n = 7$ (in some groups, 8 or 9). Phytochemistry: sesquiterpene lactones usually absent.

Comprising 185 genera and about 1,240 species, cosmopolitan, but most diverse in Australia and South Africa.

The work of Anderberg (1989, 1991a, b, c) and Karis (1993b) suggests that the tribe Inuleae (Asteraceae: Asteroideae) sensu Merxmüller et al. (1977) should be considered as three separate tribal lineages: Inuleae s.s., Gnaphalieae and Plucheeae. More recently, however, Anderberg (in this series) returned Plucheeae to Inuleae s.s. These recircumscriptions, based in part on a cladistic analysis of morphological characters, are supported by two molecular analyses (Kim and Jansen 1995; Bayer and Starr 1998), both molecular studies indicating that Inuleae s.l. are not a monophyletic lineage. In the *trn*L intron and *trn*L/*trn*F intergenic spacer analysis by Bayer and Starr (1998), Inuleae s.s. and Plucheeae together form a clade sister to the remainder of Asteroideae. Kim and Jansen (1995), using *ndh*F, also suggest a strong sister relationship of Plucheeae and Inuleae within Asteroideae. The topological relationships identified by Bayer and Starr (1998) were almost identical to those established by Karis (1993b) based on morphology. Therefore, the segregation of Gnaphalieae from Inuleae s.l. is warranted. The sister relationships of Gnaphalieae proposed by these studies remain controversial. Karis (1993b), using morphology, revealed them as sister to a clade containing the tribes Astereae and

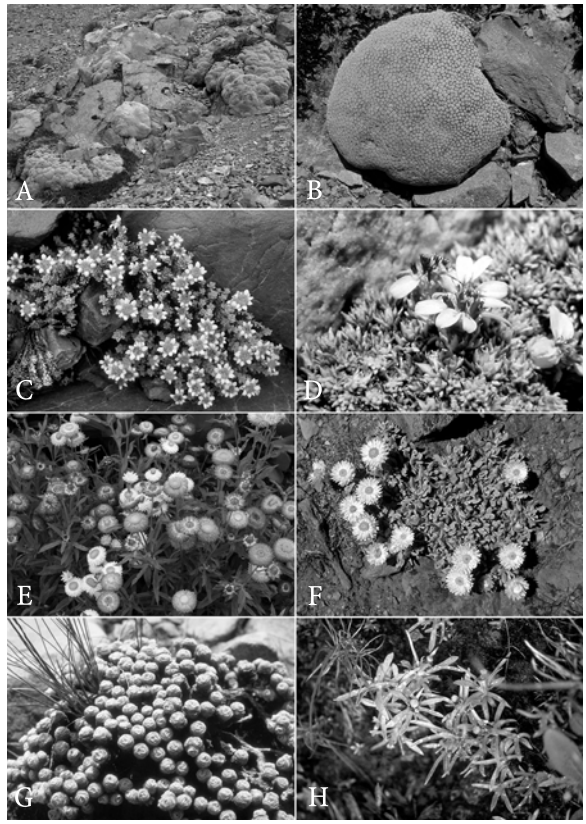

Fig. 61. Compositae-Gnaphalieae. Habit. **A**, **B** *Raoulia eximia*, cushion shrub, New Zealand. **C** *Leucogenes grandiceps*, decumbent herb, dense clusters of capitula surrounded by ring of showy modified leaves, New Zealand. **D** *Bryomorphe aretioides*, ericoid shrub, capitula with radiate outer florets, South Africa. **E** *Xerochrysum bracteatum*, upright herb, colourful papery involucral bracts, Australia. **F** *Leucochrysum albicans*, mat-forming herb, white papery involucral bracts, Australia. **G** *Mniodes pulvinulata*, suffruticose cushion, Peru. **H** *Gnaphalium supinum*, stoloniferous rosette herb, inconspicuous involucral bracts, Eurasia. (Photographs **A–C**, **F** John Lovis, **D** Marinda Koekemoer, **E** Randall Bayer, **G** Michael Dillon, **H** Ilse Breitwieser)

Anthemideae. Bayer and Starr (1998), based on *trnL* intron and *trnL*/*trnF* spacer data, proposed that Gnaphalieae are sister to Senecioneae. The RFLP (restriction fragment length polymorphism) analysis of Jansen et al. (1991) placed Gnaphalieae as sister to Inuleae (represented by *Inula* L.). Keeley and Jansen (1991) showed them as sister to a clade consisting of Inuleae and Plucheeae. Finally, the *ndhF* analysis of Kim and Jansen (1995) had Gnaphalieae in an unresolved clade containing Calenduleae, Astereae and Anthemideae. Until more information is at hand, the tribal circumscription and sister relationships of Gnaphalieae will remain controversial. Some genera which are currently part of Gnaphalieae (sensu Anderberg in Bremer 1994) will need to be relocated to other tribes but, until more data are presented, these transfers would be premature. Additionally, our current molecular work on the tribe (Bayer and Starr 1998; Bayer et al. 2000) indicates that the subtribes of Gnaphalieae, as delimited by Anderberg (1991a), are non-monophyletic and will need recircumscription once the final analyses are completed. It is for this reason that we have chosen not to place the genera within any subtribal or informal classification system, as there is no strong phylogenetic evidence yet to erect such groups. As more phylogenetic information becomes available, it will be possible to establish such groups but, at this stage, this would be premature and would lead to instability. Therefore, we decided to list the genera alphabetically. The descriptions of genera are based largely on Anderberg (1991a), except for numerous amendments made by us, especially to Australian, New Zealand and South African taxa. We recognize 185 genera, in contrast to the 167 which Anderberg (1991a) accepted. Some of the 18 additional genera are ones which were resurrected by us and some are new genera, described since Anderberg's monograph. Also, in light of recent molecular and reassessed morphological evidence, *Printzia* and *Isoetopsis* have been transferred to Astereae (Bayer and Cross 2002). A cautionary note should be expressed concerning the key to genera. It is very difficult to write a key to genera of a large and taxonomically problematical group such as Gnaphalieae. This key should be considered tentative at this point as, in many cases, it considers mainly the typical character states in each genus. Therefore, anomalous species may prove impossible to identify correctly to genus with this key.

Key to the Genera

1. Plants perennial — 2
– Plants annual or biennial — 125
2. Plants woody — 3
– Plants herbaceous — 61
3. Plants forming alpine cushions — 4
– Plants shrubby — 10
4. Plants dioecious — 5
– Plants synoecious — 6
5. Outer florets yellow; Asia — **734. *Sinoleontopodium***
– Outer florets purple to blue; South America — **692. *Mniodes***
6. Habit ericoid — **604. *Bryomorphe***
– Habit not ericoid — 7
7. Sweeping hairs on style branches apically and dorsally or dorsally only — 8
– Sweeping hairs on style branches apically only — 9
8. Central florets yellow — **725. *Raouliopsis***
– Central florets purple — **668. *Jalcophila***
9. Leaf apex apiculate; Tasmania — **719. *Pterygopappus***
– Leaf apex truncate or obtuse; New Zealand — **724. *Raoulia***
10. Habit ericoid — 11
– Habit not ericoid — 22
11. Capitulum not narrowly cylindric — 12
– Capitulum narrowly cylindric — 17
12. Leaves extremely densely set, imbricate — 13
– Leaves not extremely densely set, not imbricate — 14
13. Central florets purple — **704. *Phaenocoma***
– Central florets yellow — **631. *Dolichothrix***
14. Involucral bracts cartilaginous — **669. *Lachnospermum***
– Involucral bracts papery — 15
15. Pappus scabrid or barbellate — **664. *Hydroidea***
– Pappus distinctly plumose, at least apically — 16
16. Stereome undivided — **718. *Pterothrix***
– Stereome divided — **750. *Trichogyne***
17. Outer radiate florets present — 18
– Outer radiate florets absent — 19
18. Involucral bracts with brown papery lamina — **578. *Amphiglossa***
– Involucral bracts without lamina — **629. *Disparago***
19. Involucral bracts cartilaginous — 20
– Involucral bracts papery — 21
20. Capitulum with one floret — **738. *Stoebe***
– Capitulum with two or more florets — **633. *Elytropappus***
21. Capitula many in corymbs — **687. *Metalasia***
– Capitula solitary or only a few together — **708. *Planea***
22. Capitula heterogamous, radiate or disciform — 23
– Capitula homogamous, discoid — 44
23. Outer florets filiform or tubular — 24
– Outer florets radiate — 34
24. Central florets perfect — 25
– Central florets functionally male — 29
25. Sweeping hairs on style branches apically only — 26
– Sweeping hairs on style branches dorsally only or apically and dorsally — 27
26. Branches terminating in a thorn — **571. *Acanthocladium***
– Branches not terminating in a thorn — **700. *Ozothamnus***
27. Outer florets purple to blue — **650. *Gnaphaliothamnus***
– Outer florets white or yellow — 28

28. Capitula solitary or only a few together; North Africa **576. *Aliella***
– Capitula many in terminal panicles; Australia **623. *Cremnothamnus***
29. Leaf lamina flat 30
– Leaf lamina not flat 31
30. Receptacle paleate **703. *Petalacte***
– Receptacle epaleate **670. *Langebergia***
31. Leaf margin concave to involute **683. *Loricaria***
– Leaf margin revolute 32
32. Outer florets purple to blue 33
– Outer florets white or yellow **583. *Anderbergia***
33. Sweeping hairs on style branches dorsally only; Central and South America **616. *Chionolaena***
– Sweeping hairs on style branches apically only; South Africa **581. *Anaxeton***
34. Outer florets yellow with purple stripes abaxially 35
– Outer florets not discolourous 40
35. Receptacle paleate 36
– Receptacle epaleate 39
36. Central florets with 1–4 pappus bristles **729. *Rosenia***
– Central florets without pappus bristles 37
37. Subterranean thick woody tubers or rhizomes present **621. *Comborhiza***
– Subterranean thick woody tubers or rhizomes absent 38
38. Plants glabrous (if hairy, then with capitula congested in secondary heads) **697. *Oedera***
– Plants ± hairy or glandular-hairy, capitula generally solitary **726. *Relhania***
39. Pappus scales present **681. *Leysera***
– Pappus scales absent **589. *Antithrixia***
40. Sweeping hairs on style branches dorsally, not reaching the apex 41
– Sweeping hairs on style branches dorsally and apically 43
41. Pappus scales present **605. *Callilepis***
– Pappus scales absent 42
42. Leaf margin entire; central florets functionally male **699. *Oxylaena***
– Leaf margin not entire; central florets perfect **702. *Pentatrichia***
43. Receptacle paleate **593. *Arrowsmithia***
– Receptacle epaleate **686. *Macowania***
44. Leaf lamina flat 45
– Leaf lamina not flat 53
45. Corolla veins reaching ends of lobes; capitula solitary or only a few together 46
– Corolla veins ending below apex of lobes; capitula many in corymbs 50
46. Leaf margins entire 47
– Leaf margins not entire 48
47. Receptacle conical, involucral bracts cartilaginous **592. *Argyroglottis***
– Receptacle flat to convex, involucral bracts papery **700. *Ozothamnus***
48. Pappus of elongated scale-like awns **586. *Anisochaeta***
– Pappus of capillary bristles or scales 49
49. Central floret cypsela shorter than corolla **587. *Anisothrix***
– Central floret cypsela equal to or longer than corolla **702. *Pentatrichia***
50. Sweeping hairs on style branches dorsally and apically; style apex acute to conical **610. *Catatia***
– Sweeping hairs on style branches apically only; style apex truncate 51
51. Pappus absent **743. *Syncephalum***
– Pappus present 52
52. Pappus bristles connate **700. *Ozothamnus***
– Pappus bristles free **736. *Stenocline***
53. Leaf margin concave to involute 54
– Leaf margin revolute 56
54. Central florets yellow or white **700. *Ozothamnus***
– Central florets purple 55
55. Capitula 3–6 together, in corymbs **597. *Atrichantha***
– Capitulum solitary or 2–3 together **608. *Calotesta***
56. Capitula many in terminal panicles; Madagascar **661. *Humeocline***
– Capitula many in corymbs; Australia 57
57. Receptacle flat or convex 58
– Receptacle conical 60
58. Pappus absent **655. *Haeckeria***
– Pappus present 59
59. Anthers with distinct tails **700. *Ozothamnus***
– Anthers without distinct tails **609. *Cassinia***
60. Florets 20–30 per capitulum; inner involucral bracts with claw **667. *Ixodia***
– Florets 4–6 per capitulum; inner involucral bracts without claw **696. *Odixia***
61. Capitula homogamous 62
– Capitula heterogamous 80
62. Stereome divided 63
– Stereome undivided 69
63. Involucral bracts brownish or hyaline 64
– Involucral bracts coloured 66
64. Receptacle flat or convex **573. *Acomis***
– Receptacle conical 65
65. Pappus of bristles with flattened axis; cypsela without reddish knobs **680. *Leucophyta***
– Pappus of rudimentary bristles or of scales; cypsela with conspicuous reddish knobs **730. *Rutidosis***
66. Anther apex narrower than thecae **591. *Argentipallium***
– Anther apex as wide as thecae 67
67. Basal claw on involucral bracts distinct **678. *Leucochrysum***
– Basal claw on involucral bracts absent 68
68. Receptacle fimbriliferous; cypsela trichomes present **742. *Syncarpha***
– Receptacle not fimbriliferous; cypsela trichomes absent **737. *Stenophalium***
69. Plants dioecious, stolons usually present 70
– Plants synoecious, stolons absent 71
70. Leaves tomentose abaxially; pappus bristles connate in a ring **588. *Antennaria***
– Leaves glabrous abaxially; pappus bristles free **701. *Parantennaria***
71. Capitula solitary or only a few together 72
– Capitula many 76
72. Involucral bracts papery 73
– Involucral bracts cartilaginous **586. *Anisochaeta***
73. Involucral bracts brownish or hyaline; Asia **620. *Cladochaeta***
– Involucral bracts coloured; Australia 74
74. Basal claw on involucral bract distinct; receptacle epaleate 75
– Basal claw on involucral bract absent; receptacle paleate **577. *Ammobium***

75. Pappus bristles barbellate **584. *Anemocarpa***
– Pappus bristles plumose **678. *Leucochrysum***
76. Capitula in glomerules 77
– Capitula in panicles 78
77. Capitula pedicellate **622. *Craspedia***
– Capitula sessile **720. *Pycnosorus***
78. Receptacle conical, paleate **590. *Apalochlamys***
– Receptacle flat or convex, epaleate 79
79. Involucral bracts brownish or hyaline; Australia **607. *Calomeria***
– Involucral bracts coloured; Madagascar **661. *Humeocline***
80. Outer florets blue to purple 81
– Outer florets yellow, white or pale green 100
81. Central florets perfect 82
– Central florets functionally male or female 97
82. Sweeping hairs on style branches dorsally and apically 83
– Sweeping hairs on style branches apically only or dorsally only 90
83. Distinct outer florets radiate or absent 84
– Distinct outer florets filiform 85
84. Distinct outer florets radiate **596. *Athrixia***
– Distinct outer florets absent **730. *Rutidosis***
85. Style branches acute to conical 86
– Style branches obtuse to truncate 88
86. Pappus bristles scabrid or barbellate without shorter teeth apically 87
– Pappus bristles distinctly plumose but barbellate towards apex with shorter teeth apically **601. *Berroa***
87. Cypsela with globose hairs **600. *Belloa***
– Cypsela with elongated twin hairs **684. *Lucilia***
88. Pappus bristles free or cohering by patent cilia; Australasia **637. *Euchiton***
– Pappus bristles connate in a ring or in groups; South America 89
89. Anther tails distinct; elongated or globose twin hairs present on cypsela **685. *Luciliocline***
– Anther tails absent; short clavate twin hairs present on cypsela **614. *Chevreulia***
90. Style apex obtuse 91
– Style apex truncate 92
91. Leaf margin entire; receptacle paleate **605. *Callilepis***
– Leaf margin denticulate; receptacle epaleate **675. *Lepidostephium***
92. Stereome divided **632. *Edmondia***
– Stereome undivided 93
93. Cypsela hairs short, clavate **651. *Gnaphalium***
– Cypsela hairs globose, elongated, or absent 94
94. Capitula solitary in axils of uppermost leaves; receptacle conical **723. *Rachelia***
– Capitula clustered; receptacle flat 95
95. Receptacle paleate; leaves tomentose abaxially only **745. *Tenrhynea***
– Receptacle epaleate; leaves tomentose on both sides 96
96. Involucral bracts white; pappus bristles free; New Zealand **640. *Ewartiothamnus***
– Involucral bracts brown; pappus bristles connate in a ring; mainly South America **646. *Gamochaeta***
97. Leaf margin flat 98
– Leaf margin concave to involute 99
98. Plants synoecious **688. *Mexerion***
– Plants dioecious **624. *Cuatrecasasiella***
99. Plants not ericoid; Australia **639. *Ewartia***
– Plants ericoid; South Africa **750. *Trichogyne***
100. Sweeping hairs on style branches apically and dorsally 101
– Sweeping hairs on style branches only apically or only dorsally 110
101. Capitula many 102
– Capitula solitary or only few 106
102. Pappus bristles free or cohering by patent cilia 103
– Pappus bristles connate in a ring or in groups, in *Euchiton* apparently so 104
103. Involucral bracts white **580. *Anaphalis***
– Involucral bracts brownish or hyaline **637. *Euchiton***
104. Stereome divided; South America **647. *Gamochaetopsis***
– Stereome undivided; Eurasia, Australasia 105
105. Central florets functionally male **674. *Leontopodium***
– Central florets perfect **637. *Euchiton***
106. Involucral bracts coloured **755. *Xerochrysum***
– Involucral bracts brownish or hyaline 107
107. Style apex obtuse; stereome undivided 108
– Style apex much prolonged; stereome divided **730. *Rutidosis***
108. Outer florets filiform 109
– Outer florets radiate **706. *Philyrophyllum***
109. Leaf margin entire **637. *Euchiton***
– Leaf margin not entire **705. *Phagnalon***
110. Sweeping hairs on style branches dorsally only 111
– Sweeping hairs on style branches apically only 112
111. Outer florets filiform **576. *Aliella***
– Outer florets radiate **605. *Callilepis***
112. Involucral bracts brownish or hyaline 113
– Involucral bracts coloured 116
113. Capitula surrounded by whorl of white-lanate leaves **679. *Leucogenes***
– Capitula not surrounded by whorl of white-lanate leaves 114
114. Outer florets filiform or tubular 115
– Outer florets radiate **698. *Oreoleysera***
115. Plant forming mats **724. *Raoulia***
– Plant not forming mats **666. *Ixiolaena***
116. Stereome divided 117
– Stereome undivided 121
117. Distinct outer florets fewer than central florets or absent 118
– Distinct outer florets more numerous than central florets 120
118. Anther appendages flat, cypselae oblong 119
– Anther appendages concave, cypselae ellipsoid to turbinate **618. *Chrysocephalum***
119. Anther apex narrower than thecae **591. *Argentipallium***
– Anther apex as wide as thecae **659. *Helichrysum***
120. Capitula with < 20 florets **572. *Achyrocline***
or **659. *Helichrysum***
– Capitula with > 20 florets **715. *Pseudognaphalium***
or **659. *Helichrysum***
121. Receptacle conical **579. *Anaphalioides***
– Receptacle flat or convex 122
122. Capitula solitary or only a few together 123
– Capitula many together 124
123. Capitula solitary; New Zealand **724. *Raoulia***
– Capitula only a few together; South Africa **658. *Helichrysopsis***

124. Pappus bristles capillary; South Africa **709. *Plecostachys***
– Pappus bristles rudimentary or of scales; NE tropical Africa **615. *Chiliocephalum***
125. Capitula homogamous 126
– Capitula heterogamous 181
126. Cypsela ellipsoid or turbinate or long and rod-like 127
– Cypsela oblong or obovoid 143
127. Cypsela long and rod-like **617. *Chondropyxis***
– Cypsela ellipsoid or turbinate 128
128. Involucral bracts in one row 129
– Involucral bracts in more than one row 131
129. Pappus bristles capillary **691. *Millotia***
– Pappus bristles rudimentary or of scales 130
130. Distinct leaf glands present **748. *Toxanthes***
– Distinct leaf glands absent **732. *Scyphocoronis***
131. Involucral bracts with distinct claw 132
– Involucral bracts without claw 135
132. Centremost florets functionally male **697. *Schoenia* (*S. ayersii*)**
– Centremost florets bisexual 133
133. Style apex obtuse or truncate 134
– Style apex acute to conical **754. *Waitzia***
134. Style apex obtuse **678. *Leucochrysum***
– Style apex truncate **657. *Haptotrichion***
135. Involucral bracts herbaceous 136
– Involucral bracts papery or cartilaginous 137
136. Receptacle epaleate **712. *Podotheca***
– Receptacle paleate **694. *Neotysonia***
137. Involucral bracts cartilaginous 138
– Involucral bracts papery 139
138. Pappus bristles capillary **744. *Taplinia***
– Pappus with a few scale-like bristles **721. *Quinetia***
139. Cypsela longer than or equal to corolla 140
– Cypsela shorter than corolla 142
140. Receptacle conical **599. *Bellida***
– Receptacle flat or convex 141
141. Receptacle paleate **694. *Neotysonia***
– Receptacle epaleate **722. *Quinqueremulus***
142. Stereome divided; receptacle conical **730. *Rutidosis***
– Stereome undivided; receptacle flat **648. *Gilberta***
143. Central floret cypsela oblong 144
– Central floret cypsela obovoid 145
144. Involucral bracts brownish or hyaline **645. *Galeomma***
– Involucral bracts coloured **753. *Vellereophyton***
145. Involucral bracts brownish or hyaline 146
– Involucral bracts coloured 168
146. Receptacle paleate 147
– Receptacle epaleate 151
147. Receptacle flat or convex 148
– Receptacle conical or peg-like 150
148. Involucral bracts cartilaginous; pappus of connate scales **749. *Trichanthodium***
– Involucral bracts papery; pappus of scales absent 149
149. Capitula surrounded by whorl of leaves **619. *Chthonocephalus***
– Capitula not surrounded by whorl of leaves **626. *Decazesia***
150. Receptacle conical **733. *Siloxerus***
– Receptacle peg-like **622. *Craspedia***
151. Cypsela trichomes present 152
– Cypsela trichomes absent 162
152. Cypsela densely villous 153
– Cypsela not densely villous 156
153. Receptacle peg-like **644. *Fitzwillia***
– Receptacle conical 154
154. Leaf glands distinct **714. *Polycalymma***
– Leaf glands absent 155
155. Pappus of basally connate subplumose to plumose bristles **642. *Feldstonia***
– Pappus of short reduced flattened basally connate bristles **630. *Dithyrostegia***
156. Receptacle flat or convex 157
– Receptacle conical or peg-like 159
157. Involucral bracts cartilaginous **749. *Trichanthodium***
– Involucral bracts papery 158
158. Leaf glands distinct **635. *Eriochlamys***
– Leaf glands absent **713. *Pogonolepis***
159. Receptacle peg-like **602. *Blennospora***
– Receptacle conical 160
160. Leaf glands distinct; pappus bristles scabrid or barbellate 161
– Leaf glands absent; pappus distinctly plumose, at least apically **574. *Actinobole***
161. Capitula surrounded by whorl of leaves **693. *Myriocephalus***
– Capitula not surrounded by whorl of leaves **652. *Gnephosis***
162. Involucral bracts cartilaginous 163
– Involucral bracts papery 164
163. Bracts in more than one row **628. *Dielitzia***
– Bracts in one row **735. *Sondottia***
164. Leaves glabrous **673. *Lemooria***
– Leaves tomentose 165
165. Leaf glands distinct; receptacle conical **662. *Hyalochlamys***
– Leaf glands absent; receptacle flat or convex 166
166. Leaves alternate throughout; capitula not surrounded by whorl of leaves **677. *Leptotriche***
– Leaves opposite, at least basally; capitula surrounded by whorl of leaves 167
167. Pappus basally connate into a jagged scale-like cup **612. *Cephalosorus***
– Pappus absent **634. *Epitriche***
168. Involucral bracts herbaceous **712. *Podotheca***
– Involucral bracts papery 169
169. Inner involucral bracts conspicuously longer than outer bracts 170
– Inner involucral bracts not conspicuously longer than outer bracts 176
170. Pappus present 171
– Pappus absent **707. *Pithocarpa***
171. Pappus scabrid or barbellate 172
– Pappus distinctly plumose, at least apically 174
172. Leaves filiform, alternate throughout **636. *Erymophyllum***
– Leaves flat, opposite, at least basally 173
173. Cypsela of outer florets dorsiventrally compressed; 2 vascular bundles medial in relation to cotyledons **731. *Schoenia***
– Cypsela of outer florets not dorsiventrally compressed; 2 vascular bundles lateral in relation to cotyledons **672. *Lawrencella***
174. Receptacle flat or convex ; pappus bristles free or cohering by patent cilia **611. *Cephalipterum***
– Receptacle conical; pappus bristles connate in a ring 175

175. Cypsela densely villous with elongated twin hairs **727. *Rhodanthe***
– Cypsela not densely villous, but with globose hairs without basal cell **663. *Hyalosperma***
176. Pappus absent **746. *Thiseltonia***
– Pappus present 177
177. Pappus of jagged scales **710. *Pleuropappus***
– Pappus of flattened plumose bristles 178
178. Cypsela trichomes absent **649. *Gilruthia***
– Cypsela trichomes present 179
179. Receptacle paleate **720. *Pycnosorus***
– Receptacle epaleate 180
180. Involucral bracts usually 4, with 2 concave bracts (always present) surrounding usually 2 (sometimes 0 or 1) flat bracts **585. *Angianthus***
– Involucral bracts 7–c.22, variously flat to somewhat concave **606. *Calocephalus***
181. Central floret cypsela long, rod-like 182
– Central floret cypsela ellipsoid, turbinate, oblong, obovoid or abortive 183
182. Biennial **695. *Nestlera***
– Annual **728. *Rhynchopsidium***
183. Central floret cypsela obovoid 184
– Central floret cypsela ellipsoid, turbinate, or oblong 186
184. Capitula arranged in glomerules or spikes **747. *Tietkensia***
– Capitula solitary or only a few together 185
185. Inner bracts conspicuously longer than outer bracts, coloured **672. *Lawrencella***
– Inner bracts not conspicuously longer than outer bracts, hyaline **656. *Haegiela***
186. Central floret cypsela ellipsoid or turbinate 187
– Central floret cypsela oblong 202
187. Outer florets bilabiate **672. *Denekia***
– Outer florets radiate, filiform, tubular or corolla absent 188
188. Outer florets radiate 189
– Outer florets filiform or tubular, or corolla absent 192
189. Outer florets purple to blue; receptacle paleate **575. *Alatoseta***
– Outer florets yellow; receptacle epaleate 190
190. Outer florets yellow with purple stripes abaxially; South Africa **728. *Rhynchopsidium***
– Outer florets without purple stripes abaxially; Australia 191
191. Bract laminae filiform-subulate, densely plumose **595. *Asteridea***
– Bract laminae flat, entire to long-ciliate on margins **711. *Podolepis***
192. Central florets functionally male **598. *Basedowia***
– Central florets perfect 193
193. Leaf glands distinct 194
– Leaf glands absent 197
194. Involucral bracts brownish or hyaline 195
– Involucral bracts coloured 196
195. Involucral bracts with distinct basal claw **595. *Asteridea***
– Involucral bracts without distinct basal claw **594. *Artemisiopsis***
196. Pappus bristle one **654. *Gratwickia***
– Pappus bristles more than one **618. *Chrysocephalum***
197. Capitula surrounded by a whorl of leaves 198
– Capitula not surrounded by a whorl of leaves 200
198. Involucral bracts brownish or hyaline 199
– Involucral bracts coloured **717. *Pterochaeta***
199. Receptacle conical **751. *Triptilodiscus***
– Receptacle flat or convex **637. *Euchiton***
200. Leaves opposite, at least basally **656. *Haegiela***
– Leaves alternate throughout 201
201. Outer florets purple to blue **641. *Facelis***
– Outer florets yellow **676. *Leptorhynchos***
202. Central florets perfect 203
– Central florets functionally male 215
203. Stereome divided 204
– Stereome undivided 209
204. Involucral bracts brownish or hyaline 205
– Involucral bracts coloured 207
205. Outer florets scattered in axils of outer involucral bracts **665. *Ifloga***
– Outer florets all inside a common involucre 206
206. Florets purple **671. *Lasiopogon***
– Florets yellow **653. *Gnomophalium***
207. Florets yellow **715. *Pseudognaphalium***
– Florets purple 208
208. Capitula not surrounded by a whorl of leaves **752. *Troglophyton***
– Capitula surrounded by a whorl of leaves **753. *Vellereophyton***
209. Receptacle flat or convex 210
– Receptacle conical 213
210. Receptacle paleate **689. *Micropsis***
– Receptacle epaleate 211
211. Pappus bristles connate in a ring **646. *Gamochaeta***
– Pappus bristles free or cohering by patent cilia 212
212. Style branches truncate **651. *Gnaphalium***
– Style branches obtuse **637. *Euchiton***
213. Inner involucral bracts folded around florets **682. *Logfia***
– Inner involucral bracts not enclosing florets 214
214. Pappus present **643. *Filago***
– Pappus absent **739. *Stuartina***
215. Receptacle peg-like 216
– Receptacle flat to conical 222
216. Inner involucral bracts folded around florets 217
– Inner involucral bracts not enclosing florets 218
217. Corolla of outer florets attached obliquely to cypsela **613. *Chamaepus***
– Corolla of outer florets attached straight to cypsela **638. *Evacidium***
218. Anther appendage concave; apex narrower than thecae 219
– Anther appendage flat; apex as wide as thecae 221
219. Leaves opposite, at least basally; cypsela with trichomes **716. *Psilocarphus***
– Leaves alternate throughout; cypsela without trichomes 220
220. Pappus present **741. *Stylocline***
– Pappus absent **582. *Ancistrocarphus***
221. Pappus present **625. *Cymbolaena***
– Pappus absent **603. *Bombycilaena***
222. Receptacle flat or convex 223
– Receptacle conical 226
223. Outer florets scattered in axils of the outer involucral bracts 224
– Outer florets all inside a common involucre 225
224. Pappus bristles without patent cilia at base **750. *Trichogyne***

– Pappus bristles with patent cilia at base **665. *Ifloga***
225. Inner involucral bracts enclosing florets **690. *Micropus***
– Inner involucral bracts not enclosing florets **740. *Stuckertiella***
226. Receptacle paleate; pappus absent **660. *Hesperevax***
– Receptacle epaleate; pappus present **643. *Filago***

Genera of Gnaphalieae

571. *Acanthocladium* F. Muell.

Acanthocladium F. Muell., Fragm. 2: 155 (1861); Burbidge, Austral. J. Bot. 6: 229–284 (1958), rev.

Spiny shrub. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts papery, brownish, stereome undivided. Receptacle flat. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with globose twin hairs. Pappus bristles capillary, scabrid or barbellate, connate in groups. One species, *A. dockeri* F. Muell., Australia.

572. *Achyrocline* (Less.) DC.

Achyrocline (Less.) DC., Prodr. 6: 219 (1838); Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.
Gnaphalium subg. *Achyrocline* Less. (1832).

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in corymbs, rarely solitary. Involucral bracts papery, coloured, stereome divided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, barbellate, free. $n = 14$. Thirty-two species, Africa, Madagascar, Central and South America.

573. *Acomis* F. Muell.

Acomis F. Muell., Fragm. 4: 145 (1864); Wilson, Nuytsia 8: 479–483 (1992), reg. rev.

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, brownish, stereome divided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches with much prolonged apex, with sweeping hairs dorsally. Cypselae ellipsoid, with globose hairs without a basal cell. Pappus absent. Three species, Australia.

574. *Actinobole* Fenzl ex Endl. Fig. 63Q

Actinobole Fenzl ex Endl., Gen. Pl. suppl. 3: 70 (1843); Short, Muelleria 6: 9–22 (1985), rev.
Gnaphalodes A. Gray (1852), nom. illegit., non Mill. (1754).

Annual herbs. Leaves alternate to subopposite, flat with entire margins, tomentose on both surfaces. Capitula many, crowded together among basal leaves. Involucral bracts papery, hyaline, stereome undivided. Receptacle conical, epaleate. All florets perfect, yellow. Anthers with concave appendages.

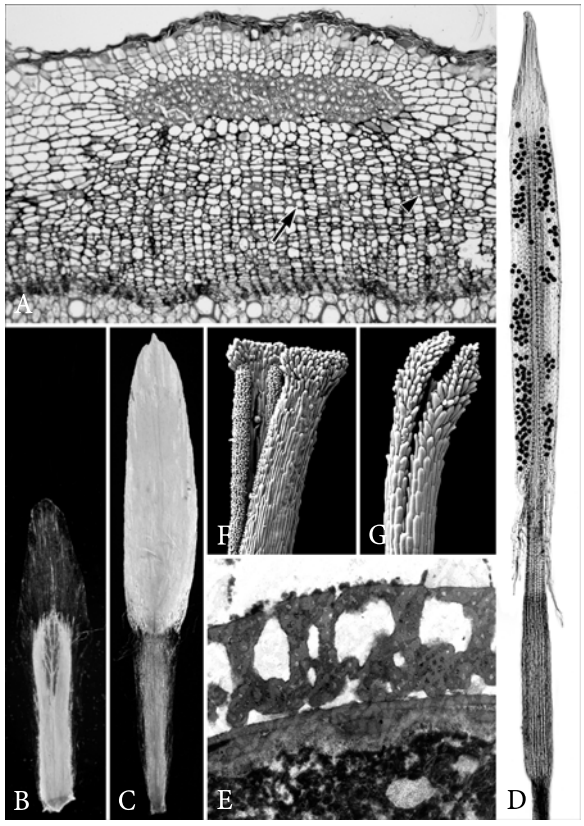

Fig. 62. Compositae-Gnaphalieae. Tribal characters. **A** *Ozothamnus aggregatus*. Transverse section of stem, fibres (*arrow*) within phloem (×185). **B, C** Papery involucral bracts. **B** *Pseudognaphalium luteoalbum*. Hyaline lamina, divided stereome (×25). **C** *Anaphalioides bellidioides*. Showy lamina, undivided stereome (×13). **D** *Ozothamnus depressus*. Stamen with ecalcarate, tailed anther (×67). **E** *Anaphalis margaritacea*. Pollen with 2-layered ectexine, TEM section (×2,600). **F, G** Style branches from central florets. **F** *Ozothamnus leptophyllus*. Separate stigmatic rows, hairs apically (SEM ×115). **G** *Ewartia catipes*. Hairs apically and dorsally (SEM ×112. 5)

Style branches truncate, with hairs apically. Cypselae obovoid, glabrous or with globose hairs without a basal cell. Pappus bristles with flattened axis, distinctly plumose, at least apically, connate in a ring. $n = 10$. Four species, Australia.

575. *Alatoseta* Compton

Alatoseta Compton, Trans. Roy. Soc. S. Afr. 19: 314 (1931); Dyer, The genera of southern African flowering plants (1975), gen. consp.

Annual herb. Leaves alternate, subterete with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, paleate. Outer florets radiate, purple. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, glabrous. Pappus a short rim. One species, *A. tenuis* Compton, Africa.

576. *Aliella* Qaiser & Lack

Aliella Qaiser & Lack, Bot. Jahrb. Syst. 106: 488 (1986); Qaiser & Lack, Bot. Jahrb. Syst. 106: 487–498 (1986), rev.

Perennial subshrubs and herbs. Leaves alternate, revolute or flat with dentate margins, sparsely tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous, brown, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, with a few elongated twin hairs. Pappus bristles capillary, barbellate, basally connate. $n = 7, 9$. Three species, Africa.

577. *Ammobium* R. Br. Fig. 63L

Ammobium R. Br. in J. Sims, Bot. Mag. ad t. 2459 (1824); Anderberg, Telopea 4: 129–135 (1990), rev.; Orchard, Telopea 5: 1–12 (1992), rev.
Nablonium Cass. (1825).

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, white, stereome undivided. Receptacle conical, paleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus of two spines. $n = 12, 13$. Three species, Australia.

578. *Amphiglossa* DC.

Amphiglossa DC., Prodr. 6: 258 (1838); Dyer, The genera of southern African flowering plants (1975), gen. consp.; Koekemoer, Bothalia 29: 65–75 (1999), rev.

Shrubs. Leaves alternate, flat to twisted with entire margins, sparsely tomentose on both surfaces. Capitula only a few together, in dense corymbs. Involucral bracts papery, brown, stereome undivided. Receptacle flat, epaleate. Outer florets radiate, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, plumose, basally connate. Nine species, Africa.

579. *Anaphalioides* (Benth.) Kirp. Fig. 62C

Anaphalioides (Benth.) Kirp., in Kirpichnikov & Kuprijanova, Trudy Bot. Inst. Akad. Nauk S.S.S.R. ser. 1, Fl. Sist. Vyssh. Rast. 9: 33 (1950); Glenny, N. Z. J. Bot. 35: 451–477 (1997), rev.; Glenny & Wagstaff, N. Z. J. Bot. 35: 441–449 (1997), phylog., Ward & Breitwieser, N. Z. J. Bot. 36: 165–171 (1998), reg. rev.

Perennial herbs or subshrubs. Leaves alternate, flat or revolute with entire margins, tomentose abaxially or on both surfaces. Capitula solitary, only a few together, or many in corymbs. Involucral bracts papery, white, stereome undivided. Receptacle conical, epaleate. Outer florets filiform, pale green. Central florets perfect, pale green. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong to narrowly oblong, generally glabrous. Pappus bristles capillary, scabrid, free. $n = 14, 28, 42$. Seven species, New Zealand and New Guinea.

580. *Anaphalis* DC. Fig. 62E

Anaphalis DC., Prodr. 6: 271 (1838); Beauverd, Bull. Soc. Bot. Genève sér. 2, 5: 146–147 (1913), gen. consp.; Koster, Blumea 20: 193–226 (1972), reg. rev.; Grierson, Notes Roy. Bot. Gard. Edinburgh 31: 389–392 (1972), reg. rev.

Subdioecious perennial herbs or shrubs. Leaves alternate, flat or revolute with entire margins, tomentose on both surfaces. Capitula many in corymbs. Involucral bracts papery, white, stereome divided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets functionally male, yellow. Anthers with flat appendages. Style branches truncate, with hairs dorsally and apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles cap-

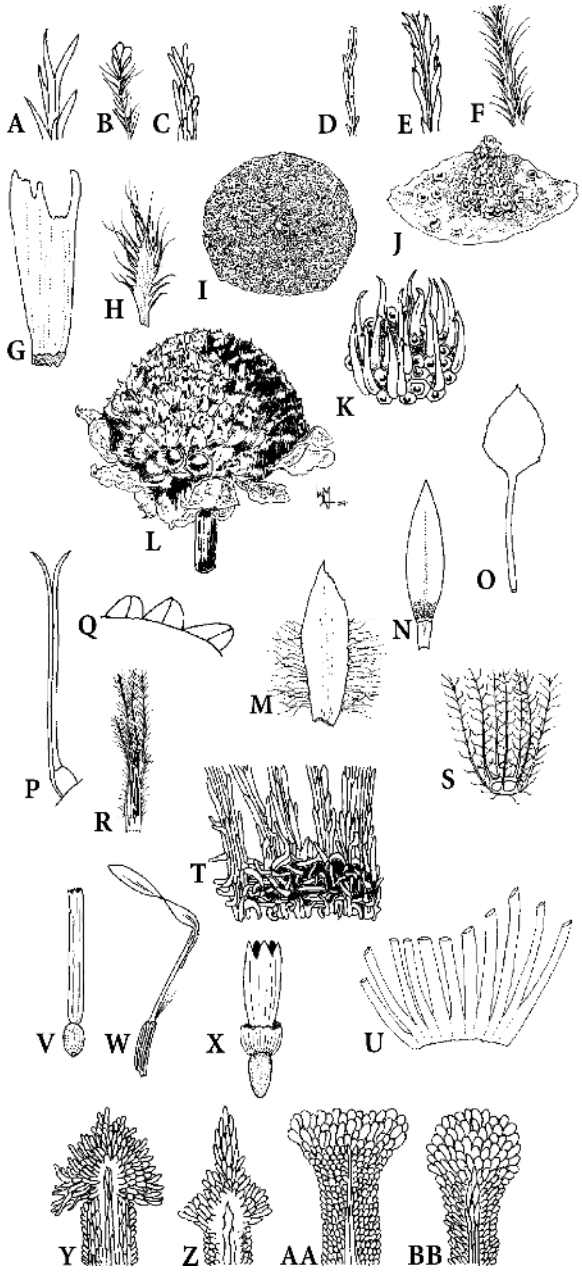

Fig. 63. Compositae-Gnaphalieae. **A** *Rhodanthe moschata*. Acute pappus apex. **B** *Hyalosperma cotula*. Clavate pappus apex. **C** *Helichrysum calvertianum*. Obtuse pappus apex. **D** *Ozothamnus bidwillii*. Scabrid pappus bristle. **E** *Haptotrichion conicum*. Barbellate pappus bristle. **F** *Rhodanthe frenchii*. Plumose pappus bristle. **G** *Relhania fruticosa*. Pappus scale. **H** *Rutidosis leptorrhynchoides*. Fimbriate pappus scale. **I** *Xerochrysum bracteatum*. Flat, honeycombed receptacle. **J** *Triptilodiscus pygmaeus*. Peg-like receptacle. **K** *Helichrysum miconiifolium*. Fimbriate receptacle. **L** *Ammobium craspedioides*. Paleaceous receptacle. **M** *Anemocarpa saxatilis*. Laminar (clawless) involucral bract. **N** *Helichrysum milfordiae*. Clawed involucral bract. **O** *Leucochrysum stipitatum*. Stipitate involucral bract. **P** *Lucilia acutifolia*. Elongated twin cypsela hair. **Q** *Actinobole oldfieldiana*. Globose twin cypsela hair. **R** *Rhodanthe anthemoides*. Pappus bristles fused into groups. **S** *Gilberta tenuifolia*. Pappus bristles fused into a ring. **T** *Pseudognaphalium luteoalbum*. Pappus bristles coherent by patent cilia. **U** *Helichrysum adenophorum*. Pappus bristles weakly coherent. **V** *Helichrysum aureum*. 'Helichrysum-type', oblong cypsela with attached floret. **W** *Macowania hamata*. 'Relhania-type', rod-like cypsela with attached floret. **X** *Gnephosis eriocarpa*. 'Gnephosis-type', obovoid cypsela with attached floret. **Y** *Lawrencella davenportii*. Triangular style apex. **Z** *Bellida graminea*. Acute style apex. **AA** *Ozothamnus lepidophyllus*. Truncate style apex. **BB** *Chrysocephalum semicalvum*. Obtuse style apex. (**P**, **Q** modified after Anderberg 1991a; **Y**–**BB** after Wilson 1992; drawings by William Murray)

illary, barbellate, free. n = 7, 13, 14, 21, 24. About 110 species, Asia, North and South America.

581. *Anaxeton* Gaertn.

Anaxeton Gaertn., Fruct. Sem. Pl. 2: 406 (1791); Lundgren, Opera Bot. 31 (1972), rev.

Shrubs. Leaves alternate, revolute with entire margins, sparsely tomentose on both surfaces. Capitula many in dense corymbs. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, basally connate. Ten species, Africa.

582. *Ancistrocarphus* A. Gray

Ancistrocarphus A. Gray, Proc. Amer. Acad. Arts 7: 355 (1868).

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts cartilaginous, hyaline, stereome undivided. Receptacle peg-like, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Style branches with much prolonged apex, with hairs dorsally. Anthers with concave appendages. Cypselae oblong, glabrous. Pappus absent. One species, *A. filagineus* A. Gray, North America.

583. *Anderbergia* B. Nord.

Anderbergia B. Nord., Ann. Wiener Mus. Naturgesch. 98: 407 (1996); Nordenstam, Ann. Wiener Mus. Naturgesch. 98, B: 403–418 (1996), rev.

Shrubs. Leaves alternate, revolute with entire margins, sparsely tomentose on both surfaces. Capitula many in dense corymbs. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, free. Six species, Africa.

584. *Anemocarpa* Paul G. Wilson Fig. 63M

Anemocarpa Paul G. Wilson, Nuytsia 8: 452 (1992); Wilson, Nuytsia 8: 447–460 (1992), rev.

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, coloured, stereome undivided. Receptacle convex, epaleate. All florets perfect, yellow. Style branches obtuse. Cypselae ellipsoid. Pappus bristles capillary, barbellate, free. Two species, Australia.

585. *Angianthus* J.C. Wendl.

Angianthus J.C. Wendl., Col. Pl. 2: 31. t. 48 (1808?), nom. cons.; Short, Muelleria 5: 143–183 (1983), rev.; Short, Muelleria 5: 185–214 (1983), rev.
Phyllocalymma Benth. (1837).
Skirrhophorus DC. (1838).

Annual herbs and a single shrub. Leaves alternate or opposite at least basally, flat with entire margins, tomentose on both surfaces. Capitula many, forming secondary heads. Involucral bracts papery, coloured, stereome undivided. General receptacle peg-like, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with globose hairs without basal cells. Pappus bristles with flattened axis, barbellate or distinctly plumose apically, connate in a ring. $n = 6, 12, 13$. Fifteen species, Australia.

586. *Anisochaeta* DC.

Anisochaeta DC., Prodr. 5: 109 (1836); Dyer, The genera of southern African flowering plants (1975), gen. consp.

Perennial subshrub. Leaves alternate, flat with deeply lobed margins, sparsely tomentose on both surfaces. Capitula only a few together, in lax corymbs. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. All florets perfect, whitish-yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, triquetrous, with few elongated twin hairs. Pappus of several elongated awns. One species, *A. mikanioides* DC., southern Africa.

587. *Anisothrix* O. Hoffm.

Anisothrix O. Hoffm. in Kuntze, Revis. Gen. Pl. 3: 129 (1898); Anderberg, Bot. Jahrb. Syst. 109: 363–372 (1988), rev.

Perennial subshrubs. Leaves alternate, flat with dentate margins, sparsely tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, with few elongated twin hairs. Pappus of scales and capillary bristles, few, barbellate, free. $n = 7$. Two species, Africa.

588. *Antennaria* J. Gaertn. Fig. 64A

Antennaria J. Gaertn., Fruct. Sem. Pl. 2: 410 (1791), nom. cons.; Bayer & Stebbins, Syst. Bot. 7: 300–313 (1982), reg. rev.; Bayer, Syst. Bot. 9: 74–83 (1984), reg. rev.; Bayer, Biol. Zentralbl. 106: 683–698 (1987), agamic complexes; Bayer, Taxon 37: 292–298 (1988), nomencl.; Bayer, Brittonia 41: 53–60 (1989), rev.; Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.; Bayer, Arctic Alpine Res. 25: 150–159 (1993), reg. rev.; Bayer & Stebbins, Canad. J. Bot. 71: 1589–1604 (1993), rev., syn.
Antennaria Link ex Fr. (1821), non J. Gaertn. (1791).

Dioecious perennial herbs or subshrubs. Leaves alternate, flat with entire margins, tomentose on both surfaces, abaxially only, or rarely glabrous. Capitula solitary, only a few together, or many in corymbs.

Involucral bracts papery, coloured, stereome undivided. Receptacle flat, epaleate. Female florets filiform, white or purplish. Male florets tubular, white or purplish. Anthers with flat appendages. Style branches truncate, with hairs dorsally and apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, barbellate, connate in a ring. n =14, 21, 28, 42, 49, 56, 70, 84. About 40 species, Asia, Europe, North and South America.

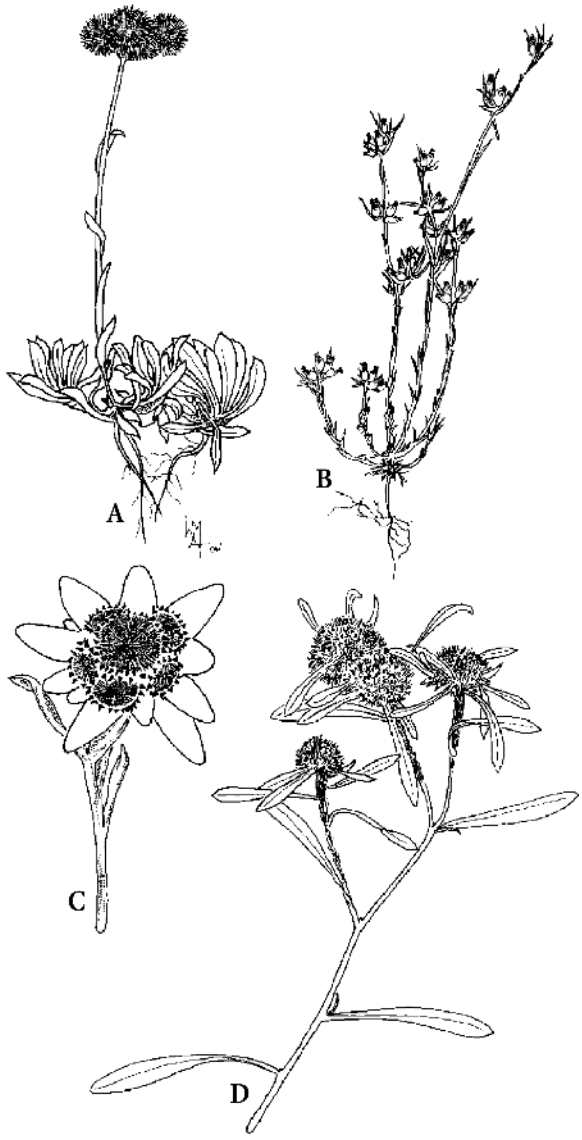

Fig. 64. Compositae-Gnaphalieae. **A** *Antennaria pulchella*. Habit (pistillate plant). **B** *Logfia gallica*. Habit. **C** *Leontopodium alpinum*. Flowering branch. **D** *Gnaphalium uliginosum*. Flowering branch. (Drawings by William Murray)

589. *Antithrixia* DC.

Antithrixia DC., Prodr. 6: 277 (1838); Bremer, Bot. Notiser 131: 449–453 (1978), rev.

Shrub. Leaves alternate or opposite, revolute or flat with entire margins, densely tomentose adaxially. Capitula solitary. Involucral bracts papery, brown, stereome undivided. Receptacle flat, epaleate. Outer florets radiate, yellow with purple bands. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae cylindrical, glabrous or with few elongated twin hairs. Pappus bristles capillary, barbellate, basally connate. One species, *A. flavicoma* DC., Africa.

590. *Apalochlamys* Cass.

Apalochlamys Cass., Dict. Sci. Nat. 56: 223 (1828).

Perennial herb. Leaves alternate, flat, broad with entire margins, tomentose on both surfaces. Capitula many in terminal panicles. Involucral bracts papery, brownish, stereome undivided. Receptacle conical, paleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glandular-hairy. Pappus bristles capillary, barbellate, connate in a ring. One species, *A. spectabilis* (Labill.) J.H. Willis, Australia.

591. *Argentipallium* Paul G. Wilson

Argentipallium Paul G. Wilson, Nuytsia 8: 455 (1992); Wilson, Nuytsia 8: 447–460 (1992), rev.

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces or only abaxially. Capitula solitary or many in terminal panicles. Involucral bracts papery, coloured, stereome divided. Receptacle convex, epaleate. Outer filiform florets yellow or absent. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse or truncate. Cypselae obovoid, with short clavate twin hairs. Pappus bristles capillary, barbellate, shortly connate in a ring. n =12. Six species, Australia.

592. *Argyroglottis* Turcz.

Argyroglottis Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 83 (1851); Burbidge, Austral. J. Bot. 6: 229–284 (1958), rev.

Shrub. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous, white, stereome un-

divided. Receptacle conical, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches conical, with hairs dorsally. Cypselae ellipsoid, with elongated twin hairs. Pappus bristles capillary, barbellate, connate in groups. n =12. One species, *A. turbinata* Turcz., Australia.

593. *Arrowsmithia* DC.

Arrowsmithia DC., Prodr. 7: 254 (1838); Dyer, The genera of southern African flowering plants (1975), gen. consp.; Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 42: 227–260 (1985), rev.

Perennial subshrub. Leaves alternate, revolute to flat with entire margins, sparsely glandular-hairy on both surfaces. Capitula solitary. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. Outer florets radiate, yellow. Central florets perfect or functionally male, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, glabrous or with few elongated twin hairs. Pappus bristles capillary, few, barbellate, free. One species, *A. styphelioides* DC., Africa.

594. *Artemisiopsis* S. Moore

Artemisiopsis S. Moore, J. Linn. Soc., Bot. 35: 331 (1902); Merxmüller, Prodromus einer Flora von Südwestafrika 139 (1967), reg. rev.

Annual herb. Leaves alternate, flat with entire margins, sparsely tomentose on both surfaces. Capitula only a few together, in dense corymbs. Involucral bracts cartilaginous, stereome divided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with few elongated twin hairs. Pappus bristles capillary, few, barbellate, free. One species, *A. villosa* (O. Hoffm.) Schweickerdt, Africa.

595. *Asteridea* Lindl.

Asteridea Lindl., Sketch Veg. Swan R. 24 (1839); Kroner, Mitt. Bot. Staatssamml. München 16: 1–268 (1980), rev.; Short, Austral. Syst. Bot 13: 739–744 (2000), reg. rev.

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts papery, hyaline, stereome forming two ribs. Receptacle flat, epaleate. Outer florets radiate, yellow to white. Central florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid or turbinate, with globose twin hairs. Pappus bristles capillary, barbellate or apically plumose, free. n = 7, 9. Nine species, Australia.

596. *Athrixia* Ker Gawl.

Athrixia Ker Gawl., Bot. Reg. 8, t. 681 (1823); Kroner, Mitt. Bot. Staatssamml. München 16: 1–268 (1980), rev.
Klenzea Sch. Bip. ex Walp. (1840).

Perennial herbs. Leaves alternate, revolute with entire or dentate margins, sparsely tomentose on both surfaces. Capitula solitary or only a few together, in lax corymbs. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple or white. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, with few elongated twin hairs. Pappus bristles capillary, barbellate, free. Fourteen species, Africa.

597. *Atrichantha* Hilliard & B.L. Burtt

Atrichantha Hilliard & B.L. Burtt, Bot. J. Linn. Soc. 82: 219 (1981); Hilliard & Burtt, Bot. J. Linn. Soc. 82: 181–232 (1981), gen. consp.; Karis, Bot. J. Linn. Soc. 102: 23–36 (1990), rev.

Shrub. Leaves alternate, flat to twisted with entire margins, sparsely tomentose adaxially. Capitula three to six in corymbs. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. Outer florets absent. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, free. One species, *A. gemmifera* (Bol.) Hilliard & B.L. Burtt, Africa.

598. *Basedowia* Pritzel

Basedowia Pritzel, Ber. Deutsch. Bot. Gesell. 36: 332 (1918).

Annual herb. Leaves alternate, flat with entire margins, very sparsely tomentose on both surfaces. Capitula only a few together, unisexual. Involucral bracts papery, white, stereome undivided. Receptacle convex, epaleate. Female florets without corolla. Male florets tubular, yellow. Style branches truncate, with hairs apically. Cypselae ellipsoid or turbinate, glabrous. Pappus usually absent, if present of capillary bristles, barbellate, connate at

base. One species, *B. tenerrima* (F. Muell. & Tate) J.M. Black, Australia.

599. *Bellida* Ewart Fig. 63Z

Bellida Ewart, Proc. Roy. Soc. Victoria ser. 2: 34, t. 10, 11 (1907); Wilson, Nuytsia 8: 361–377 (1992), rev.

Annual herb. Leaves alternate, filiform with entire margins, weakly tomentose on both surfaces. Capitula solitary. Involucral bracts papery, brownish, stereome undivided. Receptacle conical, epaleate. All florets perfect, except very innermost ones functionally male, yellow. Anthers with concave appendages. Style branches conical, with hairs dorsally. Cypselae turbinate, with elongated twin hairs. Pappus bristles capillary, barbellate, violet-coloured, free. $n = 9$. One species, *B. graminea* Ewart, Australia.

600. *Belloa* Remy

Belloa Remy in Gay, Fl. Chile 3: 336 (1848); Cabrera, Bol. Soc. Argent. Bot. 7: 79–85 (1958), rev.; Sagástegui-Alva & Dillon, Phytologia 58: 392–400 (1985), reg. rev.; Freire, Darwiniana 27: 431–490 (1986), rev.; Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, brownish, stereome usually undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches acute, with hairs dorsally. Cypselae ellipsoid to turbinate, with globose twin hairs. Pappus bristles capillary, barbellate, connate in groups. $n = 12$. About nine species, South America.

601. *Berroa* Beauverd

Berroa Beauverd, Bull. Soc. Bot. Genève sér. 2, 5: 210 (1913); Beauverd, Bull. Soc. Bot. Genève sér. 2, 5: 210–212 (1913), rev.

Perennial herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches acute, with hairs dorsally. Cypselae turbinate, with elongated twin hairs. Pappus bristles capillary, distinctly plumose, barbellate towards the apex, connate in groups. One species, *B. gnaphalioides* (Less.) Beauverd, South America.

602. *Blennospora* A. Gray

Blennospora A. Gray, J. Bot. Kew Gard. Misc. 3: 98: 172 (1851); Short, Muelleria 6: 349–358 (1987), rev.

Annual herbs. Leaves mainly alternate but often opposite, at least basally, filiform with entire margins, tomentose on both surfaces. Capitula many, forming terminal secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle peg-like, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with globose hairs without a basal cell. Pappus bristles with flattened axis, distinctly plumose, connate in a ring. $n = 11$. Two species, Australia.

603. *Bombycilaena* (DC.) Smoljan.

Bombycilaena (DC.) Smoljan., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 17: 448 (1955).
Micropus sect. *Bombycilaena* DC. (1836).

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts cartilaginous, brownish, stereome undivided. Receptacle peg-like, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches with much prolonged apex, with hairs dorsally. Cypselae oblong, glabrous. Pappus absent. $n = 14$. Three species, Asia, Europe and North America.

604. *Bryomorphe* Harv. Fig. 61D

Bryomorphe Harv., Thes. Cap. 2: 33 (1863); Dyer, The genera of southern African flowering plants (1975), gen. consp.

Shrub. Leaves alternate, twisted, revolute with entire margins, sparsely tomentose adaxially. Capitula solitary. Involucral bracts papery, brown, stereome undivided. Receptacle flat, epaleate. Outer florets radiate, white. Central florets perfect or perhaps functionally male, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae cylindrical, glabrous. Pappus bristles capillary, barbellate, free. One species, *B. aretioides* (Turcz.) Druce, Africa.

605. *Callilepis* DC.

Callilepis DC., Prodr. 5: 671 (1836); Dyer, The genera of southern African flowering plants (1975), gen. consp.
Zoutpansbergia Hutch. (1946).

Perennial herbs and a shrub. Leaves alternate or opposite, flat with entire margins, sparsely tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, paleate. Outer florets radiate, blue or white. Central florets perfect, purple. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, triquetrous, with few elongated twin hairs. Pappus of several elongated awns. Five species, southern Africa.

606. *Calocephalus* R. Br.

Calocephalus R. Br., Trans. Linn. Soc. London 12: 106 (1817).

Perennial or annual herbs. Leaves opposite, at least basally, or alternate, flat with entire margins, tomentose on both surfaces. Capitula many, forming terminal secondary heads. Involucral bracts papery, coloured, stereome undivided. Receptacle peg-like, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with globose hairs without a basal cell. Pappus bristles with flattened axis, distinctly plumose apically, connate in a ring. n = 12, 14, 28. Eleven species, Australia.

607. *Calomeria* Vent.

Calomeria Vent., Jard. Malmaison ad t. 73 (1804); Heine, Adansonia sér. 2, 7: 115–140 (1967), rev.
Humea J.E. Sm. (1804).

Biennial herb. Leaves alternate, large, flat with entire margins, weakly tomentose on both surfaces. Capitula many in large, drooping, terminal panicles composed of many small corymbs. Involucral bracts papery, pink, stereome undivided. Receptacle flat, epaleate. All florets perfect, purplish. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with short clavate twin hairs. Pappus absent. One species, *C. amaranthoides* Vent., Australia.

608. *Calotesta* P.O. Karis

Calotesta P.O. Karis, Bot. J. Linn. Soc. 102: 25 (1990); Karis, Bot. J. Linn. Soc. 102: 23–36 (1990), rev.

Shrub. Leaves alternate, flat to twisted with entire margins, sparsely tomentose adaxially. Capitula only a few together, in small clusters. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. All florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, free. One species, *C. alba* P.O. Karis, southern Africa.

609. *Cassinia* R. Br.

Cassinia R. Br., Trans. Linn. Soc. London 12: 126, nom. cons. (1817); Breitwieser & Ward, N. Z. J. Bot. 35: 125–128 (1997), reg. rev.; Orchard, Austral. Syst. Bot. 17: 469–481 (2004), rev.; Orchard, Austral. Syst. Bot. 17: 505–533 (2004), rev.; Orchard, Austral. Syst. Bot. 17: 535–566 (2004), rev.; Orchard, Austral. Syst. Bot. 17: 567–570 (2004), nomencl.; Orchard, Taxon 54: 199–201 (2005), nomencl.

Shrubs. Leaves alternate, revolute with entire margins, tomentose on both surfaces. Capitula many in corymbs. Involucral bracts papery, coloured, stereome undivided. Receptacle flat, usually paleate. Outer filiform florets, when present, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with elongated twin hairs. Pappus bristles capillary, barbellate, connate in a ring. n =14. About 20 species, Australia.

610. *Catatia* Humbert

Catatia Humbert, Mém. Soc. Linn. Normandie 25: 67, 288 (1923).

Shrubs. Leaves alternate, flat with entire margins, tomentose. Capitula many in corymbs. Involucral bracts papery, hyaline, inner involucral bracts tube-like and enclosing florets, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches conical, with hairs dorsally. Cypselae oblong, glabrous. Pappus absent or forming a small dentate rim. Two species, Madagascar.

611. *Cephalipterum* A. Gray

Cephalipterum A. Gray, J. Bot. Kew Gard. Misc. 4: 271 (1852).

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in terminal clusters. Involucral bracts papery, coloured, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with

concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with elongated twin hairs. Pappus bristles capillary with flattened axis, distinctly plumose apically, free. n =12, 14. One species, *C. drummondii* A. Gray, Australia.

612. *Cephalosorus* A. Gray

Cephalosorus A. Gray, J. Bot. Kew Gard. Misc. 3: 98, 152 (1851); Short, Muelleria 5: 143–183 (1983), rev.
Piptostemma Turcz. (1851).

Annual herb. Leaves opposite throughout, flat with entire margins, tomentose on both surfaces. Capitula many, forming terminal secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, glabrous. Pappus scale-like, connate in a ring. n =12. One species, *C. carpesioides* (Turcz.) P.S. Short, Australia.

613. *Chamaepus* Wagenitz

Chamaepus Wagenitz in K.H. Rechinger, Fl. Iran. 145: 12 (1980).

Annual herb. Leaves alternate, flat with entire margins, tomentose on both sides. Capitula only a few together. Involucral bracts cartilaginous and papery at the apex, brownish, stereome undivided. Receptacle peg-like, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches with hairs dorsally. Cypselae oblong, glabrous. Pappus absent. One species, *C. afghanicus* Wagenitz, Middle East.

614. *Chevreulia* Cass.

Chevreulia Cass., Bull. Sci. Soc. Philom. Paris 1817: 69 (1817); Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.

Perennial herbs. Leaves opposite, flat with entire margins, tomentose abaxially. Capitula solitary. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, with short clavate twin hairs. Pappus bristles capillary, barbellate, connate in a ring. About six species, South America.

615. *Chiliocephalum* Benth.

Chiliocephalum Benth., Icon. Pl. ser. 3, 2: 34, pl. 1137 (1873); Bentham, Icon. Pl. ser. 3, 2: 34, pl. 1137 (1873), reg. rev.; Anderberg, Bot. Jahrb. Syst. 110: 1–6 (1988), rev.

Perennial herb. Leaves alternate, flat with entire margins, sparsely tomentose on both surfaces. Capitula only a few together, in dense corymbs. Involucral bracts papery, yellow, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets functionally male, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, glabrous. Pappus absent. One species, *C. schimperi* Benth., northeastern tropical Africa.

616. *Chionolaena* DC.

Chionolaena DC., Prodr. 5: 397 (1836); Baker, Fl. Brasil. 6 (1882), reg. rev.; Anderberg & Freire, Notes Roy. Bot. Gard. Edinburgh 46: 37–41 (1989), reg. rev.; Freire, Ann. Missouri Bot. Gard. 80: 397–438 (1993), rev.
Pseudoligandra M.O. Dillon & Sagást. (1990).
Parachionolaena M.O. Dillon & Sagást. (1992).

Shrubs. Leaves alternate, revolute with entire margins, tomentose on both surfaces. Capitula solitary or many in corymbs or dense clusters. Involucral bracts papery, coloured, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches truncate, with hairs dorsally. Cypselae ellipsoid, generally with elongated twin hairs or glabrous. Pappus bristles capillary, barbellate, connate in a ring. n = 14. Eighteen species, Central and South America.

617. *Chondropyxis* D.A. Cooke

Chondropyxis D.A. Cooke, in Jessop & Toelken, Fl. S. Australia 3: 1612 (1986).

Annual herb. Leaves subopposite, semi-succulent, flat with entire margins, glabrous. Capitula solitary. Involucral bracts cartilaginous, hyaline. Receptacle flat. Outer florets filiform. Central florets perfect. Style branches lanceolate-subulate. Cypselae linear with dilated apex, glabrous. Pappus bristles capillary, plumose, connate in a ring. One species, *C. halophila* D.A. Cooke, Australia.

618. *Chrysocephalum* Walp. Fig. 63BB

Chrysocephalum Walp., Linnaea 14: 503 (1840).
Argyrophanes Schltdl. (1847), nom. illegit.

Perennial or annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, coloured, stereome divided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae narrowly ellipsoid, with globose hairs without a basal cell, and one cell overtopping the other. Pappus bristles capillary, barbellate, free. n =12, 24. About seven species, Australia.

619. *Chthonocephalus* Steetz

Chthonocephalus Steetz in Lehm., Pl. Preiss. 1: 444 (1845); Short, Muelleria 7: 225–238 (1990), rev.

Rosulate annual herbs. Leaves opposite, flat with entire margins, tomentose on both surfaces. Capitula many in dense secondary heads surrounded by leaves. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, paleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with globose hairs without a basal cell. Pappus absent. Four species, Australia.

620. *Cladochaeta* DC.

Cladochaeta DC., Prodr. 6: 245 (1838).

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate and with hairs apically. Cypselae oblong, with globose twin hairs. Pappus bristles capillary, barbellate, basally connate in groups. n =8, 9. Two species, Eurasia.

621. *Comborhiza* Anderb. & K. Bremer

Comborhiza Anderb. & K. Bremer, Ann. Missouri Bot. Gard. 78: 1070 (1991); Anderberg & Bremer, Ann. Missouri Bot. Gard. 78: 1061–1072 (1991), rev.

Shrubs with stems arising from subterranean, thick, woody tubers or rhizomes. Leaves alternate, flat with entire margins, sparsely tomentose abaxially. Capitula solitary. Involucral bracts papery, brown, stereome undivided. Receptacle flat to convex, paleate. Outer florets radiate, yellow with purple bands. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous or with few elongated twin hairs. Pappus scales and bristles capillary, few, barbellate, basally connate. Two species, Africa.

622. *Craspedia* G. Forst.

Craspedia G. Forst., Fl. Ins. Austral. 58 (1786); Ward & Breitwieser, N. Z. J. Bot. 36: 165–171 (1998), reg. rev.; Breitwieser et al., N. Z. J. Bot. 37: 399–412 (1999), phylog.
Richea Labill. (1800).

Perennial or annual herbs. Leaves alternate, in a basal rosette and sometimes cauline, flat with entire margins, tomentum various. Capitula many in dense glomerules. Involucral bracts papery, brownish or hyaline, stereome undivided. Receptacle peg-like, paleate. All florets perfect, white, yellow or orange. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with papillae, glandular hairs, or elongated or globose twin hairs. Pappus bristles with flattened axis, distinctly plumose, connate in a ring. n =11, 22, 33, 44, 55. About 20 species, Australia, New Zealand.

623. *Cremnothamnus* C.F. Puttock

Cremnothamnus C.F. Puttock, Austral. Syst. Bot. 7: 576 (1994); Puttock, Austral. Syst. Bot. 7: 569–583 (1994), rev.

Perennial subshrub. Leaves alternate, flat with entire margins, weakly tomentose on both surfaces. Capitula many in terminal panicles composed of many small corymbs. Involucral bracts papery, coloured, stereome undivided. Receptacle convex, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally and apically. Cypselae turbinate, with elongated twin hairs. Pappus bristles capillary, barbellate, weakly cohering in a ring. One species, *C. thomsonii* (F. Muell.) C.F. Puttock, Australia.

624. *Cuatrecasasiella* H. Rob.

Cuatrecasasiella H. Rob., Fl. Neotrop. 2, suppl.: 14 (1985); Robinson, Fl. Neotrop. 2, suppl.: 13–16 (1985), rev.; Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.

Dioecious perennial herbs. Leaves opposite, flat with entire margins, tomentose on both surfaces. Capitula solitary, sessile. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Female florets filiform, purple. Male florets purple. Anthers with flat appendages. Style

branches acute to conical, with hairs dorsally. Cypselae turbinate, glabrous. Pappus bristles capillary, barbellate, connate in a ring. Two species, South America.

625. *Cymbolaena* Smoljan.

Cymbolaena Smoljan., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 17: 452 (1955); Wagenitz, Oesterr. Bot. Z. 119: 399–403 (1971), rev.

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts cartilaginous, brownish, stereome undivided. Receptacle peg-like, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches with much prolonged apex, with hairs dorsally and apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, scabrid, cohering by patent cilia. One species, *C. griffithii* (A. Gray) Wagenitz, Middle East, Asia.

626. *Decazesia* F. Muell.

Decazesia F. Muell., Fragm. 11: 71 (1879).

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in loose globose secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, paleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with globose hairs without a basal cell. Pappus bristles with flattened axis, barbellate, connate in a ring. $n = 14$. One species, *D. hecatocephala* F. Muell., Australia.

627. *Denekia* Thunb.

Denekia Thunb., Prodr. Fl. Cap. 2: 153 (1800); Dyer, The genera of southern African flowering plants (1975), gen. consp.

Annual or perennial herb. Leaves alternate, flat with dentate margins, densely tomentose abaxially. Capitula only a few together, in dense corymbs. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. Outer florets bilabiate, blue or white. Central florets functionally male, blue or white. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with few elongated twin hairs. Pappus bristle one, capillary, plumose. One species, *D. capensis* Thunb., Africa.

628. *Dielitzia* P.S. Short

Dielitzia P.S. Short, Muelleria 7: 103 (1989); Short, Muelleria 7: 103–116 (1989), rev.

Rosulate annual herb. Leaves opposite, at least basally, narrowly linear, flat with entire margins, tomentose on both surfaces. Capitula many in dense secondary heads among the leaves. Involucral bracts cartilaginous, brown. All florets perfect, yellow. Style branches truncate, with hairs apically. Cypselae obovoid. Pappus bristles capillary, barbellate, connate in a ring. $n = 13$. One species, *D. tysonii* P.S. Short, Australia.

629. *Disparago* Gaertn.

Disparago Gaertn., Fruct. Sem. Pl. 2: 463 (1791); Levyns, J. S. African Bot. 2: 95–103 (1936), rev.; Koekemoer, Bothalia 21: 158–161 (1991), reg. rev.; Koekemoer, Bothalia 23: 197–206 (1993), rev.

Shrubs. Leaves alternate, flat to twisted, with entire margins, sparsely tomentose adaxially. Capitula only a few together, in dense corymbs. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. Outer florets, when present, radiate, purple to pink or white. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, plumose, free. $n = 9$. Seven species, Africa.

630. *Dithyrostegia* A. Gray

Dithyrostegia A. Gray, J. Bot. Kew Gard. Misc. 3, 97, 100 (1851); Short, Muelleria 5: 185–214 (1983), rev.; Short, Muelleria 7: 103–116 (1989), rev.

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in dense secondary heads surrounded by two basally connate leaves. Involucral bracts papery, hyaline, stereome undivided. Receptacle conical, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with elongated twin hairs. Pappus bristles short, flat, connate in a ring. Two species, Australia.

631. *Dolichothrix* Hilliard & B.L. Burtt

Dolichothrix Hilliard & B.L. Burtt, Bot. J. Linn. Soc. 82: 222 (1981); Hilliard & Burtt, Bot. J. Linn. Soc. 82: 181–232 (1981), rev.

Shrub. Leaves alternate, flat with entire margins, sparsely tomentose adaxially. Capitula solitary.

Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with elongated twin hairs. Pappus bristles capillary, barbellate, basally connate. One species, *D. ericoides* (Lam.) Hilliard & B.L. Burtt, Africa.

632. *Edmondia* Cass.

Edmondia Cass., Bull. Sci. Soc. Philom. Paris 1818: 75 (1818).

Perennial subshrubs. Leaves alternate, involute, adpressed, with entire margins, sparsely tomentose adaxially. Capitula solitary. Involucral bracts papery, white or pink, stereome divided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, barbellate, basally connate. Three species, Africa.

633. *Elytropappus* Cass.

Elytropappus Cass., Bull. Soc. Sci. Philom. Paris 1816: 199 (1816); Levyns, J. S. African Bot. 1: 89–103 (1935), rev.; Nordenstam, J. S. African Bot. 30: 45–48 (1964), nomencl.
Achyrocome Schrank (1824).

Shrubs. Leaves alternate, flat to twisted with entire margins, sparsely tomentose adaxially. Capitula solitary or many in dense corymbs. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. All florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, plumose, basally connate. Eight species, southern Africa.

634. *Epitriche* Turcz.

Epitriche Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 74 (1851); Short, Muelleria 5: 143–183 (1983), rev.
Pteropogon sect. *Pteropogonopsis* A. Gray (1852).

Annual herb. Leaves opposite, flat with entire margins, tomentose on both surfaces. Capitula many in dense secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style apices truncate, with hairs apically. Cypselae obovoid, glabrous. Pappus absent. One species, *E. demissus* (A. Gray) P.S. Short, Australia.

635. *Eriochlamys* Sond. & F. Muell.

Eriochlamys Sond. & F. Muell. in Sond., Linnaea 25: 488 (1853).

Annual herb. Leaves opposite, flat with entire margins, tomentose on both surfaces. Capitula many in terminal secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with globose hairs without a basal cell. Pappus absent. $n = 14$. One species, *E. behrii* Sond. & F. Muell., Australia.

636. *Erymophyllum* Paul G. Wilson

Erymophyllum Paul G. Wilson, Nuytsia 7: 105 (1989); Wilson, Nuytsia 7: 103–116 (1989), rev.

Annual herbs. Leaves alternate, filiform with entire margins, tomentose on both surfaces. Capitula only a few together, in terminal clusters. Involucral bracts papery, coloured, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with elongated twin hairs. Pappus bristles with flattened axis, barbellate, free. $n = 11, 14$. Five species, Australia.

637. *Euchiton* Cass.

Euchiton Cass., Dict. Sci. Nat. 56: 214 (1828); Koster, Blumea 20: 193–226 (1972), reg. rev.; Drury, N.Z.J. Bot. 10: 112–179 (1972), reg. rev.; Breitwieser & Sampson, Grana 36: 65–79 (1997), palynol.; Breitwieser & Sampson, Grana 36: 80–95 (1997), palynol.; Breitwieser & Ward, N. Z. J. Bot. 36: 303–304 (1998), rev.; Ward & Breitwieser, N. Z. J. Bot. 36: 165–171 (1998), rev.; Breitwieser et al., N. Z. J. Bot. 37: 399–412 (1999), phylog.
Gnaphalium sect. *Euchiton* (Cass.) DC. (1837)

Perennial or rarely annual, generally stoloniferous herbs. Leaves alternate, generally flat with entire margins, tomentose on both surfaces or abaxially only. Capitula solitary or few to many in dense clusters. Involucral bracts papery, brownish or hyaline, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple or colourless. Central florets perfect, purple or colourless. Anthers with flat appendages. Style branches obtuse, with hairs dorsally and apically. Cypselae small, oblong or larger and narrowly ellipsoid-oblong, generally with short clavate twin hairs. Pappus bristles capillary, scabrid, free or cohering by patent cilia.

n = 14. Twenty species, New Zealand, Australia, New Guinea, Asia, Oceania.

638. *Evacidium* Pomel

Evacidium Pomel, Mat. Fl. Atl. 41 (1874).

Annual herb, sometimes perennating. Leaves alternate, flat with entire margins, tomentose. Capitula only a few together. Involucral bracts cartilaginous or apically with a minute papery portion, brownish, stereome undivided. Receptacle peg-like, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches with a much prolonged sterile apex, with hairs dorsally. Cypselae oblong, with globose twin hairs. Pappus absent. One species, *E. atlanticum* Pomel, south-eastern Europe and northern Africa.

639. *Ewartia* Beauverd Fig. 62G

Ewartia Beauverd, Bull. Soc. Bot. Genève sér. 2, 2: 236 (1910); Beauverd, Bull. Soc. Bot. Genève sér. 2, 3: 253–260 (1911), rev.; Breitwieser & Ward, N. Z. J. Bot. 31: 43–58 (1993), morph.; Breitwieser & Sampson, Grana 36: 65–79 (1997), palynol.; Breitwieser & Sampson, Grana 36: 80–95 (1997), palynol.; Ward & Breitwieser, N. Z. J. Bot. 36: 165–171 (1998), rev.; Breitwieser et al., N. Z. J. Bot. 37: 399–412 (1999), phylog.

Subdioecious or dioecious, perennial, mat-forming herbs. Leaves alternate, concave with entire margins, tomentose on both surfaces. Capitula solitary or few together. Involucral bracts papery, white, stereome divided or undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets purple. Anthers with flat appendages. Style branches obtuse, with hairs dorsally and apically. Cypselae oblong to obovoid, with elongated or short clavate twin hairs. Pappus bristles capillary, scabrid, connate in a ring or in groups. n = 14, 28. Four species, Australia.

640. *Ewartiothamnus* Anderb.

Ewartiothamnus Anderb., Opera Bot. 104: 94 (1991); Anderberg, Opera Bot. 104: 1–195 (1991), rev.; Breitwieser & Ward, N. Z. J. Bot. 31: 43–58 (1993), morph.; Breitwieser & Sampson, Grana 36: 65–79 (1997), palynol.; Breitwieser & Sampson, Grana 36: 80–95 (1997), palynol.; Ward & Breitwieser, N. Z. J. Bot. 36: 165–171 (1998), rev., Breitwieser et al., N. Z. J. Bot. 37: 399–412 (1999), phylog.

Perennial herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in corymbs. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid to obovoid, glabrous. Pappus bristles capillary, scabrid, free. n = 14. One species, *E. sinclairii* (Hook. f.) Anderb., New Zealand.

641. *Facelis* Cass.

Facelis Cass., Bull. Sci. Soc. Philom. Paris 1819: 94 (1819); Beauverd, Bull. Soc. Bot. Genève sér. 2, 5: 212–220 (1913), rev.; Robinson, Fl. Neotrop. 2, suppl.: 13–16 (1985), reg. rev.; Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches acute with hairs dorsally. Cypselae turbinate, with elongated twin hairs. Pappus bristles capillary, distinctly plumose below, barbellate apically, connate in groups. n = 14. Four species, South America.

642. *Feldstonia* P.S. Short

Feldstonia P.S. Short, Muelleria 7: 108 (1989); Short, Muelleria 7: 103–116 (1989), rev.

Annual herb. Leaves opposite basally, alternate above, flat with entire margins, generally glabrous. Capitula many in terminal dense secondary heads. Involucral bracts cartilaginous, hyaline. Receptacle conical, epaleate. All florets perfect, yellow. Style branches truncate, with hairs apically. Cypselae obovoid, hairy. Pappus bristles capillary, subplumose to plumose, connate in a ring. n = 11. One species, *F. nitens* P.S. Short, Australia.

643. *Filago* L.

Filago L., Sp. Pl. 2: 927 (1753), nom. cons.; Chrtek & Holub, Preslia 35: 1–17 (1963), rev.; Wagenitz, Willdenowia 4: 37–59 (1965), rev.; Wagenitz, Ber. Deutsch. Bot. Gesell. 79: 336–342 (1966), rev.; Wagenitz, Willdenowia 4: 283–298 (1968a), reg. rev., Wagenitz, Willdenowia 5: 55–66 (1968b), rev.; Wagenitz, Willdenowia 5: 395–444 (1969), rev.; Wagenitz, Willdenowia 6: 115–139 (1970), reg. rev.; Wagenitz, Feddes Repert. 81: 107–117 (1970), rev.; Wagenitz, Israel J. Bot. 19: 260–265 (1970), reg. rev.; Wagenitz, Sida 6: 221–223 (1976), reg. rev.

Evax Gaertn. (1791).
Gifola Cass. (1819).
Filaginopsis Torr. & A. Gray (1842).
Evacopsis Pomel (1874).

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts cartilaginous, brownish, stereome undivided. Receptacle conical, epaleate. Outer florets filiform, purple. Central florets perfect or functionally male, purple. Anthers with flat appendages. Style branches with much prolonged apex, with hairs dorsally. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, scabrid, free. n = 9, 13, 14. Forty-six species, Asia, Europe, North Africa and North America.

644. *Fitzwillia* P.S. Short

Fitzwillia P.S. Short, Muelleria 7: 111 (1989); Short, Muelleria 7: 103–116 (1989), rev.

Annual herb. Leaves opposite, flat with entire margins, semi-succulent, glabrous. Capitula many in flattened secondary heads. Involucral bracts cartilaginous, hyaline. Receptacle peg-like. All florets perfect, white. Style branches truncate, with hairs apically. Cypselae obconic, villous. Pappus of scales, connate in a ring forming a cup. One species, *F. axilliflora* (W.V. Fitzg. ex Ewart & Jean White) P.S. Short, Australia.

645. *Galeomma* Rauschert

Galeomma Rauschert, Taxon 31: 557 (1981).

Annual herbs. Leaves alternate, flat with entire margins, sparsely tomentose on both surfaces. Capitula many in dense corymbs. Involucral bracts papery, hyaline, stereome divided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with globose hairs. Pappus bristles capillary, barbellate, free or cohering by patent cilia. Two species, southern Africa.

646. *Gamochaeta* Wedd.

Gamochaeta Wedd., Chlor. Andina 1: 151 (1856); Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.
Gnaphalium sect. *Gamochaeta* (Wedd.) Benth., pro parte et quoad typum (1873).

Annual or perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in head-like or spike-like clusters. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with globose twin hairs. Pappus bristles capillary, barbellate, connate in a ring. n = 14. About 50–80 species, South America.

647. *Gamochaetopsis* Anderb. & Freire

Gamochaetopsis Anderb. & Freire, Bot. J. Linn. Soc. 106: 186 (1991); Anderberg & Freire, Bot. J. Linn. Soc. 106: 173–198 (1991), rev.

Perennial herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula few together in small, flat-topped glomerules. Involucral bracts papery, brownish, stereome divided. Receptacle flat. Outer florets filiform. Central florets perfect. Style branches truncate, with hairs dorsally and apically. Cypselae oblong-elliptic, with short clavate twin hairs. Pappus bristles capillary, scabrid, connate in a ring. One species, *G. alpina* (Poepp. & Endl.) Anderb. & S.E. Freire, South America.

648. *Gilberta* Turcz. Fig. 63S

Gilberta Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 192 (1851); Wilson, Nuytsia 8: 379–438 (1992), rev.
Antheidosorus A. Gray (1851).

Annual herb. Leaves alternate, filiform with entire margins, tomentose on both surfaces. Capitula many in terminal secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect or some central ones functionally male, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with elongated twin hairs. Pappus bristles with flattened axis, distinctly plumose, connate in a ring. n = 10. One species, *G. tenuifolia* Turcz., Australia.

649. *Gilruthia* Ewart

Gilruthia Ewart in Ewart, Jean White & B. Rees, Proc. Roy. Soc. Victoria ser. 2, 22: 13 (1909).

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together, in terminal clusters. Involucral bracts papery, green, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow.

Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, glabrous. Pappus bristles with flattened axis, distinctly plumose, connate in a ring. $n = 13$. One species, *G. osbornii* Ewart & Jean White in Ewart, Jean White & B. Rees, Australia.

650. *Gnaphaliothamnus* Kirp.

Gnaphaliothamnus Kirp. in Kirp. & Kuprijanova, Trudy Bot. Inst. Akad. Nauk S.S.S.R. ser. 1, Fl. Sist. Vyssh. Rast. 9: 33 (1950), reg. rev.; Nesom, Phytologia 68: 366–381 (1990), rev.; Nesom, Phytologia 69: 1–3 (1990), rev.; Nesom, Phytologia 76: 185–191 (1994), gen. consp.

Shrub. Leaves alternate, revolute with entire margins, tomentose on both surfaces. Capitula many in corymbs. Involucral bracts papery, white or pink, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs dorsally and apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, barbellate, free. $n = 14$. One species, *G. rhodanthus* (Sch. Bip.) Kirp., Central America.

651. *Gnaphalium* L. Figs. 61H, 64D

Gnaphalium L., Sp. Pl. 2: 850 (1753); Drury, N. Z. J. Bot. 8: 222–248 (1970), rev.; Chang & Tseng, Fl. Reip. Pop. Sin. 75 (1979), reg. rev.; Jeffrey, Taxon 28: 349–351 (1979), nomencl.; Hilliard, Bot. J. Linn. Soc. 82: 267–292 (1981), gen. consp.; Hilliard & Burtt, Bot. J. Linn. Soc. 82: 233–265 (1981), nomencl.; Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.
Omalotheca Cass. (1828).
Amphidoxa DC. (1838).
Filaginella Opiz (1854).
Gnaphalium sect. *Eu-Gnaphalium* O. Hoffm., pro parte et quoad typum (1889).
Homognaphalium Kirp. (1950), quoad typum, excl. descr.

Annual or perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, scabrid, free. $n = 7$, 8, 9, 10, 14, 21, 26, 28, 29. About 80 species, cosmopolitan.

652. *Gnephosis* Cass. Figs. 63X, 65D–F

Gnephosis Cass., Bull. Sci. Soc. Philom. Paris 1820: 43 (1820); Short, Muelleria 5: 185–214 (1983), rev.; Short, Muelleria 6: 317–319 (1987), rev.; Jeffrey, Comp. Newslett. 16 (1989), nomencl.
Crossolepis Benth. (1837).
Chrysocoryne Endl. (1843).
Cyathopappus F. Muell. (1861).

Annual herbs. Leaves opposite basally, alternate above, flat with entire margins, tomentose on both surfaces. Capitula many in elongate secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle conical, epaleate. Anthers with concave appendages. All florets perfect, yellow. Style branches truncate, with hairs apically. Cypselae obovoid, with globose hairs without a basal cell. Pappus of small scales connate in a ring to form a cup or absent. $n = 6$, 12, 14. Eight species, Australia.

653. *Gnomophalium* Greuter

Gnomophalium Greuter, Willdenowia 33: 242 (2003); Hilliard & Burtt, Bot. J. Linn. Soc. 82: 181–232 (1981), reg. rev., sub *Homognaphalio*; Fayed & Zareh, Willdenowia 18: 445–453 (1989), reg. rev., sub *Homognaphalio*.
Homognaphalium Kirp. (1950), quoad descr., typo excluso.

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in dense clusters among a group of leaves. Involucral bracts papery, hyaline, stereome divided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, scabrid, cohering by patent cilia. One species, *G. pulvinatum* (Delile) Greuter, North Africa and Asia.

654. *Gratwickia* F. Muell.

Gratwickia F. Muell., Bot. Centralbl. 64: 445 (1895); Eichler, Taxon 12: 295–297 (1963), nomencl.

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together, in terminal clusters. Involucral bracts papery, yellowish, stereome divided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristle capillary, one, plumose, on central

florets only. One species, *G. monochaeta* F. Muell., Australia.

655. *Haeckeria* F. Muell.

Haeckeria F. Muell., Linnaea 25: 406 (1853); Ewart, Flora of Victoria (1930), reg. rev.; Heine, Adansonia sér. 2, 7: 115–140 (1967), rev.; Orchard, Austral. Syst. Bot. 17: 447–467 (2004), rev.
Humea sect. *Haeckeria* (F. Muell.) F. Muell. (1858).

Shrubs. Leaves alternate, revolute with entire margins, tomentose on both surfaces. Capitula many in corymbs. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with short clavate twin hairs. Pappus absent. Two species, Australia.

656. *Haegiela* P.S. Short & Paul G. Wilson

Haegiela P.S. Short & Paul G. Wilson, Muelleria 7: 259 (1990); Short & Wilson, Muelleria 7: 259–265 (1990), rev.

Annual herb. Leaves opposite, at least basally, flat with entire margins, tomentose on both surfaces. Capitula axillary, solitary. Involucral bracts papery, silvery. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow with purple apices. Anthers with flat appendages. Style branches truncate. Cypselae ellipsoid, with globose hairs without a basal cell. Pappus absent. One species, *H. tatei* (F. Muell.) P.S. Short & Paul G. Wilson, Australia.

657. *Haptotrichion* Paul G. Wilson Fig. 63E

Haptotrichion Paul G. Wilson, Nuytsia 8: 422 (1992); Wilson, Nuytsia 8: 379–438 (1992), rev.

Annual herbs. Leaves alternate, flat with entire margins, glandular-hairy on both surfaces. Capitula solitary. Involucral bracts papery, coloured, clawed, stereome undivided. Receptacle flat or convex, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate. Cypselae beaked, ellipsoid. Pappus bristles capillary, barbellate, connate in a ring to form a small cup. $n = 12$. Two species, Australia.

658. *Helichrysopsis* Kirp.

Helichrysopsis Kirp., Trudy Bot. Inst. Akad. Nauk S.S.R. ser. 1: 32 (1950).

Perennial subshrub. Leaves alternate, flat with entire margins, sparsely tomentose on both surfaces. Capitula only a few together, in dense corymbs. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with globose twin hairs. Pappus bristles capillary, plumose, basally connate. One species, *H. septentrionalis* (Vatke) Hilliard & B.L. Burtt, Africa.

659. *Helichrysum* Mill. Fig. 63C,K,N,U,V

Helichrysum Mill., Gard. Dict. abr. ed. 4: 28 (1754), corr. Pers., Syn. Pl. 2: 414 (1807), nom. et orth. cons.; Moeser, Bot. Jahrb. 43: 420–460 (1909), reg. rev.; Moeser, Bot. Jahrb. 44: 239–345 (1910), reg. rev.; Schwartz, Mitt. Inst. Bot. Hamburg 10: 1–393 (1939), reg. rev.; Hedberg, Symb. Bot. Upsal. 15: 1–424 (1957), reg. rev.; Cufodontis, Bull. Jard. Bot. Natl Belg. 36, suppl. (1966), reg. rev.; Gill, Willdenowia 12: 95–128 (1982), reg. rev.; Scott, Fl. Mascar. 109: 62–70 (1993), reg. rev.
Leontonyx Cass. (1822).

Perennial or annual herbs or sometimes shrublets. Leaves alternate, generally flat with entire margins, often tomentose. Capitula solitary or many in corymbs. Involucral bracts papery, brown, yellow, pink or white, stereome divided or undivided. Receptacle flat, epaleate or rarely paleate. Outer filiform florets yellow, or absent. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, glabrous or with elongated or short clavate twin hairs. Pappus bristles capillary, barbellate or subplumose, connate or free. $n = 7, 8, 9, 14, 21, 24, 28, 42$. About 600 species, Africa, Madagascar, Europe and Asia.

660. *Hesperevax* (A. Gray) A. Gray

Hesperevax (A. Gray) A. Gray, Proc. Amer. Acad. Arts 7: 356. (1868); Morefield, Syst. Bot. 17: 293–310 (1992), rev.
Evax [sect.] *Hesperevax* A. Gray (1857).

Annual herbs. Leaves alternate or seemingly whorled below, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts none or vestigial. Receptacle conical, paleate. Outer florets filiform, white. Central florets functionally male, lobes purple, tubes white. Cypselae ovoid, dorsiventrally compressed, glabrous. Pappus absent. Three species, North America.

661. *Humeocline* Anderb.

Humeocline Anderb., Opera Bot. 104: 138 (1991); Anderberg, Opera Bot. 104: 1–195 (1991), rev.

Perennial herb or subshrub. Leaves alternate, revolute with entire margins, tomentose. Capitula many in terminal pyramidal synflorescence. Involucral bracts papery, yellowish. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, glabrous. Pappus absent. One species, *H. madagascariensis* (Humbert) Anderb., Madagascar.

662. *Hyalochlamys* A. Gray

Hyalochlamys A. Gray, J. Bot. Kew Gard. Misc. 3: 98–101 (1851); Short, Muelleria 5: 185–214 (1983), rev.

Rosulate annual herb. Leaves opposite, at least basally, flat with entire margins, tomentose on both surfaces. Capitula many, forming dense secondary heads among the leaves. Involucral bracts papery, hyaline, stereome undivided. Receptacle conical, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, glabrous. Pappus absent. One species, *H. globifera* A. Gray, Australia.

663. *Hyalosperma* Steetz Fig. 63B

Hyalosperma Steetz in Lehm., Pl. Preiss. 1: 476 (1845); Wilson, Nuytsia 7: 75–101 (1989), rev.
Helipterum sect. *Pachypterum* Steetz in Lehm. (1845), pro parte et quoad typum.

Annual herbs. Leaves alternate, filiform with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, white or yellow, stereome undivided. Receptacle conical, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with globose hairs without a basal cell. Pappus bristles with flattened axis, plumose, connate in a ring. n = 8, 11, 12. Nine species, Australia.

664. *Hydroidea* P.O. Karis

Hydroidea P.O. Karis, Bot. J. Linn. Soc. 102: 29 (1990); Hilliard & Burtt, Bot. J. Linn. Soc. 82: 181–232 (1981), reg. rev. sub *Atricantha*; Karis, Bot. J. Linn. Soc. 102: 23–36 (1990), rev.

Shrub. Leaves alternate, twisted with revolute entire margins, sparsely tomentose on both surfaces. Capitula solitary. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. All florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, free. One species, *H. elsiae* (Hilliard) P.O. Karis, Africa.

665. *Ifloga* Cass.

Ifloga Cass., Bull. Sci. Soc. Philom. Paris 1819: 142 (1819); Fayed & Zareh, Willdenowia 17: 115–123 (1988), reg. rev.; Hilliard, Bot. J. Linn. Soc. 82: 293–312 (1981), rev.
Trichogyne sect. *Ifloga* (Cass.) DC. (1838).
Comptonanthus B. Nord. (1964), pro parte et quoad typum.

Annual herbs. Leaves alternate, concave to involute with entire margins, tomentose adaxially. Capitula only a few together, in spikes. Involucral bracts papery, brownish, stereome divided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, rarely functionally male, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with globose twin hairs. Pappus bristles capillary, distinctly plumose apically, cohering by patent cilia. n = 7. Six species, Asia, Europe, Middle East and Africa.

666. *Ixiolaena* Benth.

Ixiolaena Benth. in Endl., Enum. Pl. 66 (1837).

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous with papery tips, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Style branches truncate, with hairs apically. Anthers with concave appendages. Cypselae ellipsoid with elongated twin hairs. Pappus bristles capillary, barbellate, connate in a ring. n = 20, 30. Eight species, Australia.

667. *Ixodia* R. Br.

Ixodia R. Br. in Aiton, Hort. Kew. ed. 2. 4: 517 (1812); Copley, J. Adelaide Bot. Gard. 6: 41–54 (1982), rev.; Orchard, Brunonia 4: 185–197 (1981), gen. consp.

Shrubs. Leaves alternate, revolute with entire margins, tomentose on both surfaces. Capitula many in corymbs. Involucral bracts papery, white, stereome undivided. Receptacle conical, paleate. All florets perfect, yellow or white. Anthers with flat appendages. Style branches truncate, with hairs api-

cally. Cypselae ellipsoid, with short clavate twin hairs. Pappus absent. $n = 13$. Two species, Australia.

668. *Jalcophila* M.O. Dillon & Sagást.

Jalcophila M.O. Dillon & Sagást., Brittonia 38: 162 (1986); Dillon & Sagástegui-Alva, Brittonia 38: 162–167 (1986), rev.; Anderberg & Freire, Brittonia 42: 138–141 (1990), rev.; Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.

Perennial, alpine cushion plants. Leaves alternate, slightly revolute with entire margins, tomentose adaxially only. Capitula solitary. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Style branches truncate, with hairs dorsally. Cypselae ellipsoid to ovoid, glabrous or with glandular hairs. Pappus bristles capillary, scabrid, connate in a ring. Three species, South America.

669. *Lachnospermum* Willd.

Lachnospermum Willd., Sp. Pl. 3: 1787 (1803); Dyer, The genera of southern African flowering plants (1975), gen. consp.; Hilliard & Burtt, Bot. J. Linn. Soc. 82: 181–232 (1981), gen. consp.

Ericoid shrubs. Leaves alternate, flat to twisted with revolute entire margins, sparsely tomentose adaxially. Capitula solitary or only a few together, in dense corymbs. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. All florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with few elongated twin hairs. Pappus bristles capillary, barbellate, basally connate. Three species, southern Africa.

670. *Langebergia* Anderb.

Langebergia Anderb., Opera Bot. 104: 93 (1991); Anderberg, Opera Bot. 104: 1–195 (1991), rev.; Nordenstam, Ann. Wiener Mus. Naturgesch. 98, B: 403–418 (1996), rev.
Petalacte D. Don sect. *Ampilasia* DC. (1837).

Shrub. Leaves alternate, almost flat with revolute, entire margins, sparsely tomentose on both surfaces. Capitula many in dense corymbs. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, free. One species, *L. canescens* (DC.) Anderb., southern Africa.

671. *Lasiopogon* Cass.

Lasiopogon Cass., Bull. Sci. Soc. Philom. Paris 1818: 75 (1818); Nordenstam, J. S. African Bot. 30: 53–65 (1964), rev.

Annual herbs. Leaves alternate, flat with entire margins, densely tomentose on both surfaces. Capitula only a few together, in dense corymbs. Involucral bracts papery, brownish, stereome divided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with globose hairs. Pappus bristles capillary, plumose or barbellate, free. $n = 7$. Eight species, Africa and Middle East.

672. *Lawrencella* Lindl. Figs. 63Y, 65G

Lawrencella Lindl., Bot. Reg., Appendix to vols. 1–23: 23 (1839); Wilson, Nuytsia 8: 361–377 (1992), rev.
Helichrysum sect. *Lawrencella* (Lindl.) Benth. (1867).

Annual or perennial herbs. Leaves opposite, at least basally, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, white, yellow or pink, stereome undivided. Receptacle flat, epaleate. Outer filiform florets, when present, yellow. Central florets perfect, yellow. Anthers with concave appendages. Style branches conical, with hairs dorsally. Cypselae obovoid, with elongated twin hairs. Pappus bristles capillary, barbellate, free. $n = 8, 11$. About 35 species, Australia.

673. *Lemooria* P.S. Short

Lemooria P.S. Short, Muelleria 7: 112 (1989); Short, Muelleria 7: 103–116 (1989), rev.

Annual herb. Leaves opposite, at least basally, flat with entire margins, glabrous. Capitula many in dense secondary heads. Involucral bracts papery, hyaline. Receptacle flat to convex, epaleate. All florets perfect, yellow. Style branches truncate, with hairs apically. Cypselae obovoid, with elongated twin hairs. Pappus bristles capillary, subplumose, connate in a ring. One species, *L. burkittii* (Benth.) P.S. Short, Australia.

674. *Leontopodium* R. Br. ex Cass. Fig. 64C

Leontopodium R. Br. ex Cass., Bull. Sci. Soc. Philom. Paris 1819: 144 (1819); Beauverd, Bull. Soc. Bot. Genève sér. 2, 4:

12–55 (1912), rev.; Handel-Mazzetti, Beih. Bot. Centralb. 44, 2: 1–178 (1927), rev.

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in corymbs. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets functionally male, yellow. Anthers with flat appendages. Style branches truncate, with hairs dorsally and apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, barbellate, connate in a ring. n = 7, 12, 13, 14, 22, 24, 25, 26, 52. Fifty-eight species, Asia and Europe.

675. *Lepidostephium* Oliv.

Lepidostephium Oliv., Icon. Pl. ser. 3: 22 (1868); Kroner, Mitt. Bot. Staatssamml. München 16: 1–268 (1980), rev.

Perennial herbs. Leaves alternate, revolute with denticulate margins, sparsely tomentose on both surfaces. Capitula solitary or only a few together, in lax corymbs. Involucral bracts cartilaginous to herbaceous, stereome undivided. Receptacle flat, epaleate. Outer florets radiate, violet. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, with few elongated twin hairs. Pappus bristles capillary, barbellate, free. Two species, southern Africa.

676. *Leptorhynchos* Less.

Leptorhynchos Less., Syn. Gen. Comp. 273 (1832); Wilson, Nuytsia 12: 303–305 (1998), nomencl.; Wilson, Nuytsia 13: 607–611 (2001), rev.
Rhytidanthe Benth. (1837).

Annual or rarely perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces or adaxially only. Capitula solitary. Involucral bracts papery, brownish, stereome forming two ribs. Receptacle flat, epaleate. Outer florets tubular, yellow. Central florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with globose hairs without a basal cell, and one cell overtopping the other. Pappus bristles capillary, barbellate, free. n = 10, 12. Ten species, Australia.

677. *Leptotriche* Turcz.

Leptotriche Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 73 (1851); Munir, Adelaide Bot. Gard. 12: 101–117 (1989), reg. rev.

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in terminal secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, glabrous. Pappus bristles scale-like, connate in a ring, absent in some species. Twelve species, Australia.

678. *Leucochrysum* (DC.) Paul G. Wilson Fig. 61F

Leucochrysum (A. Cunn. ex DC.) Paul G. Wilson, Nuytsia 8: 441 (1992); Wilson, Nuytsia 8: 439–446 (1992), rev.
Helipterum sect. *Leucochrysum* A. Cunn. ex DC. (1838).

Perennial or annual herbs. Leaves alternate, flat or sometimes filiform with entire margins, tomentose or glandular. Capitula solitary. Involucral bracts papery, coloured, inner bracts clawed, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Style branches obtuse. Cypselae ellipsoid. Pappus bristles capillary, distinctly plumose, free or shortly connate. n = 9. Five species, Australia.

679. *Leucogenes* Beauverd Fig. 61C

Leucogenes Beauverd, Bull. Soc. Bot. Genève sér. 2, 2: 241–242 (1910); Molloy, N. Z. J. Bot. 33: 53–63 (1995), rev.; Ward & Breitwieser, N. Z. J. Bot. 36: 165–171 (1998), rev.; Breitwieser et al., N. Z. J. Bot. 37: 399–412 (1999), phylog.
Helichrysum sect. *Leontopodioides* Benth. (1873).

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula in a dense corymb surrounded by conspicuous whorl of leafy, white-lanate bracts. Involucral bracts papery, brownish or hyaline, stereome undivided. Receptacle conical, epaleate. Outer florets filiform, generally yellow. Central florets perfect, generally yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae narrowly oblong to ellipsoid, with elongated twin hairs. Pappus bristles capillary, scabrid, free. n = 14, 28, 56. Four species, New Zealand.

680. *Leucophyta* R. Br.

Leucophyta R. Br., Trans. Linn. Soc. London 12: 106 (1818).

Perennial herb or subshrub. Leaves alternate, flat with entire margins, densely tomentose on both surfaces. Capitula many in dense, globose secondary heads. Involucral bracts papery, hyaline, stereome divided. Receptacle conical, epaleate.

All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, glabrous. Pappus bristles with flattened axis, plumose, connate in a ring. n = 9. One species, *L. brownii* Cass., Australia.

681. *Leysera* L.

Leysera L., Sp. Pl. ed. 2, 2: 1249 (July 1763); Bremer, Bot. Notiser 131: 369–383 (1978), rev.; Anderberg & Bremer, Ann. Missouri Bot. Gard. 78: 1061–1072 (1991), phylog., gen. consp.; Fayed, Willdenowia 20: 97–102 (1991), reg. rev. *Leptophytus* Cass. (1817).

Annual herbs or subshrubs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts papery, brown, stereome undivided. Receptacle flat, paleate. Outer florets radiate, yellow with purple bands dorsally. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs apically. Cypselae cylindrical, glabrous or with few elongated twin hairs. Pappus of scales and capillary, plumose, free bristles. n = 4, 7, 8. Three species, Africa.

682. *Logfia* Cass. Fig. 64B

Logfia Cass., Bull. Sci. Soc. Philom. Paris 1819: 143 (1819). *Oglifa* Cass. (1819).

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts cartilaginous, brownish, stereome undivided. Receptacle conical, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches with much prolonged apex, with hairs dorsally and apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, scabrid, cohering by basal cilia. n = 14. Nine species, Europe, Middle East and northern Africa.

683. *Loricaria* Wedd. Fig. 65A–C

Loricaria Wedd., Chlor. Andina 1: 165 (1856) non J.V. Lamour., nom. rej. (1825); Cuatrecasas, Feddes Repert. 56: 149–172 (1954), rev.; Dillon & Sagástegui-Alva, Phytologia 59: 227–233 (1986), rev.; Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.

Dioecious shrubs. Leaves alternate, concave to involute with entire margins, tomentose adaxially only. Capitula solitary or only a few together. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, often paleate. Female florets filiform, yellow. Male florets yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, free. n = ca.14. Nineteen species, South America.

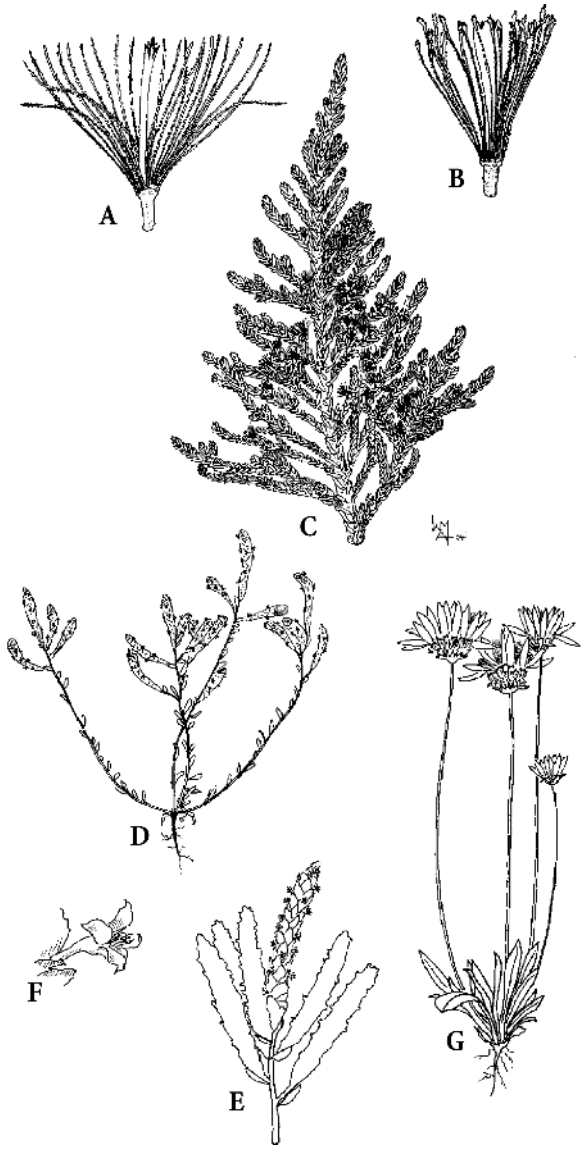

Fig. 65. Compositae-Gnaphalieae. **A** *Loricaria leptothamna*. Pistillate floret. **B**, **C** *Loricaria thuyoides*. **B** Staminate floret. **C** Flowering branch. **D**–**F** *Gnephosis uniflora*. **D** Habit. **E** Flowering branch. **F** Floret. **G** *Lawrencella davenportii*. Habit. (Drawings by William Murray)

684. ***Lucilia*** Cass. Fig. 63P

Lucilia Cass., Bull. Sci. Soc. Philom. Paris 1817: 32 (1817); Freire, Darwiniana 27: 431–490 (1986), rev.; Freire, Bol. Soc. Argent. Bot. 24: 411–413 (1986), cytol.; Zardini, Ann. Missouri Bot. Gard. 74: 431 (1987), rev.; Freire, Cladistics 3: 254–272 (1987), phylog.; Freire, Darwiniana 28: 409–411 (1987), rev.; Anderberg & Freire, Bot. J. Linn. Soc. 106: 173–198 (1991), phylog.; Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.
Oligandra Less. (1832).

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, brownish, stereome usually undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches acute to conical, with hairs dorsally. Cypselae turbinate, with elongated twin hairs. Pappus bristles capillary, barbellate, connate in groups. $n = 9, 14$. Eleven species, South America.

685. ***Luciliocline*** Anderb. & Freire

Luciliocline Anderb. & Freire, Bot. J. Linn. Soc. 106: 187 (1991); Anderberg & Freire, Bot. J. Linn. Soc. 106: 173–198 (1991), rev., phylog.

Rosulate perennial herbs. Leaves basal, flat or revolute with entire margins, tomentose on both surfaces. Capitula solitary or many in glomerules arranged in spikes. Involucral bracts brownish, stereome undivided (rarely divided). Receptacle flat. Outer florets filiform, white with purplish corolla lobes. Central florets perfect. Style branches truncate or obtuse, with hairs dorsally and apically. Cypselae ellipsoid or oblong-ellipsoid, with globose twin hairs. Pappus bristles capillary, scabrid, connate in a ring. Five species, South America.

686. ***Macowania*** Oliv. Fig. 63W

Macowania Oliv., Icon. Pl. 11: tab. 1062 (1870); Burtt & Grau, Notes Roy. Bot. Gard. Edinburgh 31: 373–376 (1972), rev.; Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 34: 253–286 (1976), reg. rev.; Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 42: 227–260 (1985), reg. rev.
Homochaete Benth. (1872).

Perennial subshrubs or shrubs. Leaves alternate, revolute or rarely flat with entire margins, sparsely tomentose adaxially, densely abaxially. Capitula solitary. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. Outer florets radiate, yellow or rarely white. Central florets perfect or functionally male, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, with few elongated twin hairs. Pappus bristles capillary, barbellate, free. Twelve species, southern Africa.

687. ***Metalasia*** R. Br.

Metalasia R. Br., Trans. Linn. Soc. London 12: 124 (1817); Karis, Opera Bot. 99: 1–150 (1989), rev.

Shrubs. Leaves alternate, twisted with revolute entire margins, sparsely tomentose adaxially. Capitula many in dense corymbs. Involucral bracts papery, white, pink or yellow, stereome undivided. Receptacle flat, epaleate. All florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, free. $n = 7$. Fifty-two species, southern Africa.

688. ***Mexerion*** G.L. Nesom

Mexerion G.L. Nesom, Phytologia 68: 249 (1990); Nesom, Phytologia 68: 247–254 (1990), rev.

Rosulate, stoloniferous, perennial herbs. Leaves, flat with entire margins, tomentose on both surfaces. Capitula arranged in glomerules or spikes. Involucral bracts brownish or hyaline, stereome undivided. Outer florets filiform, purple. Central florets functionally male, purple. Style branches with much prolonged apex, with hairs dorsally and apically. Cypselae ellipsoid or turbinate-oblong, with elongated twin hairs. Pappus bristles capillary, barbellate, connate in a ring. Two species, Mexico.

689. ***Micropsis*** DC.

Micropsis DC., Prodr. 5: 459 (1836); Beauverd, Bull. Soc. Bot. Genève sér. 2, 5: 221–228 (1913), rev.

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, paleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches with much prolonged apex, with hairs dorsally and apically. Cypselae oblong, with elongated twin hairs. Pappus absent or a brief crown. About five species, South America.

690. ***Micropus*** L.

Micropus L., Sp. Pl. 927 (1753).

Annual herb. Leaves opposite, flat with entire margins, tomentose. Capitula solitary or only a few together, in leaf axils. Involucral bracts herbaceous to cartilaginous or apically with a minute papery portion, hyaline, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches with a much prolonged sterile apex, with hairs dorsally. Cypselae aborted or reduced. Outer cypselae laterally compressed, glabrous. Pappus absent. $n = 14$. One species, *M. supinus* L., Europe, Africa.

691. ***Millotia*** Cass.

Millotia Cass., Ann. Sci. Nat. (Paris) 17: 416 (1829); Schodde, Trans. Roy. Soc. S. Australia 87: 209–241 (1963), rev.; Short, Austral. Syst. Bot. 8: 1–47 (1995), rev.; Short & Anderberg, Austral. Syst. Bot. 8: 49–55 (1995), phylog.

Annual herbs. Leaves alternate or opposite at least basally, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches acute to conical, with hairs dorsally and apically. Cypselae ellipsoid to turbinate, with elongated twin hairs. Pappus bristles capillary, barbellate, connate in a ring. $n = 8, 10, 11, 13$. Six species, Australia.

692. ***Mniodes*** (A. Gray) Benth. Fig. 61G

Mniodes (A. Gray) Benth. in Benth. & Hook. f., Gen. Pl. 2: 301 (1873); Cuatrecasas, Folia Biol. Andina 1: 1–7 (1954), rev.; Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), rev.

Dioecious, perennial, alpine cushion plants. Leaves alternate, concave to involute with entire margins, tomentose distally with an adaxial hair tuft. Capitula solitary. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Female florets filiform, purple. Male florets purple. Anthers with flat appendages. Style branches obtuse, with hairs dorsally and apically. Cypselae ellipsoid, with globose twin hairs. Pappus bristles capillary, barbellate, connate in a ring. Four species, South America.

693. ***Myriocephalus*** Benth.

Myriocephalus Benth., Enum. Pl. 61 (1837); Short, Austral. Syst. Bot 13: 729–738 (2000), rev.
Hyalolepis A. Cunn. ex DC. (1838).
Elachopappus F. Muell. (1862).

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many, clustered into dense secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle conical, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with elongated twin hairs. Pappus bristles, when present, with flattened axis, barbellate, free. $n = 8, 10, 12, 14$. Ten species, Australia.

694. ***Neotysonia*** Dalla Torre & Harms

Neotysonia Dalla Torre & Harms, Gen. Siphon. 540 (1905); Anderberg, Opera Bot. 104: 1–195 (1991), rev.; Wilson, Short & Orchard, Muelleria 7: 519–524 (1992), nomencl.
Tysonia F. Muell. (1896), nom. illegit.

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts herbaceous, brownish to hyaline, stereome undivided. Receptacle flat, paleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae pandurate, glabrous. Pappus of scales connate into a papery cup. One species, *N. phyllostegia* (F. Muell.) Paul G. Wilson ex J.W. Green, Australia.

695. ***Nestlera*** Spreng.

Nestlera Spreng., Anleit. Kenntn. Gew. 2: 568 (1818); Anderberg & Bremer, Ann. Missouri Bot. Gard. 78: 1061–1072 (1991), rev., phylog.
Columellea N.J. Jacquin (1798).
Stephanopappus Less. (1831).

Perennial herb. Leaves alternate or opposite, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together in dense corymbs. Involucral bracts papery, brown, stereome undivided. Receptacle flat, often paleate. Outer florets radiate, yellow with purple bands. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae cylindrical, with few elongated twin hairs. Pappus of scales, basally connate. $n = 5$.

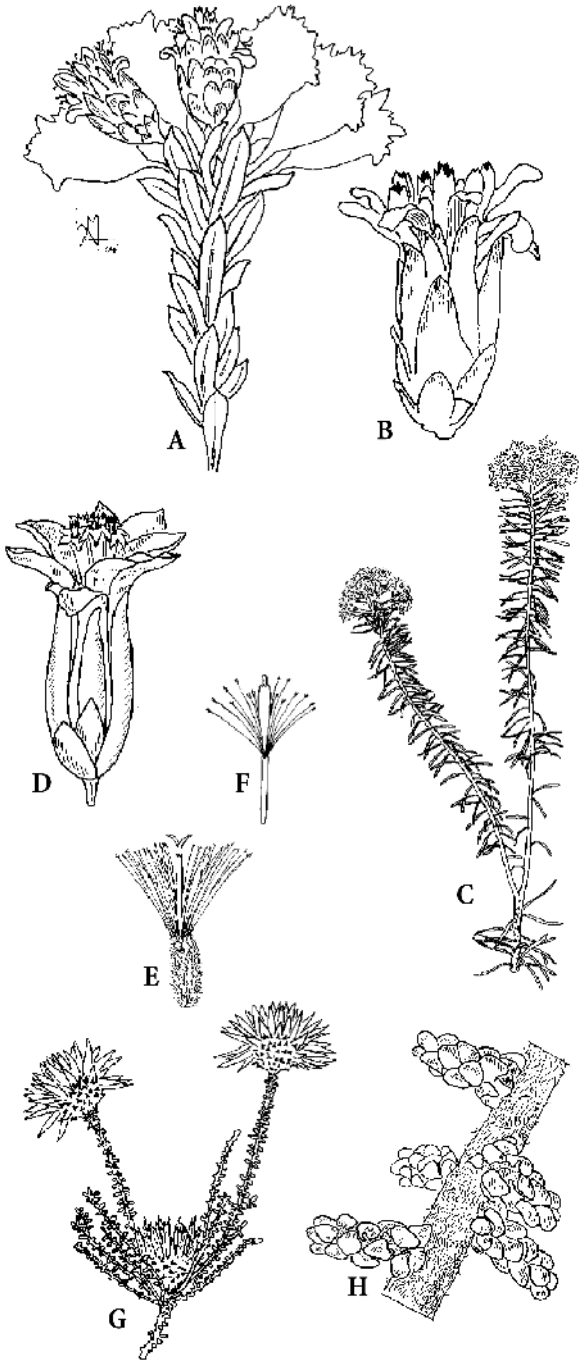

Fig. 66. Compositae-Gnaphalieae. **A**, **B** *Oedera genistifolia*. **A** Flowering branch. **B** Head. **C**, **D** *Odixia achleana*. **C** Flowering branch. **D** Head. **E–H** *Phaenocoma prolifera*. **E** Pistillate (outer) floret. **F** Staminate (central) floret. **G** Flowering branch with old and new heads. **H** Stem with leafy short shoots. (Drawings by William Murray)

One species, *N. biennis* (Jacq.) Spreng., southern Africa.

696. *Odixia* Orchard — Fig. 66C–D

Odixia Orchard, Brunonia 4: 193 (1981); Orchard, Brunonia 4: 185–197 (1981), rev.

Shrubs. Leaves alternate, revolute with entire margins, tomentose on both surfaces. Capitula many in corymbs. Involucral bracts papery, white, stereome undivided. Receptacle conical, paleate or epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with short clavate twin hairs. Pappus absent. Two species, Australia.

697. *Oedera* L. — Fig. 66A–B

Oedera L., Mant. Pl.: 291 (1771); Harvey, Fl. Cap. 3 (1865), reg. rev.; Mansfeld, Kew Bull. 6–9: 422–455 (1935), nomencl.; Anderberg & Källersjö, Bot. J. Linn. Soc. 96: 323–332 (1988), phylog.; Anderberg & Bremer, Ann. Missouri Bot. Gard. 78: 1061–1072 (1991), rev., phylog.
Eroeda Levyns (1948), nom. illegit.

Shrubs. Leaves alternate or opposite, flat with entire margins, densely tomentose on both surfaces. Capitula many in dense corymbs, surrounded by a general involucre of leaves. Involucral bracts papery, brown, stereome undivided. Receptacle flat, paleate. Outer florets radiate, yellow with purple bands. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae cylindrical, glabrous or with few elongated twin hairs. Pappus of short scales, basally connate. $n = 7$. Eighteen species, southern Africa.

698. *Oreoleysera* K. Bremer

Oreoleysera K. Bremer, Bot. Notiser 131: 450 (1978); Bremer, Bot. Notiser 131: 449–453 (1978), rev.; Anderberg & Bremer, Ann. Missouri Bot. Gard. 78: 1061–1072 (1991), rev., phylog.

Shrub. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts papery, brown, stereome undivided. Receptacle flat, epaleate. Outer florets radiate, yellow with purple bands. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae cylindrical, with elongated twin hairs. Pappus of scales and capillary, barbellate, free bristles. One species, *O. montana* (Bolus) K. Bremer, Africa.

699. *Oxylaena* Benth. ex Anderb.

Oxylaena Benth. ex Anderb., Opera Bot. 104: 53 (1991); Bentham, Icon. Pl. ser. 3, 2: 9, pl. 1109 (1873), rev. sub *Anaglypha*; Anderberg, Opera Bot. 104: 1–195 (1991), rev.

Shrub. Leaves alternate, almost flat with revolute entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. Outer florets radiate, yellow. Central florets functionally male, yellow. Anthers with concave appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, glabrous. Pappus absent. One species, *O. acicularis* (Benth.) Anderb., southern Africa.

700. *Ozothamnus* R. Br. Figs. 62A, D, F, 63D, AA

Ozothamnus R. Br., Trans. Linn. Soc. London 12: 125 (1817); Burbidge, Austral. J. Bot. 6: 229–284 (1958), rev.; Breitwieser & Ward, N. Z. J. Bot. 35: 125–128 (1997), reg. rev.; Ward & Breitwieser, N. Z. J. Bot. 36: 165–171 (1998), rev.; Breitwieser et al., N. Z. J. Bot. 37: 399–412 (1999), phylog.
Helichrysum sect. *Ozothamnus* (R. Br.) Benth. (1867).
Helichrysum subg. *Ozothamnus* (R. Br.) N.T. Burb. sect. *Ozothamnus* (R. Br.) Benth. sensu N.T. Burb. (1958).

Shrubs. Leaves alternate, flat, revolute or concave with entire margins, tomentose on both surfaces, abaxially only, or adaxially only. Capitula solitary or many in corymbs. Involucral bracts papery, brownish or hyaline or coloured, stereome undivided. Receptacle flat, usually epaleate. Outer tubular or filiform florets, when present, yellow or white. Central florets perfect, yellow or white. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, ellipsoid, ovoid, obovoid or turbinate, with elongated or short clavate twin hairs, or glabrous. Pappus bristles capillary, scabrid to barbellate, free or connate in a ring or in groups. $n = 14$. About 50 species, Australia, New Zealand, New Caledonia.

701. *Parantennaria* Beauverd

Parantennaria Beauverd, Bull. Soc. Bot. Genève sér. 2: 255 (1911); Beauverd, Bull. Soc. Bot. Genève sér. 2, 3: 253–260 (1911), rev.

Dioecious perennial herb. Leaves alternate, flat with entire margins, glabrous. Capitula solitary. Involucral bracts papery, coloured. Stereome undivided. Receptacle flat, epaleate. Female florets filiform, purple. Male florets purple. Style branches truncate, with hairs dorsally and apically. Cypselae glabrous. Pappus bristles capillary, barbellate, free. One species, *P. uniceps* (F. Muell.) Beauverd, Australia.

702. *Pentatrichia* Klatt

Pentatrichia Klatt, Bull. Herb. Boissier 3: 436 (1895).

Shrubs. Leaves alternate, flat with dentate margins, sparsely tomentose on both surfaces. Capitula solitary or only a few together in lax corymbs. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. Outer radiate florets, when present, yellow or white. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, with few elongated twin hairs. Pappus bristles capillary, few, barbellate, free. Four species, Africa.

703. *Petalacte* D. Don

Petalacte D. Don, Mem. Wern. Nat. Hist. Soc. 5: 552 (1826); Lundgren, Bot. Notiser 127: 119–124 (1974), rev.; Hilliard & Burtt, Taxon 29: 507 (1980), nomencl.; Nordenstam, Ann. Wiener Mus. Naturgesch. 98, B: 403–418 (1996), rev.

Shrub. Leaves alternate, revolute with entire margins, tomentose on both surfaces. Capitula many in dense corymbs. Involucral bracts papery, white, stereome undivided. Receptacle flat, paleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, free. One species, *P. coronata* (L.) D. Don, southern Africa.

704. *Phaenocoma* D. Don Fig. 66E–H

Phaenocoma D. Don, Mem. Wern. Nat. Hist. Soc. 5: 554 (1826); Dyer, The genera of southern African flowering plants (1975), gen. consp.; Hind, Curtis's Bot. Mag. 13: 56–62 (1996), rev.

Shrub. Leaves alternate, minute, flat with entire margins, sparsely tomentose adaxially. Capitula solitary. Involucral bracts papery, pink to rosy purple, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with elongated twin hairs. Pappus bristles capillary, barbellate, basally connate. $n = 8$. One species, *P. prolifera* (L.) D. Don, southern Africa.

705. *Phagnalon* Cass.

Phagnalon Cass., Bull. Sci. Soc. Philom. Paris 1819: 174 (1819); Qaiser & Lack, Willdenowia 15: 3–22 (1985), reg. rev.; Qaiser & Lack, Willdenowia 15: 437–450 (1986), reg. rev.; Lack & Qaiser, Pl. Syst. Evol. 155: 45–48 (1987), reg. rev. *Gnaphalon* Lowe (1868).

Perennial herbs or sometimes shrublets. Leaves alternate, revolute with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts cartilaginous or papery, brownish or hyaline, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally and apically. Cypselae ellipsoid to turbinate, with elongated twin hairs. Pappus bristles capillary, barbellate, connate in a ring. $n = 9$. Forty-three species, western Asia, Europe and northern Africa.

706. *Philyrophyllum* O. Hoffm.

Philyrophyllum O. Hoffm. in Engler & Prantl., Nat. Pflanzenfam. 4: 206, 208 (1890); Herman, Bothalia 29: 107 (1999), reg. rev.

Perennial herb. Leaves alternate, flat with dentate margins, tomentose on both surfaces. Capitula only a few together, in lax corymbs. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, paleate. Outer florets radiate, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, with few elongated twin hairs. Pappus bristles capillary, barbellate, free. Two species, Africa.

707. *Pithocarpa* Lindl.

Pithocarpa Lindl., Bot. Reg., Appendix to vols. 1–23: 23 (1839); Lewis & Summerhayes, Kew Bull. 5: 435–440 (1951), rev.; Lepschi, Nuytsia 13: 61–74 (1999), rev.

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with short clavate twin hairs. Pappus absent. $n = 13$. Two species, Australia.

708. *Planea* P.O. Karis

Planea P.O. Karis, Bot. J. Linn. Soc. 102: 32 (1990); Karis, Opera Bot. 99: 1–150 (1989), rev. sub *Metalasia*; Karis, Bot. J. Linn. Soc. 102: 23–36 (1990), rev.

Shrub. Leaves alternate, twisted, revolute with entire margins, sparsely tomentose adaxially. Capitula many in dense corymbs. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. All florets perfect, purple. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, basally connate. One species, *P. schlechteri* (L. Bolus) P.O. Karis, Africa.

709. *Plecostachys* Hilliard & B.L. Burtt

Plecostachys Hilliard & B.L. Burtt, Bot. J. Linn. Soc. 82: 206 (1981).

Perennial herbs. Leaves alternate, flat with entire margins, sparsely tomentose abaxially. Capitula many in dense corymbs. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with few elongated twin hairs. Pappus bristles capillary, barbellate, free. Two species, South Africa.

710. *Pleuropappus* F. Muell.

Pleuropappus F. Muell., Trans. Proc. Victorian Inst. Advancem. Sci. 1: 37 (1855); Short, Muelleria 5: 143–183 (1983).

Annual herb. Leaves opposite, at least basally, flat with entire margins, tomentose on both surfaces. Capitula many, forming elongated secondary heads. Involucral bracts papery, coloured, stereome undivided. Receptacle peg-like, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with globose hairs without a basal cell. Pappus of jagged-edged scales. One species, *P. phyllocalymmeus* F. Muell., Australia.

711. *Podolepis* Labill.

Podolepis Labill., Nov. Holl. Pl. 2: 56, t. 208 (1806), nom. cons.; Davis, Proc. Linn. Soc. New South Wales 81: 245–286 (1957), rev.; Short, Taxon 35: 610–613 (1986), cytol.
Stylolepis Lehm. (1828).
Panaetia Cass. (1829), pro parte et quoad typum.

Annual herbs. Leaves alternate, flat, tomentose on both surfaces. Capitula solitary or only few together. Involucral bracts papery, brownish, stereome forming two ribs. Receptacle flat, epaleate. Outer florets radiate or shortly radiate, yellow. Central florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with globose hairs without a basal cell, and one cell overtopping the other. Pappus bristles capillary, barbellate, free. n = 3, 7, 8, 9, 10, 11, 12, 20. Twenty species, Australia.

712. *Podotheca* Cass.

Podotheca Cass., Dict. Sci. Nat. 23: 561 (1822), nom. cons.; Short, Muelleria 7: 39–56 (1989), reg. rev.
Podosperma Labill. (1806), nom. rej.

Annual herbs. Leaves opposite, at least basally, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts green, herbaceous, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches acute to conical, with hairs apically. Cypselae ellipsoid to turbinate, obovoid, with elongated twin hairs. Pappus bristles with flattened axis, distinctly plumose, connate in a ring. n = 13, 14, 26. Six species, Australia.

713. *Pogonolepis* Steetz

Pogonolepis Steetz in Lehm., Pl. Preiss. 1: 440 (1845); Short, Muelleria 5: 185–214 (1983), rev.; Short, Muelleria 6: 237–253 (1986), rev.
Skirrophorus sect. *Pogonolepis* (Steetz) A. Gray (1851).

Annual herbs. Leaves alternate or opposite, at least basally, flat with entire margins, tomentose on both surfaces. Capitula forming dense secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with globose twin hairs without a basal cell. Pappus absent. n = 4, 5, 12. Two species, Australia.

714. *Polycalymma* F. Muell. & Sond.

Polycalymma F. Muell. & Sond. in Sond., Linnaea 25: 494 (1853); Short, Wilson & Nailon, Muelleria 7: 57–79 (1989), fruit morph.

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in dense terminal clusters. Involucral bracts papery, hyaline, stereome undivided. Receptacle conical, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with elongated twin hairs. Pappus bristles with flattened axis, subplumose, barbellate, free. n = 14. Three species, Australia.

715. *Pseudognaphalium* Kirp. Fig. 62B, 63T

Pseudognaphalium Kirp. in Kirp. & L.A. Kuprijanova, Trudy Bot. Inst. Akad. Nauk S.S.S.R. ser. 1, Fl. Sist. Vyssh. Rast. 9: 33 (1950); Standley, Field Mus. Nat. Hist. 18: 1419–1538 (1938), reg. rev.; D'Arcy, Ann. Missouri Bot. Gard. 62: 1033–1053 (1975), reg. rev.; Nash, Fieldiana, Bot. 24: 164–181 (1976), reg. rev.; Hilliard & Burtt, Bot. J. Linn. Soc. 82: 181–232 (1981), gen. consp.

Perennial, biennial or annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in corymbs. Involucral bracts papery, coloured, stereome divided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, barbellate, free. n = 8, 9, 10, 14, 20. About 90 species, Africa, Asia, Central, North and South America, New Zealand.

716. *Psilocarphus* Nutt.

Psilocarphus Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 340 (1841); Morefield, Madroño 39: 155–157 (1992), reg. rev.

Annual herbs. Leaves opposite, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts cartilaginous, hyaline, stereome undivided. Receptacle peg-like, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with concave appendages. Style branches with much prolonged apex, with hairs dorsally. Cypselae oblong, with short clavate twin hairs. Pappus bristles mostly absent. n = 14. Eight species, North and South America.

717. *Pterochaeta* Steetz

Pterochaeta Steetz in Lehm., Pl. Preiss. 1: 456 (1845); Wilson, Nuytsia 8: 379–438 (1992), rev.

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in loose racemes. Involucral bracts papery,

coloured, stereome forming two ribs. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, distinctly plumose, free. $n = 12$. One species, *P. paniculata* Steetz, Australia.

718. *Pterothrix* DC.

Pterothrix DC., Prodr. 6: 279 (1838); Brusse, Bothalia 20: 67–70 (1990), reg. rev.; Koekemoer, Bothalia 29: 65–75 (1999), rev.

Shrubs. Leaves alternate, flat to twisted with entire margins, sparsely tomentose adaxially. Capitula solitary or only a few together in dense corymbs. Involucral bracts papery, brown, stereome undivided. Receptacle flat, epaleate. All florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, plumose, basally connate. Six species, Africa.

719. *Pterygopappus* Hook. f.

Pterygopappus Hook. f., London J. Bot. 6: 120 (1847); Breitwieser, Bot. J. Linn. Soc. 111: 183–209 (1993), leaf anat.

Perennial, alpine cushion plant. Leaves alternate, concave with entire margins, with an adaxial tuft of stiff hairs. Capitula solitary, terminal. Involucral bracts papery, pale brown, stereome undivided. Receptacle flat, epaleate. Outer florets tubular, purple. Central florets male, purple. Anthers with flat appendages. Style branches truncate, undivided, with hairs apically. Cypselae vestigial. Outer cypselae obovate, with elongated twin hairs. Pappus bristles capillary, plumose, free. $n = 14$. One species, *P. lawrencei* Hook. f., Australia.

720. *Pycnosorus* Benth.

Pycnosorus Benth., Enum. Pl. 63 1837; Everett & Doust, Telopea 5: 39–43 (1992), rev.

Perennial or annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many, forming very dense, globose, secondary heads. Involucral bracts papery, coloured, stereome undivided. Receptacle peg-like, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style apices truncate, with hairs apically. Cypselae obovoid, with elongated twin hairs. Pappus bristles with flattened axis, plumose, connate in a ring. $n = 6, 10$. About six species, Australia.

721. *Quinetia* Cass.

Quinetia Cass., Dict. Sci. Nat. 60: 590 (1830); Anderberg, Opera Bot. 104: 1–195 (1991), rev.

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. All florets perfect, purple. Anthers with flat appendages. Style branches acute to conical, with hairs apically. Cypselae turbinate, with elongated twin hairs. Pappus of scale-like bristles, free. $n = 12$. One species, *Q. urvillei* Cass., Australia.

722. *Quinqueremulus* Paul G. Wilson

Quinqueremulus Paul G. Wilson, Nuytsia 6: 1 (1987); Wilson, Nuytsia 6: 1–5 (1987), rev.

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many, forming loose secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid with five large ligulate outgrowths at the apex, and with elongated twin hairs. Pappus, in the conventional sense, absent. One species, *Q. linearis* Paul G. Wilson, Australia.

723. *Rachelia* J.M. Ward & Breitw.

Rachelia J.M. Ward & Breitw., N. Z. J. Bot. 35: 145 (1997); Ward, Breitwieser & Lovis, N. Z. J. Bot. 35: 145–154 (1997), rev.; Breitwieser et al., N. Z. J. Bot. 37: 399–412 (1999), phylog.

Perennial herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary in axils of uppermost leaves. Involucral bracts papery, brownish, stereome undivided. Receptacle conical, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae fusiform, with projecting papillae, twin hairs absent. Pappus bristles capillary, scabrid, connate in groups. $x = 14$. One species, *R. glaria* J.M. Ward & Breitw., New Zealand.

724. *Raoulia* Hook. f. Fig. 61A, B

Raoulia Hook. f. in Raoul, Choix Pl. Nouv.-Zél. 20 (1846); Beauverd, Bull. Soc. Bot. Genève sér. 2, 4: 12–55 (1912), rev.; Ward, Mauri Ora 10: 11–19 (1982), rev.; Ward, J. Canty Bot. Soc. 16: 33–41 (1982), rev.; Ward, N. Z. J. Bot. 31:

21–28 (1993), morph.; Ward, N. Z. J. Bot. 31: 29–42 (1993), morph.; Breitwieser & Ward, Bot. J. Linn. Soc. 126: 217–235 (1998), leaf anat.; Ward, Etienne Raoul and Canterbury botany 1840–1996: (1998), history; Ward & Breitwieser, N. Z. J. Bot. 36: 165–171 (1998), rev.; Breitwieser et al., N. Z. J. Bot. 37: 399–412 (1999), phylog.
Psychrophyton Beauverd (1910).

Perennial mat-forming herbs or alpine cushion plants. Leaves alternate, flat or concave with entire margins, generally tomentose on both surfaces. Capitula solitary, sessile, terminal. Involucral bracts papery, brownish, hyaline or coloured, stereome undivided. Receptacle usually flat, epaleate. Outer florets filiform or tubular, yellow, white or purple. Central florets generally perfect, yellow, white or purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae generally oblong to obovoid, with elongated or short clavate or globose twin hairs, or rarely glabrous. Pappus bristles capillary, scabrid or barbellate, connate in groups or free. n = 14, 28, 42, 56. Twenty-three species, New Zealand.

725. *Raouliopsis* S.F. Blake

Raouliopsis S.F. Blake, J. Wash. Acad. Sci. 28: 173 (1938); Blake, J. Wash. Acad. Sci. 28: 172–177 (1938), rev.

Perennial, alpine cushion plants. Leaves alternate, concave to involute with entire margins, tomentose distally with an adaxial hair tuft. Capitula solitary, sessile. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally. Cypselae ellipsoid, glabrous. Pappus bristles capillary, barbellate, connate in a ring. Two species, South America.

726. *Relhania* L'Herit. Fig. 63G

Relhania L'Herit., Sert. Angl. 1: 24 (1789), nom. cons.; Bremer, Opera Bot. 40: 1–86 (1976), rev.; Bremer, Taxon 25: 207–208 (1976), nomencl.; Bremer, Taxon 28: 411–412 (1979), nomencl.; Anderberg & Bremer, Ann. Missouri Bot. Gard. 78: 1061–1072 (1991), rev., phylog.

Shrubs. Leaves alternate or opposite, flat with entire margins, glabrous or sparsely tomentose on both surfaces. Capitula solitary or many in dense corymbs. Involucral bracts papery, brown, stereome undivided. Receptacle flat to conical, often paleate. Outer florets radiate, yellow with purple bands. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae cylindrical, glabrous or with few elongated twin hairs. Pappus a crown of free scales. n = 5, 7. Thirteen species, southern Africa.

727. *Rhodanthe* Lindl. Fig. 63A, F, R

Rhodanthe Lindl., Bot. Reg. 1703 (1834); Wilson, Nuytsia 8: 379–438 (1992), rev.
Pteropogon A. Cunn. ex DC. (1838).
Roccardia Neck. ex Voss (1896), nom. illegit., non Raf. (1838).
Xyridanthe Lindl. (1839).
Acroclinium A. Gray (1852).
Helichrysum sect. *Rhodanthe* (Lindl.) Baill. (1886).

Annual herbs, one species a perennial. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, coloured, stereome undivided. Receptacle conical, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with elongated twin hairs. Pappus bristles with flattened axis, plumose, connate in a ring. n = 5, 7, 8, 10, 11, 14. Forty-three species, Australia.

728. *Rhynchopsidium* DC.

Rhynchopsidium DC., Mém. Soc. Phys. Genève 7: 283 (1836); Anderberg & Bremer, Ann. Missouri Bot. Gard. 78: 1061–1072 (1991), rev., phylog.
Rhynchocarpus Less. (1832), nom. illegit.

Annual herbs. Leaves alternate or opposite, flat with entire margins, glabrous or sparsely tomentose on both surfaces. Capitula solitary. Involucral bracts papery, brown, stereome undivided. Receptacle flat, paleate. Outer florets radiate, yellow with purple bands. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with elongated twin hairs. Pappus of scales, basally connate or free. n = 5. Two species, Africa.

729. *Rosenia* Thunb.

Rosenia Thunb., Nova Gen. Pl. 161 (1800); Bremer, Bot. Notiser 129: 97–111 (1976), rev.; Anderberg & Bremer, Ann. Missouri Bot. Gard. 78: 1061–1072 (1991), rev., phylog.
Polychaetia Less. (1832).

Shrubs. Leaves alternate or opposite, recurved with entire margins, tomentose on both surfaces. Capitula solitary or only a few together in dense corymbs.

Involucral bracts papery, brown, stereome undivided. Receptacle flat, often paleate. Outer florets radiate, yellow with purple bands dorsally. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae cylindrical, with few elongated twin hairs. Pappus of scales and a few, free, barbellate, capillary bristles. $n = 7, 14, 28$. Four species, southern Africa.

730. *Rutidosis* DC. Fig. 63H

Rutidosis DC., Prodr. 6: 158 (1838); Holland, Austrobaileya 4: 199–203 (1994), reg. rev.; Holland, Austrobaileya 5: 565–572 (1999), rev.

Perennial or annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts papery, brownish, stereome divided. Receptacle conical, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches with much prolonged apex, with hairs dorsally. Cypselae ellipsoid, with globose hairs without a basal cell. Pappus of scale-like bristles or broad scales, free. $n = 11, 12, 13, 19, 21, 22, 23, 26, 33, 36$. Nine species, Australia.

731. *Schoenia* Steetz

Schoenia Steetz in Lehm., Pl. Preiss. 1: 480 (1845); Wilson, Nuytsia 8: 361–377 (1992), rev.
Xanthochrysum Turcz. (1851).

Annual herbs. Leaves opposite at least basally, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, white or pink, stereome undivided. Receptacle flat, epaleate. Florets perfect, innermost functionally male, yellow. Anthers with concave appendages. Style branches acute to conical, with hairs dorsally. Cypselae obovoid, with elongated twin hairs. Pappus bristles capillary, barbellate, free. $n = 12$. Three species, Australia.

732. *Scyphocoronis* A. Gray

Scyphocoronis A. Gray, Icon. Pl. t. 854 (1851); J. Bot. Kew Gard. Misc. 4: 225 (1852); Cooke, J. Adelaide Bot. Gard. 7: 273–287 (1985), reg. rev.; Short, Austral. Syst. Bot. 8: 1–47 (1995), rev.; Short & Anderberg, Austral. Syst. Bot. 8: 49–55 (1995), phylog.

Annual herbs. Leaves alternate or opposite at least basally, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous, greenish, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches conical, with hairs dorsally. Cypselae turbinate, with elongated twin hairs. Pappus rudimentary, a small cartilaginous crown. Two species, Australia.

733. *Siloxerus* Labill.

Siloxerus Labill., Nov. Holl. pl. 2: 57 (1806); Short, Muelleria 5: 185–214 (1983b), rev.; Short, Austral. Syst. Bot. Soc. Newslett. 78: 6–7 (1994), rev.
Styloncerus Spreng. (1818), nom. illegit.
Gyrostephium Turcz. (1851).

Annual herbs. Leaves opposite at least basally, filiform with entire margins, tomentose on both surfaces. Capitula many, forming dense secondary heads. Involucral bracts papery, hyaline, stereome undivided. Receptacle conical, paleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, with globose hairs without a basal cell. Pappus bristles scale-like, free. Three species, Australia.

734. *Sinoleontopodium* Y.L. Chen

Sinoleontopodium Y.L. Chen, Acta Phytotax. Sin. 23: 457 (1985); Chen, Acta Phytotax. Sin. 23: 457–459 (1985), rev.

Dioecious, perennial, alpine cushion plant. Leaves alternate, concave to involute with entire margins, tomentose distally with an adaxial hair tuft. Capitula solitary, sessile. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Female florets filiform, yellow. Male florets yellow. Anthers with flat appendages. Style branches obtuse, with hairs dorsally and apically. Cypselae turbinate, glabrous. Pappus bristles capillary, barbellate, free. One species, *S. lingianum* Y.L. Chen, eastern Asia.

735. *Sondottia* P.S. Short

Sondottia P.S. Short, Muelleria 7: 113 (1989); Short, Muelleria 7: 103–116 (1989), rev.

Annual herbs. Leaves opposite, flat with entire margins, tomentose on both surfaces or glabrous. Capitula many in dense secondary heads. Involucral bracts cartilaginous, brownish-green or hyaline, stereome undivided. Receptacle flat, epaleate. Floret solitary, perfect, yellow. Style branches truncate, with hairs apically. Cypselae obovoid, glabrous except for long apical hairs. Pappus scale-like, connate in a laciniate cup. $n = 3$. Two species, Australia.

736. *Stenocline* DC.

Stenocline DC., Prodr. 6:218 (1838).

Shrublets. Leaves alternate, flat or revolute with entire margins, tomentose. Capitula many in corymbs. Involucral bracts papery, white or yellowish, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, glabrous. Pappus bristles capillary, barbellate, free. Three species, Madagascar and (?)Mauritius.

737. *Stenophalium* Anderb.

Stenophalium Anderb., Opera Bot. 104: 141 (1991); Robinson, Phytologia 55: 121–126 (1984), rev. sub *Stenocline*; Anderberg, Opera Bot. 104: 1–195 (1991), rev.

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together, in terminal corymbs. Involucral bracts papery, white, stereome divided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, glabrous. Pappus bristles capillary, barbellate, cohering by patent cilia. Three species, South America.

738. *Stoebe* L.

Stoebe L., Sp. Pl. 831 (1753); Levyns, J. S. African Bot. 3: 1–35 (1937), rev.; Dyer, The genera of southern African flowering plants (1975), gen. consp.; Nogueira, Bol. Soc. Brot. 51: 127–133 (1977), reg. rev.
Seriphium L. (1753).

Shrubs. Leaves alternate, twisted, revolute, with entire margins, sparsely tomentose adaxially. Capitula solitary or only a few together, in dense corymbs or spikes. Involucral bracts cartilaginous, stereome undivided. Receptacle flat, epaleate. All florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, glabrous. Pappus bristles capillary, plumose, basally connate, or rarely absent. n = 8. Thirty-four species, Africa, Madagascar and La Réunion.

739. *Stuartina* Sond.

Stuartina Sond., Linnaea 25: 521 (1853); Aston & Cooke, Muelleria 6: 255–257 (1986), rev.

Annual herbs. Leaves alternate, spathulate, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts cartilaginous, brownish, stereome undivided. Receptacle conical, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae oblong, glabrous. Pappus absent. Two species, Australia.

740. *Stuckertiella* Beauverd

Stuckertiella Beauverd, Bull. Soc. Bot. Genève sér. 2, 5: 205 (1913); Beauverd, Bull. Soc. Bot. Genève sér. 2, 5: 205–209 (1913), rev.; Dillon & Sagástegui-Alva, Fieldiana, Bot. n.s. 26: 1–70 (1991), reg. rev.

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together, in terminal clusters. Involucral bracts papery, brownish, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with globose twin hairs. Pappus bristles capillary, barbellate, connate in a ring. Two species, South America.

741. *Stylocline* Nutt.

Stylocline Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 338 (1840); Wagenitz, Oesterr. Bot. Z. 119: 399–403 (1971), rev.; Morefield, Madroño 39: 114–130 (1992), rev.

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts cartilaginous, hyaline, stereome undivided. Receptacle peg-like, epaleate. Outer florets filiform, purple. Central florets functionally male, purple. Anthers with concave appendages. Style branches with much prolonged apex, with hairs dorsally. Cypselae oblong, glabrous. Pappus bristles capillary, scabrid, free. n = 14. Seven species, North America.

742. *Syncarpha* DC.

Syncarpha DC., Ann. Mus. Natl Hist. Nat. 16: 205 (1810); Nordenstam, Comp. Newslett. 17: 2–6 (1989), rev.
Anaxeton Schrank (1824), nom. illegit. non Gaertn. (1791).
Helipterum DC., pro parte (typ. non design.) (1838), nom. illegit.
Roccardia Neck. ex Voss (1894).

Perennial herbs. Leaves alternate, flat with entire margins, densely tomentose on both surfaces. Capitula solitary or only a few together, in lax

corymbs. Involucral bracts papery, yellow, pink or brown, stereome undivided or divided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with globose twin hairs. Pappus bristles capillary, plumose or barbellate, basally connate. $n = 7, 11$. Twenty-five species, southern Africa.

743. *Syncephalum* DC.

Syncephalum DC., Prodr. 6: 282 (1838).

Shrubs. Leaves alternate, flat with entire margins, tomentose abaxially or on both surfaces. Capitula many in corymbs. Involucral bracts papery, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with short clavate twin hairs. Pappus absent. Five species, Madagascar.

744. *Taplinia* Lander

Taplinia Lander, Nuytsia 7: 37 (1989); Anderberg, Opera Bot. 104: 1–195 (1991), rev.; Lander, Nuytsia 7: 37–42 (1989), rev.

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many in terminal panicles composed of many small corymbs. Involucral bracts cartilaginous, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow below, purple above. Style branches truncate, with hairs apically. Cypselae ellipsoid, with appressed twin hairs. Pappus bristles capillary, barbellate, free. One species, *T. saxatilis* Lander, Australia.

745. *Tenrhynea* Hilliard & B.L. Burtt

Tenrhynea Hilliard & B.L. Burtt, Bot. J. Linn. Soc. 82: 232 (1981).
Rhynea DC. (1838), nom. illegit., non Scopoli (1777).

Perennial herb. Leaves alternate, flat with entire margins, sparsely tomentose abaxially. Capitula many in dense corymbs. Involucral bracts papery, white or pink, stereome undivided. Receptacle flat, paleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with few elongated twin hairs. Pappus bristles capillary, barbellate, free. One species, *T. phylicifolia* (DC.) Hilliard & B.L. Burtt, Africa.

746. *Thiseltonia* Hemsl.

Thiseltonia Hemsl., Icon. Pl. t. 2781 (1905); Wilson, Nuytsia 8: 479–483 (1992), rev.

Annual herb. Leaves alternate, filiform with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts papery, white or yellow, stereome undivided. Receptacle conical, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae obovoid, glabrous. Pappus absent. One species, *T. gracillima* (F. Muell. & Tate) Paul G. Wilson, Australia.

747. *Tietkensia* P.S. Short

Tietkensia P.S. Short, Muelleria 7: 248 (1990); Short, Muelleria 7: 239–252 (1990), rev.

Rosulate annual herb. Leaves basal, flat with entire margins, tomentose on both surfaces. Capitula many in dense secondary heads surrounded by leaves. Involucral bracts papery, brownish-green or hyaline, stereome undivided. Receptacle flat, paleate. Outer florets filiform, yellow. Central florets perfect, yellow or purplish. Style branches truncate. Cypselae obovoid, with minute hairs. Pappus absent. One species, *T. corrickiae* P.S. Short, Australia.

748. *Toxanthes* Turcz.

Toxanthes Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 176 (1851); Short, Austral. Syst. Bot. 8: 1–47 (1995), rev.; Short & Anderberg, Austral. Syst. Bot. 8: 49–55 (1995), phylog.
Anthocerastes A. Gray (1852).

Annual herbs. Leaves alternate throughout or opposite at least basally, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts cartilaginous, greenish-brown, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches conical, with hairs dorsally and apically. Cypselae narrowly turbinate, with elongated twin hairs. Pappus absent. Three species, Australia.

749. *Trichanthodium* Sond. & F. Muell.

Trichanthodium Sond. & F. Muell. in Sond., Linnaea 25: 489 (1853); Short, Muelleria 7: 213–224 (1990), rev.

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula many, forming secondary heads on terminal branches. Involucral bracts cartilaginous, hyaline, stereome undivided. Receptacle flat, epaleate. All florets perfect, yellow. Style branches truncate. Cypselae obovoid, glabrous. Pappus scale-like, connate in a ring. n = 3, 4, 7. Four species, Australia.

750. *Trichogyne* Less.

Trichogyne Less., Linnaea 6: 231 (1831); Hilliard, Bot. J. Linn. Soc. 82: 293–312 (1981), rev.; Beyers, Bothalia 25: 107–109 (1995), reg. rev.

Perennial herbs. Leaves alternate, almost flat with involute margins, sparsely tomentose adaxially. Capitula only a few together, in spikes. Involucral bracts papery, brownish, stereome divided. Receptacle flat, paleate. Outer florets filiform, purple. Central florets functionally male, yellow. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, plumose, free. Eight species, South Africa.

751. *Triptilodiscus* Turcz. Fig. 63J

Triptilodiscus Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 66 (1851); Wilson, Nuytsia 8: 379–438 (1992), rev.
Dimorpholepis A. Gray (1851).

Annual herb. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts papery, brownish, inner bracts cartilaginous, stereome divided. Receptacle conical, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with concave appendages. Style branches truncate, with hairs apically. Cypselae ellipsoid, with globose hairs without a basal cell. Pappus bristles plumose, with flattened axis, free. n = 10. One species, *T. pygmaeus* Turcz., Australia.

752. *Troglophyton* Hilliard & B.L. Burtt

Troglophyton Hilliard & B.L. Burtt, Bot. J. Linn. Soc. 82: 208 (1981).

Annual or perennial herbs. Leaves alternate, flat with entire margins, sparsely tomentose on both surfaces. Capitula solitary or only a few together, in dense corymbs. Involucral bracts papery, white, stereome divided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong with few short clavate twin hairs. Pappus bristles capillary, barbellate, free. Six species, southern Africa.

753. *Vellereophyton* Hilliard & B.L. Burtt

Vellereophyton Hilliard & B.L. Burtt, Bot. J. Linn. Soc. 82: 210 (1981).

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula only a few together. Involucral bracts papery, white, stereome divided. Receptacle flat, epaleate. Outer florets filiform, purple. Central florets perfect, purple. Anthers with flat appendages. Style branches truncate, with hairs apically. Cypselae oblong, with short clavate twin hairs. Pappus bristles capillary, barbellate, free. Seven species, southern Africa.

754. *Waitzia* J.C. Wendl.

Waitzia J.C. Wendl., Coll. Pl. 2: 13 (1808); Wilson, Nuytsia 8: 461–477 (1992), rev.

Annual herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, coloured, stereome forming two ribs. Receptacle flat, epaleate. All florets perfect, yellow. Anthers with concave appendages. Style branches conical, with hairs apically. Cypselae ellipsoid to turbinate, with globose hairs without a basal cell, and one cell overtopping the other. Pappus bristles capillary, barbellate, free. n = 10, 12. Seven species, Australia.

755. *Xerochrysum* Tzvelev Figs. 61E, 63I

Xerochrysum Tzvelev, Novosti Sist. Vyssh. Rast. 27: 151 (1990); Bayer, Kew Bull. 56: 1013–1015 (2001), nomencl.
Bracteantha Anderb. & Haegi in Anderb. (1991), nom. superfl.

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary or only a few together. Involucral bracts papery, coloured, stereome undivided. Receptacle flat, epaleate. Outer florets filiform, yellow. Central florets perfect, yellow. Anthers with concave appendages. Style branches acute, with hairs dorsally. Cypselae quadrangular, glabrous. Pappus bristles capillary, barbellate, free. n = 11, 12, 13, 14, 15. Six species, Australia.

Recently Described Genera not Included in the Key and Descriptions

Argyrotegium J.M. Ward & Breitw., N. Z. J. Bot. 41: 603–611 (2003).

Segregate of *Euchiton*. Four species, New Zealand, Australia.

Castroviejoa Galbany, L. Sáez & C. Benedí, Austral. Syst. Bot. 17: 581–591 (2004).

Segregate of *Helichrysum*. Two species, Corsica, Sardinia.

Leiocarpa P.G. Wilson, Nutysia 13: 595–605 (2001).

Formerly species of *Chrysocephalum*, *Ixiolaena*, *Leptorhynchos*. Ten species, Australia.

XV. Tribe Astereae Cass. (1819).

G. Nesom and H. Robinson

Annual or perennial herbs, subshrubs, shrubs, rarely small trees or vines, rarely partially or totally dioecious. Leaves usually alternate, opposite in a few African and Australian genera, blades simple to pinnately divided. Heads solitary or in corymbose, thyrsoid, spicate, racemose or cyme-shaped cymes, sometimes with modified secund branches; involucral bracts in (2–)3–5(–9) series, gradate to nearly equal in length, narrow, apices acute or rounded, often herbaceous, usually persistent and reflexed, sometimes caducous; receptacles flat or convex to conic or cyathiform, usually alveolate or foveolate, usually glabrous, sometimes fimbriate or with small to large pales. Ray florets in 1–2 (to many) series; corolla of ray florets usually 3–5-veined, apically acute to truncate or dentate, with yellow or white to blue limb, sometimes reduced to tube or ray florets absent; style branches supinate. Disc florets perfect and fertile or functionally male; corollas narrowly tubular or funnelform or with limb abruptly ampliate, rarely asymmetric, lobes usually 5(–4), short and erect to spreading and sharply recurved or long and recurved-coiling; thecae bases truncate or slightly auricular, rarely tailed or slightly calcarate; apical appendage flat, lanceolate, usually eglandular, rarely lacking. Pollen c. 25-µm diam. in fluid; spherical; tricolporate and echinate, with thin perforated tectum continuous between colpi. Style arms pronate (erect or convergent) at maturity, spreading radially, with separate lateral stigmatic lines and lanceolate to deltoid apical appendages, inner surface between stigmatic lines and on appendages glabrous, outer surface with sweeping hairs which are short-papillose to longer with rounded or less often pointed apices. Achenes laterally compressed and 2-nerved or angular to nearly terete and multinerved, rarely obcompressed (dorsiventrally compressed), surfaces usually with setulae, often with glands, tips of setulae often spreading or anchor-shaped, cells of achene wall usually with raphids, without phytomelanin; carpopodium usually annular; pappus usually of 1–3 or 4 series of barbellate or rarely plumose bristles, persistent or basally caducous, outer or all segments sometimes reduced to scales or awns, or pappus totally lacking.

Base chromosome number $x = 9$, reduced to $x = 8, 7, 6, 5, 3$ and 2. Variation between $x = 4, 5$ and 9 often by dysploid reduction. Limited data by Herz (1977) indicate the presence of various flavonoids, benzofurans and coumarins, unidentified alkaloids, acetylenes with methyltriyne endgroups and some matricaria esters. No pentaynene acetylenes have been found, and sesquiterpene lactones are absent or rare, which is correlated with the rarity of large non-glutinous glandular punctuations. Diterpenoids are most common in Machaerantherinae and Solidagininae, clerodanes and labdanes in many genera with glutinous or viscid leaf surfaces. Clerodanes are also common in roots of *Solidago*, triterpenoids and sterols in many members of the tribe, distinctive Baccharis-oxide is characteristic of some *Baccharis*, and shionone is found in some Asterinae.

The tribe Astereae occurs widely in temperate and tropical parts of the World. It comprises c. 3,080 species in 205 genera (in the present account); the difference in species number from a previous estimate of c. 3,100 (Nesom 1994c) primarily reflects an increase in the estimated number of species in *Olearia* (Lander 1994) and a lower, more accurate estimate for *Baccharis* (fide D. Giuliano, pers. comm.).

Astereae are part of the large subfamily Asteroideae sensu stricto. Their echinate, tricolporate, caveate pollen is characteristic of the non-Anthemidean members of that group. The closest relationship seems to be to Gnaphalieae and possibly Anthemideae. Characteristic for the tribe are the essentially ecaudate non-calcarate bases of the anthers, the totally separated stigmatic lines of the style, and the short to elongate, basically triangular

style appendages which are glabrous on the inside and have sweeping hairs or papillae on the outside. Astereae completely lack phytomelanins in the achene wall, which occur in most of the helianthoid genera. Astereae was one of the tribes originally recognized by Cassini (1819), and it has been recognized in essentially all treatments since then (Bentham 1873a; Hoffmann 1894; Cronquist 1955; Bremer 1994). There have been few problems of delimitation, but the tribe now includes *Olivaea* (De Jong and Beaman 1963), once in Helenieae, *Geissolepis* (Robinson and Brettell 1972), *Rigiopappus* (Robinson and Brettell 1973b) and *Sheareria* (Robinson 1981), once in Heliantheae, *Plagiocheilus* (Robinson and Brettell 1973d), once in Anthemideae, and *Novenia* (Nesom 1994c), once in *Lucilia* of Inuleae-Gnaphalieae. A major DNA study by Noyes and Rieseberg (1999) is the general basis for the order of subtribes followed here, with the last nine subtribes forming a North American clade having a single origin. Revisions in Nesom (1994c, 2000a) are the primary basis for the subtribal limits followed here, although the DNA data suggest that some of the basal subtribes, such as Asterinae, Brachyscominae, Hinterhuberinae and Podocominae, are somewhat artificial (Noyes and Rieseberg 1999; Lowrey and Urbatsch 2003). Particularly notable revisions of generic limits are those of *Aster* (Nesom 1994d) and *Haplopappus* (Lane and Hartman 1996). More complete descriptions of the genera in North America, Central America, the Antilles, and Hawaii can be found in Nesom (2000b). The ETS and ITS study by Roberts and Urbatsch (2004) shows where further generic revisions may be needed in Solidagininae.

Key to the Subtribes and Unplaced Genera

1. Heads of two types usually on different plants, dioecious or rarely monoecious 2
– Heads of one type 3
2. Achenes compressed **2. Hinterhuberinae** (*Aztecaster*)
– Achenes prismatic **7. Baccharidinae** (p. 310)
3. Anther bases spurred; style base bulbiform **17. *Vernoniopsis***
– Anther bases not spurred, shortly rounded, or rarely tailed; style base not or rarely broadened 4
4. Limbs of ray florets, when obvious, usually yellow or white; achenes often terete to fusiform (compressed in most *Ericameria*) 5
– Limbs of ray florets elongate and bluish to purplish or white, or limbs commonly reduced or lacking; achenes usually somewhat compressed 17
5. Style appendages of fertile disc florets hairy; involucral bracts usually thickened or keeled (Machaerantherinae and Chrysopsidinae) or not keeled (*Ericameria*) 6
– Style appendages of fertile disc florets papillose, rarely hairy; involucral bracts flattened, not keeled 8
6. Teeth and apices of leaves and involucral bracts often spinulose-tipped; pappus series often gradate; $x = 6$ and reduced **13. Machaerantherinae** p.p. (p. 328)
– Teeth and apices of leaves and involucral bracts not spinulose-tipped; inner pappus distinctly longer than outer, or pappus of equal length or nearly so; $x = 9$ and reduced 7
7. Shrubs; pappus of equal length or nearly so; $x = 9$ **758. *Ericameria***
– Herbs; inner pappus distinctly longer than outer; $x = 9$ and reduced **17. Chrysopsidinae** (p. 337)
8. Pappus (1–)2(–3)-seriate; leaves often tomentose below 9
– Pappus 1-seriate; leaves with little or no tomentum 11
9. Plants in most parts of Southern Hemisphere to Hawaii and Mexico **2. Hinterhuberinae** (p. 294)
– Shrubs or trees of St. Helena 10
10. Plants with pale hairs **756. *Commidendron***
– Plants with hairs often blackish **763. *Melanodendron***
11. Herbs to subshrubs; leaves usually sessile; mostly American 12
– Shrubs or subshrubs; leaves usually petiolate; Asian or African 14
12. Involucral bracts usually gradate, outer not or rarely leaf-like **10. Solidagininae** (p. 320)
– Involucral bracts subequal, at least outer leaf-like 13
13. Florets trimorphic, outer pistillate radiate, median pistillate; disc florets functionally male **765. *Nannoglottis***
– Florets dimorphic, radiate and disc; disc florets perfect **771. *Tonestus***
14. Disc florets with lobes unequal, outer three lobes longer **761. *Heteroplexis***
– Disc florets with lobes equal 15
15. Plants not glutinous; leaf venation strongly ascending or sublongitudinal; disc florets perfect **764. *Microglossa***
– Plants glutinous; leaves with veins single or pinnate; disc florets functionally male 16
16. Leaf venation pinnate; pappus bristles shortly united at base; ray florets in several series **768. *Psiadia***
– Leaves 1-nervate; pappus of scales; ray florets 1 or 2 **769. *Psiadiella***
17. Appendages of disc floret styles narrowly oblong to oblanceolate, longer than the stigmatic lines **11. Pentachaetinae** (p. 326)
– Appendages of disc styles deltate to lanceolate, shorter than the stigmatic lines 18
18. Involucral bracts with orange-resinous ribs or veins 19
– Involucral bracts without prominent resinous veins 22
19. Lower leaves reduced to scales; limb of disc corolla ampliate; rays few, limbs not coiling **757. *Doellingeria***
– Lower leaves usually larger than upper; limb of disc corolla variously shaped 20
20. Achenes terete or compressed with wings; involucral bracts with tips rounded or obtuse; rays coiling **12. Boltoniinae** (p. 327)

– Achenes compressed, not winged; involucral bracts with tips mostly acute; rays coiling or straight 21
21. Receptacle without obvious pales, sometimes with small scales; pistillate florets without pappus and with rigid, narrowly urceolate corollas **18. Conyzinae** (p. 339)
– Receptacle with pales peripherally grading into small scales on disc; pistillate florets with pappus; corollas not rigid nor narrowly urceolate **770. *Sarcanthemum***
22. Appendages of fertile disc styles hairy; involucral bracts mostly herbaceous or with distinct apical green herbaceous patch; pappus usually of capillary bristles 23
– Appendages of fertile disc styles papillose; involucral bracts with herbaceous parts not necessarily in distinct apical patch; pappus of bristles or reduced or lacking 26
23. Involucral bracts mostly herbaceous **767. *Oreostemma***
– Involucral bracts with herbaceous part in distinct apical green patch 24
24. Leaves entire or toothed to lobed or pinnatifid, teeth and apices commonly spinulose-tipped; pappus bristles tending to be flattened at least basally; $x = 6$ or reduced **13. Machaerantherinae** p.p. (p. 328)
– Leaves entire or rarely toothed, without spinulose tips; pappus bristles capillary; $x = 9$ or reduced 25
25. Achenes cylindrical to subcylindrical, 8–12(–18)-nerved **760. *Eurybia***
– Achenes more or less compressed, 2(–8)-nerved **14. Symphyotrichinae** (p. 334)
26. Ray florets, when present, (1–)2–4-seriate 27
– Ray florets 1-seriate 29
27. Pappus of bristles in (1–)2–3 series; limbs of ray florets sometimes elongate and coiling **8. Podocominae** (p. 312)
– Pappus reduced or lacking, rarely a single series of bristles; ray florets with limbs short or lacking 28
28. Achenes not beaked; setulae often with anchor-shaped tips; receptacles often conical or cyathiform **5. Grangeinae** (p. 304)
– Achenes often beaked; setulae without anchor-shaped tips; receptacles usually convex to flat, rarely conical **6. Lagenophorinae** (p. 307)
29. Pappus reduced or lacking; achenes strongly compressed 30
– Pappus usually of capillary bristles 31
30. Plants rosulate with heads solitary on individual scapes; limbs of ray florets not coiling; setulae of achene simple **4. Bellidinae** (p. 303)
– Plants not rosulate; heads not on individual scapes from rosettes; limbs of ray florets coiling or short; setulae of achenes with anchor-shaped tips **3. Brachyscominae** (p. 302)
31. Leaves increasing in size upwards from stem base to near middle, lowest scale-like; involucral bracts often keeled, without distinct herbaceous tips, without or with narrow hyaline margins; appendages of disc styles lanceolate 32
– Basal leaves not scale-like, often persistent; involucral bracts not keeled, mostly herbaceous or broadly hyaline-margined 34
32. Pappus bristles 1–2-seriate, apically attenuate; limbs of rays coiling **762. *Ionactis***
– Pappus bristles 2–3-seriate, apically dilated or attenuate; limbs of rays not or scarcely coiling 33
33. Bristles of pappus apically dilated; achene surfaces eglandular **759. *Eucephalus***
– Bristles of pappus apically attenuate; achene surfaces glandular **766. *Oclemena***
34. Limbs of ray florets, when present, not coiling or reflexed; $x = 9$ or 5; North America and Mexico **16. Astranthiinae** (p. 336)
– Limbs of ray florets, when present, strongly or belatedly coiling 35
35. Involucral bracts mostly herbaceous to base; receptacles not paleate; mostly Palearctic **9. Asterinae** (p. 316)
– Involucral bracts usually with broad hyaline margins; receptacles often paleate 36
36. Achenes terete to compressed; leaves alternate; $x = 8$; North America & Mexico **15. Chaetopappinae** (p. 335)
– Achenes compressed; leaves alternate or opposite; $x = 9$ and reduced; Africa and southeast to central Asia **1. Homochrominae** (p. 290)

Unplaced Genera

756. *Commidendrum* DC.

Commidendrum DC., Arch. Bot. (Paris) 2: 334 (1833).

Shrubs to small trees, hairs pale. Leaves clustered at branch tips, shortly petiolate, subcoriaceous, obovate to spathulate, gland-dotted, glutinous, tomentose to sparsely pilose abaxially, venation pinnate. Inflorescences 1-headed or corymbose, erect or in pendent clusters; involucres campanulate to hemispheric; bracts 3–5-seriate, gradate, linear-lanceolate, without resin duct, glabrous to tomentellous, margins narrowly scarious; receptacles plano-convex, epaleate. Rays 8–50, pistillate, white, short-reflexed to long-spreading. Disc florets 8–50, perfect, yellow, tube long, throat cylindrical, lobes elongate, reflexed to coiled. Achenes oblong, terete to subcompressed, 10-nerved, glabrous or sparsely setulose, eglandular; pappus 1-seriate, persistent, bristles smooth below, barbellate distally. Four species, St. Helena.

757. *Doellingeria* Nees

Doellingeria Nees, Gen. Sp. Aster. 177 (1832) [1833]; Nesom, Phytologia 75: 452–462 (1993), emend., key.

Erect perennial herbs; fibrous-rooted; glabrous to sparsely pubescent, eglandular. Leaves all cauline, lowest leaves reduced to bracts, upper petiolate, blades truncate- to cordate-based. Inflorescences corymbose; involucres cylindric-turbinate; bracts 2–4-seriate, strongly gradate, oblong to oblong-lanceolate, apically rounded to acute, with raised midrib, without herbaceous apical patch; recep-

tacles epaleate. Rays 2–11(–16), pistillate, white, limbs not coiling. Disc florets perfect, yellow, limb expanded, lobes lanceolate, reflexing to coiling; style appendages deltate. Achenes plump to compressed, glabrous to sparsely strigose, 5–9-nerved, nerves with orange duct; pappus 2–3-seriate, outer series short, longer bristles widened apically. $x = 9$. Eleven species, eastern USA, eastern Asia.

Nesom (1993) included eight Asian species in the genus, but molecular data (Brouillet et al. 2001) indicate that the North American species are primitive members of the North American clade, whereas the Asian species are more closely related to typical *Aster*.

758. *Ericameria* Nutt.

Ericameria Nutt., Trans. Amer. Philos. Soc. 2, 7: 518 (1840); Anderson, General Technical Report INT-200, USDA, Forest Service, Ogden, Utah: 29–45 (1986), key.

Evergreen ericoid shrubs, often intricately branched; often glutinous, sometimes tomentose. Leaves linear to spathulate, sessile to short-petiolate, usually gland-dotted. Heads solitary, or in thyrsoid, racemose or corymbose inflorescences; involucres subcampanulate to turbinate; bracts 3–5-seriate, subequal to strongly gradate, midvein orange-resinous; receptacles epaleate. Rays 0–10, pistillate, yellow, limbs coiling. Disc florets perfect, lobes triangular, usually equal, erect to spreading-recurved; style appendages lanceolate to linear-lanceolate, hairy. Achenes narrowly oblong, compressed or less commonly terete, 6–12-ribbed, usually strigose to sericeous; pappus 1–3-seriate, bristles persistent or caducous. $x = 9$. Thirty-one species, western USA, north-western Mexico.

759. *Eucephalus* Nutt.

Eucephalus Nutt., Trans. Amer. Philos. Soc. 2, 7: 298 (1840).

Perennials, usually rhizomatous, rarely taprooted; stems simple or distally few-branched, glabrous or pilose to tomentose, with minute glands below heads. Leaves all cauline, lowest scale-like, most large, sessile, entire. Inflorescences (1–)6–20-headed, corymbose; involucres campanulate to hemispheric; bracts 4–6-seriate, gradate, ovate to lanceolate, often convex, keeled, stramineous-indurate, tips often purplish or green, inner bract margins hyaline; receptacles plano-convex, epaleate. Rays 0(–5) or 6–20, pistillate, white to bluish, slightly coiling. Disc florets perfect, yellow, lobes deltate and erect to triangular and reflexing; style appendages linear-lanceolate. Achenes obovate, compressed, marginal nerves 2 and sometimes 1–2 nerves on each face; pappus bristles 2–3-seriate, usually broadened apically, equally long or outer shorter. $x = 9$. Eleven species, north-western USA (incl. California), western Canada.

760. *Eurybia* (Cass.) S.F. Gray

Eurybia (Cass.) S.F. Gray, Nat. Arr. Brit. Pl. 2: 464 (1821); Nesom, Phytologia 77: 256–262 (1994), comb.
Aster subg. Eurybia Cass. (1818).
Herrickia Wooton & Standl. (1913).
Weberaster Å. Löve & D. Löve (1982).

Perennial herbs, rhizomatous; stems and leaves usually glabrate, few species with stipitate glands. Leaves sessile, linear to obovate or cordate, entire to spinulose, usually 3–5-parallel-veined. Inflorescences usually corymbose, rarely 1- to few-headed; involucres turbinate to campanulate; bracts 5–7-seriate, gradate, bases indurate, usually low-keeled, apically with distinct green patch, margins usually minutely fringed; receptacles epaleate. Rays pistillate, blue and coiling or white and scarcely coiling. Disc florets perfect, becoming purplish, narrowly tubular or with long tube and expanded limb; style appendages linear-triangular. Achenes cylindric, 8–12(–18)-nerved; pappus bristles (1–)2-seriate, often stiff and flattened, often apically broadened. $x = 9$. Twenty-eight species, USA, Canada to Alaska, and north-eastern Asia.

761. *Heteroplexis* C.C. Chang

Heteroplexis C.C. Chang, Sunyatsenia 3: 266 (1937); Chen, Guihaia 5: 337–343 (1985), rev.

Scandent or trailing perennial herbs. Leaves short-petiolate, blades lanceolate; pinnately veined, margins entire to sparsely serrulate. Inflorescences with glomerules of small heads; involucres campanulate; bracts 3–4-seriate, gradate, ovate to oblong, obtuse; receptacles convex, epaleate. Pistillate florets 4–7, 1-seriate; corollas tubular, eradiate. Disc florets 4–6, perfect, yellow, funnelform, lobes lanceolate, unequal, 3 outer lobes longer; style appendages triangular. Achenes oblong-ovate, almost terete to slightly compressed, 6-nerved, sparsely setuliferous; pappus of subequal barbellate bristles. Three species, China.

762. *Ionactis* Greene

Ionactis Greene, Pittonia 3: 245 (1897); Nesom & Leary, Brittonia 44: 247–252 (1992), emend.

Perennial herbs from thick taproots or branched woody caudex, rarely rhizomatous; puberulous or glabrous. Leaves cauline, congested, basal leaves sometimes marcescent, others stiff, narrow, 1-nerved, margins sometimes scarious. Inflorescences 1–3-headed or loosely corymbose; involucres broadly turbinate to campanulate; bracts 3–6-seriate, gradate, linear-lanceolate, strongly keeled, without herbaceous tips; receptacles plano-convex, epaleate. Rays 8–21, pistillate, limbs violet to bluish or white, coiling. Disc florets perfect (one species functionally male), narrowly tubular; style appendages lanceolate. Achenes narrowly obovate, in rays (2–)3-nerved, in disc florets 2(–4)-nerved, compressed, strigose to sericeous (1 species glandular); pappus bristles 1–2-seriate, attenuate, outer series of short bristles or scales. $x = 9$. Five species, USA (4 western, 1 eastern).

763. *Melanodendron* DC.

Melanodendron DC., Prodr. 5: 279 (1836).

Trees; hairs pale to blackish; young stems tomentose. Leaves clustered on branch tips, base broad, narrowing to pseudopetiole, blade leathery, oblong to obovate, margins entire, revolute, venation pinnate, adaxially glabrous, abaxially with sparse tomentum, obscurely gland-dotted. Inflorescences corymbose; heads short-pedunculate; involucres broadly campanulate; bracts 3–4-seriate, gradate, linear-lanceolate, margins narrowly scarious, midveins distinct, not resinous; receptacles plano-convex, epaleate. Rays 20–25, pistillate, white, elongate. Disc florets c. 60–75, perfect, yellow, tubes elongate, limb narrowly funnelform, lobes deltate; style appendages deltate. Achenes prismatic to scarcely compressed, 5-nerved, glabrous, eglandular; pappus bristles 1–2-seriate, persistent, smooth below, barbellate distally. One species, *M. integrifolium* DC., St. Helena.

764. *Microglossa* DC.

Microglossa DC., Prodr. 5: 320 (1836).

Erect to scandent shrubs, not viscid nor glutinous. Leaves petiolate, membranaceous to coriaceous, oblong-lanceolate to ovate, entire or serrate, with strongly ascending secondary veins. Inflorescences of dense corymbose to subglobose cymes; involucres campanulate to turbinate; bracts 3–4-seriate, gradate, ovate to linear-lanceolate to oblong-lanceolate; receptacles plano-convex, epaleate. Rays 3–4-seriate, pistillate, white. Disc florets perfect, whitish, limbs cylindric-campanulate to funnelform, lobes deltate, recurved; style appendages lanceolate or conic and papillose at base. Achenes narrowly turbinate to obovoid, weakly 4-costate, somewhat compressed, pilose-setulose; pappus bristles 1-seriate, persistent, numerous, subequal, minutely barbellate. Circa 19 species, Africa, Madagascar, tropical Asia.

765. *Nannoglottis* Maxim.

Nannoglottis Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 27: 480 (1881); Liu et al., Mol. Phylog. Evol. 23: 307–325 (2002), phylog.; Gao & Chen, Comp. Newslett. 40: 34 (2003), gen. class.; Gao et al., Acta Bot. Yunn. 26: 189–190 (2004), gen. class.
Stereosanthus Franch. (1896).
Vierhapperia Hand.-Mazz. (1937).

Perennial herbs; stems, leaves and involucres stipitate-glandular, usually with greyish-white tomentum, especially on leaf undersides. Basal leaves large, petiolate, elliptic-lanceolate, toothed, pinnately veined, cauline leaves reduced, sessile, decurrent to clasping. Inflorescences loosely corymbose; heads large; involucres broadly campanulate; bracts 2–3-seriate, subequal, herbaceous, oblong-lanceolate. Florets trimorphic; rays pistillate, yellow. Inner pistillate florets in several series, tubular, eradiate. Disc florets functionally male, yellow, limbs broadened, tubular, lobes oblong-lanceolate, erect to spreading. Fertile achenes oblong to fusiform, subterete, 8–10-ribbed; pappus 1-seriate, caducous, slender above base in disc achenes. Nine species, south-central China.

Nannoglottis was placed in Solidagininae by Nesom (1994c) but its evolutionary origin has since been shown to be basal or near-basal in Astereae (Liu et al. 2002).

766. *Oclemena* Greene

Oclemena Greene, Leafl. Bot. Observ. Crit. 1: 4 (1903).

Perennial herbs; puberulous with coloured hairs; unbranched below inflorescence. Leaves all cauline, lowest scale-like, larger towards middle, sessile to short-petiolate, elliptic to oblanceolate, entire or serrate, gland-dotted. Inflorescences loosely

corymbose, with arching peduncles; involucres broadly turbinate; bracts 3–4-seriate, gradate, linear-lanceolate, thin-herbaceous, slightly keeled, without green patch; receptacles plano-convex, epaleate. Rays numerous, pistillate, white to pinkish-purple, long, not coiling. Disc florets perfect, pink or reddish, lobes deltate, erect; style appendages lanceolate, distally papillose. Achenes fusiform to narrowly obovate or oblong, densely gland-dotted, 4–8-nerved, often compressed with thicker marginal nerves; pappus bristles 2–3-seriate, subequal, outer series sometimes short. $x = 9$. Three species, eastern North America.

767. *Oreostemma* Greene

Oreostemma Greene, Pittonia 4, 23: 224 (1900); Nesom, Phytologia 74: 305–316 (1993), rev.
Oreastrum Greene (1896), nom. illegit., non *Oriastrum* Poepp. (1838).

Perennial, taprooted herbs, sometimes rhizomatous or with branching caudex; eglandular or stipitate-glandular; upper stems and involucres loosely tomentose. Leaves in basal rosette linear to oblanceolate, entire, 3-nerved, cauline leaves reduced. Inflorescence essentially scapose, 1-headed; involucres broadly turbinate; bracts 3–4-seriate, subequal, linear to linear-elliptic, mostly leaf-like, often with low keel, basal margins sometimes indurate; receptacles plano-convex, with subspiniform ridge-junctions, epaleate. Rays numerous, pistillate, white to purplish. Disc florets perfect, yellow to reddish, tubular, lobes deltate, erect; style appendages linear-lanceolate. Achenes narrowly cylindric, with 5–10 raised nerves, glabrous or sparsely strigose; pappus bristles 1-seriate, sometimes some in outer series short. $x = 9$. Three species, western North America.

768. *Psiadia* Jacq.

Psiadia Jacq., Pl. Rar. Hort. Schoenbr. 2: 13, t. 152 (1800).

Glabrous or glabrescent to pubescent shrubs; stems and leaves glabrous and glandular-viscid to densely tomentose. Leaves petiolate, oblong-elliptic to lanceolate, mucronate to acuminate, entire to serrate, venation pinnate. Inflorescences corymbose; peduncles to 2 cm long; involucres hemispheric; bracts 3–5-seriate, gradate, oblong to lanceolate, obtuse, margins membranaceous to hyaline; receptacles plano-convex, minutely paleate, fimbriate or glabrous. Pistillate florets several-seriate, yellow, radiate or tubular with 2–5 lobules. Disc florets functionally male, yellow, narrowly funnelform, lobes deltate, erect-spreading. Fertile achenes narrowly turbinate, not or scarcely compressed, 3–6-costate; disc achenes minute; pappus bristles 1-seriate, persistent, united at base. Circa 60 species, tropical Africa, Madagascar, Mascarenes.

769. *Psiadiella* Humbert

Psiadiella Humbert, Mém. Soc. Linn. Normandie 25: 39, 282 (1923).

Glutinous, ericoid subshrubs with sessile glands, often hirsute with pale hairs. Leaves oblanceolate to linear, entire, 1-nerved. Inflorescences corymbose, heads 2–5, disciform, densely clustered; involucres campanulate; bracts few, c. 2-seriate, unequal, glandular, obovate-oblong, apices obtuse to rounded, margins scarious; receptacles flat, bare. Pistillate florets 1 or 2, yellow, tubular, truncate apically. Disc florets 3–6, functionally male, yellow, funnelform, lobes deltate, erect; style branches lanceolate, papillose. Achenes oblong-cylindric, truncate above, weakly 4–5-costate, weakly setulose; pappus 1-seriate, of 2–8 unequal, linear to lanceolate scales. One species, *P. humilis* Humbert, Madagascar.

770. *Sarcanthemum* Cass.

Sarcanthemum Cass., Bull. Sci. Soc. Philom. Paris 1818: 74 (1818).

Shrubs; glabrous, viscous; stems erect, moderately branched. Leaves petiolate, blades oblong-oblanceolate, margins entire in basal half, deeply oblong-dentate distally. Inflorescences corymbose; involucres hemispheric; bracts 2–3-seriate, subequal, appressed, ovate-oblong, coriaceous, margins membranaceous; receptacles plane, with small scales on disc. Pistillate florets several-seriate, tubular, narrowed above, with small limb. Disc florets numerous, functionally male, yellow, thickened and fleshy at base of limb, lobes 5, equal. Fertile achenes obovoid, compressed, glabrous, striate; disc achenes minute; pappus of disc achenes of long, flexuous-tipped, basally connate scales, rudimentary on fertile achenes. One species, *S. coronopus* Cass., Rodrigues Island.

771. *Tonestus* A. Nelson

Tonestus A. Nelson, Bot. Gaz. (Crawfordsville) 37: 262 (1904); Nesom & Morgan, Phytologia 68: 174–180 (1990), emend; Brouillet et al., Sida 21: 889–900 (2004), phylog.

Perennial herbs from branching caudices or slender rhizomes; stems, leaves, and involucres stipitate-glandular or seldom eglandular. Leaves subclasping, often persistent in rosette, blades obovate, 3-veined from base, margins spinulose-toothed or entire, upper cauline leaves reduced. Inflorescences 1- to few-headed, often loosely corymbose; involucres turbinate to hemispheric or campanulate; bracts 3–4-seriate, subequal, at least outer leaf-like; receptacles plano-convex, epaleate. Rays absent or 1–2-seriate, pistillate, yellow or white, limbs long, not coiling. Disc florets perfect, yellow, narrowly tubular; style appendages lanceolate, papillose. Achenes narrowly oblong to subfusiform, terete to rather compressed, 5-, 5–8-, or 8–12-nerved, glabrous or strigose; pappus bristles 1(–2)-seriate, attenuate, sometimes with short outer series. $x = 9$. Eight species, western USA, south-western Canada.

772. *Vernoniopsis* Humbert

Vernoniopsis Humbert, Mém. Inst. Sci. Madagascar sér. B, Biol. Vég. 6: 154 (1955).

Shrubs or small trees, moderately branched; stems with dense, evanescent, bristly hairs. Leaves oblanceolate, glabrous, entire, basally cuneate and petioliform, apically rounded, venation pinnate. Inflorescences terminal, densely corymbose; involucres narrowly cylindric; bracts 4–5-seriate, strongly gradate, ovate to linear-lanceolate, short-acute, smooth outside; receptacles bare. Rays lacking. Disc florets 1–4, perfect, white, funnelform with rather abruptly widened limb, lobes linear-lanceolate, spreading to reflexed; thecae bases calcarate; style base bulbiform; style appendages deltate. Achenes cylindrical, 10-ribbed, glabrous; pappus persistent, bristles coherent in basal ring, barbellate, inner bristles longer, outer progressively shorter. One species, *V. caudata* (Drake) Humbert, Madagascar.

XV.1. Subtribe Homochrominae Benth. in Benth. & Hook. f. (1873).

Subtribe Feliciinae G.L. Nesom (1994).

Annual to perennial herbs, subshrubs, or shrubs, strigose to hirsute or villous, lanate in *Lachnophyllum*. Leaves mostly alternate, opposite in species of *Amellus*, *Felicia*, *Engleria*, *Poecilolepis* and *Jeffreya*, entire, rarely toothed or lobed. Heads solitary or few, glomerate in *Nolletia* and *Chrysocoma*; involucral bracts not keeled, often with broad hyaline margins; receptacles plane to plano-convex, with or without pales. Ray florets 1-seriate, corollas white to blue, less commonly yellow, coiling. Disc florets usually bisexual, functionally male in some; style branch appendages usually triangular-deltate, papillose. Achenes compressed, 2-nerved, eglandular (glandular in *Nolletia*), setulae with anchor-shaped tips only in *Amellus*; pappus 1–2-seriate (of bristles and scales), rarely absent (*Jeffreya*). $x = 9$, reduced to 8, 6, 5.

Key to the Genera

1. Receptacle with acuminate pales **773. *Amellus***
– Receptacle epaleate or with only small deciduous scale-like pales 2
2. Achenes epappose or with only small apical annulus **779. *Jeffreya***
– Achenes with few to many pappus bristles 3
3. Pappus bristles basally connate, falling as a unit; annuals or short-lived perennial herbs; Asia 4
– Pappus bristles not or scarcely basally connate; annual herbs to shrubs; mostly Africa (to Arabia in some *Felicia*, to Spain in *Nolletia*) 5
4. Inflorescence with heads on many branches; involucral bracts c. 3-seriate **774. *Chamaegeron***
– Heads solitary; involucral bracts 5–7-seriate **780. *Lachnophyllum***
5. Heads mostly homogamous, without ray florets 6
– Heads heterogamous, usually with ray florets 7
6. Leaves alternate; inflorescence corymbose; corollas yellow, without resin glands in lobes **775. *Chrysocoma***
– Leaves opposite; heads solitary; corollas purplish, with pairs of elongate, marginal resin glands by sinuses **784. *Roodebergia***
7. Achenes with wings containing septate resin ducts **776. *Engleria***
– Achenes not winged 8
8. Leaves opposite or alternate; heads solitary on erect peduncles; disc florets perfect or sometimes functionally male; pappus never plumose 9
– Leaves alternate; heads solitary on erect peduncles or grouped; disc florets often functionally male, less often perfect; pappus sometimes plumose 10
9. Disc floret style appendages relatively evenly low-papillose; anthers truncate at the base **777. *Felicia***
– Disc floret style appendages with a ring of markedly longer collecting hairs at the base of each; anthers slightly auriculate at the base **782. *Poecilolepis***
10. Achenes surfaces 'pocked' and appearing glandular; disc florets perfect or functionally male **781. *Nolletia***
– Achene surfaces smooth or minutely pebbled; disc florets functionally male 11
11. Achenes with tan, smooth faces, with an apical bony collar; pappus bristles scabrid; limbs of ray florets with a purple abaxial midstripe **783. *Polyarrhena***
– Achenes with black, minutely pebbled faces, without apical bony collar; pappus bristles plumose to scabrid; limbs of ray florets without an abaxial midstripe 12

12. Achenes densely white-papillose from short setulae with a rounded clavate apex, glabrous in several species; pappus of disc florets of 2 or 3 bristles, of ray florets of 1 or 2 bristles or absent
778. *Gymnostephium*
– Achenes strigose-sericeous with long, filiform setulae; pappus of disc and ray florets of 8–12 bristles
785. *Zyrphelis*

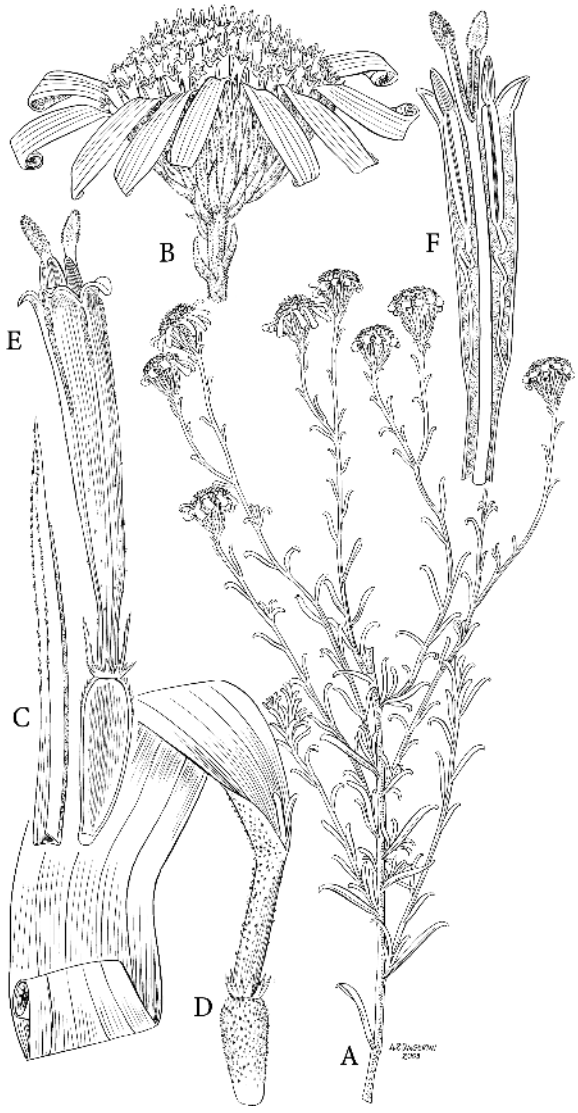

Fig. 67. Compositae-Astereae. *Amellus asteroides*. **A** Habit. **B** Capitulum with ray and disc florets. **C** Receptacular palea with reddish resin duct along keel. **D** Ray floret showing style, fertile achene with minute setulae (zwillingshaare), and coiling of older corolla limb. **E** Disc floret with fertile achene showing reddish resin ducts distally along veins of corolla throat. **F** Disc floret in longitudinal section showing anthers with spurred or tailed bases and style with paired stigmatic lines and triangular, externally papillose style appendages (Drawing by A.R. Tangerini)

Genera of Homochrominae

773. *Amellus* L. Fig. 67

Amellus L., Syst. Nat., ed. 10, 2: 1225, 1377 (1759), nom. cons.; Rommel, Mitt. Bot. Staatssamml. München 13: 579–728 (1977), rev.

Erect to spreading annual or perennial herbs or subshrubs, stems, leaves and involucres variously densely puberulous to hirsute with stiff hairs. Leaves alternate to opposite, bases sessile to nearly sessile, linear or elliptic to oblanceolate. Inflorescences 1-headed to loosely corymbose; involucres campanulate to hemispheric; bracts 3–4-seriate, subequal, linear-lanceolate, naviculate; pales linear-lanceolate. Rays 0 to 1–2-seriate, pistillate, white to purplish, coiling. Disc florets yellow, throat cylindric to funnelform, often with resin pockets along veins, lobes deltate, erect to recurved; style appendages lanceolate to linear. Achenes obovate, compressed to trigonous, 2–5(–7)-ribbed; pappus usually of c. 5, caducous, hispid bristles alternating with persistent scales. Twelve species, southern Africa.

774. *Chamaegeron* Schrenk

Chamaegeron Schrenk, Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 3: 107 (1845); Botschantzev, Fl. U.R.S.S. 25: 118–121 (1959), Engl. transl. 111–113 (1999), reg. rev.

Annual or biennial, sparingly branched herbs from weak taproot, with stipitate glands, sometimes with longer erect hairs. Leaves cauline, sessile, narrow to oblanceolate, entire or dentate, with short, fragile cartilaginous apex. Branches of inflorescence with terminal, narrowly pedunculate heads; involucres campanulate; bracts c. 3-seriate, gradate, herbaceous, inner oblanceolate, apically fimbriate, margins membranaceous; receptacles flat, glabrous. Rays 1–2-seriate, pistillate, lilac, limbs coiling. Disc corollas pale yellow, narrowly funnelform, with hairs on lower half, outer lobe separated from other triangular lobes by deeper sinuses; style appendages acuminate. Achenes elliptic-oblong to oblanceolate, glabrous or setulose; pappus bristles white, 1-seriate, connate in basal ring, caducous with ring. $x = 9$. Four species, central Asia, Iran, Afghanistan, Pakistan.

775. *Chrysocoma* L.

Chrysocoma L., Sp. Pl. 2: 840 (1753).

Perennial ericoid herbs or shrubs; glabrous, viscid. Leaves linear to oblanceolate, usually entire.

Inflorescences corymbose or with heads solitary on leafy branches, peduncles short to long; involucres hemispheric to broadly campanulate; bracts few-seriate, imbricate, margins membranaceous, subserrulate or subentire, midrib darker. Rays absent. Disc corollas yellow, base cylindric, limb narrowly funnelform, lobes triangular, erect. Achenes obovoid, somewhat compressed, pilose; pappus bristles 1-seriate, caducous, white, as long as corolla. Twenty species, southern Africa.

776. *Engleria* O. Hoffm.

Engleria O. Hoffm., Bot. Jahrb. Syst. 10: 273 (1888).

Much-branched perennial herbs or shrubs; branches terete, striate. Leaves opposite, some above subopposite, narrowly petiolate, blades membranaceous, elliptic, acute, dentate. Inflorescence diffuse, with single long-pedunculate heads terminal or appearing axillary; involucres broadly ovoid to campanulate; bracts persistent, 4–5-seriate, gradate, linear-lanceolate, outer squarrose, inner erect-spreading, margins scarious; receptacles convex, epaleate. Ray florets 0 or 1-seriate, pistillate; corollas yellow. Disc florets 20–30, perfect; corollas yellow, lobes 5, broadly triangular, recurved; style appendages linear, obtuse. Achenes obovate, rounded distally to narrow apical callus, compressed, setulose on margins and middle of faces, 1-nervate on faces, margins with narrow wings containing septate resin ducts; pappus sub-2-seriate, bristles unequal, barbellate, with shorter narrow scales outside. Two species, Angola, Namibia.

777. *Felicia* Cass.

Felicia Cass., Bull. Sci. Soc. Philom. Paris 1818: 165 (1818), nom. cons.; Grau, Mitt. Bot. Staatssamml. München 9: 195–705 (1973), rev.
Detris Adans. (1763).

Annual or perennial often ericoid herbs or shrubs; glabrous to strigose, hirtellous or pilose. Leaves alternate or opposite, sessile or bases winged, herbaceous to coriaceous, filiform to oblong, margins usually entire. Inflorescences 1-headed; peduncles long; involucres hemispheric; bracts c. 2-seriate, subequal to gradate, linear-lanceolate, dark along midline, sometimes with resin pocket distally, margins scarious. Rays 1-seriate, rarely absent, pistillate, blue, violet or rarely white or yellow. Disc florets sometimes functionally male, yellow, tubes narrow, limb narrowly funnelform, lobes deltate to lanceolate, spreading to recurved. Achenes elliptic-obovate; pappus white, 1-seriate, bristles sometimes caducous, rarely lacking in rays. $x = 9$, reduced to 8, 6, 5. Circa 85 species, Africa, Arabia.

778. *Gymnostephium* Less.

Gymnostephium Less., Syn. Gen. Comp. 185 (1832); Nesom, Phytologia 76: 85–95 (1994), rev.
Heteractis DC. (1838).

Branching subshrubs; hairs stout, usually spreading. Leaves almost all cauline, linear, entire. Inflorescences usually corymbose with numerous heads; involucres campanulate to obconic; bracts 3–4-seriate, gradate, lanceolate to linear-lanceolate, with broad scarious margins. Rays 1-seriate, pistillate, white to blue, narrow. Disc florets functionally male, yellow, narrowly funnelform, lobes triangular. Fertile achenes oblong-obovate, black at maturity, faces pebbled, eglandular, glabrous or with dense, white, papilliform setulae; pappus 1-seriate, caducous, lacking in ray florets, or with 1 or 2 plumose or barbellate bristles, disc florets with more bristles. Eight species, southern Africa.

779. *Jeffreya* Wild

Jeffreya Wild, Kirkia 9: 295 (1974).

Annual herbs; mostly glabrous, glandular-pilose below heads, stems simple below, sparsely branched above, terete, 8–10-ribbed. Lower leaves opposite, others alternate, sessile, bases subclasping, blades linear, entire or remotely serrulate, narrowly revolute, obtusely callus-tipped. Heads solitary on long peduncles; involucres broadly campanulate to subpatelliform; bracts 1–2-seriate, subequal, margins serrulate-ciliate, not hyaline. Rays 1-seriate, pistillate, elongate, white to blue or violet. Disc florets deep yellow to orange-yellow, tube cylindrical, limb campanulate, lobes deltate, erect; style appendages linear, minutely puberulous. Achenes ellipsoid, somewhat compressed, margins slightly costate, smooth, glabrous; pappus absent or a small annulus. One species, *J. palustris* (O. Hoffm.) Wild, Tanzania.

780. *Lachnophyllum* Bunge

Lachnophyllum Bunge, Beitr. Fl. Russl. 151 (1852); Botschantzev, Fl. U.R.S.S. 25: 288–289 (1959), Engl. transl. 270–271 (1999), reg. rev.

Erect, aromatic, annual or biennial herbs; with long hairs and stipitate glands, often lanate. Leaves entire, lowest petiolate, obtuse, middle leaves sessile, ovate, acuminate. Inflorescence thyrsoid to racemose; heads pedunculate; involucres broadly campanulate; bracts 5–7-seriate, gradate, recurved, outer lanceolate, herbaceous, inner linear-lanceolate, with midvein green, margins membranaceous. Rays 2-seriate, pistillate, blue to pink or violet. Disc florets yellow, with yellow ducts, tubes slender, limbs narrowly funnelform, lobes 5, lanceolate, recurving; style appendages lanceolate, hairy. Achenes oblanceolate, sericeous-villous, abruptly narrowed distally; pappus yellow, 1-seriate, bristles, basally connate. $x = 9$. Two species, central Asia.

781. *Nolletia* Cass.

Nolletia Cass., Dict. Sci. Nat. 37: 479 (1825).

Erect perennial herbs or shrubs; strigose or hispid to glabrous, rarely with stipitate glands; stems often clustered. Leaves sessile, linear to subulate. Heads solitary on branches or in subcorymbose inflorescences; peduncles long; involucres hemispheric; bracts few-seriate, gradate, linear to oblanceolate-linear, acute or acuminate, margins hyaline. Rays 1-seriate, pistillate, yellow, narrowly cylindric, apex fimbriate or 2–3(–5)-lobed. Disc florets perfect or functionally male, yellow, cylindric below, limb narrowly funnelform, lobes triangular, erect-spreading; style appendages linear. Achenes ellipsoid, surfaces puberulous to strigillose; pappus 1-seriate, of slender, caducous setae. Ten species, Africa, one to Spain.

782. *Poecilolepis* J. Grau

Poecilolepis J. Grau, Mitt. Bot. Staatssamml. München 13: 244 (1977).

Small, decumbent, annual or perennial herbs; glabrescent. Leaves alternate or opposite, fleshy, linear, entire, bases subamplexicaul. Inflorescences of axillary, aphyllous, 1-headed peduncles; involucres broadly campanulate; bracts c. 3-seriate, weakly to strongly gradate, fleshy, ovoid to oblong, margins narrowly scarious; receptacles with or without deciduous scales. Rays to 15, 1-seriate, pistillate, white, broad. Disc florets to c. 15, yellow, narrowly funnelform from short, broad tube, lobes 5, deltate, erect; anther bases slightly auriculate; style appendages short-deltate, with a basal ring of longer collecting hairs. Achenes obovate, slightly compressed, smooth, setulose, 2–3-costate; pappus setae few to 8, short, papillose to scabrid, caducous. Two species, South Africa, Cape Province, maritime.

783. *Polyarrhena* Cass.

Polyarrhena Cass., Dict. Sci. Nat. 56: 172 (1828); Grau, Mitt. Bot. Staatssamml. München 7:347–368 (1970), rev.

Ericoid shrubs; hirsute with non-glandular and/or stipitate-glandular hairs. Leaves sessile, coriaceous, ascending to recurved, linear to oblong, margins dentate to ciliate. Heads solitary on erect peduncles; involucres broadly campanulate; bracts 2–3-seriate, mostly subequal, oblong-lanceolate to linear, obtuse to acute, indurate and yellowish at base, margins narrowly scarious, narrow green patch distally, with median, yellowish, resin duct. Rays 1–2-seriate, pistillate, white, often purple adaxially. Disc florets perfect or functionally male, yellow, funnelform, lobes triangular, spreading or recurved; style sterile or with deltate appendages. Achenes ellipsoid-oblong, with pale apical collar; pappus bristles 1-seriate, caducous. $x = 9$. Four species, southern Africa.

784. *Roodebergia* B. Nord.

Roodebergia B. Nord., Acta Phytotax. Geobot. 53: 101 (2002).

Perennial herbs; primary stems repent, branches ascending, hirsute-hispid, glanduliferous; leaves opposite, sessile, narrowly elliptic, entire. Heads solitary, long-pedunculate; involucral bracts c. 10, c. 2-seriate, subequal, oblong-lanceolate, glanduliferous and sparsely setiferous. Rays lacking. Disc florets 15–25, purplish, tubular, wider above, mostly glabrous, lobes 5, triangular-ovate, each with elongate resin gland on each margin by sinus. Achenes elliptic-oblong, subglabrous, with minute setulae especially proximally; pappus 2-seriate, bristles numerous, scarcely connate at base, not falling as unit. One species, *R. kitamurana* B. Nord., southern Africa.

785. *Zyrphelis* Cass.

Zyrphelis Cass., Ann. Sci. Nat. (Paris) 17: 420 (1829); Nesom, Phytologia 76: 85–95 (1994), emend., comb.
Homochroma DC. (1836).

Perennial herbs or subshrubs; hairs stout, usually spreading; plants acaulescent or stems branching. Leaves almost all cauline, sessile, linear. Inflo-

rescences with numerous heads or less often 1-headed; peduncles long; involucres broadly campanulate to obconic; bracts c. 3-seriate, gradate, ovate to lanceolate, margins broadly scarious. Rays 1-seriate, pistillate, white to blue or yellow, narrow, tightly coiling. Disc florets usually functionally male, funnelform. Fertile achenes black at maturity, oblong-obovate, faces pebbled, eglandular, surfaces densely strigose-sericeous, setulae filiform with evenly connate tips; pappus plumose, 1-seriate, bristles 8–12, caducous. Ten species, southern Africa.

XV.2. Subtribe Hinterhuberinae Cuatrec. (1969).

Perennial herbs, subshrubs, or shrubs. Leaves alternate, opposite in *Pteronia* and *Olearia*, mostly entire, resinous-glandular, punctuate-glandular or eglandular. Heads mostly in a corymboid inflorescence; involucral bracts usually not keeled; receptacles plano-convex, with or without pales. Ray florets 1(–3)-seriate, corollas white or yellow, conspicuous or variously modified or reduced. Disc florets bisexual or sometimes functionally male; style branch appendages usually narrowly lanceolate, papillose. Achenes multinerved, mostly terete, less commonly compressed and 2-nerved, commonly glandular, setulae without anchor-shaped tips. Pappus (1–)2(–3)-seriate, usually of even-length bristles. $x = 9$.

Key to the Genera

1. Receptacles with pales 2
– Receptacles without pales 8
2. Acaulescent herbs **786. *Achnophora***
– Shrubs 3
3. Rays present and white; heads borne on abrupt leafless and ebracteose peduncles **793. *Chiliotrichum***
– Rays absent or yellow; heads sessile or borne on bracteose peduncles 4
4. Involucral bracts lacerate-ciliate-margined, scarcely indurate, persistent; ray florets often present 5
– Involucral bracts smooth-margined, indurate, easily deciduous; ray florets absent 6
5. Ray florets present; pappus of barbellate bristles equal to disc corollas in length; achenes not evidently glandular-viscid **791. *Chiliophyllum***
– Ray florets present or absent; pappus of lacerate-fimbriate scales c. half as long as disc corollas; achenes sometimes strongly glandular-viscid **792. *Chiliotrichiopsis***
6. Pappus of barbellate bristles equal to disc corolla in length **805. *Nardophyllum***
– Pappus of broad pales or scales equal or less than equal to disc corolla length 7
7. Pappus of scales 1–2 mm high; achenes strongly flattened and 2-nerved, strigose-sericeous on margins, faces glabrous **787. *Aylacophora***
– Pappus of pales equal to disc corolla in length; achenes turbinate and multinerved, evenly hirsute-strigose **811. *Paleaepappus***
8. Dioecious shrubs **788. *Aztecaster***
– Monoecious herbs, shrubs or trees 9
9. Densely branched, cupressiform, persistently aromatic shrub 10
– Herbs or shrubs not cupressiform, not notably aromatic 11
10. Pappus of narrowly subulate, caducous scales **801. *Lepidophyllum***
– Pappus of many long inner bristles and some short outer scales or bristles **812. *Parastrephia***
11. Heads homogamous, without pistillate florets 12
– Heads heterogamous, with peripheral pistillate florets 13
12. Heads in corymbose inflorescences; receptacles columnar, with florets borne on narrow convex tip **802. *Llerasia***
– Heads usually solitary at ends of branches; receptacles flat, convex, or concave **815. *Pteronia***
13. Pistillate florets tubular or subbilabiate, often 5-lobed; disc florets functionally male 14
– Pistillate florets usually with long or short limbs; disc florets perfect or functionally male 18
14. Pistillate florets edentate or scarcely dentate at tip 15
– Pistillate corollas with 4 or 5 distinct narrow lobes 16
15. Small bromeliad-like rosettiform plants with thickened, glabrous leaves; pistillate corollas not broadened distally **806. *Novenia***
– Small shrubby or subshrubby plants with pubescent, sometimes stipitate-glandular leaves; pistillate corollas ampliate above middle and slightly constricted at tip **818. *Westoniella***
16. Shrubs, often ericoid **799. *Hinterhubera***
– Erect or creeping herbs 17
17. Pappus present **797. *Flosmutisia***
– Pappus lacking **800. *Laestadia***
18. Ray achenes linear or fusiform with distinct distal rostrum **789. *Blakiella***
– Ray achenes without rostrum 19
19. Herbs 20
– Shrubs or trees 25
20. Pappus bristles plumose 21
– Pappus bristles not plumose 22
21. Disc corollas narrowly funnelform; Auckland and Campbell Islands **794. *Damnamenia***
– Disc corollas goblet-formed, with narrow tube and abruptly cyathiform limb; S Africa **804. *Mairia***
22. Disc florets functionally male 23
– Disc florets perfect 24
23. Stems branching, prostrate; leaves cauline; achenes glandular; pappus bristles almost smooth **796. *Floscaldasia***
– Stems simple, erect; leaves in a basal rosette; achenes glandular; pappus bristles scabrid to barbellate **808. *Oritrophium***
24. Rosulate herbs with narrow mostly 1-nerved leaves; inflorescences of long-pedunculate, solitary heads **790. *Celmisia***

– Robust herbs, leaf blades broad with many longitudinal veins; inflorescences racemose **813. *Pleurophyllum***
25. Disc florets functionally male 26
– Disc florets perfect 28
26. Leaves clustered at tips of branches, with weak longitudinal venation; inflorescence a sessile terminal cluster of heads; ray achenes only slightly compressed, with 9–11 ribs **810. *Pacifigeron***
– Leaves usually persistent on younger stems, with pinnate venation; inflorescences usually branched with pedunculate heads; ray achenes distinctly compressed, with 3–5 ribs 27
27. Pappus of numerous bristles almost as long as disc corollas; disc florets of one type, all functionally male **795. *Diplostephium***
– Pappus of 3–9(–14) unequal to subequal, persistent, somewhat flattened bristles; outer disc florets often pistillate **816. *Remya***
28. Anther thecae with long basal tails **814. *Printzia***
– Anther bases without tails 29
29. Ray corollas yellow 30
– Ray corollas white to bluish or purplish 31
30. Heads 1–3(–12), with obvious rays; involucre broadly campanulate **817. *Rochonia***
– Heads c. 15–40 in racemiform or thysiform inflorescence, with short pistillate florets; involucre cylindrical **798. *Guynesomia***
31. Disc corolla limbs narrowly campanulate, with slightly spreading lobes; achenes (4–)5–8-ribbed **803. *Madagaster***
– Disc corolla limbs narrowly funnelform with spreading or recurved lobes; achenes 4–5-ribbed or grooved 32
32. Involucral bracts 2–6-seriate, subglabrous to weakly tomentose, inner bracts less than 14 mm long; pappus bristles unequal in length; achenes glabrous to setulose; capitula solitary or in compound inflorescence **807. *Olearia***
– Involucral bracts 8–9-seriate, densely tomentose, inner bracts more than 14 mm long; pappus bristles equal in length; achenes densely sericeous; capitula solitary **809. *Pachystegia***

Genera of Hinterhuberinae

786. *Achnophora* F. Muell.

Achnophora F. Muell., Trans. Proc. Roy. Soc. S. Australia 6: 32 (1883).

Acaulescent perennial herbs; rhizome thick, vertical; glabrous. Leaves in basal rosette, linear, basally sheathing. Inflorescence scapiform, 1-headed; involucre nearly hemispheric; bracts c. 3-seriate, gradate, ovate to obovate, subacute, scarcely scarious distally; receptacles conical, with deciduous pales. Rays 1-seriate, pistillate, white, long. Disc florets functionally male, yellow, tubular below, narrowly funnelform above, 5(–4) lobes deltoid, erect-spreading. Achenes obovate, cuneate at base, somewhat 3–4-angled; pappus persistent, segments 8–12, sublanceolate-subulate, flat, slightly ciliate. One species, *A. tatei* F. Muell., Australia, Kangaroo Island.

787. *Aylacophora* Cabrera

Aylacophora Cabrera, Bol. Soc. Argent. Bot. 4: 261 (1953); Bonifacino & Sancho, Sida 19: 531–538 (2001), emend.

Intricately branching, subaphyllous shrubs; branches glabrous with tomentose grooves. Leaves sparse, linear, entire, acute, with evanescent tomentum. Heads terminal on branchlets, discoid; involucres broadly campanulate; bracts 5–6-seriate, gradate, ovate to oblong-lanceolate, easily deciduous, tomentose, margins smooth; receptacular pales oblong-lanceolate, conduplicate, distally ciliate, acuminate. Florets 20–25, perfect, yellow, funnelform, lobes lanceolate, erect-spreading. Achenes obovate, compressed, 2-nerved, margins and apex strigose-sericeous, faces glabrous; pappus 1-seriate, of c. 20–25 lanceolate scales c. 1.2 mm long. One species, *A. deserticola* Cabrera, central Argentina.

788. *Aztecaster* G.L. Nesom

Aztecaster G.L. Nesom, Phytologia 75: 64 (1993).

Dioecious shrubs; stems silvery-white tomentose, glabrate. Leaves densely spiralled, often in axillary fascicles, linear-oblong, entire, flocculent, glutinous, margins revolute. Inflorescences spicate; heads sessile, subtended by clustered leaves; involucres turbinate; bracts 3–4-seriate, gradate, narrowly ovate to lanceolate, yellowish to greenish-yellow, resinous, narrowly keeled, margins scarious; receptacles epaleate. Female heads with 5–10 florets; corollas narrowly tubular, 5-lobed; male heads with 8–9 functionally male florets; corollas narrowly tubular, lobes short-triangular, spreading. Fertile achenes oblong-ovate, compressed with 2 marginal nerves and 1 nerve on 1 or both faces, strigose; pappus bristles 1-seriate, numerous. Two species, Mexico.

789. *Blakiella* Cuatrec.

Blakiella Cuatrec., Webbia 24: 37 (1969).

Perennial subshrubs, hirsutulous and densely stipitate-glandular. Leaves sessile, base subauriculate, margins crenulate, revolute. Inflorescences of few clustered long-pedunculate heads; involucres cupulate-campanulate; receptacles epaleate.

Peripheral florets multiseriate, 200–270, pistillate, yellow, tube subcapillary, distally broadened, limbs short, slightly constricted at mouth. Disc florets 55–85, functionally male, yellow, tube narrow, limb campanulate, lobes triangular. Ray achenes obovate-fusiform, c. 4-nervate, base attenuate, distally short-rostrate; disc achenes narrowly cylindrical, setulose and glandular; pappus 1-seriate, bristles broadened apically in disc florets. One species, *B. bartsiifolia* (S.F. Blake) Cuatrec., Colombia, Venezuela.

790. *Celmisia* Cass.

Celmisia Cass., Dict. Sci. Nat. 37: 259 (1825), nom. cons.; Given, N. Z. J. Bot. 7: 400–418 (1969), emend.
Elcisimia B.L. Rob. (1913), nom. rej.

Perennial, mostly rosulate herbs from woody caudex; stems scapiform, bracteolate. Leaves mostly in rosettes, subcoriaceous, linear or filiform to elliptic-oblanceolate, with sheathing bases, abaxially often with white tomentum. Heads solitary; involucres broadly campanulate to hemispheric; bracts 4–5-seriate, gradate, linear; receptacles epaleate. Rays 1-seriate, pistillate, white or partly violet to purple, not or weakly coiling. Disc florets perfect, yellow to purplish, narrowly funnelform, lobes 5, broadly triangular to lanceolate, spreading; anther bases acute; style appendages linear, branches papillose to near base. Achenes elliptic to obovoid, compressed, ribs marginal and 2 or 3 on each face, glabrous to sericeous; pappus bristles numerous, unequal. $x = 9$. Circa 60 species, New Zealand, Australia.

791. *Chiliophyllum* Phil.

Chiliophyllum Phil., Linnaea 33: 132 (1836), nom. cons.

Small ericoid shrubs; stems, leaf undersides and involucres tomentose or glutinous. Leaves sessile, linear-oblong to obovate, margins entire to revolute. Heads solitary on branchlets, short-pedunculate; involucres broadly campanulate; bracts c. 15–25, 2–5-seriate, subindurate, persistent, broadly lanceolate to linear-lanceolate, acute, margins lacerate-ciliate; receptacular pales rather conduplicate. Rays c. 8 or 9, 1-seriate, pistillate, yellow, limbs broad. Disc florets perfect, yellow, narrowly tubular-funnelform, lobes lanceolate, spreading or recurved. Achenes oblanceolate, scarcely compressed, ribbed, setulose, not evidently glandular; pappus bristles 1-seriate, subequal or strongly unequal. Three species, Argentina, Chile.

792. *Chiliotrichiopsis* Cabrera Fig. 68

Chiliotrichiopsis Cabrera, Notas Mus. La Plata, Bot. 2: 172 (1937); Nesom et al., Brittonia 53: 430–434 (2001), emend.

Perennial, glutinous, ericoid shrubs; stems white-tomentose, glabrescent, brownish-lined, blackening. Leaves sessile, linear to oblanceolate, margins entire, revolute, glabrous above, tomen-

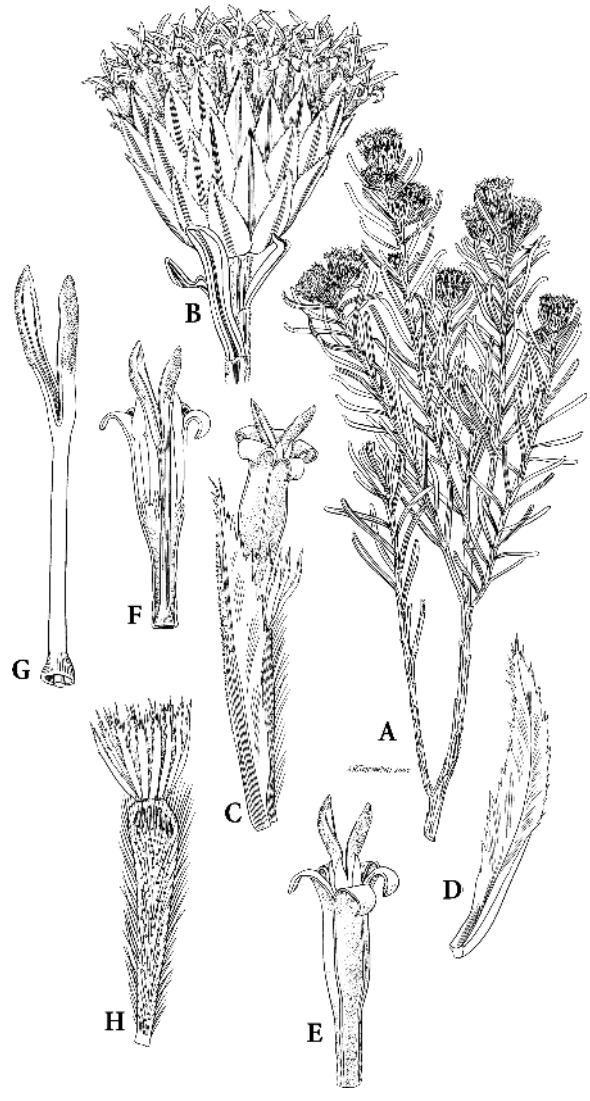

Fig. 68. Compositae-Astereae. *Chiliotrichopsis peruviana*. **A** Flowering branch. **B** Capitulum. **C** Disc floret with palea. **D** Receptacular palea. **E** Corolla and partly exserted anthers and style of disc floret. **F** Disc floret, longitudinal section. **G** Style of disc floret. **H** Achene with pappus of long scales. (Nesom et al. 2001)

tose beneath except on midvein. Heads solitary on short branches, sessile; involucre campanulate; bracts 4–5-seriate, gradate, persistent, lanceolate to oblong-lanceolate, bases pale, thickened, median nerve green, margins broadly scarious, lacerate-ciliate; receptacular pales conduplicate. Rays pistillate, yellow or absent. Disc florets perfect, yellow, narrowly funnelform, lobes triangular, recurved; style with stigmatic lines and distal papillose outer surface overlapping. Achenes oblanceolate, compressed, strigose-sericeous, with intermixed resiniferous glands, margins thickened; pappus of 10–16 lanceolate fimbriate scales half as long as corollas. Three species, Argentina, Peru.

793. *Chiliotrichum* Cass.

Chiliotrichum Cass., Bull. Sci. Soc. Philom. Paris 1817: 69 (1817).

Ericoid shrubs; stems, leaf undersides and outer involucral bracts pale tomentose. Leaves subcoriaceous, sessile, linear to oblanceolate, entire, glabrous adaxially. Heads on clustered ebracteate peduncles; involucres broadly campanulate to hemispheric; bracts 3–4-seriate, gradate, caducous, mostly indurate, oblong-lanceolate, subentire, narrowly scarious, green patches on outer bracts; receptacular pales weakly conduplicate. Rays 1-seriate, pistillate, white or violet, coiling. Disc florets perfect, yellow, tube narrow, limb narrowly campanulate, lobes lanceolate, recurved; style appendages linear, branches papillose almost to base. Achenes slender, 4–5-nerved, with long hairs and glandular dots; pappus bristles multiseriate, about as long as corollas. Two species, Argentina, Chile.

794. *Damnamenia* D.R. Given

Damnamenia D.R. Given, N. Z. J. Bot. 11: 786 (1973).

Stoloniferous herbs, with branched caudex; stems short and erect or scapiform. Primary leaves spirally inserted with imbricated bases, blades linear, glossy, glabrous, venation simple, lateral veins of base ending below blade. Inflorescences 1-headed, on long leafy scapes; involucres campanulate; bracts 2–3-seriate, subequal, linear-oblanceolate, with non-glandular hairs; receptacles obconic. Rays 1-seriate, pistillate, white to pale reddish distally. Disc florets numerous, perfect, purple or yellow, with slender tube and abruptly cyathiform limb, lobes broadly triangular, erect-spreading; anthers with slight tails; style appendages broadly triangular, with long hairs. Achenes obconic, setulose; pappus bristles c. 2-seriate, unequal, plumose. $x = 9$. One species, *D. vernicosa* (Hook. f.) D.R. Given, New Zealand.

795. *Diplostephium* Kunth

Diplostephium Kunth in H.B.K., Nov. Gen. Sp., ed. folio 4: 75 (1818); Cuatrecasas, Webbia 24: 90–194 (1969), reg. rev.

Shrubs or small trees; stems, leaf undersides and involucres puberulous to lanate or gland-dotted. Leaves usually petiolate, coriaceous, margins plane or revolute. Inflorescences 1-headed to corymbose or thyrsoid; involucres cylindric to hemispheric; bracts 4–7-seriate, gradate, ovate to oblong or linear; receptacles epaleate. Pistillate florets 1–3-seriate, white to bluish or purplish, radiate or eradiate. Disc florets functionally male or rarely perfect, yellow, green or violaceous, tubular-campanulate, lobes triangular. Achenes glabrous, setuliferous or gland-dotted; fertile achenes obovoid, 2–3-nerved, somewhat compressed; disc achenes oblong or linear, 5-nerved; pappus bristles of disc achenes dilated at tips, outer series of short setae or squamae. $x = 9$. Over 70 species, Costa Rica and Andes to Bolivia.

796. *Floscaldasia* Cuatrec.

Floscaldasia Cuatrec., Webbia 24: 194 (1969); Sklená & Robinson, Novon 10: 146–147 (2000), emend.

Minute herbaceous subshrubs; stems branching, repent, rooting, glabrous; densely foliose branches decumbent or erect. Leaves sessile, oblong or trilobed, base vaginate, margins ciliate. Heads solitary on erect hirsutulous scapes; bracteoles few; involucres campanulate; bracts 2–3-seriate, subequal, oblong-lanceolate to oblong, herbaceous; receptacles epaleate. Rays 26–45, pistillate, reddish to purplish, limbs short. Disc florets 10–12, functionally male, purplish, tube broad, limb short-campanulate, lobes deltate; style branches lanceolate, densely hairy. Fertile achenes obovoid, scarcely compressed, 2-nervate, glandular along outer margin; pappus white to brownish, subbiseriate, bristles c. 25, nearly smooth. Two species, Colombia, Ecuador.

797. *Flosmutisia* Cuatrec.

Flosmutisia Cuatrec., Anales Jard. Bot. Madrid 42: 415 (1986).

Rhizomatous, rosulate perennial herbs, pilose and minutely stipitate-glandular. Leaves sessile, elliptic-oblong to obovate. Scapes with narrow bracteoles; heads solitary; involucres broadly campanulate; bracts 4–5-seriate, subequal, oblong-lanceolate to oblanceolate, outer bracts ciliate on margins and midvein, inner bracts mostly glabrous; receptacles epaleate. Pistillate florets 2–3-seriate, white, subbilabiate, 5-lobed, outer lobes linear, the two inner lobes filiform. Disc florets functionally male, white, funnelform with expanded limb, lobes triangular, erect-spreading, pilosulous. Fertile achenes ellipsoid, compressed, densely setuliferous and glandular, obscurely 5-nerved; disc achenes slender; pappus whitish, bristles 1-seriate, barbellate. One species, *F. paramicola* Cuatrec., Colombian paramo.

798. *Guynesomia* Bonifacino & Sancho

Guynesomia Bonifacino & Sancho, Taxon 53: 675 (2004).

Shrubs. Stems glandular. Leaves sparse, sessile, linear, clasping, entire, glandular on both surfaces. Inflorescence racemiform or thyrsiform. Heads c. 15–40, pedunculate, disciform; involucres cylindric; bracts 4–5-seriate, coriaceous, ovate to linear, margins broadly membranaceous; receptacles epaleate. Pistillate florets 10–11, 1-seriate, yellow, limb 2–3 mm long, tridentate, lateral lobes reduced. Disc florets 13–16, perfect, yellow, tubular, lobes triangular, spreading. Achenes narrowly elliptic, scarcely compressed, 3–4-ribbed, glandular; pappus bristles 2-seriate, subequal. One species, *G. scoparia* (Phil.) Bonifacino & Sancho, Chile.

799. *Hinterhubera* Sch. Bip. ex Wedd.

Hinterhubera Sch. Bip. ex Wedd., Chlor. And. 1: 185 (1857); Cuatrecasas & Aristeguieta, Bol. Soc. Venez. Ci. Nat. 17: 98–104 (1956), rev.

Small ericoid shrubs, with sessile or stipitate glands and non-glandular hairs; stems defoliated below, densely covered with leaf bases or scars. Leaves linear or oblong, margins revolute. Heads disciform, sessile or pedunculate on branch tips; involucres campanulate; bracts 4–5-seriate, gradate, lanceolate to linear; receptacles epaleate. Peripheral florets 90–170, pistillate, pluriseriate, white or yellow, tubular, 4–5 lobules equal or 3 longer. Disc florets 9–60, functionally male, white or yellow, tube narrow, limb deeply divided into linear-lanceolate lobes; style appendages linear, with hair-like papillae. Fertile achenes obovate-oblong, with setulae and short-stipitate glands, with 1(–3) marginal nerves; disc achenes linear; pappus whitish to reddish, with few short outer setae, bristles of disc achenes broadened distally. Eight species, Colombia, Venezuela.

800. *Laestadia* Kunth ex Less.

Laestadia Kunth ex Less., Syn. Gen. Comp. 203 (1832).

Matted herbs, mostly procumbent, gland-dotted, glutinous, sometimes hirtellous. Leaves crowded, sessile, sometimes subclasping, oblong to spathulate, entire, 1-nerved. Heads on terminal or axillary peduncles, disciform; involucres hemispheric; bracts 2–4-seriate, subequal, reflexing, margins narrowly hyaline, outer bracts herbaceous distally; receptacle epaleate. Peripheral florets 2–4-seriate, pistillate, regular with 4 or 5 deeply cut, triangular, spreading or recurving lobes. Disc florets 15–25, functionally male, white to purple, abruptly expanded from short tube, limb cut to near base, lobes triangular. Achenes oblong to obovoid, nearly terete, 6–10-nerved, gland-dotted; epappose, callus with ring of glands or on short glandular beak. Six species, Costa Rica, Hispaniola, Andes to Bolivia, high elevations.

801. *Lepidophyllum* Cass.

Lepidophyllum Cass., Bull. Sci. Soc. Philom. Paris 1816: 199 (1816); Cabrera, Bol. Soc. Argent. Bot. 1: 48–58 (1945), rev.

Cupressiform, densely branched shrubs; glabrous, glutinous; stems subfrondiform with many short spreading branches. Leaves decussate, scale-like, closely abutting, as wide as long, rhombic, with slightly rounded keel. Heads solitary on branch tips, sessile; involucres narrowly campanulate; bracts c. 3-seriate, lanceolate, middle indurate, belatedly caducous, margins thinly scarious; receptacles epaleate. Pistillate florets 3 or 4, yellow, radiate or bilabiate with 3 outer lobes short, coiling. Disc florets few, perfect, yellow, narrowly funnelform, lobes lanceolate, recurved; style appendages linear. Achenes oblanceolate, slightly compressed, with c. 5 broad costae, papillose or glabrous; pappus of many caducous, narrowly subulate scales. $x = 9$. One species, *L. cupressiforme* (Lam.) Cass., Patagonia.

802. *Llerasia* Triana

Llerasia Triana, Ann. Sci. Nat. Bot. 4, 9: 37 (1858); Cuatrecasas, Biotropica 2: 39–45 (1970), emend.

Shrubs, small trees or vines, often gland-dotted; stems and leaf undersides pale-tomentose. Leaves short-petiolate, coriaceous, entire or dentate, pinnately veined. Inflorescences corymbose; heads homogamous; involucre cylindric; bracts 4–6-seriate, strongly gradate, mostly obtuse, mostly deciduous; receptacles columnar, epaleate, florets borne on narrow convex tip. Florets 3–15, perfect, yellow, tubular, limb slightly broader, lobes deeply cut, linear-oblong, spreading; style base bulbous, appendages triangular, hairy. Achenes narrowly prismatic, 3–5-angled, 5–9-nerved, papillose, gland-dotted or short-setulose; pappus tawny to white, 2–3-seriate. Ten species, Colombian to Bolivian Andes.

803. *Madagaster* G.L. Nesom

Madagaster G.L. Nesom, Phytologia 75: 97 (1993).

Shrubs or small trees; tomentose on young branches, leaf undersides and petioles. Leaves coriaceous, entire or distally toothed, venation pinnate. Inflorescences 1-headed to corymbose or thyrsoid; heads pedunculate; involucres campanulate to hemispheric; bracts 3–4-seriate, gradate, ovate to oblong or linear, herbaceous at tips, margins scarious; receptacles epaleate. Rays 1-seriate, pistillate, white to bluish. Disc florets numerous, perfect, yellow, limbs narrowly campanulate, lobes triangular, erect-spreading; style appendages short-triangular. Achenes narrowly oblong-fusiform, (4–)5–8-ribbed, nearly terete to slightly compressed, strigose, eglandular; pappus 1–2-seriate, bristles dilated apically, outer series shorter, unequal. Five species, Madagascar.

804. *Mairia* Nees

Mairia Nees, Gen. Sp. Aster. 247 (1832); Nesom, Phytologia 76: 85–95 (1994), emend.

Annual or perennial herbs; with flexuous hairs; stems scapiform, 1-headed. Leaves in basal rosette, thick, broadly obovate. Involucres broadly campanulate; bracts 3–4-seriate, weakly gradate, outer rows completely herbaceous, flat; receptacles epaleate. Rays 1–2-seriate, pistillate, blue or white, often with staminodia, limbs broad, weakly coiling. Disc florets perfect, yellow, funnelform, lobes ovate-deltate, erect to reflexed; style appendages lanceolate. Achenes narrowly oblong to oblanceolate, compressed, (2–)4–6-nerved, glandular, densely strigose-sericeous, paired setula tips of uneven lengths, strongly divergent; pappus 1–2-seriate, persistent, bristles plumose, sometimes with long scales outside. Three species, southern Africa.

805. *Nardophyllum* (Hook. & Arn.) Hook. & Arn.

Nardophyllum (Hook. & Arn.) Hook. & Arn., Companion Bot. Mag. 2: 44 (1836); Cabrera, Notas Mus. La Plata 17: 55–66 (1954), rev.

Gochnatia subg.(?) *Nardophyllum* Hook. & Arn. (1835).

Small spreading shrubs; stems, leaf undersides, and involucres often tomentose; branchlets sometimes spiniform, internodes often angled or with dark lines. Leaves sessile, subcoriaceous, oblong to linear, entire. Heads 1–5, terminal or axillary; involucres campanulate; bracts 3–5-seriate, gradate, caducous, oblong to lanceolate or linear, margins scarious; receptacles with narrow caducous pales. Rays lacking. Florets few, perfect, yellow, narrowly funnelform, lobes triangular to lanceolate, often recurved; style appendages lanceolate, papillose outside, branches smooth below. Achenes obovoid, compressed, 4–5-ribbed, sericeous-villous; pappus bristles as long as corollas. Seven species, Argentina, Bolivia, Chile.

806. *Novenia* S.E. Freire

Novenia S.E. Freire, Bol. Soc. Argent. Bot. 24: 296 (1986); Freire & Hellwig, Taxon 19: 124–125 (1990), comb.

Acaulescent, caespitose, perennial herbs. Leaves in rosettes, bases involute, densely villous; blades linear-lanceolate, coriaceous, with 3 grooves adaxially, glabrous. Inflorescences sessile, glomerulate, 1–4-headed; involucres cylindric; bracts c. 3-seriate, subequal, oblong-lanceolate, stramineous, indurate, glabrous, margins scarious; receptacles with reduced pales. Pistillate florets 3–9, whitish, filiform, eradiate. Disc florets functionally male, whitish, narrowly tubular, lobes oblong-triangular, erect; style branches linear-lanceolate. Achenes obovoid to oblong, compressed, with (5–)6 whitish nerves, with sparse filiform setulae; pappus bristles 2–3-seriate, persistent. $x = 9$. One species, *N. acaulis* (Wedd. ex Benth. in Benth. & Hook. f.) S.E. Freire & F. Hellw., Andes from northern Argentina to southern Peru.

807. *Olearia* Moench

Olearia Moench, Supp. Meth. 254 (1802), nom. cons.; Cross et al., Pl. Syst. Evol. 235: 99–120 (2002); Comp. Newslett. 40:

11 (2004), phylog.
Steetzia Sonder (1853).

Shrubs; glabrous or glutinous to variously pubescent, hairs sometimes stellate. Leaves cauline, alternate or opposite, broadly ovate to linear, often tomentose abaxially. Heads terminal or axillary, solitary or in corymbose to thyrsoid inflorescences, sessile to pedunculate; involucres cylindric to hemispheric; bracts persistent, 2–6-seriate, herbaceous, linear to lanceolate, margins scarious, sometimes resin duct along midvein; receptacles epaleate. Rays 1-seriate, rarely lacking, white to blue or purple, coiling. Disc florets few to numerous, perfect, yellow or purplish, narrowly funnelform, lobes 5, deltate or lanceolate, recurving; anthers shortly calcarate. Achenes terete or slightly compressed, usually 5-ribbed, glabrous or setulose; pappus bristles persistent, often in 2 unequal series. $x = 9$. Circa 180 species, Australia, New Zealand, New Guinea.

A molecular-phylogenetic study (Cross et al. 2002) indicates that *Olearia* is polyphyletic as currently defined, with species divided into three or four primary, phyletically disparate clades, with several other smaller ones variously dispersed. Formal taxonomic changes await more detailed sampling and analysis.

808. *Oritrophium* (Kunth) Cuatrec.

Oritrophium (Kunth) Cuatrec., Cié. (Mexico) 21: 21 (1961); Cuatrecasas, BioLlania ed. espec. 6: 287–303 (1997), rev.; Nesom, Sida 18: 523–526 (1998), emend.
Aster L. sect. *Oritrophium* Kunth (1818).

Perennial herbs from thick erect to horizontal rhizome. Leaves mostly in basal rosettes, bases usually densely hairy, blades oblanceolate to linear, glabrous to sericeous. Inflorescences scapose, 1-headed, bracteoles linear-subulate; involucres subhemispheric to broadly cylindric or turbinate; bracts 2–3-seriate, gradate to subequal, linear to oblong-lanceolate, obscurely veined; receptacles epaleate. Rays 1–2-seriate, pistillate, white, coiling. Disc florets functionally male, narrowly funnelform, lobes triangular, erect; style branches linear, long-papillose. Ray achenes fusiform, 5-veined, several-angled or compressed, glabrous to sericeous, eglandular; disc achenes linear, 4–5-veined; pappus 1-seriate, bristles subequal. $x = 9$. Circa 21 species, mostly Andean, Venezuela to Bolivia, two in Mexico.

809. *Pachystegia* Cheeseman

Pachystegia Cheeseman, Man. N. Z. Fl., ed. 2, 910 (1925); Cross et al., Pl. Syst. Evol. 235: 99–120 (2002), phylog.

Robust spreading shrubs; leaf undersides, peduncles and involucres densely tomentose. Leaves stoutly petiolate with broadly clasping bases, blades coriaceous, entire, glabrous adaxially. Heads solitary on long peduncles; involucres subglobose to urn-shaped, becoming hemispheric; bracts to 9-seriate, ovate to lanceolate, outer obtuse, inner acute or with needle-like recurved tips; receptacles epaleate. Rays 2–3-seriate, pistillate, white, not or weakly coiling. Disc florets numerous, perfect, yellow, tubes slender, limbs narrowly funnelform-tubular, lobes 5, lanceolate, spreading, with distinct yellowish ducts; style appendages linear, obtuse. Achenes oblong-linear, grooved, densely sericeous; pappus tawny, 1-seriate, bristles slightly thickened distally. $x = 9$. One species, *P. insigne* Cheeseman, New Zealand.

810. *Pacifigeron* G.L. Nesom

Pacifigeron G.L. Nesom, Phytologia 76: 160 (1994).

Shrubs, younger parts with arachnoid tomentum, persisting in axils. Leaves clustered at branch tips, coriaceous, obovate-spathulate, entire. Inflorescences of clustered subsessile heads imbedded in tomentum; involucres campanulate; bracts c. 18–24, 2–3(–4)-seriate, gradate, broadly lanceolate, yellowish with 3(–5) orange veins; receptacles epaleate. Rays c. 18–26, 1(–2)-seriate, pistillate, white or cream, orange-veined, limbs spreading. Disc florets functionally male, orange-veined, funnelform, limb enclosed in long hairs, lobes broadly lanceolate. Fertile achenes fusiform, slightly compressed, with 9–11 raised orange-resinous nerves when young, setulose, eglandular; pappus bristles 30–45, outer series short. One species, *P. rapensis* (F. Br.) G.L. Nesom, Polynesia, Rapa Island.

811. *Paleaepappus* Cabrera

Paleaepappus Cabrera, Bol. Soc. Argent. Bot. 11: 273 (1969); Bonifacino & Sancho, Sida 19: 531–538 (2001), emend.

Small, divaricately branched shrubs, young branchlets thorn-like; young branches, young leaves and involucres tomentose. Leaves small, subcoriaceous, sessile, oblong to spathulate, entire, caducous. Heads solitary on bracteose branches, discoid; involucres campanulate; bracts

4–5-seriate, gradate, broadly lanceolate, short-acute, entire, indurate, caducous; receptacles with conduplicate pales. Rays absent. Florets numerous, perfect, yellow, tubes narrow, limbs narrowly campanulate, lobes triangular; style appendages lanceolate, papillose, branches smooth below. Achenes oblong-obovoid, sericeous-villous; pappus 2-seriate, of linear-lanceolate scales, as long as corollas. One species, *P. patagonicus* Cabrera, Patagonia.

812. *Parastrephia* Nutt.

Parastrephia Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 449 (1841); Nesom, Phytologia 75: 347–357 (1993), rev.

Ericoid to cupressiform shrubs, resinous to partly tomentose. Leaves alternate, sessile, coriaceous, scale-like to linear, midvein depressed and tomentose abaxially, remainder of leaf glabrous. Heads solitary or in small clusters, disciform; involucres narrowly campanulate; bracts 3–4-seriate, gradate, oblong to oblong-lanceolate, obtuse to acute, persistent, mostly indurate, margins thin and scarious; receptacles epaleate. Pistillate florets 1-seriate, yellow, tubular or with small limb. Disc florets perfect, yellow, narrowly funnelform, lobes lanceolate, recurved; style appendages lanceolate, papillose to base of branches. Achenes obovoid, compressed, c. 4-ribbed, 2 marginal, sericeous; pappus bristles 2-seriate, some outer scales or bristles short. Three species, Argentina, Chile, Bolivia and Peru.

813. *Pleurophyllum* Hook. f.

Pleurophyllum Hook. f., Fl. Antarctica 1: 30 (1844); Cross et al., Pl. Syst. Evol. 235: 99–120 (2002), phylog.

Robust, perennial, rosulate herbs; silvery-sericeous to white-tomentose. Leaves sessile, basal leaves large, broadly elliptic to obovate, subacute, entire or denticulate, coriaceous to subcarnose, with 30–40 parallel veins; cauline leaves narrowly elliptic, with 5–9 veins. Scapes racemose; involucres depressed-hemispheric; bracts 2–3-seriate, subequal, linear-lanceolate, pilose to lanate; receptacles epaleate. Rays 15–30(?), 1–3-seriate, pistillate, whitish to purplish, limbs short or elongate, 3-lobed or deeply tripartite. Disc florets 60 or more, perfect, purple, tube cylindric, limb campanulate, lobes 4 or 5, long-ovate, recurving; style appendages deltate. Achenes elongate, compressed in ray florets, subquadrate in disc florets, ribbed, densely setulose; pappus bristles 2–3-seriate, sordid, scabrous to subplumose, unequal. Three species, New Zealand, sub-Antarctic islands south of New Zealand.

814. *Printzia* Cass.

Printzia Cass., Dict. Sci. Nat. 37: 488 (1825); Anderberg, Opera Bot. 104: 1–195 (1991), emend.

Perennial herbs or small shrubs; stems and leaf undersides pale-tomentose; leaves subsessile, narrowly elliptic to ovate. Inflorescences thyrsoid or with heads solitary; peduncles short; involucral bracts 2–5-seriate, gradate to subequal, lanceolate to ovate, dark in middle, margins pale; receptacle epaleate. Rays pistillate, 1-seriate, violet to white, yellowish or greenish, often coiled, rarely filiform, staminodes sometimes present. Disc florets numerous, perfect, yellow, narrowly funnelform; lobes 5, triangular, recurving; anther thecae with long basal tails; style appendages lanceolate, weakly papillate. Achenes mostly terete, c. 10-nerved, setuliferous; pappus bristles 1–2-seriate, tips often subplumose. Six species, southern Africa.

The genus is re-incorporated in Astereae on the basis of a DNA study by Bayer and Cross (2002), in spite of the long-tailed anther bases.

815. *Pteronia* L.

Pteronia L., Sp. Pl., ed. 2, 2: 1176 (1763), nom. cons.; Gen. Pl., ed. 6, 414 (1764); Hutchinson & Phillips, Ann. S. African Mus. 9: 277–329 (1917), rev.

Shrubs or shrublets; grey-tomentellous, scabridulous, gland-dotted or glabrous. Leaves alternate or opposite, sometimes rather fleshy, sessile to petiolate, linear or ovate-oblong to oblanceolate, entire to serrulate-ciliate. Heads usually solitary, peduncles short; inflorescences sometimes corymbiform or (*P. fasciculata* L. f.) numerous single-flowered heads aggregated into a second-order head; involucres ovoid to cylindric; bracts 4–7-seriate, gradate, broadly ovate to linear-oblong, margins membranaceous to subscarious; receptacles often fimbriate, epaleate. Rays absent. Florets 1 to many, perfect, yellow to orange, narrowly funnelform or limbs campanulate-cylindric, lobes oblong-linear to deltate, erect. Achenes turbinate, often contracted at apex, villous to glabrous; pappus bristles c. 2-seriate, persistent, white, stramineous, or reddish to purple, often connate into basal ring. Circa 80 species, southern and south-western Africa to Zambia.

816. ***Remya*** W. Hillebrand ex Benth. in Benth. & Hook. f.

Remya W. Hillebrand ex Benth. in Benth. & Hook. f., Gen. Pl. 2, 1: addend. 536 (1873); Wagner & Herbst, Syst. Bot. 12: 601–608 (1987), rev.

Weakly erect or sprawling shrubs, densely tomentose to glabrous. Leaves narrowly elliptic to broadly ovate or lanceolate, glabrous adaxially, margins toothed. Inflorescences loosely corymbose; involucres ovoid to globose or hemispheric; bracts 4–5-seriate, gradate, coriaceous to chartaceous, ovate to linear-oblong, margins narrowly scarious; receptacles epaleate. Rays 12–20, pistillate, cream-coloured, limbs short. Disc florets dimorphic in two species; outer pistillate, tubular; inner functionally male, yellow, goblet-shaped. Fertile achenes narrowly obovoid, compressed, 3–4-angled, with 1 or 2 nerves on each face, glabrous to strigose; pappus of 3–9(–14) unequal to subequal, persistent non-barbellate awns, sometimes reduced in inner disc. $x = 9$. Three species, Hawaii.

817. ***Rochonia*** DC.

Rochonia DC., Prodr. 5: 345 (1836); Humbert, Fl. Madag. 189, III, 1: 311–317 (1960), reg. rev.

Subshrubs or shrubs, stipitate-glandular, stems, leaf undersides and involucres tomentose. Leaves sessile, mostly subcoriaceous, elliptic or lanceolate to obovate, entire or dentate, 1- or 3-nerved from base. Inflorescences terminal, 1-headed to corymbose; peduncles short to long; involucres hemispheric; bracts 3–4-seriate, gradate, ovate to oblong-lanceolate, margins scarious; receptacles epaleate. Rays 1–2-seriate, 14 to c. 35, pistillate, yellow, coiling. Disc florets numerous, perfect, yellow, narrowly funnelform, tube short, lobes triangular, erect; style appendages deltate. Achenes oblong, slightly fusiform, compressed, 5–10-costate, setuliferous; pappus bristles 2-seriate, persistent, subequal or outer shorter. Four species, Madagascar.

818. ***Westoniella*** Cuatrec.

Westoniella Cuatrec., Phytologia 35: 472 (1977).

Erect shrubs or prostrate to pulvinate herbs, glabrous to white-woolly, often gland-dotted. Leaves imbricate, sessile, rigid, linear to elliptic, margins revolute, entire to serrate or digitate, tomentose beneath. Heads solitary or in glomerulae. Involucres campanulate; bracts 4–5-seriate, subequal, glabrous to woolly; receptacles epaleate. Pistillate florets 2–4-seriate, white to reddish or purple, filiform-tubular or slightly broadened distally, contracted and minutely 5-toothed apically. Disc florets functionally male, tubular, purple to reddish, lobes 5, triangular, erect. Fertile achenes obovate, compressed, 2-nerved or with weak nerve on each face, strigose to sericeous, usually with glands apically; pappus bristles 1-seriate, as long as corollas. Six species, Costa Rica, Panama.

XV.3. Subtribe Brachyscominae G.L. Nesom (1994).

Annual to perennial herbs. Leaves alternate, entire to toothed or lobed, eglandular or stipitate-glandular. Heads solitary to few; involucral bracts not keeled, commonly with broad hyaline margins; receptacles plane to conical, epaleate. Rays 1-seriate, pistillate, white to blue, coiling. Disc florets bisexual, functionally male in *Ceratogyne* and some species of *Calotis*, corollas short-tubed; style appendages deltate, papillose. Achenes obovate, 2-nerved, flat, commonly winged in *Brachyscome*, eglandular, faces and margins usually with setulae with anchor-shaped tips; pappus absent or highly reduced, less commonly of bristles, 1-seriate. $x = 9$, reduced to 8, 7, 6, 5, 4, 3, 2.

Key to the Genera

1. Achenes distally Y- or T-shaped with widely spreading arms, with wings involute on one side; pappus lacking **821.** ***Ceratogyne***
– Achenes without distal arms or projections; pappus usually present 2
2. Disc florets mostly perfect; pappus of short or minute scales or absent **819.** ***Brachyscome***
– Disc florets usually functionally male; pappus of subulate to spreading awns, often retrorsely barbed **820.** ***Calotis***

Genera of Brachyscominae

819. ***Brachyscome*** Cass.

Brachyscome Cass., Bull. Sci. Soc. Philom. Paris 1816: 199 (1816); Davis, Proc. Linn. Soc. New South Wales 73: 142–241 (1948), rev.

Brachycome Cass. corr. Cass. (1825), in wide use in horticulture, and arguably the correct orthography.

Annual or perennial herbs, sometimes rhizomatous; glabrous or tomentose to stipitate-glandular; stems erect or spreading. Leaves in rosettes or

cauline, entire to pinnatisect. Peduncles usually long; involucres campanulate to hemispheric; bracts 2–3-seriate, subequal, oblong, obtuse, herbaceous, margins narrowly hyaline; receptacles convex-conical. Rays 1–2-seriate, numerous, white, blue, pink or yellow. Disc florets numerous, mostly perfect, yellow, limbs narrowly campanulate, lobes triangular-lanceolate, spreading or recurved; anther appendage rarely lacking; style appendages deltate to long-triangular. Achenes terete to compressed, glabrous to setulose or tuberculate, sometimes winged; pappus absent or of small white scales. $x = 9$, reduced to 8, 7, 6, 5, 4, 3 or 2. Circa 70 species, Australia, New Guinea, New Zealand, New Caledonia.

820. *Calotis* R. Br.

Calotis R. Br., Bot. Reg. 6: pl. 504 (1820); Davis, Proc. Linn. Soc. New South Wales 77: 146–188 (1952), rev.

Annual or perennial herbs, prostrate to erect, sometimes stoloniferous, glabrate to hispid or hirsute. Leaves cauline and/or basal, petiolate or sessile, usually toothed or pinnately lobed. Inflorescences 1-headed or leafy-cymose; involucres campanulate to subglobose; bracts 2–3(–4)-seriate, subequal, herbaceous; receptacles flat to conical, sometimes with small scales. Rays 1- to several-seriate, limbs blue or purple to white or yellow, sometimes vestigial. Disc florets usually functionally male, yellow, limb campanulate, lobes deltate-lanceolate, erect to spreading. Achenes obconical, glabrous or strigose to tuberculate, sometimes winged; pappus of (1–)2–25 subequal erect to spreading awns, often retrorsely barbed or ciliate, sometimes with alternating low scales, rarely of 12–15 short-plumose bristles or absent. $x = 8$, reduced to 7, 5, 4. Circa 28–30 species, mostly Australia.

821. *Ceratogyne* Turcz.

Ceratogyne Turcz., Bull. Soc. Imp. Naturalistes Moscou 24: 68 (1851).

Annuals or short-lived perennials; taproot weak; stems strigose, non-glandular; erect or ascending from rosette. Leaves sessile, obovate or those subtending heads smaller. Inflorescences seriate-cymose; heads sessile in terminal or overtopped clusters; involucral bracts bracteole-like, 2–5, 1-seriate; receptacles plano-convex. Rays 3–6, whitish; limbs short. Disc florets c. 3–6, functionally male, narrowly funnelform, lobes 3 or 4, deltate-ovate. Fertile achenes lobed, Y- or T-shaped, compressed, winged, involute on one face, anchor-shaped setulae on faces, lobe margins and base; epappose. One species, *C. obionoides* Turcz., south-eastern Australia.

XV.4. Subtribe Bellidinae Willk. (1870).

Tribe Bellideae Cass. ex D. Don (1830).
Tribe Bellieae DC. ex Godr. (1850)

Herbs. Leaves alternate in basal rosette, wide, entire to serrate-dentate, eglandular. Heads solitary on scapes; involucral bracts flat, completely herbaceous, 2(–3)-seriate; receptacles conical, epaleate. Ray florets 1-seriate, limbs long, white or pink-tinged. Disc florets bisexual, with short tube; style branches with deltate papillose appendages. Achenes obovate, compressed, with pair of thick marginal ribs, eglandular, setulae without anchor-shaped tips; pappus absent or a short laciniate crown, apical callus narrow. $x = 9$.

Key to the Genera

1. Pappus absent or a ring of very short bristles; involucral bracts 2-seriate **822. *Bellis***
– Pappus with outer ring of 4–6(–10) scales alternating with inner ring of bristles; involucral bracts 1-seriate **823. *Bellium***

822. *Bellis* L.

Bellis L., Sp. Pl. 886 (1753); Webb, Atlas Fl. Europaea 4: 111–112 (1976), reg. rev.; Fiz et al., Mol. Phylog. Evol. 25: 157–171 (2002), phylog.

Annual or short-lived perennial herbs, sometimes rhizomatous, roots fibrous; stems usually scapiform. Leaves in rosette, sometimes some on lower stem, spathulate to oblanceolate, entire to toothed. Involucres shallowly cupulate; bracts (1–)2-seriate, subequal, ovate or oval, evenly herbaceous; receptacles conical or hemispheric to flat. Rays pistillate, limbs white above, often pink or purple below, closing upwards at night. Disc florets perfect, yellow, tubular, tube very short, nearly stipe-like, lobes erect. Achenes obovate, short-strigose or ciliate-margined to glabrous, sometimes with sessile glands; pappus absent or a short crown of bristles. $x = 9$. Circa 8 species, Europe, widely introduced.

823. *Bellium* L.

Bellium L., Mant. Pl. 2: 157 (1771).

Annual or perennial herbs; acaulescent or rarely caulescent; pilosulous. Leaves elliptic-obovate to spathulate, bases long-petioliform, tips rounded to obtuse, margins entire. Involucres broadly campanulate to hemispheric; bracts crowded 1-seriate, equal, herbaceous in middle, margins scarious, tips obtuse, rather fimbriate; receptacles hemispheric to conical. Rays pistillate, limbs white, often reddish below, not coiling. Disc florets perfect, yellow, narrowly campanulate from short tube, lobes 4 or 5, broadly triangular, erect. Achenes oblong-obovoid, setulose on sides; pappus of 4–6(–10) barbellate bristles as long as achene, alternating with short scales. $x = 9$. Four species, southern Europe.

XV.5. Subtribe Grangeinae Benth. in Benth. & Hook. f. (1873); Fayed, Mitt. Bot. Staatssamml. München 15: 425–476 (1979), rev.

Annual to perennial herbs, usually glandular. Leaves alternate, pinnatifid to pinnatisect. Heads solitary or few in a loosely corymbose inflorescence, involucral bracts not keeled; receptacles often conical, with or without pales. Ray florets usually 2–4-seriate, corolla limb absent or barely exceeding the involucre, white greenish-yellow or purplish. Disc florets perfect or often functionally male, corollas commonly 4-lobed; style branch appendages deltate, papillose. Achenes compressed, 2-nerved, eglandular or glandular, setulae sometimes with anchor-shaped tips; pappus absent, of a few short bristles, or a low crown of basally connate scales. $x = 9$, apparently reduced to 8 in *Erodiophyllum*.

Key to the Genera

1. Receptacles with pales 2
– Receptacles epaleate 3
2. Florets of 2 types, outer florets tubular, without limbs; receptacles plane **825. *Ceruana***
– Florets of 3 types, outer pistillate florets radiate; receptacles highly convex to conical **831. *Erodiophyllum***
3. Pappus of 3–50 elongate, separate, slender or flattened bristles 4
– Pappus rudimentary or lacking, rarely with 1 or 2 bristles 8
4. Heads heterogamous, with peripheral pistillate florets 5
– Heads homogamous, without differentiated pistillate florets 6
5. Pappus of 3–8 short bristles; receptacles conic **824. *Akeassia***
– Pappus usually of 12–50 long bristles; receptacles plano-convex **838. *Nidorella***
6. Achenes broadly winged; pappus segments fused at base **833. *Grangeopsis***
– Achenes not winged; pappus segments not fused at base 7
7. Annuals; pappus of c. 10 flattened, persistent bristles in 1 series **828. *Dacryotrichia***
– Erect perennial herbs; pappus 2–3-seriate, numerous, unequal, slender caducous bristles **836. *Heteromma***
8. Perennial herbs; corollas of pistillate florets bilabiate, with lobules on inner side **839. *Plagiocheilus***
– Annual or short-lived perennial herbs; corollas of pistillate florets not bilabiate 9
9. Disc florets functionally male 10
– Disc florets perfect 11
10. Anthers without apical appendage; receptacles flat **826. *Colobanthera***
– Anthers with distinct apical appendage; receptacles cup-shaped, with pistillate florets borne on both inner and outer surfaces of cup **827. *Cyathocline***
11. Pistillate corollas radiate 12
– Pistillate corollas not radiate, sometimes 4-dentate at apex 14
12. Achene with a cartilaginous apical crown or cup; pappus lacking; ray florets in 1–4 series **830. *Egletes***
– Achene without cartilaginous apical crown or cup; pappus of minute teeth or triangular scales 13
13. Leaves pinnatifid with often coarsely toothed oblong or lanceolate lobes; plants hispid to hirsute; receptacle hemispheric to conical **835. *Gyrodoma***
– Leaves simple, entire; plants densely glanduliferous; receptacle convex to toroid **873. *Mtonia***
14. Receptacle flat or scarcely convex **834. *Grauanthus***
– Receptacle hemispheric to conical or columnar 15
15. Pappus a papillose rim, or with 1 or 2 bristles, or lacking; disc corollas campanulate, lobes not spreading **829. *Dichrocephala***
– Pappus a partially fused corona with a lacerate rim or paleaceous teeth; disc corollas with widely spreading lobes **832. *Grangea***

Genera of Grangeinae

824. *Akeassia* J.-P. Lebrun & Stork

Akeassia J.-P. Lebrun & Stork, Candollea 48: 332 (1993).

Much-branched annual herbs, longer branches prostrate-decumbent; stems and leaves weakly puberulous. Leaves sessile, obovate, narrowed to base, venation weakly pinnate. Heads clustered among distal leaves, 3–6, subsessile, subglobose; involucral bracts subbiseriate, subequal, oblanceolate; receptacles conical. Pistillate florets 1–3-seriate, yellow, short-cylindrical, 4-toothed. Disc florets bisexual, yellow, tube short, limb campanulate, glandular, lobes 4, as wide as long. Ray and disc achenes alike, subcylindric or ellipsoid, glandular, setulae with anchor-shaped tips; pappus of (3–)5–8 short bristles. One species,

A. grangeoides J.-P. Lebrun & Stork, western Africa and Congo.

825. *Ceruana* Forssk.

Ceruana Forssk., Fl. Aegypt.-Arab. 74: 153 (1775).

Erect, coarse, annual or short-lived perennial herbs; sparsely hirsute, gland-dotted. Leaf bases slender with short decurrent margins, blades obovate, entire to serrate-pinnatifid. Inflorescences cymose with racemose branches; heads on short peduncles, overtopped by branches; involucre hemispheric; bracts c. 2-seriate, subequal, narrowly oblong, acute, herbaceous, margins very narrowly scarious; receptacles plane, with pale, lanceolate, fimbriate, caducous pales. Florets yellow. Pistillate florets 1-seriate, filiform, with minute stipitate glands, with 4 narrow apical lobes. Disc florets perfect, tube short, limb abruptly campanulate, lobes 5, broadly triangular, scarcely spreading, with slender yellowish ducts. Achenes oblanceolate to oblong-obovoid, setulose; pappus of short, basally connate, bristle-like scales or setae. One species, *C. pratensis* Forssk., northern and western Africa.

826. *Colobanthera* Humbert

Colobanthera Humbert, Mém. Soc. Linn. Normandie 25: 35, 281 (1923).

Small, erect to spreading, annual or short-lived perennial herbs, branching mostly from base; leaves, peduncles and involucres with subsessile glands. Basal leaves subpetiolate, narrowly oblanceolate, cauline leaves sessile, subamplexicaul, sublinear, usually entire. Heads terminal and axillary, solitary on long peduncles; involucres broadly campanulate; bracts subbiseriate, subequal, obtuse, margins scarious, blackish; receptacles flat. Rays 2–3-seriate, c. 25, pistillate, white or yellow, narrow, tubes almost lacking. Disc florets c. 10, functionally male, campanulate from slender tube, lobes deltoid, erect-spreading; thecae without apical appendage; style branches oblong-lanceolate. Achenes oblong, slightly fusiform, with many small setulae; pappus none. One species, *C. waterlotii* Humbert, Madagascar.

827. *Cyathocline* Cass.

Cyathocline Cass., Ann. Sci. Nat. (Paris) 17: 419 (1829).

Erect, annual or perennial herbs; hirsute to glandular. Leaves sessile, usually with basal auricles, pinnatifid with pointed teeth. Inflorescences loosely cymose with corymbose branches; peduncles short; involucres broadly campanulate to hemispheric; bracts c. 3-seriate; subequal, linear-lanceolate, narrowly acute, 1-nerved, herbaceous medially, margins scarious, ciliate; receptacles cup-shaped, bearing multiseriate pistillate florets on outer and inner surfaces of cup. Florets yellow to purple. Pistillate florets filiform with small oval limbs. Disc florets few, only in centre of receptacle cup, functionally male, limb campanulate from slender tube, lobes broadly triangular, spreading. Fertile achenes obovoid to fusiform, glabrous; pappus lacking. $x = 9$. Three species, tropical Asia.

828. *Dacryotrichia* Wild

Dacryotrichia Wild, Garcia de Orta, ser. Bot. 1: 67 (1973).

Annual herbs; pilose, sparsely glandular; stems erect or spreading. Leaves sessile, often narrowed, subauriculate, pinnatisect, with 2–6 linear to spathulate lobes. Inflorescences loosely cymose, c. 10-headed; peduncles 1–2 cm long; involucres hemispheric; bracts 2–3-seriate, oblong to obovate, acute to obtuse, margins hyaline; receptacles plano-convex. Ray florets absent. All florets perfect, orange-yellow, broadly funnelform, lobes broadly triangular, erect; style appendages lanceolate, subobtuse. Achenes narrow with base attenuate, sparsely glandular, biseriate setulae bearing single, caducous, narrowly vesicular cell on lower half of apex; pappus persistent, white, bristles c. 10, flattened, with some shorter outer bristles. One species, *D. robinsonii* Wild, Zambia.

829. *Dichrocephala* L'Hér. ex DC.

Dichrocephala L'Hér. ex DC. in Guill., Arch. Bot. (Paris) 2: 517 (1833).

Annual herbs; straggling to erect; pilose or glabrescent. Leaf bases clasping-auriculate, blades lyrate-pinnatifid, coarsely serrate or serrate-crenate. Inflorescences paniculate; heads subglobose; involucral bracts 1–2-seriate, subequal, oblong to elliptic, apices rounded to obtuse, margins membranaceous; receptacle convex to columnar-ellipsoid, tuberculate to pitted. Rays multiseriate, pistillate, greenish, yellow-white, or purplish, tubular, 2–4-dentate or regularly lobed. Disc florets yellow or reddish, rotate-campanulate from short tubes, lobes 4–5, deltate to broadly triangular, erect to spreading. Achenes obovoid to turbinate, mostly glabrous with glands basally

and distally; pappus absent, a narrow rim or of 1 to few caducous, short bristles. Ten species, Africa, Madagascar, Indonesia, tropical and south-western Asia.

830. *Egletes* Cass.

Egletes Cass., Bull. Soc. Philom. Paris 1817: 153 (1817); Shinners, Lloydia 12: 239–247 (1949), rev.; Lloydia 12: 248–250 (1949), emend.

Erect to procumbent, taprooted, annual herbs; stems much-branched, viscid with usually stipitate glands. Leaf bases petiolate to sessile, subclasping, blades obovate to spathulate, lobed or toothed to pinnatifid or bipinnatifid. Heads usually solitary and axillary or few in loosely corymbose inflorescences, short-pedunculate; involucres hemispheric to cupulate; bracts 2–3-seriate, subequal, thin-herbaceous, lanceolate; receptacles conical. Rays 1–4-seriate, pistillate, white, filiform, limbs short. Disc florets perfect, yellow, tubular-funnelform, 3–5-lobed. Achenes oblong to narrowly obovate, glabrous or gland-dotted, or with hooked setulae, apical callus a whitish, sometimes flaring crown or cup; pappus bristles absent. $x = 9$. Circa 8 species, neotropical to south-western USA (southern Texas).

831. *Erodiophyllum* F. Muell.

Erodiophyllum F. Muell., Fragm. (Mueller) 9: 119 (1875).

Coarse, erect or ascending perennial herbs; stems, leaves, and involucres hirsute with white hairs. Leaves herbaceous, lyrate-pinnatifid. Inflorescences terminal or axillary, 1-headed, pedunculate; involucres campanulate to hemispheric; bracts c. 2-seriate, subequal, oblong to oblong-linear, herbaceous; receptacles convex or conical, outer 4–7 rows among pistillate florets with ovate pales which become indurate with recurved points. Rays 1-seriate, blue to purple or white. Tubular pistillate florets 4–7-seriate. Central florets functionally male, yellow, tubes short, limbs narrowly funnelform, lobes deltate, spreading or recurved. Fertile achenes obovoid-obconic, glabrous, apex indurate; pappus of minute scales fused to crenate rim. $x = 8$. Two species, Australia.

832. *Grangea* Adans.

Grangea Adans., Fam. Pl. 2: 121, 563 (1763).

Annual herbs, suberect to prostrate. Leaves pinnatifid. Inflorescences opposite to leaves or terminal and corymbose, 3–6-headed; involucres hemispheric to subglobose; bracts 1–2-seriate, subequal, inner with membranaceous margins; receptacles hemispheric or conical, naked. Pistillate florets 2- to many-seriate, yellow, campanulate or narrowly funnelform, cylindric below, 2–4-dentate. Disc florets perfect, yellow, campanulate or rotate-campanulate, cylindric below, 4–5-lobed. Achenes subterete, ellipsoid, compressed or 4-angled, apex sometimes cartilaginous, sometimes constricted; pappus obsolete, a lacerate coroniform rim, or toothed. Ten species, Africa, Madagascar, tropical Asia.

833. *Grangeopsis* Humbert

Grangeopsis Humbert, Mém. Soc. Linn. Normandie 25: 34, 281 (1923).

Small, branching perennial herbs, stoloniferous; stems, leaves and involucres with thin tomentum. Leaves larger in basal rosette, basal leaves obovate to oblanceolate, bases petioliform, cauline leaves oblong-spathulate. Heads solitary on long peduncles; involucres campanulate to hemispheric; bracts c. 3-seriate, subequal, herbaceous, oblong to spathulate, obtuse, margins scarious; receptacles convex. Rays lacking. Florets yellow, tube short, limb broadly campanulate, lobes (4–)5, subdeltoid, spreading. Achenes broadly obovate, broadly winged, ciliate, with rounded to narrow apex and lacking nerves on faces; pappus of 10–12 hyaline, lanceolate, unequal scales, 1/2–9/10 as long as corollas, bases fused into ring. One species, *G. perrieri* Humbert, Madagascar.

834. *Grauanthus* Fayed

Grauanthus Fayed, Mitt. Bot. Staatssamml. München 15: 484 (1979).

Erect or ascending annual or perennial herbs, leaves and involucres hirsute. Leaves sessile, dentate to lyrato-pinnatifid, generally lanceolate to linear. Inflorescences subcorymbose; peduncles short; involucres cupuliform; bracts 2–3-seriate, subequal, outer bracts narrow, obtuse, 1-nerved, inner bracts oblong-obovate, margins hyaline, ciliate; receptacles plano-convex, tuberculate, centre subacuminate. Pistillate florets c. 3-seriate, whitish-yellow, tubular with broadened limb, 3- or 4-dentate. Disc florets yellow, tube short with broadly funnelform limb, lobes 5, oblong-triangular, erect. Achenes yellow, subcylindric, partial nerve on face, margins setulose, disc

achenes somewhat smaller; pappus lacking. Two species, tropical Africa.

835. *Gyrodoma* Wild

Gyrodoma Wild, Kirkia 9: 294 (1974).

Decumbent or ascending annual herbs; branching from base; stems, leaves and outer involucral bracts hispid to hirsute. Basal leaves short-petiolate, upper leaves attenuate to clasping base, generally oblong or oblanceolate, coarsely toothed to pinnatifid with oblong or lanceolate lobes. Heads solitary on long peduncles; involucres broadly campanulate to subpatelliform; bracts c. 2-seriate, subequal, margins membranaceous; receptacles hemispheric-conical. Rays 1-seriate, pistillate, white to pale blue, linear, recurved. Disc florets yellow, tube short, limb widely funnelform, lobes cut to basal 1/3 of limb, triangular, spreading; style appendages obtuse. Achenes narrowly turbinate, minutely setulose; pappus of minute scales c. 0.1 mm long. One species, *G. hispida* (Vatke) Wild, Mozambique.

836. *Heteromma* Benth. in Benth. & Hook. f.

Heteromma Benth. in Benth. & Hook. f., Gen. Pl. 2: 286 (1873).

Erect perennial herbs; pubescent. Leaves entire to serrate-dentate or lyrate-pinnatifid, bases decurrent on stem. Inflorescences corymbose; involucres hemispheric; bracts 2–3-seriate, gradate, outer bracts narrow, inner bracts apically membranaceous. Rays lacking. Florets yellow, tube short, limb campanulate, lobes 5, triangular, erect-spreading; style appendages short-triangular, hirtellous. Achenes oblong-obovoid, usually 3-ribbed, glandular, setulose; pappus 2–3-seriate, numerous unequal, caducous bristles. Three species, southern Africa.

837. *Mtonia* Beentje

Mtonia Beentje, Kew Bull. 54: 97 (1999).

Erect, densely glanduliferous, annual herbs; leaves sessile, narrowly elliptic to lanceolate, entire, pilose. Inflorescences corymbose; heads 3–4 mm high, crowded at tips of branches; peduncles short, with stipitate glands; involucral bracts 2–3-seriate, subequal, oblong-lanceolate; receptacles convex to toroid, spiculiferous. Rays 2–3-seriate, c. 30–40, yellow, limbs short, erect. Disc florets numerous, yellow, narrowly funnelform, with sticky glands; 5-lobed. Achenes setuliferous; pappus a minutely dentate ring. One species, *M. glandulifera* Beentje, eastern Africa.

838. *Nidorella* Cass.

Nidorella Cass., Dict. Sci. Nat. 37: 459, 469 (1826); Wild, Bol. Soc. Brot. 43: 209–243 (1969), rev.

Erect annual or perennial herbs; nearly glabrous to hirsute or lanate. Leaves mostly cauline, sessile to pseudopetiolate or subamplexicaul, obovate to linear-spathulate, entire to pinnatisect. Inflorescences corymbose with subglobose or cymose clusters of heads; involucre hemispheric or campanulate; bracts 1–3-seriate, subequal, midrib often glandular to pilose, margins hyaline. Rays 2–3-seriate, pistillate, yellow, limb short or 3–4(–5)-lobed. Disc florets few to many, usually perfect, yellow, funnelform, lobes triangular, erect-spreading; style appendages broad, base cordate and with larger papillae. Achenes obovoid or ellipsoid, pubescent, often glandular; pappus bristles persistent, 5 to c. 30. $x = 9$. Circa 15 species, tropical and southern Africa.

839. *Plagiocheilus* Arn. ex DC.

Plagiocheilus Arn. ex DC., Prodr. 6: 142 (1838).
Polygyne Phil. (1864).

Erect to creeping perennial herbs; pilose to hirsute on leaf-base margins, leaf surfaces or sometimes on stems. Petioles winged with broadened bases, leaf blades pinnately to bipinnately dissected. Heads solitary on axillary peduncles or short-pedunculate in small terminal clusters; involucres campanulate to hemispheric; bracts c. 3-seriate, mostly subequal, ovate to oblong, blunt, margins hyaline. Ray florets multiseriate, pistillate, white, shortly bilabiate with 1 or 2 smaller lobules adaxially. Disc florets functionally male, greenish-yellow to reddish-brown, tube slender, limb narrowly funnelform, lobes deltate to oblong-lanceolate, erect to spreading. Achenes oblong, constricted but not beaked, setula tips anchor-shaped; pappus lacking. $x = 9$. Seven species, South America.

XV.6. Subtribe Lagenophorinae G.L. Nesom (1994).

Annual to perennial herbs or subshrubs. Leaves alternate, mostly in a basal rosette. Heads borne singly on scapose stems or few in a loose panicle; involucral bracts herbaceous; receptacles plane to convex, conical in *Pytinicarpa*, sometimes concave

in *Thespis*, epaleate. Ray florets (1–)2–4-seriate, white, limb reduced, usually not coiling, sometimes reflexing. Disc florets often functionally male; style branch appendages deltate to lanceolate, mostly papillose. Achenes compressed, 2-nerved, usually with persistent or deciduous glands at the apex or beak; setulae without anchor-shaped tips; pappus often absent. $x = 9$.

Key to the Genera

1. Pappus of 6–20, rather stout or persistent, barbellate bristles 2
– Pappus none or with distorted caducous bristles 3
2. Perennial herbs from short woody stolons; leaves all basal; pistillate corollas radiate **844. *Pappochroma***
– Annual herbs in small spreading clumps; leaves alternate; pistillate corollas eradiate **851. *Thespis***
3. Heads with 9 or fewer florets, only 1 or 2 disc florets **849. *Sheareria***
– Florets in heads 15 or more 4
4. Disc corollas goblet-shaped, tube abruptly opening into a broad limb; pistillate florets radiate 5
– Disc corollas tubular to funnelform, gradually opening into the limb; pistillate corollas with or without limb 8
5. Annual or perennial herbs, not aromatic; leaves herbaceous, flat-margined, sometimes subclasping but not basally dilated or sheathing, basal leaves often persistent but cauline leaves continuing unreduced in size halfway to nearly completely up the stem 6
– Perennial herbs to subshrubs or shrubs, at least some species aromatic; leaves thickened to coriaceous, usually with revolute or deflexed margins, basally dilated and sheathing, evenly arranged along stems or in rosulate clusters 7
6. Pistillate florets 2–5(–10)-seriate; corollas greenish-white to pink or purplish; pappus lacking **843. *Myriactis***
– Pistillate florets 2-seriate, c. 11, disc florets c. 11; pistillate corollas whitish; pappus lacking or with caducous scraggly bristles **848. *Rhynchospermum***
7. Leaves of current year in a rosulate or subrosulate cluster; heads on long, scapiform peduncles; anthers with a short apical appendage **840. *Keysseria***
– Leaves densely and more or less evenly arranged on stems; heads without evident peduncle; anthers without an apical appendage **845. *Piora***
8. Heads radiate; limb of ray florets strongly developed; achenes with glands 9
– Heads disciform; limbs of pistillate florets rudimentary or absent 10
9. Involucral bracts narrowly lanceolate to linear, acute to acuminate; receptacles convex **841. *Lagenophora***
– Involucral bracts elliptic-obovate to oblong, rounded to obtuse; receptacles sharply acute **846. *Pytinicarpa***
10. Disc florets perfect, more numerous than pistillate florets; involucral bracts c. 6, ciliate; achenes obcompressed(?) **847. *Rhamphogyne***
– Disc florets functionally male, less numerous than pistillate florets; involucral bracts 9–16, denticulate; achenes compressed 11
11. Achene beak conspicuous; ovaries of disc florets completely absent; leaves entire **842. *Lagenocypsela***
– Achene beak rudimentary or absent; ovaries of disc florets present, sterile; leaves toothed **850. *Solenogyne***

Genera of Lagenophorinae

840. *Keysseria* Lauterb.

Keysseria Lauterb., Feddes Repert. Spec. Nov. Regni Veg. 13: 241 (1914); Koster, Nova Guinea, Bot. 24: 597–608 (1966), reg. rev.

Perennial, aromatic, spreading herbs or subshrubs, branches erect or ascending. Leaves fleshy to coriaceous, linear-terete or elliptic to spathulate, glabrous to tomentose, sometimes glandular, margins entire to shallowly dentate. Heads solitary, often nodding, peduncles scapiform with 1–6 leaf-like bracteoles; involucres campanulate or hemispheric; bracts 2–4-seriate, subequal, herbaceous, midrib prominent, usually glandular, margins membranaceous, distally fringed. Rays 2–3-seriate, pistillate, white to purplish, short, linear, recurving. Disc florets perfect or functionally male, yellow to pinkish, funnelform, limb abruptly widened, lobes (3–)4(–5), triangular. Fertile achenes obovate to elliptic, glabrate; pappus absent. $x = 9$. Twelve species, Indonesia, Hawaii.

841. *Lagenophora* Cass.

Lagenophora Cass., Bull. Sci. Soc. Philom. Paris 1816: 199 (1816), nom. et orth. cons.; Cabrera, Blumea 14: 285–307 (1966), rev.
Lagenifera Cass. (1816), orth. var. rej.

Perennial stoloniferous herbs or subshrubs, often matted; usually puberulous; stems erect or procumbent. Leaves cauline or mostly in rosette, sessile to petiolate, linear to spathulate, entire or dentate. Heads solitary, long-pedunculate; involucres turbinate to subrotate; bracts 2–3-seriate, subequal, more than 10, narrowly oblong, acute or obtuse, herbaceous, entire or denticulate, margins scarious. Rays 1–4-seriate, pistillate, white to purple, coiling. Disc florets fewer than rays, perfect or functionally male, yellow to reddish, lobes 4 or 5, triangular, erect to spreading. Achenes obovate to oblanceolate, subfusiform, with short, glandular and viscid beak or with glandular apical rim; pappus lacking. $x = 9$. Fourteen species, south-eastern Asia, Australasia, Pacific islands, Central America, South America.

842. ***Lagenocypsela*** Swenson & K. Bremer

Lagenocypsela Swenson & K. Bremer, Austral. Syst. Bot. 7: 270 (1994).

Small, perennial, rosettiform herbs; with erect caudex. Leaves in rosette, linear or petiolate with lanceolate blades, glabrous, entire. Inflorescences 1-headed, on erect pilose peduncles; involucres campanulate; bracts 9–16, 2–3-seriate, gradate, rounded, 1-nerved, margins scarious, denticulate. Pistillate florets 1–2-seriate, red-purple, filiform, minutely toothed distally. Disc florets few, functionally male, red-purple, narrowly campanulate, lobes deltate, erect. Achenes fusiform, short-beaked, glabrous; pappus lacking. Two species, New Guinea.

843. ***Myriactis*** Less.

Myriactis Less., Linnaea 6: 127 (1831); Cabrera, Blumea 14: 285–307 (1966), rev.; Wang & Peng, Comp. Newslett. 41: 58–59 (2004), typ.

Perennial herbs, often rhizomatous, subglabrous to hirsute-villous. Leaves cauline, bases rather clasping, blades oblanceolate to ovate or orbicular, crenate-dentate to pinnatisect. Heads 1 to many, sometimes in subthyrsoid inflorescences, pedunculate; involucres cupuliform to hemispheric; bracts 2–4-seriate, subequal to gradate, herbaceous, oblong-lanceolate, with basally keeled midrib. Rays c. 10–45 or more, 2–5(–10)-seriate, fertile or sterile, greenish-white to purplish in age. Disc florets perfect or functionally male, yellow or green, goblet-shaped, lobes 4 or 5, lanceolate, spreading to reflexing. Achenes obovate to oblanceolate, faces shiny, eglandular, apex short-beaked or in disc achenes erostrate, gland-dotted; pappus absent. $x = 9$. Two species, tropical America, eastern Asia, Indonesia, Philippines.

844. ***Pappochroma*** Raf.

Pappochroma Raf., Fl. Tellur. 2: 48 (1836) [1837]; Nesom, Phytologia 76: 426 (1994), emend.
Lagenithrix G.L. Nesom (1994).
Lagenopappus G.L. Nesom (1994).

Perennial herbs from short stolons, often in mats; stems and leaves hispid-pilose, stipitate-glandular or eglandular. Leaves all basal, thick, oblanceolate to spathulate, entire to distally crenate, 1–3-nerved. Heads solitary, sessile or on bracteolate scapes; involucres hemispheric; bracts 2–3-seriate, subequal, oblong-lanceolate, 1-nerved, herbaceous except for scarious margins, often purple-tinged. Rays 25–36, 1–4-seriate, white, narrow, straight. Disc florets perfect or functionally male, yellow, funnelform, tube linear, lobes 4 or 5, triangular. Fertile achenes oblanceolate-oblong, 2–4-nerved, glabrous except for viscid glands distally, slightly constricted or with neck distally; pappus 1–2-seriate, persistent, bristles 12–50. Nine species, Australia.

845. ***Piora*** J.T. Kost.

Piora J.T. Kost., Nova Guinea, Bot. 24: 596 (1966).

Ericoid shrubs; aromatic, glabrous, stems, leaf undersides and involucres gland-dotted; stems erect, virgately branched. Leaves caducous below, sessile, with short, sheathing bases, blades coriaceous or fleshy, 1-nerved, linear, obtuse, margins entire, recurved. Heads solitary, on short, sparsely bracteolate peduncles; involucres obconic-campanulate; bracts 3–4-seriate, gradate, mostly linear-lanceolate, acute, 1-nerved. Rays c. 40, 2–3-seriate, pistillate, bluish-white, not coiling. Disc florets c. 30, functionally male, yellow, narrowly funnelform, lobes 4, lanceolate, erect, with orange ducts; anthers with minute, indistinct apical appendages. Achenes oblong-obovate, triangular, truncate apically; pappus lacking. One species, *P. ericoides* J.T. Kost., New Guinea.

846. ***Pytinicarpa*** G.L. Nesom

Pytinicarpa G.L. Nesom, Phytologia 76: 136 (1994); Nesom, Sida 19: 513–518 (2001), emend.

Perennial, eglandular, rhizomatous herbs. Leaves in basal rosettes, oblanceolate to linear, with 3 parallel veins, entire or distally toothed, sparsely villous. Scapes with few filiform bracts; heads solitary; involucres campanulate; bracts 2–4-seriate, all but outermost subequal, oblong, tips rounded, with thin orange midvein, margins scarious, laciniate to ciliate; receptacles sharply conic. Rays 1-seriate, pistillate, white, tube hairy, limbs 4-veined, coiling. Disc florets functionally male, orange-veined, tube short, limb tubular-campanulate, lobes deltate, erect. Fertile achenes narrowly oblong, base narrowed, neck short, (1–)2(–3)-ribbed on each surface, glabrous, eglandular; pappus lacking. Two species, New Caledonia and Fiji.

847. ***Rhamphogyne*** S. Moore

Rhamphogyne S. Moore, J. Bot. 52: 146 (1914); Swenson & Bremer, Austral. Syst. Bot. 7: 265–273 (1994), emend.

Small, perennial, caespitose herbs. Leaves densely inserted, linear-oblanceolate, entire or pinnatifid. Heads small, solitary, sessile, disciform; involucres narrowly campanulate; bracts c. 6, acute, ciliate. Peripheral florets 1-seriate, pistillate, yellow, tubular, 3-lobed. Disc florets more numerous than pistillate florets, perfect, yellow, limb narrowly funnelform, lobes 3 or 4, ovate-triangular, erect-spreading, anthers inserted near base of corolla; style branches acute, hairy. Achenes elliptic-obovate, long- and sometimes sinuously beaked, glabrous; pappus lacking. Two species, Rodrigues Island, New Guinea.

848. *Rhynchospermum* Reinw.

Rhynchospermum Reinw., Syll. Pl. Nov. 2: 7 (1825).

Erect perennial herbs; puberulous. Leaves petiolate, blades herbaceous, elliptic to oblanceolate, remotely dentate. Inflorescences racemose-spicate to thyrsoid; peduncles usually widely diverging; heads subdiscoid; involucres hemispheric; bracts 3–4-seriate, weakly gradate, oblong, with distal green patch, margins narrowly scarious, apices obtuse, fimbriate. Rays c. 11, 2-seriate, pistillate, whitish, limbs short, elliptic. Disc florets c. 11, perfect, yellowish, tubes short, narrow, limb campanulate, lobes 4, broadly triangular, erect; style appendages oblong-ovate. Achenes obovate, gland-dotted distally, ray achenes with apical neck; pappus lacking or of up to 10 scraggly, whitish, caducous bristles. $x = 9$. One species, *R. verticillatum* Reinw., eastern and south-eastern Asia.

849. *Sheareria* S. Moore

Sheareria S. Moore, J. Bot. 13: 227, t. 165 (1875).

Small annual herbs; sparsely pilose; stems erect, costate; branches sparse, divergent. Leaves small, bract-like, linear, entire. Inflorescences mostly 1-headed; involucres campanulate; bracts 6 or 7, c. 2-seriate, gradate, ovate to oblong, concave, without obvious venation. Rays 3 or 4, pistillate, white, with broad limb, apex weakly 5-crenulate. Disc florets 1 or 2, functionally male, yellow, tube slender, limb narrowly funnelform, lobes deltate, erect; style undivided. Fertile achenes oblong, trigonous, with narrowly winged, denticulate ribs, glabrous; pappus lacking. Two species, China.

850. *Solenogyne* Cass.

Solenogyne Cass., Dict. Sci. Nat. 50: 493 (1827); Davis, Proc. Linn. Soc. New South Wales 75: 88–194 (1948), rev.; Adams, Brunonia 2: 3–65 (1979), rev.

Rosulate perennial herbs; glabrous to pilosulous. Leaves in rosette, oblanceolate to spathulate with cuneate or pseudopetiolate base, dentate distally. Heads solitary on elongate peduncles, disciform; involucres broadly campanulate to hemispheric; bracts c. 3-seriate, subequal, herbaceous, oblong, obtuse or rounded, denticulate, margins not or narrowly scarious. Pistillate florets 3–4-seriate, greenish or red-tinged, filiform, oblique or with minute limbs. Disc florets fewer than pistillate, functionally male, white or greenish to reddish, tube narrow, limb narrowly campanulate, with (3–)4(–5) erect, deltate lobes; style branches hairy. Achenes oblong-obovate, short-beaked or beakless, smooth, glabrous, mostly non-glandular; pappus lacking. $x = 9$. Three species, Australia, Tasmania.

851. *Thespis* DC.

Thespis DC. in Guill., Arch. Bot. (Paris) 2: 517 (1833).

Spreading annual herbs, puberulous to pilose. Leaves sessile to petiolate, blades ovate to obovate, entire to serrate-dentate. Heads in small corymbose cymes, short-pedunculate, discoid; involucres hemispheric; bracts c. 2-seriate, subequal, glabrous, oblong, concave, with broad green band, margins scarious. Pistillate florets multiseriate; corollas minutely tubular or lacking. Disc florets few, functionally male, pale, shortly funnelform, lobes 4, oblong-ovate, erect, with orange resin ducts; anther appendages reduced to small apiculus. Fertile achenes ellipsoid, multinerved, eglandular, not or slightly compressed, finely papillose; pappus 1-seriate, of 6–13 scabrid bristles shorter than achene, sometimes lacking in disc florets. Three species, south-eastern Asia.

XV.7. Subtribe Baccharidinae Less. (1830).

Subf. Baccharidoideae Burmeist. (1837).
Tribe Heterothalaminae Endl. (1837).

Trees, woody shrubs, or vines, rarely herbs or subshrubs, often dioecious. Leaves alternate, rarely opposite, entire to serrate or pinnatisect, commonly gland-dotted. Inflorescences congested corymbose to thyrsoid; involucral bracts flat, mostly herbaceous; receptacles with or without pales. Female heads with florets tubular or with short white limbs,

central florets sometimes appearing functionally male; male heads with pistillate florets absent or 1–2-seriate; disc style branches with short, papillose appendages. Achenes small, terete to compressed, multinerved, usually eglandular, glandular in some *Baccharis* and *Archibaccharis*, setulae without anchor-shaped tips; pappus 1-seriate, persistent, bristles often apically dilated. $x = 9$.

Key to the Genera

1. Female heads with a few central functionally male florets **852. *Archibaccharis***
– Female heads without male florets 2
2. Male and female florets in totally separate heads; plants totally dioecious or rarely monoecious **853. *Baccharis***
– Male heads with 2 outer series of pistillate florets; female heads paleate, male heads epaleate **854. *Heterothalamus***

Genera of Baccharidinae

852. *Archibaccharis* Heering

Archibaccharis Heering, Jahrb. Hamburg Wissensch. Anst. 21, Beih. 3: 40 (1904); Jackson, Phytologia 32: 81–194 (1975), rev.; Nesom, Phytologia 71: 152–159 (1991), emend.
Hemibaccharis S.F. Blake (1924).

Perennial herbs, shrubs or vines, functionally dioecious, with stipitate or sessile glands, not glutinous; stems straight, twining or zigzag. Leaves petiolate or sessile. Inflorescences terminal or axillary, strongly cymose or corymbose, unisexual or vestigially gynomonoecious. Involucral bracts 3–5-seriate, gradate. Female heads with outer florets pistillate, central florets appearing bisexual but anthers and achenes usually sterile; pistillate florets radiate to tubular, sometimes with staminodes. Male heads with gynoecia usually sterile. Fertile achenes compressed, ovate to oblong, 2–5(–7)-nerved, mostly 3-angled; pappus 1-seriate, bristles not elongating at maturity, usually dilated apically in staminate florets and sometimes in pistillate florets. $x = 9$. Thirty-two species, mostly Mexico, Central America, 1 or 2 in South America.

853. *Baccharis* L.

Baccharis L., Sp. Pl. 860 (1753), nom. cons.; Barroso, Rodriguésia 40: 3–273 (1976), reg. rev.; Barroso & Bueno, Fl. Illustr. Catarin., Compostas 5, subtribo Baccharidinae: 769–777, 784–1065 (2002), reg. rev.; Cuatrecasas, Revista Acad. Colomb. Ci. Exact. 13: 5–102 (1967), reg. rev.; Hellwig, Mitt. Bot. Staatssamml. München 29: 1–456 (1990), rev.; Mahler & Waterfall, Southw. Naturalist 9: 189–202 (1964), reg. rev.; Matuda, Anales Inst. Biol. Univ. Nac. Mexico 28: 143–174 (1957), reg. rev.
Molina Ruiz & Pav. (1794), nom. illegit. non Cav. (1790).
Sergilus Gaertn. (1791).
Tursenia Cass. (1825).
Pingraea Cass. (1826).
Baccharidastrum Cabrera (1937).
Baccharidiopsis G.M. Barroso (1976).
Neomolina Hellwig (1993), nom. illegit. non Honda & Sakis. (1930).

Small trees, shrubs or perennial herbs, dioecious or rarely monoecious; stems sometimes winged. Leaves rarely opposite, scale-like or absent, lamina linear to ovate, obovate or pinnatisect, glabrous to glandular-dotted and glutinous, rarely tomentose. Inflorescence corymbose or thyrsoid, spicate, racemose or 1-headed; heads unisexual, discoid. Involucres cylindric to hemispheric; bracts 3–8-seriate, gradate; receptacles plano-convex, usually epaleate. Female florets filiform-tubular; staminate heads with florets mostly whitish to purplish, funnelform, lobes cut nearly to base of limb, spreading-reflexing; style branches rudimentary. Achenes compressed or nearly terete, glabrous or hairy, 5–10(–12)-nervate; pappus 1–3-seriate, bristles sometimes caducous, in female florets usually elongating beyond involucre, in male florets often apically broadened. $x = 9$. Circa 360 species (fide Daniel Giuliano, pers. comm.), mostly of tropical America, north into central and coastal USA.

Hellwig (1990, 1993, 1996) proposed and formally recognized segregate genera from within *Baccharis* and made nomenclatural combinations for representative species, but he has not completed or extended his conceptual modifications. In a study of Baccharidinae, Giuliano (2001) has reviewed and modified the infrageneric taxonomy and also proposed to recognize several segregate genera, but with concepts which minimally intersect or overlap with those of Hellwig (1990, 1993, 1996).

854. *Heterothalamus* Less.

Heterothalamus Less., Linnaea 5: 145 (1830); Barroso & Bueno, Fl. Illustr. Catarin., Compostas 5, subtribo Baccharidinae: 777–784 (2002), rev.

Polygamo-dioecious, more or less ericoid shrubs, densely branched, often slightly glutinous. Leaves linear to elliptical. Inflorescences of small ter-

minal clusters of heads, often overtopped by lateral branches; involucres hemispheric; bracts 3–4-seriate, weakly to strongly gradate, oblong to linear, pale at base, green along midvein distally, margins hyaline; receptacles convex to subconical. Female heads with navicular pales, with only yellowish, filiform, short-rayed, pistillate florets. Male heads epaleate, with outer, sterile, pistillate florets 2-seriate, limbs short; inner florets functionally male, lobes deltate, reflexing. Fertile achenes 3- or 5-angled, glabrous; pappus bristles short; male achenes sterile; pappus bristles broadened apically. Two species, southern Brazil, Uruguay.

XV.8. Subtribe Podocominae G.L. Nesom (1994).

Annual to perennial herbs, often gland-dotted. Leaves alternate, entire to toothed or divided. Heads mostly solitary, paniculate or corymbose in some genera; involucral bracts herbaceous to thickened or slightly keeled; receptacles planoconvex, epaleate. Ray florets 2–3-seriate, corollas white to bluish (yellow in *Kippistia*), limbs coiling. Disc florets bisexual or often functionally male; style appendages usually lanceolate to linear, papillose. Achenes 2-nerved, compressed, often with a neck or beak, distally glandular, setulae without anchor-shaped tips; pappus bristles (1–)2–3-seriate, often with a much shorter outer series. $x = 9$.

Key to the Genera

1. Plants from America 2
– Plants from Australia 7
2. Achenes with a distinct neck or beak 3
– Achenes apically rounded or truncate, without a beak or neck 4
3. Vestiture arachnoid; leaves cauline, densely overlapping, not clasping; heads 20–35 mm wide, 1–2 on leafy stems; disc ovaries sterile **855. *Asteropsis***
– Vestiture glabrate to scabrous or hispid-pilose, never arachnoid; leaves cauline, basal leaves sometimes persistent, loosely disposed along long internodes, clasping to subclasping; heads (5–)7–15(–17) mm wide, solitary on scapose stems; disc ovaries fertile **869. *Podocoma***
4. Leaves herbaceous, not rigid, mostly oblanceolate, entire to serrate or pinnately dissected 5
– Leaves rigid, linear and entire or apically trifurcate, or pinnately dissected 6
5. Leaves all basal or basal and lower cauline; heads solitary on scapose stems; disc ovaries sterile; achenes eglandular **860. *Inulopsis***
– Leaves primarily cauline, basal leaves persistent in some species; heads on leafy stems; disc ovaries fertile; achenes glandular **865. *Laennecia***
6. Stems and leaves sessile- or punctate-glandular, also arachnoid; disc ovaries fertile **866. *Microgynella***
– Stems and leaves densely stipitate-glandular, not arachnoid; disc ovaries sterile **870. *Sommerfeltia***
7. Achenes with a short neck or long beak 8
– Achenes apically rounded or truncate, without a neck or beak 11
8. Achenes with a long, filiform beak; receptacles flat or nearly so; involucres reflexed after fruiting **863. *Ixiochlamys***
– Achenes with a short neck 9
9. Achenes with a prominently narrowed, basal extension below the seed, basal extension densely tufted with stiff, appressed hairs **872. *Vittadinia*** p.p.
– Achenes without a narrowed, basal extension below the seed, hairs at base not denser than on surface 10
10. Achenes c. 2 mm long, with short, broad neck; pappus bristles 2-seriate, the outer distinctly shorter than the inner; involucral bracts incurved after fruiting **857. *Dichromochlamys***
– Achenes c. 1 mm long, with a short, narrow neck; pappus bristles 1-seriate; involucral bracts never incurved **864. *Iotasperma***
11. Achenes usually with 2 to numerous facial nerves between the lateral nerves (facial nerves absent in six species of *Vittadinia*) 12
– Achenes with only a pair of lateral nerves, these variable in thickness, sometimes obscure or absent 14
12. Achenes with a prominently narrowed, basal extension below the seed, basal extension densely tufted with stiff, appressed hairs **872. *Vittadinia*** p.p.
– Achenes narrowly oblong to obovate or oblanceolate, without a narrowed, basal extension below the seed, hairs at achene base not denser than on achene surface 13
13. Disc florets with fertile ovaries; achenes usually with 3 pairs of facial nerves; herbs from a woody rootstock **856. *Camptacra***
– Disc florets with sterile ovaries; fertile achenes with one pair of facial nerves, rarely none; woody-based shrubs or shrublets **871. *Tetramolopium***
14. Achenes with a prominently narrowed, basal extension below the seed, basal extension densely tufted with stiff, appressed hairs **872. *Vittadinia*** p.p.
– Achenes without a narrowed, basal extension below the seed, hairs at achene base not denser than on achene surface 15
15. Disc florets with fertile ovaries; pappus of ray and disc achenes similar 16
– Disc florets with sterile ovaries; pappus of ray and disc achenes different 17
16. Ray florets with yellow corollas, ovaries often sterile; disc corollas 4-merous; achenes usually apically truncate, with a correspondingly broad pappus insertion **864. *Kippistia***
– Ray florets with white to bluish corollas, ovaries fertile; disc corollas 5-merous; achenes usually rounded to a narrow pappus insertion **868. *Peripleura***
17. Disc corollas with 5 lobes; pappus of ray achenes of equal length bristles, pappus of disc achenes of unequal bristles or of bristles and scales **867. *Minuria***

– Disc corollas with 3–4 lobes; pappus of ray achenes of scales or scales and bristles, pappus of disc (sterile) achenes of bristles 18
18. Leaves oblanceolate; ray achenes with pappus of scales and bristles **858. *Dimorphocoma***
– Leaves linear; ray achenes with pappus of scales 19
19. Erect or decumbent herbs; leaves cauline; heads terminal, solitary; pappus scales of ray achenes lanceolate **859. *Elachanthus***
– Sessile herbs with clustered leaves; heads clustered among leaf bases; pappus scales of ray achenes broadly obovate **862. *Isoetopsis***

Genera of Podocominae

855. *Asteropsis* Less.

Asteropsis Less., Syn. Gen. Comp. 188 (1832); Nesom, Phytologia 76: 101–105 (1994), relat.

Perennial herbs; stems, leaves and involucres loosely tomentose-villous. Leaves densely spirally inserted, sessile, non-clasping, 1-nerved, linear, entire. Inflorescences terminal, 1- to few-headed; involucres hemispheric, 20–30 mm wide; bracts 4–5-seriate, slightly gradate, linear-lanceolate, with long-attenuate, reddish tips. Rays multiseriate, to 100 or more, pistillate, white, limbs long. Disc florets functionally male, yellow, tubular, lobes narrowly triangular; style branches linear, papillae hair-like. Fertile achenes broadly obovate, apex short-beaked, surfaces sericeous, eglandular; pappus bristles c. 2-seriate, persistent, capillary. One species, *A. macrocephala* Less., southern Brazil, Uruguay.

856. *Camptacra* N.T. Burb.

Camptacra N.T. Burb., Brunonia 5: 11 (1982); Lander, Nuytsia 6: 61 (1987), comb.

Erect perennial herbs from rootstock; loosely tomentose to subglabrous, glandular. Leaves cauline, sessile, linear to oblong, entire to trifid at tip. Heads solitary on long peduncles; involucres broadly campanulate to hemispheric; bracts 3–4-seriate, oblong to linear-lanceolate, with or without membranaceous margins. Rays 1–2-seriate, pistillate, white to bluish, limbs narrow, short. Disc florets perfect, yellow, tube short, limb funnelform, lobes triangular, erect-spreading. Achenes narrowly elliptic to elliptic-oblong, bases not extended nor more densely hairy, dark or purplish when mature, glandular, each face with 3 slender, non-vascularized ribs; pappus bristles 1–2-seriate, persistent. $x = 9$. Two species, Australia.

857. *Dichromochlamys* Dunlop

Dichromochlamys Dunlop, J. Adelaide Bot. Gard. 2: 235 (1980).

Decumbent annual herbs; stems and leaves villous to woolly, rarely glabrous, glandular. Leaves cauline, spathulate, cuneate at base, apex coarsely toothed. Inflorescences 1-headed, on long, densely glandular peduncles; involucres hemispheric to subglobose; bracts 4–5-seriate, strongly gradate, lanceolate, apices acuminate, median bracts with broad, white, scarious margins; receptacles conical, densely glandular, edge with fine hairs. Florets 100–150. Rays numerous, multiseriate, pistillate, white to pink. Disc corollas perfect, yellow. Achenes obovate, smooth, constricted and glandular distally, sericeous on basal 3/4; pappus bristles persistent, multiseriate, uneven, outer series short. One species, *D. dentatifolia* (F. Muell.) Dunlop, central Australia.

858. *Dimorphocoma* F. Muell. & Tate

Dimorphocoma F. Muell. & Tate, Trans. Proc. Roy. Soc. S. Australia 6: 107 (1883).

Small, ascending annual herbs, with non-glandular hairs. Leaves cauline, lower leaf bases attenuate, upper subamplexicaul, oblanceolate, entire, midvein prominent. Heads solitary, pedunculate; involucres cup-shaped; bracts c. 8, 2-seriate, subequal, lanceolate, herbaceous with scarious margins. Rays 7 or 8, 1-seriate, pistillate, white, limbs short, narrow. Disc florets 3 or 4, functionally male, yellow, tubular, lobes 3 or 4. Fertile achenes obovate, without neck, sericeous-villous; pappus 2-seriate, outer row of many bristles, inner row of c. 6 equally long linear-lanceolate scales; disc florets with 3 or 4 pappus bristles. Two species, Australia.

859. *Elachanthus* F. Muell.

Elachanthus F. Muell., Linnaea 25: 410 (1853).

Small, erect or decumbent annual herbs; glabrous or puberulous, non-glandular. Leaves cauline, sessile, linear, entire. Heads solitary, pedunculate, disciform; involucres campanulate; bracts c. 2-seriate, subequal with few outer bracts smaller, oblong to oblanceolate, obtuse, herbaceous with scarious margins. Pistillate florets 2–3-seriate, white, tubular, narrowed and 2- or 3-lobed apically. Disc florets 2–5, functionally male, yellow, narrowly funnelform from narrow tube, lobes 3–5. Fertile achenes narrowly obovate to obconical,

slightly compressed, without neck, minutely setulose to sericeous-villous; pappus c. 2-seriate, of lanceolate scales; slender disc achenes with pappus of 1–3 linear, basally connate scales or 3 or 4 bristles. Two species, southern Australia.

860. *Inulopsis* (DC.) O. Hoffm.

Inulopsis (DC.) O. Hoffm. in Engler & Prantl, Nat. Pflanzenfam. IV/5: 145, 149 (1890); Nesom, Phytologia 76: 115–124 (1994), rev.
Haplopappus Cass. sect. *Inulopsis* DC. (1836).

Perennial herbs from rhizomes; leaves and stems glabrate to hirsute-villous, sometimes gland-dotted, resinous. Leaves all basal or some cauline, obovate to linear, with 1 or 2 pairs of longitudinal veins from base. Heads solitary on scapes; involucre hemispheric to turbinate; bracts 2–4-seriate, outer 1/2–3/4 as long as inner, lanceolate to lanceolate-oblong, herbaceous, 1-nerved. Rays 1-seriate, pistillate, white, tube with biseriate hairs. Disc florets functionally male, yellow, orange-veined, narrowly funnelform, lobes deltate, erect. Achenes oblanceolate to elliptic, sometimes with extra rib on each face, eglandular, strigose-sericeous, apical neck vestigial; pappus bristles (1–)2–3-seriate, subequal, attenuate, often with short outer setae. $x = 9$. Four species, southern Brazil, Paraguay, eastern Bolivia.

861. *Iotasperma* G.L. Nesom

Iotasperma G.L. Nesom, Phytologia 76: 144 (1994).

Erect, taprooted annual herbs; surfaces hispid-pilose, sparsely glandular. Leaves cauline, sessile, subclasping, oblanceolate-oblong, coarsely toothed distally. Inflorescences loosely corymbose; involucres shallowly cupulate; bracts c. 2-seriate, subequal, elliptic-lanceolate, green, 3-nerved, stipitate-glandular, margins scarious, inner bracts basally indurate. Rays (1–)2–3-seriate, pistillate, white to purplish. Disc florets functionally male, yellow, tube linear, limb subabruptly funnelform, lobes short-triangular. Achenes obovate to elliptic-obovate, sclerified, setuliferous, rounded to narrow, gland-dotted bases and apices, prominent apical callus bearing 6–10(–15), 1-seriate, caducous, bristles. Two species, Australia.

862. *Isoetopsis* Turcz.

Isoetopsis Turcz., Bull. Soc. Imp. Naturalistes Moscou 34, 1: 174, t. 3 (1851); Robinson & Brettell, Phytologia 26: 73–75 (1973), relat.

Sessile, rosulate annual herbs, glabrous. Leaves linear, with pale broad bases. Heads sessile among leaf bases; involucral bracts c. 2-seriate, subequal, oblong-ovate, obtuse, pale below, green distally, margins narrowly pale to scarious. Rays 5–6, pistillate, apomictic(?), greenish or purplish distally, tubular, narrowed to lobed tip, lobes usually 3, triangular with setiform tip; bulbous style base with numerous fibrous strands entering achene. Disc florets 2–3, functionally male, pale yellowish, with slender tube, limb flaring, lobes 4; stamen appendages small, ovate-oblong. Fertile achenes obovate, nearly terete, 2-nervate, without neck, sericeous; pappus of c. 8 persistent, obovate, obtuse, broadly costate scales. One species, *I. graminifolia* Turcz., Australia.

863. *Ixiochlamys* F. Muell. & Sond. ex Sond.

Ixiochlamys F. Muell. & Sond. ex Sond., Linnaea 25: 466 (1853); Dunlop, J. Adelaide Bot. Gard. 24: 241–252 (1980), rev.

Annual or perennial herbs to small shrubs; glabrous to pilose or hirsute, often stipitate-glandular. Leaves cauline, sessile, entire to pinnately lobed. Heads solitary, pedunculate; involucres broadly campanulate; bracts 3–4-seriate, gradate, herbaceous, lanceolate to linear, reflexed after anthesis, glabrous or glandular. Rays several-seriate, pistillate, white to pink, limbs often short. Disc florets usually fewer than rays, functionally male or perfect, yellow, funnelform from slender tube, lobes triangular, erect. Fertile achenes smooth, with few or no hairs or glands, apically narrowed into filiform beak; pappus bristles persistent, often with shorter outer bristles. Four species, western and central Australia.

864. *Kippistia* F. Muell.

Kippistia F. Muell., Rep. Pl. Babbage's Exped. 12 (1858); Lander & Barry, Nuytsia 3: 215–219 (1980), emend.

Small, compact, aromatic shrubs. Leaves small, linear, fleshy, glabrous. Heads solitary on branchlets, short-pedunculate; involucres broadly conical; bracts 2–3-seriate, subequal, linear-lanceolate, fimbriate apically. Rays c. 2-seriate, pistillate, fertile or sterile, yellow, limbs rather short. Disc florets perfect, yellow, narrowly funnelform, lobes triangular, erect; style appendages densely hairy. Ray achenes oblong-linear, sparsely setulose basally; disc achenes elliptic, compressed, glabrous; pappus bristles unequal, free or bases fused into cup or tube, tube

sometimes surmounted by fewer long bristles. One species, *K. suaedifolia* F. Muell., southern Australia, gypsophilous.

865. *Laennecia* Cass.

Laennecia Cass., Dict. Sci. Nat. 25: 91 (1822); Nesom, Phytologia 68: 205–228 (1990), rev.

Annual to short-lived perennial, taprooted herbs, white-tomentose or coarsely hairy, often gland-dotted. Leaves sessile, lanceolate or oblanceolate to oblong, toothed to pinnately lobed, rarely entire. Inflorescences spicate or racemose to loosely thyrsoid or corymbose; involucres turbinate; bracts 2–5-seriate, gradate, with greenish midvein. Pistillate florets several-seriate, white, filiform-tubular, eradiate and apically fimbriate or short-radiate. Disc florets perfect, cream to yellowish, tubular-funnelform, expanded near lobe bases, lobes lanceolate. Achenes oblanceolate-elliptic to obovate, faces usually with sessile or subsessile glands; pappus bristles 1–2-seriate, often caducous, with or without short outer setae or scales. $x = 9$. Seventeen species, south-western USA, Mexico to northern South America (Andean).

866. *Microgynella* Grau

Microgynella Grau, Mitt. Bot. Staatssamml. München 12: 185 (1975), nom. nov.; Nesom, Phytologia 76:101–105 (1994), emend.
Microgyne Less. (1832), nom. illegit. non Cass. (1827).

Perennial herbs to subshrubs; caudex woody; stems, leaves and involucres gland-dotted, resinous, sparingly hispid and with arachnoid hairs. Leaves densely spirally inserted, linear, mostly apically trifid with linear lobes. Heads solitary, on long peduncles; involucres broadly campanulate; bracts 2–3-seriate, subequal, narrowly oblong to linear, herbaceous with hyaline margins, inner bracts white-indurate at base. Rays 2-seriate, pistillate, reddish. Disc florets perfect, reddish, narrowly funnelform from slender tube, lobes deltate. Achenes broadly oblanceolate-conical, apically truncate, not constricted above, densely sericeous and gland-dotted; pappus c. 2-seriate, bristles reddish-brown. One species, *M. trifurcata* (Less.) Grau, south-eastern Brazil, Argentina, Uruguay.

867. *Minuria* DC.

Minuria DC., Prodr. 5: 298 (1836); Lander & Barry, Nuytsia 3: 221–237 (1980), rev.

Erect annual herbs to small shrubs; glabrous to puberulous or tomentose, non-glandular. Leaves alternate or opposite, sessile, linear to ovate or oblanceolate, entire to serrulate or dentate. Heads solitary to rarely clustered, pedunculate; involucres campanulate; bracts 3–4-seriate, weakly gradate, linear to lanceolate, herbaceous with greenish midvein and tip, margins scarious. Rays 2–3-seriate, pistillate, limbs white, blue or violet, narrow. Disc florets functionally male, yellow, narrowly funnelform, lobes (4–)5, triangular, recurving. Fertile achenes linear-lanceolate to obovate, narrowed distally without neck, setulose, with free pappus bristles; disc achenes with pappus of unequal bristles, bristles and scales, or cup of fused scales with 1–8 bristles, bristles usually more densely barbellate distally. $x = 9$. Ten species, Australia.

868. *Peripleura* (N.T. Burb.) G.L. Nesom

Peripleura (N.T. Burb.) G.L. Nesom, Phytologia 76: 131 (1994).
Vittadinia A. Rich. subg. *Peripleura* N.T. Burb. (1982).

Erect annual or perennial herbs; strigose or puberulous to stipitate-glandular. Leaves cauline, sessile, usually linear-elliptic, entire or with few teeth or lobes. Heads solitary on leafy stems, sometimes pedunculate; involucres broadly campanulate; bracts weakly gradate with few outer bracts, obtuse to acuminate, margins narrow, membranaceous. Rays 1–2-seriate, pistillate, white to purplish, short, narrow. Disc florets perfect, yellow, tubes longer than limb, lobes deltate, erect-spreading. Achenes obovate, apically rounded to pappus, without narrowed base or tuft of hairs, faces glandular; pappus bristles 1(–2)-seriate, mostly 1.5–2.5 times as long as achene, belatedly caducous in species with basally coherent bristles. $x = 9$. Nine species, Australia.

869. *Podocoma* Cass.

Podocoma Cass., Bull. Sci. Soc. Philom. Paris 1817: 137 (1817); Nesom & Zanowiak, Phytologia 76: 106–114 (1994), emend.
Podopappus Hook. & Arn. (1836).

Perennial herbs, rhizomatous; usually coarsely pubescent, eglandular. Basal leaves often persistent, cauline leaves clasping. Inflorescences 1-headed or loosely corymbose; involucres campanulate, (5–)7–15(–17) mm wide; bracts 3–5-seriate, strongly gradate, stiffly indurate,

narrowly lanceolate or oblong-lanceolate, greenish along middle, without orange resin ducts. Rays 2–5-seriate, pistillate, white or purple, rarely yellow, coiling or filiform and erect. Disc florets fewer than rays, perfect, cream-coloured, tubes long, limbs shorter, narrowly funnelform, sometimes orange-veined, lobes deltate, erect. Achenes strigose, eglandular, apically with broad or filiform neck; capillary pappus bristles in 2(–3) series or with the outer series short. $x = 9$. Circa 9 species, south-eastern South America.

870. *Sommerfeltia* Less.

Sommerfeltia Less., Syn. Gen. Comp. 189 (1832); Nesom, Phytologia 76: 101–105 (1994), emend.

Perennial herbs or subshrubs, from woody caudex; stems, leaves, and involucres with dense sessile or short-stipitate glands. Leaves densely spirally arranged, stiff, entire to pinnately dissected, tips spinose. Inflorescence 1-headed to loosely corymbose; peduncles long; involucres broadly campanulate; bracts 3–4-seriate, gradate, lanceolate to linear, thick and indurate, greenish in middle, carinate, without orange veins, sides hyaline. Rays 1-seriate, pistillate, white. Disc florets functionally male, yellow, narrowly funnelform, lobes triangular, erect. Fertile achenes narrowly obovate, apically rounded, margins and bases strigose-sericous, faces gland-dotted and sparsely hairy; pappus bristles 2-seriate, whitish, elongate, scarcely barbellate. Two species, southern Brazil, Uruguay, Argentina.

871. *Tetramolopium* Nees

Tetramolopium Nees, Gen. Sp. Aster. 202 (1832); Lowrey, Allertonia 4: 204–262 (1986), rev.; van Royen, Alpine Fl. New Guinea 4: 3245–3311 (1983), reg. rev.
Luteidiscus St. John (1974).

Monoecious or gynomonoecious; erect to decumbent shrubs or subshrubs; often stipitate-glandular or gland-dotted; branching sympodial. Leaves clustered at stem tips, sessile or petiolate, lanceolate to spathulate, entire to dentate or shallowly lobed. Inflorescences 1-headed or corymbose with 6–50 heads; peduncles bracteolate; involucres cylindric to turbinate or hemispheric; bracts 3–4-seriate, gradate, lanceolate to linear-lanceolate. Rays 5–250, pistillate, yellow or white. Disc florets perfect or functionally male, yellow or maroon, limb campanulate, lobes lanceolate, erect to spreading. Achenes obovoid to rarely fusiform-cylindric, faces 0–7-nervate, glabrous, stipitate-glandular and/or strigose; pappus bristles 1–2-seriate, unequal. $x = 9$. Thirty-eight species, New Guinea, north-eastern Australia, Hawaii.

872. *Vittadinia* A. Rich.

Vittadinia A. Rich., Voy. Astrolabe 250 (1832); Burbidge, Brunonia 5: 1–72 (1982), rev.

Annual to perennial herbs or small shrubs; strigose to hispid or hirsute, often glandular. Leaves cuneate-spathulate to oblanceolate, rarely elliptic to linear-terete, sometimes lobed. Heads solitary at tips of branches; peduncles short or long; involucres broadly campanulate; bracts 3–4-seriate, gradate but weakly overlapping, mostly linear, margins narrowly scarious. Rays 2- to several-seriate, pistillate, white to bluish, short, narrow. Disc florets perfect, yellow, narrow tube longer than limb, lobes deltate, erect. Achenes oblanceolate or cuneate, with narrow base bearing tuft of setulae, apex with broad short neck, faces with 3–5(–6) slender, often short, false nerves, glandular; pappus bristles 2–3-seriate, persistent, not coherent, c. as long as achene. $x = 9$. Twenty species, Australia.

XV.9. Subtribe Asterinae (Cass.) Dumort. (1827).

Subtribe Heterochrominae Benth. (1873), nom. non rite public.

Herbs. Leaves alternate, mostly entire, sometimes serrate, with or without glandular dots. Inflorescence corymbose or heads solitary; involucral bracts flat, mostly herbaceous; receptacles epaleate. Ray florets usually present, 1-seriate, with long white or blue limbs, short in *Psychrogeton*. Disc florets bisexual; style branches with short, papillose appendages. Achenes obovate, compressed, 2-nerved, often with glands, setulae without anchor-shaped tips; pappus (1–)2(–3)-seriate, persistent, of equal lengths or with short outer series. $x = 9$.

Key to the Genera

1. Disc florets functionally male; pistillate florets tubular or with short erect limbs **883. *Psychrogeton***
– Disc florets perfect; pistillate florets lacking or long-radiate 2
2. Caespitose plants with scapose single-headed inflorescences **873. *Arctogeron***

– Plants non-caespitose; with usually branching inflorescences 3
3. Outer involucral bracts leaf-like, strongly differentiated from smaller inner bracts **876. *Callistephus***
– Outer involucral bracts not strongly differentiated from inner bracts 4
4. Pappus of all achenes short or lacking 5
– Pappus of at least disc florets over 1 mm long 6
5. Pappus totally lacking **882. *Miyamayomena***
– Pappus bristles not over 1 mm long **880. *Kalimeris***
6. Halophytic, subsucculent plants; involucral bracts glabrous; pappus after anthesis becoming 3–4 times longer than achene **885. *Tripolium***
– Plants not halophytic; not subsucculent; pappus not noticeably elongating after anthesis 7
7. Involucral bracts gradate in 3–5 series 8
– Involucral bracts subequal to weakly gradate, in 2–3 series 10
8. Ray florets present and fertile, with ray corollas shorter than pappus **884. *Rhinactinidia***
– Ray florets sterile or lacking 9
9. Ray florets lacking **877. *Crinitaria***
– Ray florets usually present but sterile **878. *Galatella***
10. Leaves with recurved margins and cuspidate tips; subshrubs **875. *Asterothamnus***
– Leaf margins mostly flat; plants mostly strictly herbaceous 11
11. Pappus sordid-grey to brown or reddish, bristles shorter and sometimes lacking in ray florets **879. *Heteropappus***
– Pappus usually white or sordid white, alike in ray and disc achenes 12
12. Pappus of only slender bristles, without short outer series **874. *Aster***
– Pappus with inner series of slender bristles and outer series of short, flat bristles **881. *Kemulariella***

Genera of Asterinae

873. *Arctogeron* DC.

Arctogeron DC., Prodr. 5: 260 (1836); Tamamschyan, Fl. U.R.S.S. 25: 135–136 (1959), Engl. transl. 125–127 (1999), reg. rev.

Caespitose, perennial herbs; with branching woody caudex; older stem bases covered by marcescent leaves. Young leaves in apical rosettes, bases somewhat sheathing, with c. 5 stiff marginal cilia, blades narrow, almost setaceous. Inflorescences of many erect, flexuously haired scapes bearing single heads; involucres campanulate; bracts 3-seriate, not or weakly gradate, green, lanceolate, acuminate, carinate, densely hairy along keel, margins white-membranaceous; receptacles flat. Rays pistillate, white or pinkish, limbs oblong-ovate, coiling. Disc florets yellow, narrowly funnelform, lobes 5, triangular, recurved. Achenes oblong, somewhat ribbed, densely sericeous; pappus white, multiseriate, bristles as long as disc corollas. One species, *A. gramineum* DC., Siberia.

874. *Aster* L.

Aster L., Sp. Pl. 872 (1753). [*Aster* Tourn. ex L., Syst. ed. 1. 1735.]; Grierson, Notes Roy. Bot. Gard. Edinburgh 26: 67–163 (1964), reg. rev.; Lippert, Mitt. Bot. Staatssamml. München 11: 153–258 (1973), rev.; Tamamschyan, Fl. U.R.S.S. 25: 77–110 (1959), Engl. transl. 72–104 (1999), reg. rev.

Bellidiastrum Scop. (1760), nom. et orth. cons. prop.

Perennial herbs or shrubs. Leaves basal or cauline or both. Inflorescence 1-headed to corymbose or loosely thyrsoid; involucres hemispheric to campanulate; bracts several-seriate, subequal to weakly gradate, linear, mostly herbaceous; receptacles plano-convex, glabrous to spinulose or puberulous. Rays pistillate, white, bluish, pink or purplish, limbs coiling. Disc florets usually yellow, tubular to narrowly funnelform, lobes triangular, erect to spreading. Achenes obovate and compressed to cylindric, setuliferous, often gland-dotted; pappus 1–2-seriate, bristles barbellate, few or no short bristles outside. $x = 9$. Circa 180 species, mostly Eurasia and Africa, one species Arctic and western North America.

875. *Asterothamnus* Novopokr.

Asterothamnus Novopokr., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 13: 334 (1950); Tamamschyan, Fl. U.R.S.S. 25: 124–129 (1959), Engl. transl. 25: 117–121 (1999), reg. rev.

Much-branched subshrubs, rhizomatous, stems finely puberulous to greyish-tomentose. Leaves sessile, small, oval to linear, margins revolute. Heads solitary or 3–5 in corymbose groups, pedunculate; involucres obovoid to hemispheric or campanulate; bracts 3–4-seriate, gradate, oblong-lanceolate to linear, margins membranaceous, whitish, midrib prominent, brownish or reddish; receptacles flat, margins of alveolae with some teeth as long as young achenes. Rays 1-seriate or lacking, pistillate, blue, violet or whitish-pink, limbs long. Disc florets yellow, lobes triangular, spreading-recurved. Achenes ovoid to oblanceolate or subfusiform, 3-angled, 1 convex and 2 flat sides, extra rib on convex side, appressed-setulose; pappus white or sordid; bristles as long as disc corollas. Seven species, Eurasia.

876. *Callistephus* Cass.

Callistephus Cass., Dict. Sci. Nat. 37: 491 (1825), nom. cons. *Callistemma* Cass. (1817).

Annual herbs, sparingly branched; stems erect, pilose-hirsute. Leaves mostly cauline, glabrous to strigose, eglandular, lower leaves petiolate, blades coarsely toothed, upper leaves reduced, sessile, spathulate. Inflorescences 1-headed or corymbose to thyrsoid with few heads; involucres hemispheric; bracts 2–3(–5)-seriate, leaf-like, long-ciliate proximally, inner 1–2 series membranous-scarious, often white, broadest distally; receptacles plano-convex. Rays 1–2-seriate, pistillate, bluish, reddish or white. Disc florets yellow, tube short, limbs abruptly expanded, lobes deltate-lanceolate, erect to spreading; style appendages broadly lanceolate. Achenes compressed, with thickened marginal nerves, strigose-sericeous, eglandular; inner pappus bristles caducous, outer series of short bristles or squamae. $x = 9$. One species, *C. chinensis* (L.) Nees, northern China, also cultivated.

877. *Crinitaria* Cass.

Crinitaria Cass., Dict. Sci. Nat. 37: 460 (1825); Tzvelev, Fl. U.R.S.S. 25: 173–183 (1959), Engl. transl. 163–172 (1999), reg. rev.
Linosyris Cass. (1825), nom. illegit. non *Linosyris* C.G. Ludw. (1757).
Pseudolinosyris Novopokr. (1918).

Biennial herbs to subshrubs; glabrous to scabrous or gland-dotted, often tomentose in inflorescence; stems branched from base or at tip. Leaves cauline, sessile, narrow with 1 prominent nerve, margins often involute. Inflorescences corymbose to 1-headed; involucres cylindric to turbinate; bracts 3–5-seriate, subequal to gradate, herbaceous to subcoriaceous, oblong to linear-subulate, margins partly scarious; receptacles convex to elongate. Rays lacking. Florets 4–40, yellow or partly pink, tubes slender, limbs narrowly campanulate, lobes (4–)5, lanceolate; style bases sometimes bulbous; style appendages lanceolate. Achenes obovate to linear, sericeous-villous or gland-dotted, ribs obscure, often 1 or 2 on sides; pappus bristles whitish to pinkish, 2(–3)-seriate, sometimes basally connate. $x = 9$. Thirteen species, Eurasia.

878. *Galatella* Cass.

Galatella Cass., Dict. Sci. Nat. 37: 463, 488 (1825); Tzvelev, Fl. U.R.S.S. 25: 138–172 (1959), Engl. transl. 128–161 (1999), reg. rev.
Aster L. subg. *Galatea* Cass. (1818).

Perennial herbs with nodose rhizome; stems erect, mostly unbranched. Leaves sessile, oblong to narrowly linear, entire, often gland-dotted, 1- or 3-veined. Inflorescences corymbose, occasionally 1-headed; heads pedunculate; involucres obconic to subhemispheric; bracts 3–4-seriate, gradate, herbaceous, lanceolate-ovate to oblong, acute to obtuse, glabrous or puberulous, with 1–3(–5) veins, margins partly membranaceous; receptacles slightly convex, alveole margins dentate. Peripheral florets, 0 to 1–20, usually sterile, limbs pinkish- or bluish-violet. Disc florets 5–60(–100), yellow, narrowly funnelform, lobes lanceolate; style appendages lanceolate or ovate-triangular. Achenes oblong, somewhat compressed, without obvious ribs; pappus bristles whitish to pinkish-violet, 2–3-seriate, connate into basal ring. $x = 9$. Circa 30 species, south-central Europe, Russia, Iran and India to western China.

879. *Heteropappus* Less.

Heteropappus Less., Syn. Gen. Comp. 189 (1832).

Short-lived herbs; puberulous to hispid; stems branching at base or in inflorescence. Leaves herbaceous, sessile to pseudopetiolate, larger and non-persistent in rosette, cauline leaves linear to oblong or obovate, 1- or weakly 3-nerved, margins entire or remotely serrate. Inflorescences 1-headed or corymbose; involucres obconic to rotate; bracts 2–3-seriate, subequal, herbaceous, lanceolate to linear-lanceolate, margins scarcely scarious; receptacles plano-convex. Rays 1-seriate, pistillate, white, blue or purplish, coiled. Disc florets yellow, narrowly funnelform, lobes triangular, erect, often zygomorphic; style appendages triangular. Achenes obovate, compressed, 2-ribbed, sericeous; pappus bristles sordid to reddish, often with outer scales, pappus sometimes reduced in rays. $x = 9$. Circa 20 species, central and eastern Asia.

880. *Kalimeris* (Cass.) Cass.

Kalimeris (Cass.) Cass., Dict. Sci. Nat. 37: 464 (1825); Gu & Hoch, Ann. Missouri Bot. Gard. 84: 762–814 (1997).
Aster L. subg. *Kalimeris* Cass. (1822).

Perennial taprooted herbs; rhizomatous; stems branched above. Basal leaves petiolate, non-persistent, upper leaves reduced, lanceolate to oblanceolate or linear, entire, coarsely toothed or lobed, glabrous to strigose, sometimes glandular.

Inflorescences 1-headed on leafy peduncles or corymbose; involucres hemispheric to campanulate; bracts 2–3-seriate, gradate, lanceolate to obovate, pale-indurate at base, distally green-herbaceous; receptacles convex to subconical. Rays 10–30, pistillate, white to pinkish or bluish, limbs short, not coiling. Disc florets yellow, tubes short, limbs campanulate, lobes lanceolate. Achenes obovoid, compressed, with 2(–4) nerves, glandular and often strigose; pappus bristles short, 1-seriate, sometimes reddish. $x = 9$. Eight species, eastern Asia, also cultivated.

881. *Kemulariella* Tamamschyan

Kemulariella Tamamschyan in Komarov, Fl. U.R.S.S. 25: 580 (1959); Tamamschyan, Fl. U.R.S.S. 25: 110–118 (1959), Engl. transl. 25: 104–111 (1999), reg. rev.

Perennial herbs or subshrubs; stems 1 or many from nodular rhizomes, glabrous below or with articulate to hooked hairs. Leaves sessile, ovate to linear-lanceolate, entire or toothed. Heads usually solitary, pedunculate; involucres broadly campanulate to hemispheric; bracts 2–3-seriate, subequal to weakly gradate, herbaceous, oblong-lanceolate to linear; receptacles convex, conical or hemispheric, alveole margins narrowly membranaceous. Rays 1–2-seriate, pistillate, limbs purple or pinkish. Disc florets yellow, narrowly funnelform, lobes triangular. Achenes oblong, not or slightly compressed, angular with 3 narrow ribs, appressed-setulose; inner pappus bristles 1-seriate, scales or short flat bristles outside. $x = 9$. Six species, Caucasus.

882. *Miyamayomena* Kitam.

Miyamayomena Kitam., Acta Phytotax. Geobot. 33: 409 (1982).
Gymnaster Kitam. (1937), nom. illegit. non *Gymnaster* F. Schütt (1891).

Erect perennial herbs; rhizomes short; stems branched at top. Leaves glabrous or with short, coarse hairs, basal leaves with winged petioles, oblong to ovate-oblong, margins coarsely incised-toothed, cauline leaves sparse, smaller. Inflorescences loosely corymbose; heads long-pedunculate; involucres subglobose to campanulate; bracts 2–3-seriate, subequal, lanceolate; receptacles conical. Rays 1–2-seriate, pistillate, limbs blue or white, coiling. Disc florets numerous, yellow, lobes 5; style appendages deltate to lanceolate, hairy. Achenes oblong, compressed, glabrous, margins ribbed; pappus lacking. $x = 9$. Five species, Japan.

883. *Psychrogeton* Boiss.

Psychrogeton Boiss., Fl. Orient. 3: 156 (1875); Grierson, Notes Roy. Bot. Gard. Edinburgh 27: 101–147 (1967), rev.

Perennial to biennial herbs; stems usually clustered, from caudex or rhizomes; hispid to tomentose. Leaves in basal rosettes or cauline, herbaceous, lanceolate or oblanceolate to rounded, entire to pinnatifid. Inflorescences corymbose or with erect peduncles; involucres obconical to rotate; bracts c. 3-seriate, subequal, lanceolate to linear-lanceolate, margins rather broadly scarious, green patch narrow; receptacles plano-convex. Pistillate florets 1–2-seriate, white to pink or purple, tubular or with short erect limb. Disc florets functionally male, rarely perfect, yellow, narrowly funnelform, lobes somewhat unequal, erect. Achenes obovate or oblanceolate, compressed, 2-nervate, sericeous; pappus bristles whitish. $x = 9$. Twenty species, central Asia, western China.

884. *Rhinactinidia* Novopokr.

Rhinactinidia Novopokr., Trudy Bot. Inst. Akad. Nauk S.S.S.R. ser. 1, Fl. Sist. Vyssh. Rast. 7: 114, 134 (1948); Tamamschyan, Fl. U.R.S.S. 25: 129–135 (1959), Engl. transl. 121–125 (1999), reg. rev.
Rhinactina Less. (1832), non *Rhinactina* Willd. (1807).
Krylovia Schischk. (1949).
Borkonstia Ignatov (1983).

Erect perennial herbs, from branching caudex; puberulous to pilose. Leaves mostly in basal rosette, herbaceous, base cuneate or petiolate, blade obovate-oblanceolate, entire to remotely toothed. Inflorescences 1-headed to loosely corymbose; involucres campanulate to hemispheric; bracts 3–4-seriate, gradate, ovate to oblong-lanceolate, mostly indurate, green distally, tips short-acute, short-fringed, margins narrowly scarious; receptacles plano-convex, smooth. Rays 1-seriate, pistillate, pale purple, belatedly coiling. Disc florets yellow or purplish, narrowly funnelform, lobes 5, oblong-triangular, somewhat zygomorphic, erect. Achenes ellipsoid-oblong, compressed, 2-nerved, sericeous, gland-dotted; pappus bristles whitish, inner apically broadened, outer shorter. Four species, central Asia.

885. *Tripolium* Nees

Tripolium Nees, Gen. Sp. Aster. 152 (1832).

Biennials to short-lived perennials, from fibrous-rooted rhizome or caudex, glabrous. Leaves subsucculent, basal leaves oblanceolate-spathulate, usually 3-nerved, petiole as long as blade; cauline leaves sessile. Inflorescences loosely corymbose, usually 5–20-headed; involucres campanulate; bracts (1–)2–3(–4)-seriate, gradate, lanceolate to oblong, obtuse to rounded, evenly thin-herbaceous, 3–5-nerved; receptacles plano-convex. Rays 10–30, sometimes lacking, pistillate, blue to purple or white. Disc florets tubular-funnelform, lobes lanceolate. Achene faces strigose, sometimes gland-dotted; pappus 1–2-seriate, bristles subequal, accrescent after anthesis to 11–12 mm, sometimes caducous. $x = 9$. One species, *T. pannonicum* (Jacq.) Dobrocz., Eurasia, halophilic, widely introduced.

XV.10. Subtribe Solidagininae O. Hoffm. (1890).

Herbs or shrubs. Leaves alternate, mostly entire, less often serrate, with glandular dots, stipitate glands, or eglandular. Inflorescences corymbose to thyrsoid, sometimes with secund branches, or heads solitary; involucral bracts flat, usually basally indurate with herbaceous apical patch; receptacles with or without pales. Ray florets 1-seriate or lacking; limbs yellow, sometimes white, or lacking. Disc florets bisexual, functionally male in *Amphiachyris*, *Amphipappus* or *Petradoria*; style branches short to long, with papillose collecting appendages. Achenes terete, multinerved, eglandular, setulae without anchor-shaped tips; pappus usually 1-seriate, persistent, greatly reduced in the *Gutierrezia* lineage. $x = 9$, reduced to 8, 5, 4.

Key to the Genera

1. Pappus absent or a short corona or of minute scales; $x = 5$ or 4 (or 8) 2
– Pappus of barbellate bristles or (in some shrubs) of scales; $x = 9$ 5
2. Shrubs; ray florets barely exceeding the involucre; $x = 4$ or 8 **898. *Gymnosperma***
– Herbs or low subshrubs; ray florets conspicuously exceeding the involucre; $x = 5$ 3
3. Disc florets functionally male; disc pappus of 5–8 basally united, linear-spathulate scales **887. *Amphiachyris***
– Disc florets bisexual; disc pappus absent, a low corona, or a ring of lanceolate scales 4
4. Heads terminal; ray florets present, disc florets usually more than 3; pappus 1–2-seriate, of stiff scales, united or reduced in some species, usually longer in disc **897. *Gutierrezia***
– Heads axillary; ray florets absent, disc florets 3, white; pappus 2-seriate, of apiculate scales c. as long as the corollas **908. *Thurovia***
5. Shrubs 6
– Herbs or subshrubs 18
6. Pappus of scales, thick and flattened bristles or of short bristles of dissimilar length, often different on ray and disc achenes 7
– Pappus of bristles, similar on ray and disc achenes 10
7. Plants spinescent; heads in a compact corymbose cluster; disc florets functionally male; ray pappus of 15–20 flattened, paleate bristles c. 1 mm long, disc pappus of tortuous-twisted bristles c. 3 mm long **888. *Amphipappus***
– Plants not spinescent; heads solitary or few in a loose corymbose cluster; disc florets bisexual; pappus of awns or scales 8
8. Leaves linear-lanceolate, 3-nerved, resinous-viscid, arcuate; heads discoid, eradiate; pappus of paleate awns **909. *Vanclevea***
– Leaves linear to oblanceolate or spathulate, 1-nerved, not resinous-viscid or arcuate; heads discoid or radiate; pappus various 9
9. Heads radiate; involucral bracts ovate; receptacles epaleate; pappus 1–2-seriate, of thick, broadly flattened, barbellate, bristle-like scales **886. *Acamptopappus***
– Heads discoid; involucral bracts oblanceolate; receptacles paleate; pappus 1-seriate, of 5–8 flattened, linear-lanceolate scales **894. *Eastwoodia***
10. Disc corollas regular to slightly irregular; pappus 1–3-seriate, bristles sometimes apically dilated 11
– Disc corollas strongly zygomorphic; pappus 1-seriate, bristles apically attenuate 14
11. Rays present; involucral bracts not ranked; eastern USA and Caribbean Islands 12
– Rays often absent, when present yellow; involucral bracts ranked or not ranked; western USA and northwestern Mexico 13
12. Rays yellow; achenes with 8–10 whitish raised nerves; pappus 2–3-seriate; areoles of leaves subisodiametric with recessed resinous borders; eastern USA **891. *Chrysoma***
– Rays white; achenes 5-nerved; pappus 1-seriate; leaf surfaces punctate-resinous; Caribbean Islands **896. *Gundlachia*** p.p.
13. Pappus bristles apically dilated or attenuate; heads in compact corymbose clusters; rays present or absent; involucral bracts in distinct vertical ranks **892. *Chrysothamnus***
– Pappus bristles apically dilated; heads sessile to short-pedicellate, 2–4 in glomerules, the aggregation loosely corymbose; rays lacking; involucral bracts not ranked **899. *Hesperodoria***
14. Leaves hirtellous, not resinous; stems densely foliate with acicular leaves and axillary clusters; without ray florets **890. *Chihuahuana***
– Leaves not hirtellous, resinous, usually punctate; without many axillary clusters of leaves; with or without ray florets 15
15. Broom-like shrubs with dense, erect, virgate branches; branches strongly ridged; leaves widely spaced on new growth, rather erect, not persisting below **910. *Xylovirgata***

– Shrubs unbranched or with many ascending branches, not broom-like; branches terete to weakly ridged; leaves rather persistent, rather evenly and closely spaced 16
16. Leaves involute but appearing terete; without or with 1–3 ray florets **896. *Gundlachia*** p.p.
– Leaves narrow but distinctly flattened; ray florets 5–15 17
17. Involucral bracts weakly gradate; inflorescences corymbose; stems minutely papillate-scabrous **900. *Medranoa***
– Involucral bracts strongly gradate; inflorescences loosely thysiform; stems glabrous **901. *Neonesomia***
18. Rays white 19
– Rays yellow or absent 20
19. Ray corollas white, disc corollas yellow; achenes glabrous; involucral bracts not keeled, with 3–7 parallel, longitudinal veins, without an apical patch **902. *Oligoneuron*** p.p.
– Ray and disc corollas white; achenes densely strigose-sericeous; involucral bracts keeled, with a single midvein, with a green, sharply delimited apical patch **905. *Sericocarpus***
20. Heads solitary on leafless or bracteate stems **907. *Stenotus***
– Heads in corymbose, racemose (*Columbiadoria*), thyrsoid or secund (*Solidago*) clusters 21
21. Plants taprooted 22
– Plants fibrous-rooted from a rhizome or caudex 23
22. Leaves net-veined, oblanceolate; inflorescence branches racemose or weakly corymbose; disc florets bisexual; pappus bristles in 1 series **893. *Columbiadoria***
– Leaves with 3–5 raised, parallel veins; inflorescences distinctly corymbose; disc florets functionally male; pappus bristles in 2–3 series **904. *Petradoria***
23. Leaves resinous or punctate or both, but not stipitate-glandular; involucral bracts usually indurate at least below, commonly with a sharply delimited, green apical patch **903. *Oreochrysum***
– Leaves stipitate-glandular; involucral bracts primarily herbaceous and even-textured 24
24. Leaves linear to narrowly oblanceolate, distinctly punctate; disc corollas not orange-veined 25
– Linear mostly broader, punctate (*Oligoneuron*) or not (*Solidago*); disc corollas with orange-resinous veins 26
25. Basal leaves persistent, cauline leaves reduced; heads discoid, rays absent; involucral bracts in vertical ranks **889. *Bigelowia***
– Leaves all cauline; heads radiate; rays 15–25; involucral bracts not in vertical ranks **895. *Euthamia***
26. Inflorescence strongly corymbose; disc corolla lobes erect; pappus bristles in (1–)2 series **902. *Oligoneuron*** p.p.
– Inflorescence secund to thyrsoid, rarely weakly corymbose; disc corolla lobes reflexing-coiling; pappus bristles in 1 series **906. *Solidago***

Genera of Solidagininae

886. *Acamptopappus* (A. Gray) A. Gray

Acamptopappus (A. Gray) A. Gray, Proc. Amer. Acad. Arts 8: 634 (1873); Lane, Madroño 35: 247–265 (1988), rev.
Aplopappus sect. *Acamptopappus* A. Gray (1849).

Taprooted shrubs; stems decumbent, becoming spinescent, with bark shredding. Leaves lanceolate to obovate, 1-nerved, entire, non-resinous. Inflorescences 1-headed or loosely corymbose; involucres broad; bracts c. 3-seriate, broad with broad laciniate-hyaline margins, base yellowish, tips green, reflexed. Rays 0 or 5–14, pistillate, yellow. Disc florets perfect, yellow, funnelform, lobes lanceolate, reflexing; style appendages triangular-lanceolate. Achenes obconical, densely sericeous, with mixed appressed-tortuous and longer ascending-spreading setulae; pappus 1–2-seriate, of subequal awned scales, attenuate in ray achenes, spathulate in disc achenes, rarely also with few short setae. $x = 9$. Two species, south-western USA.

887. *Amphiachyris* (DC.) Nutt.

Amphiachyris (DC.) Nutt., Trans. Amer. Philos. Soc. 2, 7: 313 (1840); Lane, Syst. Bot. 4: 178–189 (1979), rev.
Brachyris Nutt. sect. *Amphiachyris* DC. (1836).

Taprooted annual herbs; glabrous. Leaves linear to lanceolate, 1(–3)-nerved, punctate, abaxially with glandular hairs. Inflorescences corymbose to thyrsoid; heads pedunculate; involucres narrowly campanulate to turbinate; bracts 1–2(–3)-seriate, gradate, 1-nerved, indurated and whitish-glutinous basally, nerve not green-margined, margins hyaline; receptacles glabrous or pilosulous. Rays 7–12, pistillate, yellow or orange-tinged. Disc florets functionally male, yellow, tube short, lobes deltate, erect. Ray achenes obovate, plump, 4–9-ribbed, strigose-sericeous, setulae slightly clavate at tips; ray pappus a low crown or ring of scales; disc pappus of 5–8 white, basally united, linear scales with spathulate tips. $x = 4, 5$. Two species, south-central USA.

888. *Amphipappus* Torr. & A. Gray ex A. Gray

Amphipappus Torr. & A. Gray ex A. Gray, Boston J. Nat. Hist. 5: 107 (1845); Porter, Amer. J. Bot. 30: 481–483 (1943), rev.

Shrubs, with branchlets and leaves glabrous, becoming leafless and spinescent; bark pale. Leaves short-petiolate, obovate to narrowly elliptic, entire. Inflorescences corymbose; involucres turbinate-cylindric; bracts 7–12, c. 3-seriate, gradate, ovate to elliptic, outer bracts keeled. Rays (0–)1–2, pistillate, yellow, slightly exceeding involucre. Disc

florets 3–7, functionally male, yellow, narrowly funnelform, lobes lanceolate, reflexing. Fertile achenes oblong-elliptic, somewhat compressed, villous; pappus bristles 15–20, in 1 series, slender, flattened, paleaeform, basally fused; disc achenes shorter; pappus tortuous-twisted. $x = 9$. One species, *A. fremontii* Torr. & A. Gray ex A. Gray, south-western USA.

889. *Bigelowia* DC.

Bigelowia DC., Prodr. 5: 326 (1836), nom. cons.; Anderson, Sida 3: 451–465 (1970), rev.; Syst. Bot. 2: 209–218 (1972), rev.

Subshrubs from short caudex, with short rhizomes; glabrous, initially viscid; stems nearly scapiform. Leaves in persistent basal rosette, sessile, linear to oblanceolate, 3-nerved, entire, gland-dotted, cauline leaves reduced to linear bracteoles. Inflorescences densely flat-corymbose; involucres turbinate-cylindric; bracts 3–4-seriate, unequal, more or less ranked, narrowly lanceolate to nearly linear, weakly keeled, green-tipped. Rays absent. Florets 2–6, perfect, yellow, tubular, lobes lanceolate, recurving; style appendages lanceolate. Achenes turbinate to subcylindric, slightly compressed to subquadrate, with 4 or 5 thin resinous nerves, sparsely strigose; pappus 1(–2)-seriate, with few bristles of uneven lengths. $x = 9$. Two species, south-eastern USA.

890. *Chihuahuana* Urbatsch & R.P. Roberts

Chihuahuana Urbatsch & R.P. Roberts, Sida 21, 1: 245 (2004).

Densely branched shrubs. Leaves closely persistent and in axillary clusters, erect, 3–10 mm long, sessile, acicular, hirtellous with uniseriate conic hairs, bases rather decurrent, apices sharply acute, in section narrowly triangular with thickened midrib composed mostly of bundle of fibers. Heads solitary; involucre campanulate; bracts gradate, to 5–6 mm long. Rays lacking. Florets 8–10; corollas yellow, hairy, lobes ovate-lanceolate, unequal. Achenes sericeous, pappus of bristles. $x = 9$. One species, *C. purpusii* (Brandegee) Urbatsch & R.P. Roberts, northern Mexico.

891. *Chrysoma* Nutt.

Chrysoma Nutt., J. Acad. Nat. Sci. Philadelphia 7: 67 (1834); Cronquist, Vasc. Fl. SE U.S., Asteraceae 1: 134 (1980), reg. rev.

Evergreen shrubs; glabrous, glutinous. Leaves sessile to shortly petiolate, oblanceolate to narrowly elliptic, entire, 1-nerved, veinlets in recessed reticulum. Inflorescences cymose; heads sessile to subsessile; involucres cylindric; bracts 3–4(–5)-seriate, gradate, ranked, lanceolate, stramineous, with orange-resinous midvein from base to apex. Rays (0–)1–2(–3), pistillate, yellow. Disc florets (2–)3–4(–5), perfect, yellow, elongate-tubular, lobes lanceolate, spreading to recurving; style appendages linear-triangular. Achenes turbinate-oblong, with 8–10 raised pale nerves, densely strigose-sericeous; pappus bristles 2–3-seriate, of uneven lengths. $x = 9$. One species, *C. pauciflosculosa* (Michx) Greene, south-eastern USA.

892. *Chrysothamnus* Nutt.

Chrysothamnus Nutt., Trans. Amer. Philos. Soc. 2, 7: 323 (1840), nom. cons. prop.; Nesom & Baird, Phytologia 75: 74–93 (1993), emend.

Suffrutescent herbs or rounded shrubs, much-branched; stems often resinous. Leaves linear to spathulate-oblanceolate, 3-nerved, gland-dotted, often varnished, glabrous to variously pubescent. Inflorescences corymbose; involucres turbinate-cylindric; bracts 4–5-seriate, gradate, ranked, ovate-lanceolate to triangular-lanceolate, with golden-resinous midvein, usually with apical green patch. Rays few or none, pistillate, yellow. Disc florets 4 or 5, perfect, yellow, tubular, gradually or abruptly broadened into limb; style appendages linear. Achenes narrowly ellipsoid, 5–10(–15)-nerved, subterete, glabrous to sericeous, sometimes glandular near apex; pappus bristles 2–3-seriate, of unequal lengths, tips sometimes broadened. $x = 9$. Circa 13 species, south-western Canada, western USA, north-central Mexico.

893. *Columbiadoria* G.L. Nesom

Columbiadoria G.L. Nesom, Phytologia 71: 249 (1991).

Perennial taprooted subshrubs; stems strict. Leaves sessile, eglandular or obscurely punctuate-glandular, not resinous, sparsely scabrous-hispidulous, oblanceolate, entire, net-veined, reduced upwards, basal leaves usually not persistent. Inflorescence racemose to loosely corymbose, with 5–15+ heads; involucres cylindric-turbinate, bracts 5–6-seriate, gradate, lanceolate, basal 2/3 white-indurate, distal half not or slightly keeled, apex green. Rays c. 5 or 8, pistillate, yellow, not or

scarcely coiling. Disc florets perfect, yellow, lobes deltate, erect; style appendages linear-lanceolate, much longer than stigmatic lines. Achenes narrowly oblong, slightly compressed, 8-nerved, moderately strigose; pappus bristles 1-seriate, apices attenuate. One species, *C. hallii* (A. Gray) G.L. Nesom, north-western USA.

894. *Eastwoodia* Brandegee

Eastwoodia Brandegee, Zoe 4: 397 (1894); Lane, Madroño 35: 247–265 (1988), rev.

Glabrous, usually glutinous shrubs; older stems with white shedding bark. Leaves not reduced above, sometimes in axillary fascicles, yellow-green, linear to oblanceolate, 1-nerved, margins entire, sparsely ciliate. Inflorescences 1-headed to corymbose; involucres hemispheric to campanulate, impressed at base; bracts 3–5-seriate, gradate, stiffly erect, resiniferous, oblanceolate, indurate below, distal half green, margins narrowly scarious; receptacles with oblanceolate, caducous scales. Rays absent. Florets 30–40, perfect, yellow, cylindric to funnel-shaped, lobes lanceolate, spreading or reflexing; style appendages lanceolate. Achenes narrowly obconical, 3–4-angled, strigose-sericeous especially on angles; pappus of 5–8 linear-lanceolate scales as long as corollas. $x = 9$. One species, *E. elegans* Brandegee, USA (California).

895. *Euthamia* Nutt. ex Cass.

Euthamia Nutt. ex Cass., Dict. Sci. Nat. 37: 471 (1825); Sieren, Rhodora 83: 551–579 (1981), rev.

Perennial herbs, rhizomatous; glabrous to scabridulous. Leaves cauline, sessile, linear to linear-lanceolate, 1–3(–5)-veined, punctate, rather glutinous. Inflorescence flat- or rounded-corymbose, with glomerate subclusters of heads; involucres cylindric to turbinate or hemispheric; bracts 3–5-seriate, gradate, ovate to oblong, obtuse, mostly chartaceous, glutinous, somewhat fimbrillate; receptacles sometimes pilosulous. Rays 15–25, pistillate, yellow. Disc florets (2–)7–15(–20), perfect, yellow, expanded-tubular, lobes lanceolate, spreading; style appendages lanceolate. Achenes oblong to narrowly turbinate, subterete, faintly 2–4-nerved, strigose; pappus bristles 1-seriate. $x = 9$. Eight species, mostly central and south-eastern USA, one south-western Canada to Baja California Norte.

896. *Gundlachia* A. Gray

Gundlachia A. Gray, Proc. Amer. Acad. Arts 16: 100 (1880); Lane, Brittonia 48: 532–541 (1996), rev.
Xylothamia G.L. Nesom, Y.B. Suh, D.R. Morgan & B.B. Simpson (1990).

Evergreen, resinous, punctate shrubs. Stems non- to many-branched. Leaves usually evenly spaced, spreading to appressed, sessile to short-petiolate, linear to obovate or spathulate, flat to involute-terete. Inflorescences terminal, racemose to corymbose or thyrsoid; heads 1–5 in clusters or hidden by leaves; involucres cylindric to narrowly obconic; bracts 2–5-seriate, linear-lanceolate to ovate, with apical resin pocket, bases white-indurate, margins translucent. Rays 3–8 or lacking, pistillate, corollas white to yellow, sometimes drying purplish, 1–6.5 mm long. Disc florets 3–50, white to yellow, lobes slightly irregular, laxly recurved; style appendages linear-lanceolate to ovate. Achenes turbinate to cylindric, sparsely pilose to sericeous; pappus bristles c. 40, subequal. $x = 9$. Six species, Caribbean, Mexico, USA (Texas).

Revisions (Urbatsch and Roberts 2004) based on DNA studies (Urbatsch et al. 2003; Roberts and Urbatsch 2004) greatly expand *Gundlachia* to include the type of *Xylothamnia* Nesom et al., but exclude most of the latter genus (see *Chihuahuana* Urbatsch & R.P. Roberts, *Medranoa* Urbatsch & R.P. Roberts, *Neonesomia* Urbatsch & R.P. Roberts and *Xylovirgata* Urbatsch & R.P. Roberts).

897. *Gutierrezia* Lag.

Gutierrezia Lag., Gen. Sp. Pl. [Elench. Hort. Matriti] 30 (1816); Solbrig, Contr. Gray Herb. 197: 3–42 (1966), rev.; Lane, Syst. Bot. 10: 7–28 (1985), rev.
Greenella A. Gray (1880).

Annual or perennial, taprooted herbs or small shrubs. Leaves decurrent, linear to lanceolate or spathulate, punctate and glutinous, glabrous, entire. Heads solitary or 3–6 in clusters; involucres cylindric to campanulate; bracts 2–4-seriate, gradate, stramineous, 1- or 2-nerved, bases white-indurate; receptacles flat to columnar, with uncinate hairs. Rays (0–)1–30, pistillate, yellow or white, coiling. Disc florets perfect, yellow or white, lobes deltate, erect; style appendages linear-lanceolate. Achenes tan to purplish-black, clavate to cylindric, multinerved, setulose between ribs, tips of setulae divergent or clavate to bulbous; pappus 1–2-seriate, of stiff scales, fused or reduced in some species. $x = 4$. Sixteen species, mostly

Mexico, also south-western USA, south-western South America.

898. *Gymnosperma* Less.

Gymnosperma Less., Syn. Gen. Comp. 194 (1832), nom. nov.
Selloa Spreng. (1819), nom. illegit. non *Selloa* Kunth (1818).

Glabrous, glutinous shrubs. Leaves sessile, decurrent, linear to narrowly lanceolate, oblanceolate or elliptic, uniform up to inflorescence, entire, 1- or 3-nerved, punctate. Inflorescences corymbose, containing compact glomerules of sessile to subsessile heads; involucres turbinate-cylindric to elliptic-obovoid; bracts 2–4-seriate, gradate, mostly white-indurate, little or no green at apices. Rays 4–9, pistillate, yellow. Disc florets 4–6, perfect or functionally male, orange-yellow, tubular-funnelform, lobes lanceolate, reflexing-coiling; style appendages lanceolate. Achenes columnar or fusiform to compressed, strigillose, without evident ribs; pappus near-absent or a minute corona. $x = 4$ or 8. One species, G. *glutinosa* (Spreng.) Less., south-western USA, south to Guatemala.

899. *Hesperodoria* Greene

Hesperodoria Greene, Leafl. Bot. Observ. Crit. 1: 173 (1906); Hall, Publ. Carnegie Inst. Wash. 389: 35, 218–222 (1928), rev.

Perennial herbs or shrubs; stems glabrous to hirtellous, white-barked with age. Leaves thick, linear-lanceolate to oblanceolate, with 3 parallel nerves, entire, surfaces glabrous to scabrous, one species punctate and resinous. Inflorescences loosely corymbose, with 2–4-headed glomerules or cymose clusters; involucres turbinate to cylindric-turbinate; bracts 5–6-seriate, subequal to gradate, not ranked, oblong-lanceolate, tips greenish, with or without glandular midline. Ray florets absent. Florets c. 10–20, perfect, yellow, tubular-funnelform, lobes deeply cut, triangular; style appendages linear-lanceolate. Achenes subterete, 5–8-nerved, sparsely sericeous; pappus 1–2-seriate, bristles persistent, apically broadened. $x = 9$. Two species, USA (Utah, northern Arizona).

900. *Medranoa* Urbatsch & R.P. Roberts

Medranoa Urbatsch & R.P. Roberts, Sida 21:254 (2004).

Shrubs to 2 m, resinous; branches numerous, ascending, mostly terete, bark smooth; internodes 1–4 mm long, green, scabridulous. Leaves evergreen, sessile, punctate, narrowly elliptic to ovate, flat-canaliculate, base decurrent. Inflorescences terminal, 1-headed or corymbose; involucral bracts 2–3-seriate, weakly gradate, mostly chartaceous. Rays 5–11; ligules elliptic, 3–7 mm long. Disc florets 15–22; corollas pale yellow, 4–5 mm long, lobes spreading or recurved, unequal, 0.8–2.2 mm long, style branches thickened with doubled veins, appendages narrowly linear. Achenes turbinate, pilose; pappus bristles c. 80, setose, subequal. $x = 9$. One species, *M. parrasana* (S.F. Blake) Urbatsch & R.P. Roberts, Mexico (Coahuila and Zacatecas).

901. *Neonesomia* Urbatsch & R.P. Roberts

Neonesomia Urbatsch & R.P. Roberts, Sida 21: 252 (2004).

Shrubs to 3 m, much-branched, aromatic; twigs ridged, internodes 2–10 mm long. Leaves linear, elliptic to narrowly oblanceolate, flat with midrib raised abaxially, with flagelliform hairs, margins entire to minutely ciliate. Heads terminal, solitary or loosely paniculate; involucre usually turbinate; bracts gradate, linear, blunt to subacute, thick, resinous, stramineous with apical glandular patch. Rays 5–15; corollas white to yellow, 2–5 mm long. Disc florets 8–20; corollas 3.5–5 mm long, tube poorly differentiated from asymmetric 5-lobed limb, lobes 0.9–3.3 mm long. Achenes strigose to sericeous; pappus of setose bristles. $x = 9$. Two species, Mexico, USA (Texas).

902. *Oligoneuron* Small

Oligoneuron Small, Fl. SE U.S., ed. 1, 1188 (1903); Nesom, Phytologia 75: 1–44 (1993), emend.
Unamia Greene (1903).

Erect perennial herbs from short rhizomes; stems usually unbranched below inflorescence. Leaves narrowly lanceolate or broadly elliptic, parallel- or net-veined, entire or serrulate, often gland-dotted, basal leaves often persistent. Inflorescences corymbose, flat-topped; involucres turbinate to campanulate or hemispheric; bracts 2–6-seriate, gradate, oblong to obovate, with 3–7+ translucent veins. Rays pistillate, yellow to white. Disc florets perfect, yellow, limbs narrowly campanulate, lobes narrowly triangular, spreading; style appendages lanceolate to linear. Achenes oblong-fusiform, terete to slightly compressed, glabrous, with 5–7(–10–20) thin longitudinal subsurface nerves; pappus (1–)2-seriate, bristles equal to subequal,

apically attenuate or clavate. $x = 9$. Six species, eastern North America.

Significant features of *Oligoneuron*, particularly the flat-topped inflorescence and gland-dotted leaves, are shared with genera of Solidagininae other than *Solidago* L. (Nesom 1993), and species of *Oligoneuron* do not hybridize with those of typical *Solidago*, within which hybrids in many combinations are easily formed. Recent molecular evidence (Beck et al. 2004), however, indicates that these six species probably arose evolutionarily from within typical *Solidago*, where they may be better treated.

903. *Oreochrysum* Rydb.

Oreochrysum Rydb., Bull. Torrey Bot. Club 33: 152 (1906).

Viscid perennial herbs; rhizomes slender, with scale leaves; stems puberulous or hirtellous and with stipitate glands. Basal and lower cauline leaves petiolate, persistent, spathulate to oblanceolate, upper cauline leaves slightly reduced, usually subclasping, broadly ovate-lanceolate to oblanceolate. Inflorescences densely corymbose, flat-topped; involucres campanulate to hemispheric; bracts 3–4-seriate, subequal, herbaceous, outer ovate, inner broadly lanceolate to oblong, with 1 (or 3) non-resinous veins. Rays 12–20, pistillate, yellow. Disc florets perfect, narrowly tubular-funnelform, lobes triangular, spreading; style appendages linear. Achenes fusiform, compressed, glabrous, with 12–16 raised whitish nerves; pappus 2(–3)-seriate, bristles equal. $x = 9$. One species, *O. parryi* (A. Gray) Rydb., western USA, north-western Mexico.

904. *Petradoria* Greene

Petradoria Greene, Erythea 3: 13 (1895); Anderson, Trans. Kansas Acad. Sci. 66: 632–684 (1963), rev.

Suffrutescent herbs from stout taproot or branching caudex; gland-dotted, resinous. Leaves persistent in rosette, little reduced upwards, coriaceous, linear to lanceolate or oblanceolate, margins entire to scabrous, with 3–5 parallel veins, venation prominulous. Inflorescences densely paniculate-corymbose; involucres cylindric to cylindric-turbinate; bracts 3–6-seriate, gradate, usually in ranks, ovate to oblong, apices truncate to attenuate, sometimes weakly keeled. Rays 1–3, pistillate, yellow. Disc florets (1–)2–4(–5), functionally male, yellow, tubular-funnelform, lobes lanceolate; style branches linear-lanceolate. Achenes cylindric to slightly compressed, 6–9-nerved, glabrous; pappus 2-seriate, of attenuate bristles. $x = 9$. One species, *P. pumila* (Nutt.) Greene, south-western USA.

905. *Sericocarpus* Nees

Sericocarpus Nees, Gen. Sp. Aster. 148 (1832) [1833]; Nesom, Phytologia 75: 45–54 (1993), key.
Oligactis Raf. (1836) [1837], nom. illegit. non *Oligactis* (Kunth) Cass. (1825).

Perennial herbs from rhizomes; puberulous to glabrous, gland-dotted. Leaves basal and cauline, sessile, linear to oblanceolate or elliptic-oblanceolate. Inflorescences corymbose, flat-topped, with glomerate clusters of heads; involucres cylindric to turbinate; bracts 2–6-seriate, gradate, coriaceous, keeled, gibbous and whitish-indurate below, with green patch distally. Rays 3–8, pistillate, white, not coiling. Disc florets perfect, white or cream-coloured, funnelform; style appendages lanceolate to linear-lanceolate. Achenes narrowly obconical to nearly cylindric, with 4–8 partially sunken nerves, strigose-sericeous; pappus 2–3-seriate, of equal, apically broadened bristles. $x = 9$. Five species, USA.

906. *Solidago* L.

Solidago L., Sp. Pl. 878 (1753); Cronquist, Vasc. Fl. SE U.S., Asteraceae 1: 116–133 (1980), reg. rev.; Tamamschyan, Fl. U.R.S.S. 25: 31–50 (1959), Engl. transl. 25: 31–50 (1999), reg. rev.; Taylor & Taylor, Sida 10: 223–251 (1984), reg. rev.
Brachychaeta Torr. & A. Gray (1842).
Brintonia Greene (1895).

Perennial herbs from rhizome or caudex, rarely thickly taprooted. Leaves linear or linear-lanceolate to ovate, some 3-nerved, entire to toothed, some gland-dotted. Inflorescence cylindric to pyramidal or racemose with secund or arcuate branches; involucres cylindric to turbinate; bracts 3–4-seriate, gradate, with an orange-glandular midrib, often with green patch apically; receptacles sometimes with caducous pales. Rays pistillate, yellow to white, usually coiling. Disc florets perfect, yellow, tubular-funnelform, lobes often deeply cut, lanceolate; style appendages lanceolate. Achenes fusiform-cylindric, 5–8-nerved, glabrous to strigose; pappus bristles 1-seriate, whitish. $x = 9$. Circa 100 species, mostly North America, eight Mexico, one South America, 10–20 Eurasia.

907. *Stenotus* Nutt.

Stenotus Nutt., Trans. Amer. Philos. Soc. 2, 7: 334 (1840).

Perennial herbs from woody, branched caudices; stems crowded, short, glabrous to tomentose, not resinous nor gland-dotted, sometimes with stipitate glands. Leaves mostly in rosette, linear to linear-oblanceolate or spathulate, entire, parallel nerves usually 3. Heads solitary on mostly leafless peduncles; involucres campanulate to hemispheric; bracts 2–3(–4)-seriate, strongly to weakly gradate, herbaceous with hyaline margins, 3(–5)-nerved. Rays usually present, pistillate, yellow, broad, slightly coiling. Disc florets perfect, yellow, gradually expanded; style appendages lanceolate to linear-lanceolate. Achenes subterete to compressed, strigose-sericeous; pappus bristles 1–2-seriate, subequal, caducous. $x = 9$. Six or seven species, Canada, western USA, north-western Mexico.

908. *Thurovia* Rose

Thurovia Rose, Contrib. U.S. Natl Herb. 3: 321 (1895).

Annual or short-lived perennial herbs; taprooted or roots laterally perennating; stems branched in upper half. Leaves cauline, linear, ascending-appressed, reduced upwards. Inflorescence spicate; heads solitary in leaf axils, usually 10–20 per stem, sessile or subsessile; involucres narrowly turbinate; bracts 5–9-seriate, subequal, outer shorter, herbaceous, inner mostly whitish-indurate with small herbaceous tips. Rays absent. Florets 3, perfect, white or pale yellow, limbs expanded, lobes lanceolate, spreading-recurved; style appendages linear. Achenes obconical, subterete, white-sericeous with thick setulae; pappus 2-seriate, of c. 10 erose, subulate scales as long as corollas. $x = 5$. One species, *T. triflora* Rose, south-eastern Texas.

909. *Vanclevea* Greene

Vanclevea Greene, Pittonia 4: 50 (1899); Anderson & Weberg., Great Basin Naturalist 34: 151–160 (1974), rev.

Shrub; glabrous, glutinous; stems with shedding epidermis or whitish bark. Leaves rigid, spreading to falcate-recurved, linear-lanceolate, entire. Heads solitary or 2–5 in an open cyme; involucres broadly turbinate; bracts 3–5-seriate, strongly gradate, narrowly elliptic-lanceolate, attenuate, inner sometimes slightly squarrose at tips. Rays absent. Florets c. 30, perfect, yellow, funnelform from short tube, lobes deltate, erect; style appendages narrowly triangular-lanceolate. Achenes narrowly cylindric, subterete, c. 5–8-nerved, glutinous, sparsely strigose; pappus of (12–)15–18 flattened narrow segments. $x = 9$. One species, *V. stylosa* (Eastw.) Greene, Utah, Arizona.

910. *Xylovirgata* Urbatsch & R.P. Roberts

Xylovirgata Urbatsch & R.P. Roberts, Sida 21: 255 (2004).

Virgately branched shrubs to 1 m; stems slender; branches strongly ridged and angled. Leaves present mostly on new growth, not persistent, widely spaced, rather erect, 2–15 mm long, c. 1 mm wide, resinous, not obviously punctate. Heads terminal, solitary or in loose racemes; involucres campanulate to turbinate; bracts strongly gradate, with thickened apical glandular structure. Rays 3–6, limbs 2- or 3-toothed, 2.3–3.0 mm long, c. 1 mm wide. Disc florets 7–14; corollas yellow, often drying purplish, 4.0–4.5 mm long, lobes 5, unequal, 1.3–2.3 mm long. Achenes sericeous; pappus bristles setose, c. 30, subequal. $x = 9$. One species, *X. pseudobaccharis* (S.F. Blake) Urbatsch & R.P. Roberts, Mexico (Coahuila).

XV.11. Subtribe Pentachaetinae G.L. Nesom (2000).

Annual herbs, eglandular. Leaves alternate, entire, filiform or linear to narrowly oblanceolate. Heads solitary and long-pedunculate; involucral bracts in 2–4 gradate series, with hyaline margins, not keeled; receptacles plano-convex, epaleate. Ray florets with corollas yellow, white in some *Pentachaeta*, strongly coiling. Disc florets with style branch appendages linear-lanceolate, much longer than the stigmatic lines. Achenes terete to slightly compressed, narrowly oblong to oblanceolate in outline, beaked in *Tracyina*, eglandular; setulae without anchor-shaped tips; pappus 1(–2)-seriate, of persistent bristles frequently in multiples of 5, sometimes laterally dilated at the base and partially connate, or sometimes completely lacking, or of long scales (*Rigiopappus*). $x = 9$.

Key to the Genera

1. Achenes beaked; pappus of bristles; involucral bracts distinctly unequal, gradate in 3–4 series **913. *Tracyina***
– Achenes not beaked; pappus of bristles or scales; involucral bracts in 2–3 equal or subequal series 2
2. Pappus of bristles; receptacles epaleate **911. *Pentachaeta***
– Pappus of long scales; receptacles paleate between ray and disc florets **912. *Rigiopappus***

Genera of Pentachaetinae

911. *Pentachaeta* Nutt.

Pentachaeta Nutt., Trans. Amer. Philos. Soc. 2, 7: 336 (1840); Van Horn, Univ. Calif. Publ. Bot. 65: 1–41 (1973), rev.

Annual, taprooted herbs, obscurely haired. Leaves narrowly oblanceolate to linear or filiform, entire, ciliate. Heads solitary, pedunculate; involucres campanulate; bracts in 2 equal or 3 subequal series, herbaceous; receptacles epaleate. Pistillate florets white, yellow or reddish, non-radiate or radiate, coiling. Disc florets perfect, yellow, tubular-funnelform, lobes 3 or 5, shallow, with fringe of hairs. Achenes oblanceolate, terete to slightly compressed, strigose; pappus 1-seriate, 3–5, c. 10 or c. 20 barbellate bristles, sometimes broadened and partially connate at base or completely lacking. Six species, USA (California), Baja California Norte.

912. *Rigiopappus* A. Gray

Rigiopappus A. Gray, Proc. Amer. Acad. Arts 6: 548 (1965); Robinson & Brettell, Phytologia 26: 69–70 (1973), relat.; Ornduff & Bohm, Madroño 23: 53–55 (1975), relat.

Annual, taprooted, hirsutulous herbs. Leaves ascending to erect, linear, entire. Heads solitary on long, leafy or bracteolate peduncles; involucres broadly turbinate; bracts 2-seriate, subequal, linear-oblong to lanceolate, acute, hirsutulous, partially clasping outer achenes; receptacles paleate between ray and disc florets. Rays 3, 5 or 8(–15), pistillate, rarely absent, yellow, often purple-tinged. Disc florets perfect, yellow, narrowly cylindrical, lobes 2–4, deltate, with fringe of hairs. Achenes narrowly cylindric to slightly fusiform or compressed, strigose with apically clavate setulae, transversely rugose; pappus of (0–)3–5 stiff, white, subulate scales. One species, *R. leptocladus* A. Gray, north-western USA.

913. *Tracyina* S.F. Blake

Tracyina S.F. Blake, Madroño 4: 74 (1937); Ornduff & Bohm, Madroño 23: 53–55 (1975), relat.

Annual, taprooted herbs; glabrous or loosely pilose below heads. Leaves cauline, ascending to appressed, linear-oblanceolate, entire, margins ciliate. Heads solitary on peduncles; involucres cylindric to broadly ovoid; bracts 3–4-seriate, distinctly unequal, linear-lanceolate, caducous; receptacles epaleate. Rays 12–20, pistillate, pale- or greenish-yellow, red-tinged, filiform, erect. Disc florets 15–25, greenish-yellow, red-tinged, filiform-tubular, lobes triangular-ovate, erect, fringed with papillae. Achenes beaked, narrowly cylindrical to linear-fusiform, 5-nerved, narrowed to slender strigose beak; pappus 1–2-seriate, of numerous, fragile, bristles. One species, *T. rostrata* S.F. Blake, California.

XV.12. Subtribe Boltoniinae G.L. Nesom (2000).

Perennial, herbs or shrubs (*Chloracantha*), rhizomatous, with persistently green stems and leaves, thorny in *Chloracantha*, glabrous. Leaves alternate, essentially all cauline, entire or few-toothed. Inflorescences with heads solitary or very loosely corymbose to thyrsoid; involucral bracts primarily herbaceous, apically rounded to obtuse, with three orange-resinous nerves; receptacles convex to conical, epaleate. Rays 1-seriate, white to slightly bluish, coiling. Disc florets bisexual, corollas orange-veined; style branch appendages deltate, papillose. Achenes terete and multinerved or flattened, 2-nerved and winged (*Boltonia*), setulae without anchor-shaped tips; pappus of bristles or awns. $x = 9$.

Key to the Genera

1. Achenes flattened and winged; pappus of 2 lateral awns **915. *Boltonia***
– Achenes terete, without wings; pappus of bristles 2
2. Herbs; stems 7–20 cm tall, thornless; leaves persistent **914. *Batopilasia***
– Subshrubs; stems 50–250 cm tall, usually with green thorns; leaves quickly deciduous **914. *Chloracantha***

Genera of Boltoniinae

914. *Batopilasia* G.L. Nesom & Noyes

Batopilasia G.L. Nesom & Noyes, Sida 19: 81 (2000).

Perennial, caespitose, glabrous herbs from thin woody rhizomes and caudices; stems usually 1–2-branched. Rosette leaves persistent, sessile, elliptic-oblanceolate, entire, 1-nerved to faintly 3-nerved; cauline leaves few, reduced to linear bracts. Heads solitary, erect on near-naked peduncles. Involucral bracts 3–4-seriate, gradate, thin-herbaceous with scarious margins and 1–3 filiform nerves, elliptic-oblanceolate, obtuse to acute; receptacles plano-convex. Rays 9–18, fertile,

white, sometimes purplish when dry, coiling at tips. Disc florets 24–29, perfect, not inflated nor indurated, lobes triangular, erect. Achenes strigose, terete to slightly compressed, with (2–3–)4(–5) orange nerves; pappus bristles 1-seriate, with few outer setae. $x = 9$. One species, *B. byei* (S.D. Sundb. & G.L. Nesom) G.L. Nesom & Noyes, north-western Mexico.

915. *Boltonia* L'Hér.

Boltonia L'Hér., Sert. Angl. 27 (1788) [1789]; Cronquist, Vasc. Fl. SE U.S., Asteraceae 1: 168–169 (1980), reg. rev.

Glabrous perennial herbs, with rhizomes or short caudices; stems ribbed. Leaves mostly cauline, entire, oblanceolate to lanceolate, sessile, sometimes decurrent. Inflorescence leafy, corymbose to thyrsoid; heads few to many, pedunculate. Involucres shallowly cupulate; bracts 2–4(–5)-seriate, gradate to subequal, narrowly oblong to lanceolate, with orangish midrib; receptacles convex to conical. Rays 20–40, pistillate, limbs white to bluish, rarely pink. Disc florets yellow, cylindrical, tubes short, throat with orange resin ducts. Achenes compressed, elliptical to elliptic-obovate, often winged, often with orangish ducts, faces sometimes pubescent; pappus absent, a short corona, or of some small bristles and 2(–4) longer thick bristles. $x = 9$. Five species, eastern North America.

916. *Chloracantha* G.L. Nesom et al.

Chloracantha G.L. Nesom, Y.B. Suh, D.R. Morgan, S.D. Sundb. & B.B. Simpson, Phytologia 70: 378 (1991).

Glabrate glaucous perennial subshrubs; stems erect, branches sharply ascending and sometimes modified as thorns. Leaves cauline, 1-nerved, oblanceolate, usually entire, early deciduous. Inflorescences loosely corymbose. Involucres broad; bracts 4–5-seriate, gradate, oblong-elliptic to lanceolate, each with (1–)3(–5) orange-resinous veins, apices rounded to lanceolate, margins hyaline; receptacles plano-convex. Rays 10–33, pistillate, white. Disc florets yellow with orange-resinous veins, narrowly funnelform, lobes deltate. Achenes compressed, 5(–6)-nerved, glabrous; pappus bristles 1–2-seriate, usually few shorter setae outside. $x = 9$. One species, *C. spinosa* (Benth.) G.L. Nesom, south-western USA (east to Louisiana), south through Mexico to Panama.

XV.13. Subtribe Machaerantherinae G.L. Nesom (1994).

Annual or perennial herbs to subshrubs (*Xylorhiza*) or small shrubs (*Hazardia*), stipitate-glandular or resinous-glandular, sometimes eglandular. Leaves alternate, entire to toothed, uncommonly lobed to pinnatifid, teeth commonly spinulose-tipped. Heads solitary to few, rarely in a loosely corymbose inflorescence; involucral bracts usually in 4–8 strongly gradate series, commonly with an apical herbaceous patch; receptacles convex, with or without pales. Ray florets 1(–2)-seriate, corollas yellow, white, or blue. Disc florets bisexual, rarely functionally male; style branch appendages narrowly triangular, hairy. Achenes multinerved, commonly obconic, eglandular; setulae without anchor-shaped tips; pappus 2–3(–4)-seriate, of bristles graduated in length and with a tendency to be flattened, at least basally. $x = 6$, reduced to 5, 4, 3, 2.

Key to the Genera

1. Style branch appendages truncate or subulate to deltate or broadly ovate 2
– Style branch appendages narrowly triangular to linear-lanceolate 4
2. Ray florets absent, outermost disc (tubular) florets zygomorphic with ray-like extensions **925. *Lessingia***
– Ray florets present 3
3. Ray florets fertile, corollas yellow; disc florets functionally male; stems and leaves without tomentose vestiture **918. *Benitoa***
– Ray florets sterile, corollas white to blue or pink; disc florets fertile (stamens and ovaries); stems and leaves usually densely to loosely tomentose **919. *Corethrogyne***
4. Rays white or blue 5
– Rays yellow or absent 9
5. Perennial, spring-flowering subshrubs; heads mostly 13–19 mm high, solitary; rays with lamina mostly 15–30 mm long **934. *Xylorhiza***
– Annual or perennial, summer- and fall-flowering herbs or weak subshrubs; heads mostly 3–12 mm high, solitary or loosely clustered; rays with lamina mostly 7–15 mm long 6
6. Leaves deeply pinnatifid to bipinnatifid throughout, at least many of the teeth and lobes sharply acute with bristle tips, bristles 0.2–1 mm long; plants annual; pappus of subulate bristles, dorsiventrally flattened near base, bases overlapping **926. *Machaeranthera***
– Leaves entire to toothed or lobed, if pinnatifid to bipinnatifid throughout, then lobes often rounded, with or without an apiculum but not bristle-tipped; plants annual to strongly perennial; pappus of filiform to subulate bristles, terete to flattened near base, bases overlapping or not overlapping 7

7. Plants strongly perennial, usually with a branched caudex; receptacles covered with scales 0.3–3.0 mm long, often forming an alveolate reticulum; pappus bristles subulate, flattened near the base, bases strongly overlapping **932. *Xanthisma*** p.p.
– Plants taprooted annuals or short-lived perennials; receptacles naked (or scales rarely to 0.5 mm long); pappus bristles filiform, not flattened near base (or slightly so), bases not (or slightly) overlapping 8
8. Ray florets with prominent pappus; leaves entire to toothed and plants variously pubescent with glandular and/or non-glandular hairs **920. *Dieteria***
– Ray florets with pappus absent or present; if pappus present, then leaves pinnatifid to bipinnatifid throughout or (if leaves entire to toothed) plants glabrous except for bristles or apiculate or bristle-tipped teeth on leaf margins **917. *Arida***
9. Disc corollas with limb campanulate, abruptly broadened from tube into limb 10
– Disc corollas narrowly funnelform, gradually broadened into limb 15
10. Pappus of numerous antrorsely barbellate bristles; achenes strigose 11
– Pappus a corona or of short scales or a few, slender, caducous awns or awn-like bristles; achenes glabrous or glabrate 12
11. Ray florets absent; plants perennial **924. *Isocoma***
– Ray florets present; plants annual (or biennial?) **930. *Rayjacksonia***
12. Heads without a basal concavity; pappus absent, a low crown of scales, or a lacerate corona 13
– Heads with distinct concavity at the peduncle insertion; pappus of 2–5(–12), white, flattened, basally caducous awns 14
13. Rays inconspicuous, barely longer than involucre; achenes strongly flattened; pappus a hyaline corona; heads sessile to short-pedunculate (0.5–1 mm) in a distinctly corymbose arrangement **931. *Stephanodoria***
– Rays conspicuous, much longer than the involucre; achenes plump, nearly terete to 4–6-sided; pappus absent, a low crown of awn-like scales, or a lacerate corona; heads solitary or long-pedunculate (1–5 cm) in a loosely corymbose arrangement **933. *Xanthocephalum***
14. Taprooted annuals or perennials with solid stems from drier habitats; leaves punctuate-resinous; achenes plump, not winged; pappus of smooth or minutely antrorsely barbellate awns **921. *Grindelia***
– Fibrous-rooted annuals with hollow stems from wet habitats; leaves not evidently punctate or resinous; achenes flattened, winged; pappus of retrorsely barbellate bristle-like awns **927. *Olivaea***
15. Heads solitary; receptacles paleate; pappus a ring of awn-like scales 3–6 mm long **932. *Xanthisma*** p.p.
– Heads solitary or in a corymbose arrangement; receptacles epaleate; pappus of numerous barbellate bristles 16
16. Plants from South America; leaves usually coriaceous, usually toothed or lobed; heads often solitary on long nearly leafless peduncles, seldom aggregated; outer involucral bracts not leaf-like **922. *Haplopappus***
– Plants from North America; leaves herbaceous to coriaceous, entire to lobed; heads often numerous on stems; outer involucral bracts sometimes leaf-like 17
17. Shrubs **923. *Hazardia***
– Herbs or weak subshrubs 18
18. Basal leaves persistent, strongly reduced upwards, foliar teeth or lobes, if present, usually not bristle-tipped; heads usually racemose to spicate, less commonly solitary or loosely corymbose **929. *Pyrrocoma***
– Basal leaves usually not persistent, reduced upwards or not, foliar teeth, if present, usually bristle-tipped; heads solitary or commonly loosely corymbose 19
19. Leaves usually spinulose-toothed or lobed, rarely entire, cauline leaves usually reduced in size upwards, not subtending the heads; outer involucral bracts not leaf-like **932. *Xanthisma*** p.p.
– Leaves entire, cauline leaves even-sized, continuing up the stems and subtending the heads; outer involucral bracts leaf-like **928. *Oonopsis***

Genera of Machaerantherinae

917. *Arida* (R.L. Hartm.) D.R. Morgan & R.L. Hartm.

Arida (R.L. Hartm.) D.R. Morgan & R.L. Hartm., Sida 20, 4: 1410 (2003).

Machaeranthera Nees sect. *Arida* R.L. Hartm. (1990).

Annual or rarely short-lived perennial herbs, usually taprooted (rhizomatous in *A. blepharophylla* (A. Gray) D.R. Morgan & R.L. Hartm.). Stems erect to ascending, often much-branched, 10–40 cm, glabrous to variously pubescent with glandular and non-glandular hairs. Leaves entire, dentate, lacerate to deeply pinnatifid or bipinnatifid. Heads solitary to loosely thyrsoid-corymbose; involucres turbinate to depressed hemispheric; bracts 4–8-seriate, gradate, appressed, spreading or reflexed, densely stipitate-glandular to glabrous, bases glabrous, apices with glandular and non-glandular hairs, not bristle-tipped; receptacles indistinctly alveolate, naked or nearly so, convex. Ray florets pistillate, fertile, laminas light to dark blue (absent in *A. carnosa* (A. Gray) D.R. Morgan & R.L. Hartm.). Disc florets perfect, corollas yellow, tubular, lobes triangular, erect. Achenes narrowly oblong, slightly compressed laterally, with 5–11 filiform nerves per face, moderately to densely pubescent; pappus of white filiform bristles in 2–3 poorly defined series. $x = 5$. Nine species, western USA, northern Mexico.

918. *Benitoa* D.D. Keck

Benitoa D.D. Keck, Leafl. W. Bot. 8: 26 (1956).

Erect, annual, taprooted herbs, scented, viscid, with dark, tack-shaped glands throughout. Leaves narrowed to clasping base, linear-lanceolate to oblanceolate, entire, upper leaves bract-like, apic-

ulate. Inflorescences loosely cymose-paniculate; involucres cylindric-turbinate; bracts c. 6-seriate, gradate, subpersistent, linear-lanceolate, green along middle, with spreading, slender tips bearing glandular globule. Rays 5–8(–14), pistillate, yellow, coiling. Disc florets 9–12, functionally male, yellow, tubes long, limbs abruptly broadened, lobes deeply cut, linear-lanceolate, erect. Fertile achenes maculate, triangular and 3-nerved, narrowed distally; pappus of 3–8 caducous bristles. $x = 5$. One species, *B. occidentalis* (H.M. Hall) D.D. Keck, California.

919. *Corethrogyne* DC.

Corethrogyne DC., Prodr. 5: 215 (1836); Saroyan et al., Madroño 47: 89–96 (2000), rev.

Perennial herbs, white-tomentose, commonly glabrescent, sometimes with stipitate glands. Leaves petiolate to sessile, linear to obovate, entire to toothed. Inflorescences simple to spicate or loosely corymbose; heads 1–5(–20); involucres hemispheric to turbinate; bracts 3–8-seriate, gradate, often with green apical patch, tips often spreading to deflexed. Rays 10–40, 1-seriate, pistillate but sterile, white to blue or pink, limbs straight to slightly coiling. Disc florets perfect, yellow, tubes long, limbs narrowly cylindrical, lobes narrowly triangular; style appendages deltate to ovate. Fertile achenes terete or compressed, 5–8-ribbed, strigose-sericeous; pappus bristles 1–2-seriate, tawny, without short outer series. $x = 5$. One species, *C. californica* DC., north-western USA (Oregon) to Baja California Norte.

920. *Dieteria* Nutt.

Dieteria Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 300 (1840).
Machaeranthera Nees subg. *Dieteria* (Nutt.) Greene (1896).

Taprooted herbs, erect to ascending, much-branched, 10–100 cm tall, glabrous or with glandular and/or non-glandular trichomes. Leaves entire to irregularly serrate or dentate, usually with spine-tipped teeth. Heads solitary or in loose panicles; involucres turbinate, campanulate, or hemispheric; bracts 3–12-seriate, gradate, appressed, spreading or reflexed, bases indurate, apices herbaceous. Rays pistillate, white, blue or purple. Disc florets perfect, yellow, funnelform, glabrate, lobes triangular, erect. Achenes linear to obovate, compressed, faces smooth or 4–6-ribbed, glabrous to strigose; pappus bristles 40–50, 1–3-seriate, white to tawny. $x = 4$. Three species, western USA, Mexico.

Ray flowers are sterile or absent in *Dieteria canescens* (Pursh) Nutt. var. *shastensis* (A. Gray) D.R. Morgan & R.L. Hartm.

921. *Grindelia* Willd.

Grindelia Willd., Gesell. Naturf. Freunde Berlin Mag. [Neuesten Entdeck. Gesamten Naturk.] 1: 259 (1807); Steyermark, Ann. Missouri Bot. Gard. 21: 433–608 (1934), rev.; Bartoli & Tortosa, Kurtziana 27: 327–359 (1999), rev.; Lane, Jepson Man.: 271–274 (1993), reg. rev.
Prionopsis Nutt. (1840).

Annual or biennial herbs to subshrubs, taprooted to stoloniferous; with punctate or stipitate glands or eglandular, often glutinous. Leaves mostly oblong-lanceolate, entire to spinulose, glandular-toothed or pinnatifid. Inflorescences usually 1-headed; involucres campanulate; bracts 4–8-seriate, subequal or gradate, bases usually sclerified, tips erect to spreading or reflexed. Rays present or absent, pistillate, yellow to orange. Disc florets perfect or functionally male, or outer perfect and central male, tubular, throat usually abruptly expanded, lobes triangular; style appendages obtuse-rounded. Achenes sometimes dimorphic, usually thick-walled, smooth or sculptured, compressed to subquadrate, disc achenes sometimes compressed with many thin nerves; pappus bristles white, usually caducous, 2–4, slender to broad. $x = 6$. Circa 70 species, USA, Mexico, southern Andes.

The achenes of *Grindelia* may be uniform or dimorphic. They are winged in some rhizomatous South American species. The pappus usually has few bristles but some South American species have up to 18, and the North American *G. ciliata* (Nutt.) Spreng. and South American *G. prunelloides* (Less.) Bartoli & Tortosa have 2–4 series of 39–50 bristles which may be basally connate. The inflorescences are loosely corymbose in some Mexican species.

922. *Haplopappus* Cass.

Haplopappus Cass., Dict. Sci. Nat. 56: 168 (1828), nom. cons.; Tortosa & Bartoli, Bol. Soc. Argent. Bot. 37: 115–133 (2002), rev.; Urbatsch et al., Comp. Newslett. 40: 35 (2003), phylog.

Perennial herbs, subshrubs or shrubs; usually glabrous and glutinous to stipitate-glandular;

stems nearly acaulescent to caulescent and branching. Leaves coriaceous, sessile, entire or dentate to pinnately lobed. Inflorescences on scapiform peduncles with scale-like bracteoles and 1 head, or corymbose to thyrsoid; involucres campanulate to hemispheric; bracts 3–6-seriate, gradate, coriaceous, tips acute to spiniform, appressed to recurved; receptacles plano-convex, epaleate. Rays 1-seriate, pistillate or sterile, yellow to purple, limbs not or weakly coiling. Disc florets numerous, perfect, yellow, narrowly funnelform, lobes 5, broadly triangular to lanceolate, erect. Achenes prismatic or turbinate, angular to terete or slightly compressed; pappus 1–3-seriate, white, yellowish or reddish, bristles unequal, scabrid. $x = 6, 5$. Circa 70 species, southern South America.

The South American *Haplopappus* sect. *Diplostephioides* (Benth. & Hook. f.) Blake has been treated as the genus *Llerasia* Triana (Cuatrecasas 1970). All North American and Central American species identified as *Haplopappus* have been transferred to other genera (summary by Lane and Hartman 1996). Of the 4 sections of South American *Haplopappus*, sects. *Haplopappus* and *Gymnocoma* Nutt. are closely related to each other; sects. *Polyphylla* Hall and *Xylolepis* Hall may be congeneric with *Hazardia* Greene, based on morphological and chemical evidence (Clark 1979; Brown and Clark 1981, 1982). Only a single South American species (*Haplopappus glutinosus* Cass., the generitype) has so far been included in molecular-based phylogenetic analyses.

923. *Hazardia* Greene

Hazardia Greene, Pittonia 1: 28 (1887); Clark, Madroño 26: 105–127 (1979), rev.

Suffrutescent herbs or shrubs. Leaves usually clasping or subclasping, deciduous, coriaceous, glutinous, entire or toothed, glabrous to tomentose, sometimes gland-dotted. Inflorescences spicate, racemose, narrowly thyrsoid or cymose, rarely 1-headed; involucres cylindric to turbinate or campanulate; bracts 5–9-seriate, gradate. Rays 0 or 3–25, pistillate, fertile or sterile, yellow or drying red-purple. Disc florets perfect or functionally male, yellow, tube narrow, limb tubular to narrowly funnelform, lobes triangular-ovate, erect. Achenes fusiform to cuneate, subterete to compressed, 4–5-nerved, glabrous to sericeous; pappus of many reddish-brown capillary bristles. $x = 4, 5, 6$. Thirteen species, western USA, western Mexico.

924. *Isocoma* Nutt.

Isocoma Nutt., Trans. Amer. Philos. Soc. 2, 7: 320 (1840); Nesom, Phytologia 70: 9–114 (1991), rev.

Erect, perennial subshrubs; often glutinous, glabrous to villous, tomentose or hispidulous. Leaves linear to oblanceolate or obovate, 1-nerved, entire to toothed or pinnatifid, teeth usually spinose-tipped. Inflorescence corymbose or 1-headed; heads sessile to subsessile; involucres turbinate or campanulate; bracts (3–)4–6-seriate, gradate, oblong to linear, chartaceous to subcoriaceous with herbaceous tips. Rays absent. All florets perfect, yellow with orange veins, limb abruptly expanded, lobes triangular, erect, marginal florets curving outwards as tube elongates. Achenes obpyramidal, terete to subterete, sericeous, 3–11-ribbed, ribs sometimes resinous; pappus bristles 2(–3)-seriate, uneven. $x = 6$. Sixteen species, Mexico, south-western USA.

925. *Lessingia* Cham.

Lessingia Cham., Linnaea 4: 203 (1829); Lane, Jepson Man.: 304–306 (1993), reg. rev.; Markos & Baldwin, Syst. Bot. 26: 168–183 (2001), phylog.

Annual, erect to decumbent, taprooted herbs; glabrous to white-tomentose, gland-dotted, often with tack-shaped glands. Leaves in basal rosettes, petiolate, obovate to spathulate, entire to serrate or pinnately lobed, sometimes spinose-tipped; cauline leaves smaller, sessile. Inflorescences glomerulous, spicate, or thyrsoid; involucres cylindric to turbinate or campanulate; bracts 3–7-seriate, imbricate, green-tipped. Florets 5–30, all perfect, yellow, lavender, rose or white; outer florets zygomorphic, all 5 lobes becoming ray-like; inner florets tubular-funnelform, lobes linear; style appendages truncate to subulate. Achenes turbinate, villous; pappus of many unequal, reddish-brown bristles, separate or united into clusters, or of 5 paleaceous awns. $x = 5$. Seven to 10 species, south-western USA, Baja California Norte.

926. *Machaeranthera* Nees

Machaeranthera Nees, Gen. Sp. Aster. 224 (1832) [1833]; Turner, Phytologia 62: 207–266 (1987), rev.; Hartman, Phytologia 68: 439–465 (1990), emend.
Hesperastrum A. Gray (1865).

Annual to perennial herbs, taprooted, erect or ascending; stems, leaves and involucres glabrous or with glandular or non-glandular hairs. Leaves

pinnatifid to bipinnatifid, spinulose. Heads solitary or in panicles, pedunculate; involucres turbinate to hemispheric; bracts 3–6-seriate, gradate, appressed to spreading or reflexed, base whitish-indurate, distally herbaceous. Rays pistillate, white to blue or purple, coiling. Disc florets perfect, yellow, funnelform, lobes triangular, erect. Achenes obovate, strigose, slightly compressed, rather thick-walled, faces 4–9-ribbed; pappus white to tawny, 1–3-seriate. $x = 4$. Two species, western USA, Mexico.

Molecular data (Morgan 2003) indicate that *Oonopsis* (Nutt.) Greene, *Pyrrocoma* Hook. and *Xanthisma* DC. arose evolutionarily from within the branches of what had recently been considered the genus *Machaeranthera* (sensu Hartman 1990). Accordingly, Morgan and Hartman (2003) have divided the genus into four smaller monophyletic genera, including *Machaeranthera* s. str., *Xanthisma*, *Arida* (R.L. Hartman) D.R. Morgan & R.L. Hartman, and *Dieteria* Nutt., which more closely reflect the hypothesized evolutionary patterns.

927. *Olivaea* Sch. Bip. ex Benth.

Olivaea Sch. Bip. ex Benth. in Hook., Ic. Pl. t. 1103 (1872); De Jong & Beaman, Brittonia 15: 86–92 (1963), rev.
Oligonema S. Wats. (1891), nom. illegit. non *Oligonema* Rostaf. (1875).
Golionema S. Wats. (1891).

Erect, mostly immersed, aquatic annuals from taproot, simple and glabrous below water surface, cymosely branched and stipitate-glandular above; stems hollow. Leaves sessile, linear to lanceolate, entire, lobed in deciduous submerged leaves. Heads solitary on leafy peduncles, in groups of few to 20; involucres hemispheric; bracts c. 3-seriate, basally fused, chartaceous, herbaceous distally. Rays 25–50, 1-seriate, pistillate, yellow, coiling. Disc florets perfect, yellow, tubular, lobes triangular, erect. Achenes quadrate or oblanceolate, compressed, 2–3-winged or 2-nerved, glabrous, shiny; pappus of 2–12 caducous, unequal bristles. $x = 6$. Two species, south-western Mexico.

928. *Oonopsis* (Nutt.) Greene

Oonopsis (Nutt.) Greene, Pittonia 3: 45 (1896); Hall, Publ. Carnegie Inst. Wash. 389: 34, 86–95 (1928), rev.
Stenotus Nutt. sect. *Oonopsis* Nutt. (1840).

Perennial herbs, with taproots and branched caudices; glabrous or sparsely tomentose. Leaves little reduced upwards, few leaves subtending heads, linear to narrowly oblanceolate or lanceolate. Inflorescences 1-headed, loosely corymbose with up to 12 heads, or subglomerate; involucres hemispheric to cylindric-turbinate; bracts 3–6-seriate, gradate, bases chartaceous, distally green, sharply acuminate. Rays 6–15, pistillate, yellow, not or weakly coiling. Disc florets perfect; yellow, funnelform, short-tubed, lobes triangular, erect. Achenes prismatic or narrowly turbinate, strigose or glabrous; pappus of rather few, brownish, rigid, unequal bristles. $x = 5$. Four or 5 species, north-central USA.

929. *Pyrrocoma* Hook.

Pyrrocoma Hook., Fl. Bor.-Am. 1: 306 (1833); Brown, Jepson Man.: 330–331 (1993), reg. rev.
Homopappus Nutt. (1840).

Erect or decumbent perennial herbs from taproot or caudex; stems, leaves and involucres glabrous or tomentose to sericeous, often punctuate- or stipitate-glandular. Leaves oblanceolate to elliptic or linear, entire or spinulose-dentate to laciniate; upper leaves reduced. Inflorescences 1-headed or spicate to loosely corymbose; involucres hemispheric to narrowly campanulate; bracts 2–6-seriate, equal to gradate, oblanceolate to oblong or linear, herbaceous and totally yellow-green or with indurate whitish base and apical green patch. Rays 10–80, pistillate, yellow, corollas sometimes reduced. Disc florets perfect, yellowish, tubular-funnelform, lobes deltate, erect. Achenes compressed or 3–4-angled with several nerves between angles, glabrous to strigose or sericeous; pappus of few, brownish, rigid, unequal bristles. $x = 6$. Circa 14 species, western USA, western Canada.

930. *Rayjacksonia* R.L. Hartm. & M.A. Lane

Rayjacksonia R.L. Hartm. & M.A. Lane, Amer. J. Bot. 83: 368 (1996).

Annual to short-lived perennial, taprooted herbs; stems, bracts and leaves with sessile or stipitate glands. Leaves linear to oblanceolate, marginal teeth and apices bristle-tipped. Inflorescence with 1–70 heads per plant, loosely thyrsoid-cymose. Involucres hemispheric; bracts 4–5-seriate, subequal, linear to lanceolate, 1-nerved, apices erect to spreading or recurved. Rays pistillate, 18–46, yellow. Disc florets perfect, throat abruptly expanded, lobes erect-spreading. Achenes strigose-sericeous, dimorphic, in ray florets broadly ellipsoid to obovoid, thick-walled, 3-angled with 0–4 ribs

on sides, in disc florets broadly ellipsoid-clavate, compressed, walls thinner, faces 5–9-ribbed; pappus bristles 3–4-seriate, unequal, thick and flattened, persistent. $x = 6$. Three species, central and south-western USA, north-eastern Mexico.

931. *Stephanodoria* Greene

Stephanodoria Greene, Erythea 3: 12 (1895); Nesom, Phytologia 82: 107–113 (1997), rev.

Perennial herbs; stems, leaves and involucres stipitate-glandular and hirtellous-pilosulous. Basal leaves persistent, narrowed to petiole, blades obovate to oblong-elliptic, entire, upper leaves reduced, sessile. Inflorescence loosely corymbose, with clusters of 2–6 sessile to subsessile heads; involucres turbinate; bracts 5–7-seriate, gradate, tips spreading to reflexed. Rays 20–30, pistillate, golden-yellow. Disc florets perfect, yellow, outer bending outwards from elongating tubes. Achenes oblanceolate to oblong-elliptic, compressed, 2–3-nerved, stramineous, mostly glabrous, strigose at apex; pappus a hyaline, erose corona, sometimes awn-like to one side. $x = 6$. One species, *S. tomentella* (B.L. Rob.) Greene, central Mexico, gypsophilous.

932. *Xanthisma* DC.

Xanthisma DC., Prodr. 5: 94 (1836); Semple, Rhodora 76: 1–19 (1974), rev.
Eriocarpum Nutt. (1840).
Sideranthus Nutt. ex Nees (1840).
Machaeranthera Nees subg. *Sideranthus* (Nutt. ex Nees) R.L. Hartman (1990).

Taprooted herbs, erect or spreading or sprawling, often much-branched, 3–100 cm tall, glabrous or with glandular or non-glandular hairs. Leaves entire or serrate to bipinnatifid, teeth usually bristle-tipped. Heads solitary or in loose panicles; involucres turbinate to hemispheric or campanulate; bracts 2–8-seriate, gradate, appressed, spreading or reflexed, bases chartaceous, apices herbaceous; receptacles with laciniate scales. Rays pistillate, white, pink, purple or yellow, sometimes absent, coiling. Disc florets perfect, yellow, tubular, lobes triangular, erect. Achenes often dimorphic, elliptic to obscurely cordate, ray achenes 3-sided, disc achenes compressed laterally, with faces 3–9-nerved, sparsely to densely pubescent; pappus of white to tawny bristles, often flattened proximally, in 2–4 series, or of awn-like scales. $x = 5$, reduced to 4, 3, and 2. Seventeen species, western USA, northern Mexico.

Xanthisma in its expanded sense comprises the unispecific genus *Xanthisma* and the former *Machaeranthera* Nees sections *Blepharodon* (DC.) R.L. Hartm., *Sideranthus* (Nutt. ex Nees) R.L. Hartm., *Havardii* (R.C. Jacks.) R.L. Hartm., and *Stenoloba* R.L. Hartm. (sensu Hartman 1990). The genus is distinguished by its short, turbinate, thick-walled, densely pubescent fruits, leaves with marginal spines, and chromosome numbers based on $x = 4$. Rays are either cyanic (blue, purple, pink or white) or yellow.

933. *Xanthocephalum* Willd.

Xanthocephalum Willd., Gesell. Naturf. Freunde Berlin Mag. [Neuesten Entdeck. Gesamten Naturk.] 1: 140 (1807); Lane, Syst. Bot. 8: 305–316 (1983), rev.; Nesom, Phytologia 66: 482–487 (1989), emend.

Annual or perennial herbs, taprooted or rhizomatous; glandular, often glutinous; stems erect or prostrate. Leaves sessile, sometimes decurrent, oblanceolate, entire or spinulose-toothed. Inflorescences 1-headed or loosely corymbose; involucres hemispheric to campanulate; bracts 2–4-seriate, gradate, white-indurate basally, green distally. Rays (0–)14–62, pistillate, yellow to orange-yellow. Disc florets perfect, yellow, tube narrow, limb abruptly expanded. Achenes compressed, subterete or 4–6-sided, thick-walled without prominent ribs, glabrous to strigillose; pappus absent, a lacerate crown, with awn-like scales or rarely with short bristles, usually shorter in rays. $x = 6$. Six species, western USA, Mexico.

934. *Xylorhiza* Nutt.

Xylorhiza Nutt., Trans. Amer. Philos. Soc. 2, 7: 297 (1840); Watson, Brittonia 29: 199–216 (1977), rev.

Perennial herbs to small shrubs; glabrous to villous or tomentose, sometimes with stipitate glands; stems often white. Leaves sessile, linear to lanceolate, oblanceolate or oblong, mostly 1-nerved, margins entire to spinulose-dentate. Heads solitary on naked peduncles; involucres campanulate to hemispheric; bracts 3–6-seriate, gradate, narrowly lanceolate, keeled, bases white-indurate, tips green. Rays 1–2-seriate, (4–)12–60, pistillate, white to blue or purple, coiling. Disc florets perfect, yellow, tubes slender, limbs narrowly funnelform, lobes ovate-deltate, erect-spreading, resin ducts pale to yellow. Achenes fusiform to

linear or ovate, somewhat compressed, 4-nerved, sericeous; pappus bristles 2–3-seriate, stout, often flattened, unequal. $x = 6$. Eight species, western USA, Mexico.

XV.14. Subtribe Symphyotrichinae
G.L. Nesom (1994).

Annual or usually perennial herbs, rarely shrubs (*Ampelaster*), eglandular to glandular. Leaves alternate, entire or rarely toothed, not lobed. Inflorescence with heads solitary to few or numerous, loosely corymbose, thyrsoid, or with branches secund; involucral bracts flat, usually with a herbaceous apical patch; receptacles flat, epaleate. Ray florets 1(–2–4)-seriate, corollas white to blue, coiling. Disc florets bisexual; style appendages lanceolate, hairy. Achenes obovoid to cylindric, terete or usually slightly to strongly compressed, multinerved, eglandular, setulae without anchor-shaped tips; pappus bristles 1-seriate (2-seriate in *Symphyotrichum* sect. *Conyzopsis*, often 2-seriate in *Canadanthus*). $x = 9$, reduced to 8, 7, 6, 5, 4.

Key to the Genera

1. Plants annual to short-lived perennial, usually arising from a slender taproot 2
– Plants perennial, usually arising from long or short rhizomes and fibrous roots 4
2. Heads and upper stems stipitate-glandular; ray achenes epappose **938. *Psilactis*** p.p.
– Plants completely eglandular; ray achenes pappose 3
3. Involucral bracts evenly herbaceous and of equal length; pistillate florets in 2–4 series in a broad outer zone, lamina absent or rudimentary to filiform and short; disc florets fewer than ray florets; pappus bristles in 2 series, all of equal length **939. *Symphyotrichum*** sect. ***Conyzopsis***
– Involucral bracts with a green, rhombic apical patch, basally indurate, gradate in length; pistillate florets in 1(–2) series, lamina prominent or strongly reduced; disc florets more numerous than ray florets; pappus bristles of equal length and in a single series **939. *Symphyotrichum*** sect. ***Oxytripolium*** p.p.
4. Ray achenes epappose **938. *Psilactis*** p.p.
– Ray achenes pappose 5
5. Involucral bracts with a sharply delimited green apical patch or zone, lower portion of involucral bract indurate 6
– Involucral bracts evenly herbaceous, without a distinctive green apical patch 7
6. Plants trailing or climbing (not twining) vines; stems perennial; achenes narrowly cylindric to slightly fusiform, with 9–12 ribs **936. *Ampelaster***
– Plants mostly erect, sometimes leaning but never trailing nor even subscandent; stems annual; achenes narrowly obovate, flattened to varying degrees, with (2–)3–10(–11) ribs **939. *Symphyotrichum*** p.p.
7. Leaves linear, parallel-veined, not clasping; rays white; achenes terete **935. *Almutaster***
– Leaves lanceolate to elliptic-lanceolate, net-veined, subclasping; rays purple; achenes strongly flattened **937. *Canadanthus***

Genera of Symphyotrichinae

935. *Almutaster* Å. Löve & D. Löve

Almutaster Å. Löve & D. Löve, Taxon 31: 356 (1982).

Perennial rhizomatous herbs, lower parts glabrous, stipitate-glandular above. Leaves sessile, thick, narrow, longitudinally 3–5-nerved. Inflorescence with 1 or few heads or loosely corymbose or thrysoid with 5–10(–30) heads; involucre broad; bracts in 3–4(–5) subequal series, herbaceous without indurated bases. Rays 15–30(–45) in 1 series, pistillate, white to lilac-tinged. Disc florets perfect, tubular, lobes deltate, erect. Achenes fusiform, terete, 7–10-nerved, sparsely strigose; pappus 1-seriate, of many attenuate, subequal bristles. $x = 9$. One species, *A. pauciflorus* (Nutt.) Å. & D. Löve, central Canada to Mexico.

936. *Ampelaster* G.L. Nesom

Ampelaster G.L. Nesom, Phytologia 77: 250 (1994).

Weak, diffusely branched shrubs; stems scrambling, hirsutulous or pilosulous. Leaves sometimes evergreen, oblanceolate, narrowed to auriculate base, 1-nerved. Heads 1 or 2–8 in loose, short-pedunculate clusters; involucres broad; bracts 4–6-seriate, gradate, thick, low-keeled, linear-oblong to narrowly spathulate, bases white, apices herbaceous, spreading-reflexed. Rays 40–70, pistillate, pink or lavender. Disc florets perfect, tubular. Achenes cylindrical to slightly fusiform, glabrous, with 9–12 usually whitish ribs; pappus 1-seriate, bristles attenuate. $x = 9$. One species, *A. carolinianus* (Walter) G.L. Nesom, eastern USA coastal plain.

937. *Canadanthus* G.L. Nesom

Canadanthus G.L. Nesom, Phytologia 77: 250 (1994).

Perennial thin-rhizomatous herbs; stems single, simple, with long-stipitate glands. Leaves cauline, sessile, clasping, lanceolate, entire to serrate, eglandular, lowest leaves much reduced. Inflorescences usually loosely corymbose, usually with 3–20 heads on leafy peduncles, sometimes

heads solitary; involucre turbinate to hemispheric; bracts 2–3-seriate, subequal, linear-lanceolate, thin-herbaceous, stipitate-glandular, without indurated base or apical green patch, inner bracts often slightly keeled. Rays 25–40, pistillate, purple, coiling. Disc florets perfect, tubular, lobes short, erect. Achenes oblanceolate, strongly compressed, 4–8-nerved; base narrow, stipitate; pappus bristles 1(–2)-seriate, attenuate. $x = 9$. One species, *C. modestus* (Lindl.) G.L. Nesom, USA (Alaska south to Montana, Michigan), east to south-eastern Canada (New Brunswick).

938. *Psilactis* A. Gray

Psilactis A. Gray, Mem. Amer. Acad. Arts 2, 4: 71 (1849); Morgan, Syst. Bot. 18: 290–308 (1993), rev.

Annual or perennial herbs, usually taprooted; stems, involucral bracts and often leaves stipitate-glandular, sometimes tomentose. Lower leaves obovate to linear-lanceolate, early deciduous, upper leaves entire, subclasping. Inflorescence loosely thyrsoid to corymbose or with branches 1-headed; involucre broad, bracts 2–4-seriate, subequal to gradate, outer bracts indurate along basal margins. Rays pistillate, white to bluish, coiling. Disc florets perfect, tubular. Ray achenes fusiform to obovate, subterete, 5–14(–18)-nerved, short-strigose, epappose; disc achenes slightly longer, with pappus bristles 1-seriate. $x = 9, 4, 3$. Six species, mostly USA (Texas) and Mexico, one to Andes of northern South America.

939. *Symphyotrichum* Nees

Symphyotrichum Nees, Gen. Sp. Aster. 135 (1832) [1833]; Nesom, Phytologia 77: 267–296 (1994), comb.
Tripolium Nees sect. *Oxytripolium* DC. (1836).
Virgulus Raf. (1836) [1837].
Tripolium Nees subg. *Astropolium* Nutt. (1840).
Brachyactis Ledeb. (1845).
Virgulaster Semple (1985).

Mostly perennial herbs, with rhizomes or short caudex, fibrous-rooted. Leaves petiolate to sessile and clasping, linear to cordate, entire or toothed. Inflorescence cylindrical to diffusely thyrsoid or corymbose; involucres narrowly campanulate to hemispheric; bracts 3–7-seriate, gradate to subequal, mostly with pale indurated bases and herbaceous tips. Rays pistillate; usually long, white to blue or purplish, coiling. Disc florets perfect, yellow, usually purplish at tips, gradually expanded, lobes deltate, erect to spreading. Achenes narrowly obovate, compressed, (2–)3–5(–6)-nerved, sparsely strigose to glabrous; pappus bristles 1(–2)-seriate. $x = 8, 7, 6, 5, 4$. Circa 92 species, mostly North America, some Mexico and South America, few widely naturalized.

Symphyotrichum subg. *Symphyotrichum* (incl. *Conyzanthus* Tamamsch., *Brachyactis* Ledeb.) includes species with $x = 8$, 7 and 6, and 5, while subg. *Virgulus* (Raf.) Nesom (incl. *Lasallea* Greene, *Virgulaster* Semple) primarily those with independently derived $x = 5$. Hybrids and backcrosses between the two ($x = 13$) are common and stabilized in some areas (Nesom 1994d).

XV.15. Subtribe Chaetopappinae G.L. Nesom (2000).

Annual or short-lived perennial herbs. Leaves alternate, oblong to oblanceolate-spathulate, entire. Heads mostly solitary; involucral bracts flat to convex, not keeled, with broad, hyaline margins; receptacles usually without pales. Rays 1-seriate, pistillate, blue to white, strongly coiling. Disc florets sometimes functionally male; style appendages obtuse or truncate to triangular. Achenes eglandular or glandular, terete and multinerved (most *Chaetopappa*) or obovate, flattened, and 2-nerved (*Monoptilon*, some *Chaetopappa*); setulae without anchor-shaped tips; pappus of persistent bristles or scales, or of bristles and scales, commonly in multiples of 5 (in *Chaetopappa*), or absent. $x = 8$.

Key to the Genera

1. Stems erect to ascending; capitula on distinct peduncles; achenes 2–5-, 8-, or 10-nerved, flattened to terete **940. *Chaetopappa***
– Stems prostrate to decumbent; capitula closely subtended by foliar bracts; achenes 2-nerved, flattened **941. *Monoptilon***

940. *Chaetopappa* DC.

Chaetopappa DC., Prodr. 5: 301 (1836); Shinners, Wrightia 1: 63–89 (1946), rev.; Nesom, Phytologia 64: 448–456 (1988), key.
Distasis DC. (1836).

Annual or perennial herbs; stems erect or decumbent. Heads terminal, involucres broadly conical to hemispheric; bracts 2–6-seriate, gradate, elliptic to linear-lanceolate; receptacles flat to slightly convex. Rays 6–20, white or drying bluish. Disc florets perfect or central florets functionally male, yellow,

tubular; style appendages shallowly to narrowly triangular. Achenes terete to compressed, 2–5- or 8–10-nerved, sparsely strigose, sometimes gland-dotted; pappus a hyaline crown, hyaline scales, awn-like bristles, alternating scales and bristles or nearly lacking. $x = 8$. Eleven species, south-central USA, north-eastern Mexico.

941. *Monoptilon* Torr. & A. Gray ex A. Gray

Monoptilon Torr. & A. Gray ex A. Gray, Boston J. Nat. Hist. 5: 106 (1845); Keil, Jepson Man.: 319 (1993), reg. rev. *Eremiastrum* A. Gray (1854).

Annual taprooted herbs, radiating branches prostrate to decumbent; stems, leaves and involucres minutely glandular, hispid-hirsute, hairs long, white. Leaves small. Heads sessile; involucres campanulate; bracts 1(–2)-seriate, equal, linear-lanceolate, purple-tipped. Rays 12–21, white or rose to purple-tinged. Disc florets mostly perfect, yellow with orange veins, tubular-funnelform; style appendages obtuse to truncate. Achenes obovate, compressed, 2-nerved, sparsely strigose; pappus a short, toothed cup and single apically plumose bristle or 1–12 barbellate bristles alternating with scales. $x = 8$. Two species, south-western USA, north-western Mexico.

XV.16. Subtribe Astranthiinae G.L. Nesom (2000).

Annual, biennial or perennial herbs. Leaves alternate, spathulate to linear, entire or few-toothed, eglandular. Heads solitary; involucral bracts not keeled, with broad, hyaline margins; receptacles convex to conical, usually epaleate, paleate in *Geissolepis*. Ray florets 1-seriate, corollas white to bluish or pinkish above (rarely yellow in *Townsendia*), usually with a lavender to blue or pink abaxial midstripe, not reflexing or coiling. Disc florets with short-tubed corollas; style branch appendages triangular-lanceolate, papillose. Achenes oblanceolate to obovate, compressed, 2(–3)-ribbed, commonly with setulae with anchor-shaped or uncinate tips (achenes winged and fringed with setulae with anchor-shaped tips in *Dichaetophora*); pappus 1-seriate, of barbellate bristles or a low crown of setae/bristles and scales (2-awned in *Dichaetophora*). $x = 9$; $x = 5$ in *Astranthium*, reduced to 4 and 3; $x = 3$ in *Dichaetophora*.

Key to the Genera

1. Pappus of numerous bristles, often short; $x = 9$ **945. *Townsendia***
– Pappus of scales, awns, or essentially absent 2
2. Plants succulent, prostrate; pappus of 6–8 narrowly triangular scales, scale margins with uncinate cilia; $x = 9$ or 8; receptacles paleate **944. *Geissolepis***
– Plants herbaceous, erect to decumbent; pappus of 2 awns or essentially absent; $x = 5$ or reduced; receptacles epaleate 3
3. Achenes without wings or fringed margins; pappus absent or a barely perceptible corona **942. *Astranthium***
– Achenes winged, hairs of marginal fringe with anchor-shaped tips; pappus of 2 thin, barbellate awns, usually with additional minute awns **943. *Dichaetophora***

Genera of Astranthiinae

942. *Astranthium* Nutt.

Astranthium Nutt, Trans. Amer. Philos. Soc. 2, 7: 312 (1840); De Jong, Publ. Mus. Michigan State Univ., Biol. Ser. 2: 429–528 (1965), rev.

Annual, biennial or perennial taprooted herbs; stems erect to creeping, sparsely to densely hairy. Some leaf bases clasping, lower leaves spathulate-obovate, upper leaves narrower. Heads solitary, on usually long peduncles; involucres campanulate to hemispheric; bracts 2(–3)-seriate, subequal, broadly oblanceolate to linear-lanceolate, thin-herbaceous; receptacles conical. Rays 10–65(–85), pistillate, limbs white above. Disc florets perfect, yellow, tube short, limb rather abruptly expanded, lobes deltate, erect; style appendages lanceolate-acute. Achenes 2-ribbed, faces smooth to papillose, glabrous or with anchor-shaped setulae; pappus absent or crown of short setae or scales. $x = 3, 4, 5$. Eleven species, Mexico to south-central USA.

943. *Dichaetophora* A. Gray

Dichaetophora A. Gray, Mem. Amer. Acad. Arts 2, 4: 73 (1849); Shinners, Wrightia 1: 90–94 (1946), rev.

Annuals from thin taproot; stems erect or decumbent, sparsely strigose. Leaves oblanceolate, entire. Heads terminal, solitary; peduncles 2–9 cm long; involucres hemispheric; bracts 2-seriate, subequal, long-ciliate; receptacles convex to conical. Rays 15–25, pistillate, limbs white above. Disc florets perfect, yellow, tubes short, abruptly expanded into limb. Achenes obovate to broadly elliptic, faces with thickened, elliptic central area surrounded by paler, glabrous wing-like margins, setulae on central area and edges of wings anchor-shaped; pappus of 2 thin

awns, usually minute additional awns along callus rim. $x = 3$. One species, *D. campestris* A. Gray, USA (south-central Texas, north-eastern Mexico).

944. *Geissolepis* B.L. Rob.

Geissolepis B.L. Rob., Proc. Amer. Acad. Arts 2, 27: 177 (1892).

Perennial prostrate herbs, with fibrous-rooted stolons; stems and peduncles sparsely pilose, glabrescent. Leaves linear-oblanceolate, succulent, strigose adaxially along midvein. Heads on thick, axillary, bracteate peduncles; involucre broadly turbinate; bracts 4–5-seriate, strongly gradate, thick; receptacles steeply conic; paleae obovate, midvein resinous. Rays 8–12, pistillate, orange-yellow with orange resin ducts. Disc florets orange-yellow with orange veins, funnelform, gradually expanded; style appendages triangular. Achenes obovate-triangular, slightly compressed, outer achenes 3–4-angled, with c. 8 pale ribs, with orange resin pockets distally, strigose with anchor-shaped setulae; pappus of 6–8 narrow pales, margins ciliate. $x = 8$ or 9. One species, *G. suaedifolia* B.L. Rob., central Mexico.

945. *Townsendia* Hook.

Townsendia Hook., Fl. Bor.-Am. 2: 16 (1834); Beaman, Contr. Gray Herb. 183: 1–151 (1957), rev.; Reveal, Great Basin Naturalist 30: 23–52 (1970), rev.

Annual, biennial or perennial herbs, taprooted or rarely stoloniferous; stems and leaves mostly strigose. Leaves basal or also cauline, spathulate to linear. Heads terminal, solitary; involucres hemispheric to campanulate; bracts 2–7-seriate, gradate, usually broadly hyaline-ciliate-margined; receptacles convex, rarely conical. Rays white or bluish to pinkish, one species yellow. Disc florets perfect, yellow, lobes deltate, erect or incurved. Achenes oblanceolate to obovate, compressed, 2(–3)-ribbed, smooth or papillose, glabrate or with anchor-shaped setulae; pappus 1-seriate, of barbellate bristles or short bristles and squamellae, ray pappus sometimes shorter than in disc. $x = 9$. Twenty-six species, western North America, incl. two in Mexico.

XV.17. Subtribe Chrysopsidinae G.L. Nesom (1994).

Annual to perennial herbs. Leaves alternate, mostly entire, commonly with sessile or stipitate glands. Heads solitary or in loosely thyrsoid inflorescences; involucral bracts keeled; receptacles epaleate. Ray florets 1-seriate, yellow, rarely white, coiling or not coiling. Disc florets bisexual, with large rectangular-prismatic crystals in the throat; style appendages narrowly lanceolate, hairy. Achenes multinervate, usually eglandular; setulae without anchor-shaped tips; pappus 2–3(–4)-seriate, the inner 1–2 series of flattened bristles, outer of much shorter setae, bristles, or scales. $x = 9$, reduced to 7, 6, 5, 4, 3.

Key to the Genera

1. Rays white; South America **949. *Noticastrum***
– Rays yellow; North America 2
2. Leaves densely and closely white-woolly-tomentose; achenes narrowly oblong and strongly flattened, with 7–9 thin, closely adjacent, superficial white nerves on each side; stems with one head **952. *Tomentaurum***
– Leaves variously pubescent but not white-woolly-tomentose; achenes not as above; stems with 1–numerous heads 3
3. Leaves linear, parallel-nerved or with a strong tendency for parallel veins, veins with associated massive sclerenchyma, prominently superficial and forming raised ridges 4
– Leaves obovate to oblanceolate, net-veined, veins not strongly sclerenchymatous, not raised above lamina 5
4. Taprooted annuals to weak perennials; pappus 1-seriate; leaves with minute but evident lacunae on the abaxial surface; $x = 6$ **947. *Croptilon***
– Rhizomatous perennials; pappus 2-seriate, of bristles and a short outer series of setae; leaves without lacunae on the abaxial surface; $x = 9$ **951. *Pityopsis***
5. Pubescence of coarse, stiff, osteolate hairs; $x = 9$ **948. *Heterotheca***
– Pubescence of fine, flexible, flagelliform hairs; $x = 5$ 6
6. Achenes obovate to linear-oblong in outline, nearly terete to slightly flattened, with 5–10 ribs, ribs often with orange-resinous oil ducts; pappus 2-seriate; stems mostly with 2–numerous heads **946. *Chrysopsis***
– Achenes fusiform-cylindric, with 8–16 whitish, superficial ribs; pappus 1-seriate or 2-seriate; stems mostly with 1 head **950. *Osbertia***

Genera of Chrysopsidinae

946. *Chrysopsis* (Nutt.) Elliott

Chrysopsis (Nutt.) Elliott, Sketch Bot. S. Carolina 2: 333 (1824), nom. cons.; Semple, Rhodora 83: 323–384 (1981), rev.; Nesom, Phytologia 71: 109–121 (1991), emend.
Diplopappus Cass. (1817).
Inula L. sect. *Chrysopsis* Nutt. (1818).

Annual or rhizomatous perennial herbs, pubescence woolly or sericeous, sometimes arach-

noid; stems erect to decumbent. Leaves sessile, basal and lower cauline spathulate to oblanceolate. Inflorescence terminal, corymbose. Involucres hemispheric to turbinate; bracts (2–)3–5-seriate, gradate, linear, not herbaceous; receptacles flat. Rays 13–34, pistillate, yellow. Disc corolla lobes deltate, erect. Achenes obovate to linear-oblong, nearly terete, strigose, ribs 5–10, sometimes with orange ducts; pappus 2-seriate, inner bristles long, outer bristles short. x = 5, 3. Circa 11 species, coastal south-eastern USA.

947. *Croptilon* Raf.

Croptilon Raf., Fl. Tellur. 2: 47 (1836) [1837]; Smith, Rhodora 67: 217–238 (1965), rev.; Smith, Sida 9: 59–63 (1981), emend.
Isopappus Torr. & A. Gray (1842).

Annual to weak perennial taprooted herbs, usually sparsely hispid, usually stipitate-glandular. Leaves sessile, linear to narrowly oblanceolate or lanceolate, often falcate, entire to serrate, long-ciliate basally, parallel veins 3, arachnoid hairs in abaxial areoles. Involucres narrowly turbinate to subcylindric; bracts 3–5-seriate, gradate, lanceolate to linear-lanceolate. Rays 5–10, pistillate, yellow to orangish, coiling. Disc corollas yellow, lobes triangular, erect. Achenes elongate, terete to few-angled, with 6–14 superficial pale nerves, strigose to sericeous, resin ducts present in 1 species; pappus 1-seriate, bristles persistent, rigid, reddish-brown. x = 6, 5, 4. Three species, south-eastern USA to north-eastern Mexico.

948. *Heterotheca* Cass.

Heterotheca Cass., Bull. Sci. Soc. Philom. Paris 1817: 137 (1817); Semple, Syst. Bot. 13: 547–558 (1988), rev.; Nesom, Phytologia 69: 282–294 (1990), rev.; Semple, Univ. Waterloo Biol. Ser. 37: i–iv, 1–164 (1996), rev.

Annual or perennial taprooted or rhizomatous herbs, often hispid-pilose, often aromatic or viscid, glands sessile or short-stipitate. Leaves entire or shallowly toothed, basal often petiolate, upper sessile. Inflorescences 1-headed or corymbose with few heads. Involucres campanulate; bracts 4–8-seriate, gradate, lanceolate, rigid; receptacles plano-convex. Rays absent or pistillate, yellow to orangish, coiling. Disc corollas slightly expanded above. Achenes cylindrical and 8–14-nerved or compressed with 2 ribs, glabrous to short-strigose or sericeous; pappus bristles tawny to whitish, sometimes a crown of short bristles or lacking. x = 9. Circa 25–30 species, USA, Canada, Mexico.

Three sections include sect. *Heterotheca* with ray achenes 3-angled, epappose and usually glabrous, and disc achenes compressed; sect. *Phyllotheca* (Nutt.) Harms with all achenes cylindric to slightly compressed, pappose and setulose; and sect. *Ammodia* (Nutt.) Harms without any short outer pappus series.

949. *Noticastrum* DC.

Noticastrum DC., Prodr. 5: 279 (1836); Zardini, Revista Mus. La Plata, Secc. Bot. 13: 313–424 (1985), rev.
Aplopappus (*Haplopappus*) sect.(?) *Leucopsis* DC. (1836).
Leucopsis (DC.) Baker (1882).

Perennial herbs or subshrubs, scapiform with basal rosettes or with stolons, decumbent to erect; pubescence non-glandular, stipitate-glandular and/or woolly. Leaves often copiously silky near base. Inflorescence 1- to few-headed. Involucre campanulate to turbinate; bracts 3–6-seriate, gradate, linear-lanceolate, often reddish-margined. Rays pistillate, white to purplish, rarely yellow. Disc corollas yellow, throat tubular, lobes short, erect. Achenes subfusiform, somewhat compressed, setuliferous, with 16–26 costae, usually 5–10 of these prominent, carpopodium asymmetric; pappus to 4-seriate, bristles usually tawny, some short outer bristles present. x = 9. Circa 19 species, Andean, southern South America.

950. *Osbertia* Greene

Osbertia Greene, Erythea 3: 14 (1895); Turner & Sundberg, Pl. Syst. Evol. 151: 229–239 (1986), rev.; Nesom, Phytologia 71: 132–135 (1991), emend.

Erect, perennial, stoloniferous herbs, pilose and eglandular to puberulous and glandular with septate glandular hairs; stems usually single. Leaves of basal rosette linear-oblanceolate to elliptical; cauline leaves reduced, clasping. Heads solitary; peduncles long. Involucres hemispheric to turbo-campanulate; bracts 4–6-seriate, gradate, linear-lanceolate; receptacles convex, alveolae deep. Rays pistillate, yellow, often purplish beneath, not coiling. Disc florets perfect, yellow, tube and limb weakly delimited. Achenes terete-fusiform, appressed-villous, with 8–16 superficial nerves, carpopodium asymmetric; pappus bristles 1-seriate, also a short outer series in 1 species. x = 5. Three species, Mexico, Guatemala.

951. *Pityopsis* Nutt.

Pityopsis Nutt., Trans. Amer. Philos. Soc. 2, 7: 317 (1840); Semple & Bowers, Univ. Waterloo Biol. Ser. 29: 1–34 (1985), rev.

Perennial herbs from short fibrous-rooted rhizomes, silky-sericeous with mostly appressed hairs, often stipitate-glandular. Leaves mostly basal or basal and cauline, reduced on upper stem, linear to lanceolate or oblanceolate, sometimes falcate, entire, parallel-veined. Inflorescence corymbose, with few to many heads. Involucre mostly cylindric-turbinate; bracts 4–8-seriate, lanceolate, usually with apical green patch. Rays 8–35, pistillate, yellow, coiling. Disc corollas gradually expanded, lobes deltate, erect. Achenes fusiform, terete to slightly compressed, strigose; pappus 2-seriate, outer bristles shorter. $x = 9$. Circa seven species, south-eastern USA, one into Mexico, Central America.

952. *Tomentaurum* G.L. Nesom

Tomentaurum G.L. Nesom, Phytologia 71: 129 (1991).

Perennial, scapose herbs from slender rhizomes, tomentose, thicker uniseriate hairs absent, with sessile or short-stipitate orange-tipped glands. Leaves in basal rosette or with clasping bases on lower part of stem, sessile, obovate to oblanceolate, entire. Heads solitary, nodding in bud. Involucres hemispheric; bracts 5–6-seriate, gradate, narrowly ovate-lanceolate, margins purplish with hyaline flange, outer bracts herbaceous, inner herbaceous only distally; receptacles plano-convex. Rays 16–21, pistillate, yellow, coiling. Achenes linear-oblong, compressed, each side 7–9-nerved, densely white-sericeous; pappus of 45–60 white bristles in several series, a few short outer setae. One species, *T. niveum* (S. Wats.) G.L. Nesom, north-western Mexico.

XV.18. Subtribe Conyzinae Horan. (1847).

Tribe Erigeroneae Gren. & Godr. (1850).

Annual to perennial herbs. Leaves alternate, mostly entire, less commonly toothed to lobed. Heads solitary to few in a loosely corymboid inflorescence, densely paniculate in some *Conyza*; involucral bracts persistent, not keeled, with orange-resinous veins; receptacles usually convex, epaleate. Ray florets 1(–3)-seriate; corollas white to blue, rarely yellow, coiling, reflexing or straight. Disc florets bisexual, with orange resin canals along veins; style branch appendages deltate, papillose. Achenes 2-nerved (rarely multinerved), compressed, eglandular; setulae without anchor-shaped tips; pappus 1–2(–3)-seriate, inner series of barbellate bristles, outer of scales or setae. $x = 9$ ($x = 5$, reduced to 4 and 3 in *Aphanostephus*).

Key to the Genera

1. Pistillate florets tubular or with short erect limbs 2
– Pistillate florets with long limbs 3
2. Perennial herbs from woody rhizomes or tubers; achenes subcylindrical **954. *Apopyros***
– Annual or perennial herbs without tubers; achenes compressed **955. *Conyza***
3. Shrubs **956. *Darwiniothamnus***
– Herbs 4
4. Achenes 4-angled to fusiform-cylindrical 5
– Achenes compressed 6
5. Leaves broad to linear-lanceolate to pinnatifid; hairs of stems and leaves appressed to spreading; achenes usually 4-angled, thick-walled, with subsurface nerves **953. *Aphanostephus***
– Leaves filiform to linear-oblanceolate; stems and leaves long-pilose with ciliate hairs; achenes fusiform-cylindrical, with numerous, raised, orange-resinous nerves **960. *Neja***
6. Rays yellow; plants taprooted **958. *Hysterionica***
– Rays white or bluish to pinkish (rarely yellow); plants taprooted or rhizomatous 7
7. Involucral bracts usually with 1 resinous longitudinal vein **957. *Erigeron***
– Involucral bracts with 3 longitudinal veins **959. *Leptostelma***

Genera of Conyzinae

953. *Aphanostephus* DC.

Aphanostephus DC., Prodr. 5: 310 (1836); Turner, Phytologia 56: 81–101 (1984), rev.

Annual or perennial taprooted, erect to decumbent herbs; hairs soft to stiff. Leaves sessile or petiolate, oblanceolate to linear-lanceolate, entire to pinnatifid. Heads solitary; involucres broadly to depressed hemispheric; bracts 3–5-seriate, weakly gradate, ovate-lanceolate, not reflexing with age, margins broadly scarious; receptacles convex to conical. Rays pistillate, 1(–2)-seriate, white above, with purplish median stripe beneath, closing upwards at night, not coiling. Disc corollas yellow, tubular to funnelform, tube or limb sometimes swollen and indurate, lobes deltate, erect. Achenes 4-angled or sometimes subterete, with 4–12 grooves or ribs, strigose or glabrous; pappus of short cilia, or with awns with or without bristle

tips. $x = 5$ reduced to 4 or 3. Four species, south-central USA, Mexico.

Aphanostephus differs in chromosome number and morphology, achene morphology (including vestiture), and pappus structure from all other members of subtribe Conyzinae, but molecular data (Noyes 2000) indicate that its evolutionary origin was sister to a group of Caribbean species of *Erigeron* L.

954. *Apopyros* G.L. Nesom

Apopyros G.L. Nesom, Phytologia 76: 177 (1994).

Erect perennial herbs, from rhizomes or tubers, stiffly pilose-hirsute to nearly glabrous, eglandular. Leaves cauline, stiffly erect, shiny-indurate, sessile, entire, 3(–5)-nerved, basal leaves scale-like. Inflorescence 1-headed or thyrsoid-corymbose; involucres broadly campanulate; bracts 3–4-seriate, weakly gradate, with resinous midvein, margins narrowly hyaline. Peripheral florets pistillate, tubular, with 3–4 triangular teeth. Disc florets narrowly tubular, base a wide indurate disc. Achenes subcylindric, strigose, eglandular, nerves 5, orange-resinous when young, becoming paler; pappus bristles (1–)2-seriate, attenuate, sometimes with short outer series. Two species, Brazil, Paraguay, Argentina.

955. *Conyza* Less.

Conyza Less., Syn. Gen. Comp. 203 (1832), nom. cons.; Cuatrecasas, Webbia 24: 198–228 (1969), reg. rev.; Wild, Bol. Soc. Brot. 43: 247–276 (1969), reg. rev.; Zardini, Bol. Soc. Argent. Bot. 17: 31–46 (1976), rev.
Conyzella Fabric. (1759).
Leptilon Raf. (1818).

Annual or perennial herbs, nearly glabrous to coarsely hispid-pilose. Leaves linear to oblanceolate, entire to pinnatifid. Inflorescences broadly ellipsoid to columnar or corymbose; involucres cylindric to hemispheric; bracts 2–4-seriate, subequal to weakly gradate, outer bracts with 3 resinous nerves; receptacle sometimes a hypanthium-like cup. Peripheral florets pluriseriate, pistillate, whitish, eradiate or with rudimentary limbs. Disc florets 3–35, perfect, whitish, tubular-funnelform, tube c. 2/3 of length. Achenes glabrous to sparsely strigose; pappus bristles 1-seriate, sometimes lengthening after anthesis, rarely with short outer series of setae. $x = 9$. Circa 60–100 species, primarily tropical and subtropical, some introduced pantropically.

Species of *Conyza* native to Africa apparently are more similar and perhaps more closely related to genera of subtribe Grangeinae. Molecular data indicate that American *Conyza*, as currently viewed, is polyphyletic, having arisen several times from within the nexus of *Erigeron* L. (Noyes 2000). The taxonomy of subtribe Conyzinae is currently under review (Nesom, unpubl. data).

956. *Darwiniothamnus* Harling

Darwiniothamnus Harling, Acta Horti Berg., Bd. 20, 3: 108 (1962).

Shrubs, glabrous to strigose, sometimes minutely glandular. Leaves clustered at ends of branches, narrowly linear to oblanceolate or lanceolate, sessile or short-petiolate, entire to mucronate. Inflorescences leafy-bracteate corymbose or nearly 1-headed; buds erect; involucres cupulate to hemispheric; bracts 4–6-seriate, strongly gradate, 1-nerved. Peripheral florets pistillate, pluriseriate, whitish, limbs exceeding involucre, coiling. Disc florets yellow, tubular-funnelform, constricted in lower 1/2–1/3, limb sometimes strongly inflated. Achenes oblong, sparsely to densely strigose, somewhat dimorphic, ray achenes compressed, 2(–4)-nerved, disc achenes shorter and broader, 3–5(–6)-nerved; pappus bristles 1-seriate. $x = 9$. Two species, Galapagos Islands.

957. *Erigeron* L.

Erigeron L., Sp. Pl. 683 (1753); Botschantzev, Fl. U.R.S.S. 25: 191–288 (1959), Engl. transl. 25: 180–269 (1999), reg. rev.; Cronquist, Brittonia 6: 121–302 (1947), rev.; Cronquist, Intermount. Fl. 5: 305–351 (1994), reg. rev.; Halliday, Fl. Eur. 4: 116–120 (1976), reg. rev.; Nesom, Phytologia 66: 415–455 (1989), rev.; 67: 67–93 (1989), emend.; 72: 157–208 (1992), rev.; Solbrig, Contr. Gray Herb. 191: 3–79 (1962), rev.
Trimorpha Cass. (1817).
Polyactis Less. (1832).
Achaetogeron A. Gray (1849).
Astradelphus Remy (1849).
Wyomingia A. Nelson (1899).

Annual to perennial herbs, rarely shrubs, with caudex or rhizomes; stems, leaves, involucres glabrous to variously pubescent, often with stipitate glands. Basal rosettes sometimes persistent, cauline leaves linear to lanceolate or spathulate, entire to pinnatifid. Inflorescences 1-headed or corymbose to thyrsoid; involucres turbinate

to hemispheric; bracts 2–4(–7)-seriate, equal to strongly gradate, with 1(–3) resinous veins; receptacles flat to conical. Rays 1–4-seriate, rarely absent, white to blue or pink, rarely yellow, reflexing, coiling, or straight. Disc florets yellow, limb sometimes inflated; style appendages lanceolate, acute or obtuse. Achenes compressed with 2–4 ribs, seldom subterete with 6–14 ribs, glabrous to strigose; pappus bristles 1-seriate, sometimes caducous or lacking, sometimes with short outer setae, scales, or a corona. $x = 9$. Circa 400 species, North to South America, West Indies, Galapagos, Eurasia.

In the analysis of molecular data by Noyes (2000), subtribe Conyzinae comprises *Erigeron*, American *Conyza* Less., *Trimorpha* Cass., *Darwiniothamnus* Harling, the four genera of the *Leptostelma* group (*Leptostelma* D. Don, *Hysterionica* Willd., *Neja* D. Don, *Apopyros* Nesom), and *Aphanostephus* DC., but the cladistically basal and terminal taxa of the subtribe are *Erigeron*. Formal recognition of any of these genera, for consistency in cladistic classification, would require further and much finer generic splitting of species traditionally considered to be *Erigeron*. Nesom (1989, 1990, 1994a) and Nesom and Noyes (1999) have divided the species of 'traditional' North and Central American *Erigeron* into 21 sections, emphasizing variation in habit, vestiture, inflorescence structure, bud position, lamina behaviour, cypsela morphology, and other features. Australian species formerly identified as *Erigeron* have been transferred to other genera (Nesom 1994b, 1998 [2000]), as has a Mexican species (Nesom and Noyes 2000).

958. *Hysterionica* Willd.

Hysterionica Willd., Gesell. Naturf. Freunde Berlin Mag. [Neuesten Entdeck. Gesamten Naturk.] 1: 140 (1807).

Annual or perennial taprooted herbs; caudex simple; stems sometimes branched at base. Leaves closely inserted, little reduced above, blades oblanceolate, glandular-pubescent. Heads 1 to several, peduncles short or long; involucres hemispheric; bracts 1–2-seriate, subequal, lanceolate, acute, glandular-pubescent and hirsute outside. Rays 1–3-seriate, pistillate, yellow or white, limbs broad to filiform. Disc florets yellow, tubular, lobes deltoid, erect. Achenes compressed, setulose; pappus 2-seriate, of bristles and an outer series of short linear scales. $x = 9$. Seven species, south-eastern South America.

959. *Leptostelma* D. Don

Leptostelma D. Don in Sweet, Brit. Fl. Gard. ser. 2, 38 (1830).

Coarse perennial herbs, erect from decumbent bases; stems, leaves and involucres often puberulous to hispid; stems often broad with broad pith. Leaves cauline, herbaceous, broadly inserted, narrowed to base, rarely pseudopetiolate, blades ovate to oblanceolate, venation pinnate, margins serrate. Inflorescences corymbose to rather subumbellate; heads large; peduncles short to long; involucres campanulate; bracts 2–3-seriate, subequal, herbaceous to chartaceous, oblong-lanceolate, 3-nerved, margins scarious. Rays 1–2-seriate, 80 or more, pistillate, whitish to creamy or yellow, narrow, not coiling. Disc florets yellow, tube slender, limb narrowly funnelform, lobes 5, lanceolate, erect. Achenes obovate-oblong, somewhat compressed, 2–3-nerved, mostly glabrous; pappus white, 1–3-seriate, of 30–40 flexuous bristles. $x = 9$. Five species, south-eastern South America.

960. *Neja* D. Don in Sweet

Neja D. Don in Sweet, Hort. Brit. (Sweet), ed. 2, 299 (1830); Espinar, Darwiniana 22: 537–549 (1980), reg. rev.

Perennial herbs, usually from taproot or branched caudex. Leaves mostly basal, filiform to linear-oblanceolate, crinkly-pilose with long cilia. Heads solitary, long-pedunculate or on sparsely bracteolate stems; involucre broadly turbinate to hemispheric; bracts 2–4-seriate, gradate, narrowly triangular. Rays pistillate, 1-seriate, yellow or white. Disc florets yellow, tubular, lobes deltate, erect. Achenes fusiform-cylindrical, with 7–10 prominulous, orange-resinous nerves, strigose between nerves; pappus bristles 1–3-seriate, outer series scarcely differing or of short setaceous bristles or scales. Circa six species, south-eastern South America, Cuba.

Recently Described or Reinstated Genera not Included in the Key and Descriptions

Allittia P.S. Short, Muelleria 20: 54 (2004).

Segregate of *Brachyscome*. Two spp., south-eastern Australia and Tasmania.

Cuniculotinus Urbatsch, R.P. Roberts and Neubig, Sida 21: 1618 (2005).

Solidagininae. One sp., *Cuniculotinus* (*Chrysothamnus*) *gramineus* (H.M. Hall) Urbatsch, R.P. Ro-

berts & Neubig (= *Petradoria discoidea* L.C. Anderson), western USA.

Herrickia Wooton & Standley [reinstated], Contr. U.S. Natl Herb. 16: 186 (1913).

Eurybia sect. *Herrickia* (Wooton & Standley) G.L. Nesom.

Machaerantherinae grade. Four spp., southwestern USA.

Hullsia P.S. Short, Muelleria 20: 58 (2004).

Segregate of *Brachyscome*. One sp., *H. argillicola* P.S. Short, north Australia.

Lorandersonia Urbatsch, R.P. Roberts and Neubig, Sida 21: 1619 (2005).

Solidagininae. Seven spp., western USA and northwestern Mexico.

Nestotus R.P. Roberts, Urbatsch & Neubig, Sida 21: 1650 (2005).

Solidagininae. Two spp., western USA.

Novaguinea D.J.N. Hind, Kew Bull. 59: 177 (2004).

Lagenophorinae. One sp., *N. rudalliae* D.J.N. Hind, New Guinea.

Pembertonia P.S. Short, Muelleria 20: 62 (2004).

Brachyscome sect. *Heteropholis* F. Muell. One sp., *P. latisquamata* (F. Muell.) P.S. Short, western Australia.

Toiyabea R.P. Roberts, Urbatsch & Neubig, Sida 21: 1652 (2005).

Solidagininae. One sp., *T.* (*Haplopappus*) *alpina* (L.C. Anderson & S. Goodrich) R.P. Roberts, Urbatsch & Neubig, western USA.

Triniteurybia Brouillet, Urbatsch & R.P. Roberts, Sida 21: 898 (2004).

Basal grade to Machaerantherinae. One sp., *T. aberrans* (A. Nelson) Brouillet, Urbatsch & R.P. Roberts, western USA.

XVI. Tribe Anthemideae Cass. (1819).

Tribe Cotuleae Benth. (1868).

Tribe Ursinieae H. Rob. & Brettell (1973).

Ch. Oberprieler, R. Vogt and L.E. Watson

Annual, biennial or perennial, hapaxanthic or pollacanthic herbs, subshrubs or shrubs, rarely spinescent. Indumentum rarely absent, usually of short biseriate glandular hairs (glands) and uniseriate basifixed, T-shaped medifixed or stellate hairs. Leaves usually alternate, rarely opposite or basally crowded, generally variously dissected, dentate, serrate, lobed, pinnatifid to pinnatisect, rarely entire, sometimes vermiform, rarely succulent. Capitula solitary or in lax to dense corymbs, panicles or racemes, or in glomerules, often pedunculate, rarely sessile, heterogamous and radiate or disciform, or homogamous and discoid. Involucres often hemispherical, sometimes obconical, cylindrical or urceolate. Phyllaries in 2–7 rows, imbricate, sometimes with one to several resin canals, almost always with scarious margins and apex. Receptacles flat, meniscoid, hemispherical, conical or narrowly conical, glabrous or hairy, paleate or epaleate. Paleae persistent or caducous, flat or canaliculate, sometimes with a central resin canal. Ray florets female and fertile or sterile, or neuter; limb white, white with a yellow base, yellow, or rarely blue-violet, pinkish or reddish. Outer disc florets (in disciform capitula) in one to several rows, female, usually fertile; corolla tubular and with 0–5 apical lobes, usually yellow, rarely absent. Central disc florets hermaphrodite or functionally male; corolla tubular or funnel-shaped, actinomorphic, rarely slightly zygomorphic, yellow or rarely whitish or reddish, with 3–6 apical lobes; lobes rarely with central resin sacs. Stamens equal in number to and alternating with the corolla lobes; upper part of the filament with cells with thickened walls, forming a split cylindrical or balusterform anther collar (filament collar); anthers usually with an ovate, triangular or subtriangular to subulate apical appendage, generally rounded, rarely shortly tailed at the base; pollen usually spiny, sometimes rugose or smooth, tricolporate (hexa-panto-colporate in *Adenanthellum*); exine ecaveate (caveate in *Ursinia*), with a thick foot layer, large basal columellae (lacking or only occasionally or vestigially found in *Ursinia*) with distal branches (branches complex and interwoven in *Artemisia* and *Crossostephium*), and a double

tectum formed by infratectal columellae of uniform length (Vezey et al. 1994). Style with a slender or bulbous base, usually situated on a cup-shaped stylopodium (nectary); style branches usually free, sometimes (in functionally male florets) fused, usually linear, rarely elliptic or ovate in outline, apically truncate, penicillate, and usually with two parallel, sometimes curved, papillate stigmatic areas on their adaxial surfaces. Achenes various in form, often obovoid, obconical or cylindrical in outline and circular, triquetrous or angled in cross-section, sometimes dorsiventrally flattened and elliptic or rhombic in cross-section, usually with more or less prominent ribs, sometimes even winged, sometimes without ribs; apex ecoronate and marginally rounded or truncate, or with an entire to lacerate (sometimes adaxially more developed) corona, or with a corona ('pappus') formed by individual, sometimes basally fused, scales or bristle-like scales, or with an (usually adaxial) auricle; pericarp without a carbonised layer, from extremely thin and delicate to thick and sclerified, often with resin ducts or sacs and specialised, myxogenic epidermal cells. Embryo sac development monosporic or tetrasporic, rarely bisporic. Base chromosome numbers generally $x = 9$, sometimes $x = 10$, rarely $x = 6$, 7, 8, 11, 13 or 17.

Comprising 111 genera with c. 1,800 species, distributed worldwide (extratropical) but with main concentrations in central Asia, the Mediterranean region and southern Africa.

Members of the tribe are well known as aromatic plants, and some are utilised for their pharmaceutical and/or pesticidal value. Three main classes of chemical substances are of considerable systematic significance: acetylenes (Greger 1977), sesquiterpene lactones (Seaman 1982) and flavonoids (Bohm and Stuessy 2001). All recent molecular studies based on coding and/or non-coding sequences from the chloroplast genome (Kim and Jansen 1995; Bayer and Starr 1998; Panero and Funk 2002) indicate a more or less well-supported sister-group relationship of Anthemideae with Astereae. This is also supported by a cladistic study of the family based on morphological and phytochemical characters by Karis (1993b). The circumscription of Anthemideae remains relatively unchanged since early, artificial classification systems (Lessing 1832; Hoffmann 1894; Bentham 1873a) and more recent ones (Poljakov 1967; Reitbrecht 1974; Heywood and Humphries 1977; Bremer and Humphries 1993), with *Cotula* and *Ursinia* included in the tribe despite considerable debate (Bentham 1873a; Robinson and Brettell 1973c; Heywood and Humphries 1977; Jeffrey 1978; Gadek et al. 1989; Bruhl and Quinn 1990, 1991; Bremer and Humphries 1993; Kim and Jansen 1995). The tribe was monographed on the basis of a mostly morphological phylogeny (Bremer and Humphries 1993), but there is little congruence with any of the previous classifications. To complicate matters further, molecular phylogenies for the tribe as a whole (Watson et al. 2000) are largely incongruent with either the morphological phylogeny (Bremer and Humphries 1993) or the previously proposed classifications (Poljakov 1967; Reitbrecht 1974; Heywood and Humphries 1977). This is also true for molecular phylogenies for the Mediterranean genera alone (Francisco-Ortega et al. 1997; Oberprieler and Vogt 2000; Oberprieler 2002, 2004a, b, 2005). There is little support for monophyly of most of the subtribes of Bremer and Humphries (1993), and there is substantial disagreement with previously proposed sister-group relationships of genera and subtribes. A molecular phylogeny for the tribe based on the chloroplast gene *ndh*F (Watson et al. 2000) revealed a basal grade of Southern Hemisphere genera which are sister to a mostly Northern Hemisphere clade. The latter consists of a basal grade of predominantly Asian genera, which includes generic assemblages related to *Artemisia* and *Chrysanthemum* (i.e. the former *Dendranthema*), sister to a monophyletic group of Mediterranean and more widespread, northwestern Eurasian genera. This monophyletic clade was also found to be characterised by a large, 15-bp deletion in nrDNA ITS (Francisco-Ortega et al. 1997; Oberprieler and Vogt 2000; Oberprieler 2002, 2004a, b, 2005). A strongly supported clade within this monophyletic group included a large number of Mediterranean and Macaronesian genera of the tribe (e.g. genera allied to *Argyranthemum*, *Chamaemelum* and *Leucanthemum*). In addition to findings of *ndh*F (Watson et al. 2000) and ITS studies (Francisco-Ortega et al. 1997), this group is also characterised by an apomorphic 5-bp deletion in the *trn*L-*trn*F intergenic spacer of the chloroplast genome (Oberprieler and Vogt 2000). Molecular studies also have helped to resolve generic delimitation and circumscription in several groups of the tribe, and have led to their formal recognition. Oberprieler (2001), using ITS data, provided evidence that *Anthemis* subg. *Anthemis* is more closely related to *Tripleuro-*

spermum than to *A.* subg. *Cota*, which resulted in the resurrection of *Cota* as an independent genus. Oberprieler (2002) also clarified the delimitation of *Chamaemelum* and *Cladanthus* which was formalised with new combinations (Oberprieler and Vogt 2002). Additional studies by Kornkven et al. (1998, 1999) and Torrell et al. (1999) and (more comprehensively) of Watson et al. (2002) and Vallès et al. (2003) have shown that generic delimitation in subtribe *Artemisiinae* sensu Bremer and Humphries (1993) is problematic. For this treatment, we followed the results of the cited papers, insofar as the segregate genus *Seriphidium* is merged with *Artemisia*. In addition, the generic independence of several other small genera of this subtribe (i.e. *Sphaeromeria*, *Neopallasia*, *Crossostephium*, *Filifolium*) is questionable (Watson et al. 2002). However, we refrained from merging them into *Artemisia* until a more complete sampling of molecular and morphological data is available. Accordingly, due to the lack of a comprehensive study for *Tanacetum*, it is presently treated in the broad sense of Bremer and Humphries (1993). Further investigations may lead to considerable rearrangements in and around this polyphyletic genus. Clearly, the subtribal classification proposed by Bremer and Humphries (1993) needs to be revised on the basis of expanded molecular and more detailed morphological data. In the present treatment, therefore, genera are arranged in a linear manner according to the results of Watson et al. (2000), i.e. in a primarily geographic representation of the members of the tribe, beginning with the southern African representatives, followed by the central and eastern Asian ones, and ending with the Mediterranean genera. Within these four major groups (three grades and the Mediterranean clade), genera are arranged alphabetically. However, to retain as much information as possible concerning several generic assemblages, monophyletic groups of genera were retained and named after one of their members whenever possible.

Key to the Genera

1. Receptacle distinctly paleate with paleae subtending florets (in *Anthemis*, rarely with the marginal part of receptacle epaleate; in *Schistostephium* and *Tanacetum*, rarely with the central part of receptacle epaleate) 2
– Receptacle completely epaleate (sometimes pilose or hirsute) or capitula few-flowered and presence of paleae unclear 51
2. Ray florets present 3
– Ray florets absent 28
3. Limb of ray florets yellow or white with a yellow base, rarely abaxially reddish 4
– Rays white (without a yellow base) or pink to reddish on both sides 13
4. Phyllaries in 2 unequal rows, the outer scarious with very wide margins, the inner connate and densely villous; paleae densely villous **967. *Eriocephalus***
– Phyllaries imbricate and subequal, not in 2 unequal rows; paleae glabrous or sparsely villous 5
5. Achenes ± circular or quadrangular in cross-section, with or without distinct ribs 6
– Achenes dorsiventrally flattened, with prominent lateral ribs or wings 11
6. Apex of achene with a corona of 5–10 large ovate or circular scales and sometimes 5 additional subulate scales **989. *Ursinia***
– Apex of achene with a shallow corona, an auricle, or rarely a few small scales, or ecoronate 7
7. Achenes of disc florets with 5 distinct ribs 8
– Achenes of disc florets with c. 10 distinct, often tuberculate ribs, or without distinct ribs 9
8. Leaves linear, entire or apically few-lobed (southern Africa) **989. *Ursinia***
– Leaves elliptical or obovate-spathulate, serrate (W Mediterranean) **1060. *Lepidophorum***
9. Indumentum of stellate hairs **1054. *Mecomischus***
– Plants glabrous or with an indumentum of basifixed or medifixed hairs 10
10. Corolla of disc florets basally saccate, adaxially clasping the upper half or more of achene; indumentum of basifixed hairs **1053. *Cladanthus***
– Corolla of disc florets basally not saccate, not clasping the apex of achene; indumentum of medifixed hairs or lacking **1033. *Anthemis***
11. Achenes with distinct lateral wings, without additional ribs **1029. *Anacyclus***
– Achenes without distinct lateral wings, if winged, then wings only narrow and achenes with additional ribs 12
12. Achenes with 2 lateral ribs and rarely with an additional adaxial rib; pericarp rather thin **1028. *Achillea***
– Achenes with 2 lateral ribs or narrow wings and 3–10 additional ribs on each face; pericarp rather thick **1034. *Cota***
13. Achenes dorsiventrally flattened, with prominent lateral ribs or wings 14
– Achenes ± circular or quadrangular in cross-section, with or without distinct ribs 18
14. Phyllaries in 2 unequal rows, the outer scarious with very wide margins, the inner connate and densely villous; paleae densely villous **967. *Eriocephalus***
– Phyllaries imbricate and subequal, not in 2 unequal rows; paleae glabrous or sparsely villous 15
15. Achenes with distinct lateral wings, without additional ribs 16
– Achenes without distinct lateral wings, if winged, then wings only narrow and achenes with additional ribs 17
16. Leaves vermiform; corolla of disc florets basally deeply and equally saccate, clasping apex of achene both adaxially and abaxially **1031. *Leucocyclus***

– Leaves pinnatisect; corolla of disc florets basally only slightly saccate, clasping apex of achene only adaxially **1029. *Anacyclus***
17. Achenes with 2 lateral ribs and rarely with an additional adaxial rib; pericarp rather thin **1028. *Achillea***
– Achenes with 2 lateral ribs or narrow wings and 3–10 additional ribs on each face; pericarp rather thick **1034. *Cota***
18. Phyllaries in 2 unequal rows, the outer scarious with very wide margins, the inner connate and densely villous; paleae densely villous **967. *Eriocephalus***
– Phyllaries imbricate and subequal, not in 2 unequal rows; paleae glabrous or sparsely villous 19
19. Achenes conspicuously villous **972. *Lasiospermum***
– Achenes glabrous, sometimes papillose 20
20. Indumentum of stellate hairs **1054. *Mecomischus***
– Plants glabrous or indumentum of basifixed or medifixed hairs 21
21. Phyllaries in 1–2 rows, readily deciduous at maturity; paleae subulate, readily deciduous; apex of achenes broadened into a bowl-shaped corona with radiating teeth or lobes; achenes persistent at maturity **1033. *Anthemis***
– Phyllaries imbricate, not readily deciduous at maturity; paleae persistent or readily deciduous; apex of achenes without a bowl-shaped corona; achenes deciduous or persistent at maturity 22
22. Apex of achenes with 5–10 large, obovate scales and sometimes 5 additional subulate scales **989. *Ursinia***
– Apex of achenes with a shallow corona, an auricle, or sometimes small scales, or ecoronate 23
23. Achenes without distinct ribs, sometimes 3–4-angled or 3–4-ribbed 24
– Achenes with 5–20 distinct ribs 26
24. Anthers caudate **974. *Osmitopsis***
– Anthers ecaudate 25
25. Pericarp very thin, formed only by mucilage cells in longitudinal rows; corolla of disc florets basally saccate, laterally clasping the apex of achene **1052. *Chamaemelum***
– Pericarp rather thick, with scattered mucilage cells; corolla of disc florets basally not saccate **1033. *Anthemis***
26. Achenes with 5 ribs **1035. *Gonospermum***
– Achenes with (6–)10 or more ribs 27
27. Shrubs with opposite (rarely alternate) leaves; achenes with 10–18 ribs; pericarp without myxogenic cells; anthers with polarised endothecial tissue (southern Africa) **984. *Eumorphia***
– Herbs or subshrubs with alternate leaves; achenes with 10 smooth or tuberculate ribs; pericarp with myxogenic cells; anthers with unpolarised endothecial tissue (N Hemisphere) **1033. *Anthemis***
28. Pericarp with resin sacs or ducts 29
– Pericarp without resin sacs or ducts (but often with glandular hairs) 34
29. Achenes densely villous **972. *Lasiospermum***
– Achenes glabrous or with glandular hairs only 30
30. Achenes with 2 lateral and 0–1 adaxial ribs; pericarp with a single resin sac or with 5 longitudinal resin canals 31
– Achenes with 4–18 ribs (sometimes with 2 more distinct lateral ribs and 3 additional inconspicuous ones); pericarp with longitudinal rows of resin sacs in ribs or scattered epidermal resin sacs 32
31. Annual herbs; pericarp with a single resin sac apically in the adaxial rib **1069. *Lonas***
– Perennial herbs and shrubs; pericarp with 5 longitudinal resin canals along vascular bundles **1028. *Achillea***
32. Perennial herbs; pericarp with scattered epidermal resin sacs; indumentum of basifixed hairs **1030. *Heliocauta***
– Shrubs or shrublets; pericarp with longitudinal rows of resin sacs in ribs; indumentum of stellate hairs or absent 33
33. Achenes with a corona of basally united, fimbriate scales; anthers with an apical appendage without a resin sac **963. *Hymenolepis***
– Achenes apically rounded or with a short, thickened rim (sometimes with a pseudo-pappus of long-stalked glands); anthers with an apical appendage with or without a resin sac **962. *Athanasia***
34. Phyllaries in 2 unequal rows, the outer scarious with very wide margins, the inner connate and densely villous; paleae densely villous **967. *Eriocephalus***
– Phyllaries imbricate and subequal, not in 2 unequal rows; paleae glabrous or sparsely villous 35
35. Apex of achenes with a corona of 5–10 large, obovate scales and sometimes 5 additional subulate scales **989. *Ursinia***
– Apex of achenes with a shallow corona, an auricle, or of small scales, or ecoronate 36
36. Corolla of disc florets 4-lobed; central part of receptacle epaleate **987. *Schistostephium***
– Corolla of disc florets 5-lobed; receptacle paleate throughout 37
37. Achenes dorsiventrally flattened 38
– Achenes circular or quadrangular in cross-section 41
38. Achenes with 2 lateral and 1 adaxial, flimsy ridges; pericarp consisting only of large myxogenic cells in longitudinal rows **1055. *Rhetinolepis***
– Achenes with prominent lateral wings or ribs; pericarp with scattered myxogenic cells 39
39. Achenes with distinct lateral wings, without additional ribs **1029. *Anacyclus***
– Achenes without distinct lateral wings, if winged, then wings only narrow and achenes with additional ribs 40
40. Achenes with 2 lateral ribs and rarely with an additional adaxial rib; pericarp rather thin **1028. *Achillea***
– Achenes with 2 lateral ribs or narrow wings and 3–10 additional ribs on each face; pericarp rather thick **1034. *Cota***
41. Corolla of disc florets basally saccate and clasping apex or more of achene; achenes ecoronate 42
– Corolla of disc florets basally not saccate, not clasping apex of achene; achene coronate or ecoronate 44
42. Pericarp formed only of longitudinal rows of myxogenic cells; achenes only with 2 lateral and 1 adaxial, flimsy ridges; indumentum absent or of basifixed hairs **1052. *Chamaemelum***
– Pericarp without or with scattered myxogenic cells; achenes 3–5-angled, with more conspicuous ribs; indumentum absent or of basifixed or medifixed hairs 43

43. Corolla of disc florets clasping only apex of achene; indumentum absent or of medifixed hairs **1056. *Santolina***
– Corolla of disc florets clasping upper half of achene (laterally even more); basal part of floret persistent on achene; indumentum densely sericeous, greyish-white, of basifixed hairs **1032. *Otanthus***
44. Capitula in a long panicle **999. *Artemisia***
– Capitula solitary or in lax to dense corymbs 45
45. Leaves opposite **985. *Gymnopentzia***
– Leaves alternate 46
46. Anthers caudate (southern Africa) **971. *Inulanthera***
– Anthers not caudate (N Hemisphere) 47
47. Indumentum exclusively of basifixed hairs 48
– Indumentum absent or of medifixed hairs 49
48. Stems sparsely branched and leafy; capitula in dense corymbs **1013. *Handelia***
– Stems loosely branched and almost leafless; capitula in lax corymbs **1017. *Sclerorhachis***
49. Capitula in dense corymbs **1035. *Gonospermum***
– Capitula solitary or in lax corymbs 50
50. Only marginal florets subtended by paleae; leaves pinnate with linear and pungent segments; plant suffruticose **1037. *Tanacetum*** (*T. paleaceum*)
– All florets or at least the central ones subtended by paleae; leaves variously divided, but never with pungent segments; annuals or perennials **1033. *Anthemis***
51. Ray florets present 52
– Ray florets absent 122
52. Ray florets yellow or white with a yellow base, rarely abaxially reddish 53
– Rays florets white (without a yellow base) or pink, reddish, bluish-violet on both sides 74
53. Corolla of disc florets apically 4-lobed 54
– Corolla of disc florets apically 5-lobed 55
54. Achenes tetragonal in cross-section, apex with minute scales **970. *Inezia***
– Achenes dorsiventrally flattened, with 2 distinct lateral, wing-like ribs, apex ecoronate (rays not true ray florets but outer disc florets with one corolla lobe expanded to a limb) **964. *Cotula***
55. Pericarp with resin sacs or ducts 56
– Pericarp without resin sacs or ducts 62
56. Resin sacs or ducts in ribs of achene 57
– Resin ducts vallecular between ribs of achene 58
57. Shrubs or shrublets; achenes circular in cross-section, with 10–18 rounded ribs, some of them with resin sacs **986. *Phymaspermum***
– Annual herb; achenes dorsiventrally flattened, with 2 lateral broad wings, both with resin ducts **975. *Adenoglossa***
58. Adaxial ribs of achenes basally fused into a ± distinct callus 59
– Ribs of achenes basally not fused into a callus 60
59. Achenes with an adaxial auricle as long as or even longer than corolla **1064. *Glossopappus***
– Achenes with an adaxial auricle much shorter than corolla **1063. *Coleostephus***
60. Limb of ray florets white with a yellow base **1066. *Mauranthemum***
– Limb of ray florets yellow, sometimes becoming red 61
61. Limb of ray florets golden yellow **1062. *Chrysanthoglossum***
– Limb of ray florets pale yellow **1068. *Rhodanthemum*** (*Rh. maresii*)
62. Achenes of ray florets triquetrous in cross-section, winged; achenes of disc florets laterally flattened and adaxially and abaxially winged or sometimes terete to prismatic 63
– Achenes of ray florets similar to achenes of disc florets; all achenes circular (or sometimes triangular) in cross-section, always without wings 66
63. Shrubs or shrublets **1048. *Argyranthemum***
– Annual herbs 64
64. Indumentum of glandular hairs; wings of achenes with apical spines **1050. *Heteranthemis***
– Indumentum absent or of basifixed, eglandular hairs; wings of achenes (if present) without apical spines 65
65. Corolla of disc florets red; achenes of disc florets laterally flattened and adaxially and abaxially winged **1051. *Ismelia***
– Corolla of disc florets yellow; achenes of disc florets prismatic with a narrow adaxial wing or terete and inconspicuously ribbed **1049. *Glebionis***
66. Annual herbs 67
– Shrubs, subshrubs, or perennial herbs 70
67. Leaves 3(–5)-lobed **998. *Tridactylina***
– Leaves variously pinnatisect 68
68. Achenes 3-angled; ray florets fertile; indumentum absent **1058. *Endopappus***
– Achenes with 5–7 ribs; ray florets sterile; indumentum of medifixed hairs 69
69. Limb of ray florets yellow; achenes of disc florets ecoronate, with 1 adaxial, 2 lateral and 2 abaxial ribs **1043. *Prolongoa***
– Limb of ray florets white with a yellow base; achenes of disc florets with a scarious corona, and with 5–7 ribs **1041. *Hymenostemma***
70. Achenes densely hairy **1011. *Trichanthemis***
– Achenes glabrous or with sessile glands 71
71. Achenes without myxogenic cells **1037. *Tanacetum***
– Achenes with myxogenic cells on ribs 72
72. Apex of achenes with scarious corona **1042. *Leucanthemopsis***
– Apex of achenes ecoronate, marginally rounded 73
73. Basally strongly woody shrublets with few-lobed leaves, lobes linear **993. *Brachanthemum***
– Perennial herbs or subshrubs; leaves with rather broad lobes, rarely entire or serrate **994. *Chrysanthemum***
74. Annual herbs 75
– Shrubs, shrublets, or perennial herbs 95
75. Corolla of disc florets (3–)4-lobed 76
– Corolla of disc florets 5-lobed 80
76. Ray florets stalked **964. *Cotula***
– Ray florets sessile 77
77. Capitula very small (2–5 mm); phyllaries in 1–2 rows; leaves 3–5-lobed **1036. *Nananthea***
– Capitula larger; phyllaries in 2–5 rows; leaves variously pinnatisect 78
78. Achenes of central disc florets without myxogenic cells **981. *Oncosiphon***
– Achenes of central disc florets with myxogenic cells 79
79. Achenes with 5, mainly adaxial ribs **1044. *Matricaria***
– Achenes inconspicuously 3-ribbed or without distinct ribs **977. *Foveolina***
80. Achenes with resin sacs or ducts 81

– Achenes without resin sacs or ducts (but often with glandular hairs) 86
81. Achenes with 10 ribs and 10 longitudinal, vallecular resin ducts between ribs **1066. *Mauranthemum***
– Achenes without or with 3–5 ribs, with apical resin sacs or resin ducts in ribs 82
82. Achenes with (1–)2(3–5) abaxial-apical resin sacs, and 2 lateral and 1 adaxial distinct ribs **1038. *Tripleurospermum***
– Achenes with resin canals or resin sacs in ribs 83
83. Achenes somewhat dorsiventrally flattened and with 2 lateral, inconspicuous ribs; corolla lobes with central resin sacs **1047. *Aaronsohnia***
– Achenes with 3 or more ± distinct ribs, sometimes slightly flattened; corolla lobes without or sometimes with central resin sacs 84
84. Achenes of ray florets laterally winged, wings with apical teeth; apex with an adaxial auricle **1057. *Daveaua***
– Achenes of ray florets terete or sometimes flattened but not winged, variously ribbed 85
85. Achenes with 5 adaxial-lateral ribs and a small corona or auricle; lateral ribs with resin canals **1044. *Matricaria***
– Achenes with 3 adaxial-lateral, rounded ribs and 2 abaxial weaker ribs; 3–5 resin canals or apical resin sacs in the ribs; apex of achene with a corona of 7–10 obovate scales **1059. *Heteromera***
86. Achenes actinomorphic, with 5–10 equidistantly arranged, equal ribs 87
– Achenes without ribs or with unequally arranged, ± unequal ribs 90
87. Ray florets yellowish-white; leaves 3–5-lobed **998. *Tridactylina***
– Ray florets white; leaves variously pinnatisect 88
88. Achenes with myxogenic cells scattered over the pericarp; ribs rather inconspicuous; apex with an erose-denticulate, sometimes unilateral corona **1033. *Anthemis***
– Achenes with myxogenic cells on the ridges of the 10 distinct ribs, ecoronate 89
89. Indumentum of medifixed hairs; phyllaries with brown scarious margins **1040. *Castrilanthemum***
– Indumentum absent or of basifixed hairs; phyllaries with pale to light brown scarious margins **1070. *Nivellea***
90. Achenes with 1 adaxial and 2 lateral thick ribs and with 2–3 adaxial weaker ribs; apex with an adaxial stiff auricle **1071. *Otospermum***
– Achenes with mainly adaxial-lateral ribs or with inconspicuous ribs; apex with an entire or scaly corona, or a scarious auricle 91
91. Pericarp and corona white and spongy, abaxially thin (southern Africa) **977. *Foveolina***
– Pericarp not white and spongy; corona scarious (N Hemisphere) 92
92. Achenes laterally pilose; apex of disc achenes with a fimbriate whitish corona; apex of ray achenes with auricle **1022. *Microcephala***
– Achenes glabrous, but often with sessile glands; apex of achenes various 93
93. Achenes somewhat dorsiventrally flattened and with 2 lateral weak ribs; corolla lobes with central resin sacs **1047. *Aaronsohnia***
– Achenes with 3 or more adaxial and lateral, distinct ribs; corolla lobes with or without central resin sacs 94
94. Achenes with 5 adaxial-lateral ribs; apex with an auricle or a small corona **1044. *Matricaria***
– Achenes with 3 adaxial-lateral ribs; apex with a stiff corona **1058. *Endopappus***
95. Corolla of disc florets (3–)4-lobed 96
– Corolla of disc florets 5-lobed 100
96. Ray florets stalked **964. *Cotula***
– Ray florets sessile 97
97. Leaves entire, lanceolate to linear (ericoid) 98
– Leaves lobed or pinnatisect 99
98. Receptacle glabrous; pericarp without myxogenic cells **970. *Inezia***
– Receptacle hairy; pericarp with myxogenic cells in rounded, scattered groups **988. *Thaminophyllum***
99. Receptacle hairy; leaves with few oblong to rounded, mucronate lobes **973. *Lidbeckia***
– Receptacle glabrous; leaves 1–2-pinnatisect **968. *Hilliardia***
100. Apex of achenes with a corona of 4–12 linear to obovate-oblong scales at least half as long as the corolla, or with many (25–50) bristle-like scales as long as or longer than the corolla 101
– Apex of achenes marginally rounded, or with an auricle, an entire corona, or a corona of short scales 103
101. Apex of achenes with 25–50 bristle-like scales equalling or exceeding the corolla in length **1007. *Allardia***
– Apex of achenes with a corona of 4–12 linear to obovate-oblong scales half as long as or equalling the corolla in length 102
102. Pericarp densely hairy **1011. *Trichanthemis***
– Pericarp glabrous **1010. *Richteria***
103. Achenes with resin sacs or canals 104
– Achenes without resin sacs or canals (but often with glandular hairs) 110
104. Achenes with 5 or c. 10 longitudinal, vallecular resin ducts between ribs 105
– Achenes with resin ducts or sacs in ribs, or with abaxial-apical resin sacs 107
105. Achenes c. 1 mm long **1066. *Mauranthemum***
– Achenes more than 1 mm long 106
106. Leaves entire, dentate-serrate, or up to 3-pinnatisect, sessile; florets not becoming reddish at maturity; achenes with c. 10 rounded ribs **1065. *Leucanthemum***
– Leaves 1–3-pinnatisect, long-petiolate; florets becoming reddish at maturity; achenes with 5 or c. 10 protruding, often wing-like ribs **1068. *Rhodanthemum***
107. Achenes circular or somewhat compressed in cross-section, with 10–18 distinct ribs 108
– Achenes triquetrous or flattened in cross-section, with 2 lateral and 1 adaxial ribs 109
108. Pericarp with myxogenic cells; achenes with 10–18 rounded ribs; resin sacs only in some of the ribs; shrubs or shrublets **986. *Phymaspermum***
– Pericarp without myxogenic cells; achenes with 10 ribs, all of them with longitudinal resin canals; perennial herb **961. *Adenanthellum***
109. Achenes dorsiventrally flattened, laterally winged, with 2 lateral resin canals **978. *Leucoptera***
– Achenes triquetrous, with 2 lateral and 1 adaxial ribs, laterally not winged, with (1–)2(–3–5) abaxial-apical resin sacs **1038. *Tripleurospermum***

110. Achenes of ray florets triquetrous, winged; achenes of disc florets laterally compressed and 2-winged, sometimes terete **1048. *Argyranthemum***
– Achenes of ray florets and disc florets subequal, not winged, terete 111
111. Pericarp with myxogenic cells 112
– Pericarp without myxogenic cells 116
112. Apex of achene with an entire or scaly corona 113
– Apex of achene marginally rounded 115
113. Indumentum of medifixed hairs; apex of achene with an entire, flimsy corona **1042. *Leucanthemopsis***
– Indumentum of basifixed hairs; apex of achene with an oblique, entire corona or with a corona of 2–6 scales 114
114. Apex of achene with a corona of 4–6 separate, mainly abaxial, subulate scales unequal in length (eastern Asia) **1024. *Opisthopappus***
– Apex of achene with an oblique, adaxially longer corona, or of one large adaxial and one smaller abaxial scale (South Africa) **976. *Cymbopappus***
115. Basally strongly woody shrublets; leaves few-lobed with linear lobes; involucres hemispherical to cylindrical, up to 7 mm in diameter; capitula with 1–10 ray florets; limb of ray florets up to 8 mm long, broadly elliptical to elliptical **993. *Brachanthemum***
– Herbs or subshrubs; leaves entire, serrate, or with rather broad lobes; involucres meniscoid, (6–)8–20(–40) mm in diameter; capitula with more than 10 ray florets; limb of ray florets 8–60 mm long, elliptical to linear **994. *Chrysanthemum***
116. Leaves opposite 117
– Leaves alternate 118
117. Shrubs with entire to few-lobed leaves (southern Africa) **984. *Eumorphia*** (*E. prostrata*)
– Creeping, suffruticose perennial with serrate-pinnatifid leaves (Iberian peninsula) **1045. *Phalacrocarpum***
118. Apex of achenes with an entire, toothed, lobed, or scaly, acute corona; receptacle glabrous 119
– Apex of achenes ecoronate, marginally rounded, or with a rounded rim; receptacle glabrous or sparsely hairy 120
119. Glabrous shrub; leaves serrate, crowded at the end of the woody branches **1023. *Nipponanthemum***
– Perennial herbs or basally woody subshrubs; indumentum absent or present; leaves variously pinnatisect **1037. *Tanacetum***
120. Ray florets sterile; receptacle glabrous **1021. *Leucanthemella***
– Ray florets fertile; receptacle glabrous or sparsely hairy 121
121. Leaves entire, narrowly linear; receptacle sparsely hairy **996. *Hulteniella***
– Leaves variously lobed or dissected; receptacle glabrous **992. *Arctanthemum***
122. Achenes with dark vallecular resin canals between pale ribs and with myxogenic cells on the ribs 123
– Achenes without vallecular resin canals, with or without ribs and myxogenic cells 125
123. Annual herb **1061. *Chlamydophora***
– Perennial herbs or subshrubs 124
124. Adaxial ribs of achenes basally fused into a ± distinct callus **1067. *Plagius***
– Achene base without an adaxial callus **1065. *Leucanthemum***
125. Disc florets apically (3–)4-lobed 126
– Disc florets apically 5(–6)-lobed 139
126. Achenes dorsiventrally flattened with 2 lateral ± distinct ribs or wings 127
– Achenes terete or only slightly dorsiventrally flattened, sometimes triquetrous 130
127. Shrublets or subshrubs; capitula in lax to dense corymbs (rarely solitary) **987. *Schistostephium***
– Annual or perennial herbs; capitula solitary 128
128. Capitula sessile in leaf axils; outer disc florets without corolla and with style persistent and spinescent in fruit **966. *Soliva***
– Capitula pedunculate; outer disc florets with corolla and with style not persistent in fruit 129
129. Outer disc florets with corolla inflated and with a hollow space between the outer and the inner epidermis; central disc florets female-sterile **965. *Leptinella***
– Outer disc florets with corolla not inflated; central disc florets fertile **964. *Cotula***
130. Outer disc florets with corolla inflated and with a hollow space between the outer and the inner epidermis **965. *Leptinella***
– Outer disc florets with corolla not inflated 131
131. Perennials 132
– Annuals 133
132. Capitula discoid; all florets hermaphrodite; achenes with 5 distinct ribs and an apical corona of scales; pollen spiny; indumentum of basifixed hairs **1014. *Lepidolopsis***
– Capitula disciform, with an outer row of female florets; achenes without conspicuous ribs, apically rounded; pollen smooth; indumentum of medifixed hairs **1001. *Filifolium***
133. Capitula disciform, with an outer row of female florets 134
– Capitula discoid; all florets hermaphrodite 136
134. Delicate, somewhat succulent herb; capitula smaller than 5 mm in diameter **1036. *Nananthea***
– Habit variable; capitula usually larger than 5 mm in diameter 135
135. Pericarp either white and spongy with 1 adaxial and 2 lateral weak ribs, abaxially thin, or achenes almost terete and thin-walled all around **97. *Foveolina***
– Pericarp not white and spongy; achenes with 5 adaxial-lateral ribs **1044. *Matricaria***
136. Achenes without myxogenic cells **981. *Oncosiphon***
– Achenes with myxogenic cells 137
137. Achenes with an apical corona covered with myxogenic cells **980. *Myxopappus***
– Achenes ecoronate or with a corona not covered with myxogenic cells 138
138. Achenes with myxogenic cells on the abaxial surface (southern Africa) **977. *Foveolina***
– Achenes with myxogenic cells on all sides (northern Africa, Near East) **1039. *Brocchia***
139. Capitula disciform, with an outer row of female florets 140
– Capitula discoid; all florets hermaphrodite 163
140. Pollen spiny (sometimes with short spines only) 141
– Pollen smooth 150
141. Achenes triquetrous with 1 adaxial and 2 lateral, thick ribs and sometimes with 2 abaxial weaker ribs, abaxi-

ally and apically with 2 distinct (sometimes 1 or 3–5) resin sacs **1038. *Tripleurospermum***
– Achenes various, not with abaxial-apical resin sacs 142
142. Annuals 143
– Perennial herbs, subshrubs or shrubs 145
143. Achenes somewhat dorsiventrally flattened and with 2 lateral weak ribs **1047. *Aaronsohnia***
– Achenes circular in cross-section 144
144. Pericarp either white and spongy with 1 adaxial and 2 lateral weak ribs, abaxially thin, or achenes almost terete and thin-walled all around **977. *Foveolina***
– Pericarp not white and spongy; achenes with 5 adaxial-lateral ribs **1044. *Matricaria***
145. Achenes dorsiventrally flattened, with or without lateral wings **969. *Hippia***
– Achenes terete, without wings 146
146. Achenes sparsely to densely hairy; receptacle hairy **1006. *Artemisiella***
– Achenes glabrous; receptacle glabrous 147
147. Style branches brownish; corolla lobes erect; pericarp without myxogenic cells **997. *Phaeostigma***
– Style branches yellowish; corolla lobes spreading; pericarp with or without myxogenic cells 148
148. Pericarp with myxogenic cells **990. *Ajania***
– Pericarp without myxogenic cells 149
149. Achene apex marginally rounded **990. *Ajania***
– Achene apex with a short to well-developed, entire to dentate, acute rim (or sometimes with an adaxial auricle) **1037. *Tanacetum***
150. Achene apex with a corona or with small scales **1000. *Crossostephium***
– Achene apex marginally rounded, ecoronate 151
151. Capitula arranged in lax to dense corymbs, generally erect 152
– Capitula arranged in long panicles, rarely in racemes or spiciform or subglobose synflorescences, sometimes pendent 154
152. Annual herbs **991. *Ajaniopsis***
– Perennial herbs 153
153. Central disc florets functionally male, compressed into a resinous mass; achenes obliquely obovoid, always without ribs (E Asia) **1001. *Filifolium***
– Central disc florets hermaphrodite; achenes rarely obovoid, usually obovoid-oblong to cylindrical and with 3–5 ribs (North America) **1005. *Sphaeromeria***
154. Corolla lobes glabrous 155
– Corolla lobes hairy 157
155. Capitula 30–50-flowered **1005. *Sphaeromeria***
– Capitula usually with fewer than 30 florets 156
156. Central disc florets of two kinds; outer perfect, inner completely sterile with reduced ovaries; annual or biennial herbs **1003. *Neopallasia***
– Central disc florets all perfect or all female-sterile with reduced ovaries; annuals, biennials, and perennials **999. *Artemisia***
157. Outer female florets without corolla; indumentum of stellate hairs **1002. *Mausolea***
– Outer female florets with corolla; indumentum absent or of basifixed, medifixed, or stellate hairs 158
158. Indumentum of stellate hairs **1019. *Kaschgaria***
– Indumentum absent or of basifixed or medifixed hairs 159
159. Achenes hairy 160
– Achenes glabrous (but with glands) 161
160. Shrublet with older branches forming long spines **1004. *Picrothamnus***
– Plant without spinescent branches **999. *Artemisia***
161. Capitula 30–50-flowered **1005. *Sphaeromeria***
– Capitula usually with fewer than 30 florets 162
162. Capitula densely congested into glomerules arranged in a spike, or rarely capitula solitary in interrupted, partly congested spikes; marginal female florets in the axils of canaliculate involucral bracts **1027. *Turaniphytum***
– Capitula usually forming a long panicle, sometimes much reduced and racemose, spiciform or subglobose; involucral bracts not canaliculate **999. *Artemisia***
163. Achenes triquetrous with 1 adaxial and 2 lateral, thick ribs and sometimes with 2 abaxial weaker ribs, abaxially and apically with 2 distinct (sometimes 1 or 3–5) resin sacs **1038. *Tripleurospermum***
– Achenes various, not with abaxial-apical resin sacs 164
164. Capitula in panicles, in racemes, or in spiciform to subglobose synflorescences (densely aggregate at the stems in *Marasmodes*) 165
– Capitula solitary or in lax to dense corymbs, sometimes in a pseudo-umbel 167
165. Apex of achenes marginally rounded, ecoronate **999. *Artemisia***
– Apex of achenes with a corona of scales 166
166. Pericarp without myxogenic cells **1014. *Lepidolopsis***
– Pericarp with myxogenic cells mainly abaxially and on the ribs **979. *Marasmodes***
167. Annual herbs 168
– Perennial herbs, subshrubs, or shrubs (in *Pseudohandelia*, sometimes biennial and monocarpic) 175
168. Pollen smooth **995. *Elachanthemum***
– Pollen spiny 169
169. Pericarp of all achenes without myxogenic cells **1037. *Tanacetum***
– Pericarp of at least the central achenes with myxogenic cells 170
170. Achenes without ribs or with 2 lateral weak ribs 171
– Achenes with 3 or more, ± distinct ribs 172
171. Achenes without ribs, circular in cross-section; apex truncate to marginally rounded; pericarp with longitudinal rows of myxogenic cells; corolla lobes without central resin sacs; indumentum of medifixed hairs **1025. *Stilpnolepis***
– Achenes somewhat dorsiventrally flattened and with 2 lateral weak ribs; apex with an adaxial auricle, sometimes marginally rounded; pericarp with myxogenic cells abaxially; corolla lobes sometimes with central resin sacs; indumentum of basifixed hairs **1047. *Aaronsohnia***
172. Achenes with unbranched hairs adaxially between ribs **1022. *Microcephala***
– Achenes glabrous 173
173. Indumentum absent or of medifixed hairs **1033. *Anthemis***
– Indumentum of basifixed hairs 174
174. Achene apex with a corona covered with myxogenic cells **980. *Myxopappus***
– Achene apex marginally rounded or with a corona not covered with myxogenic cells **977. *Foveolina***
175. Achenes with a corona of 4–20 linear, bristle-like to obovate-elliptical scales at least as long as the achene 176

– Achenes ecoronate or with a corona of short scales, an auricle, or an acute or rounded rim 178
176. Pericarp glabrous or sparsely hairy; corona scales brownish **1008. *Cancrinia***
– Pericarp densely hairy; corona scales white 177
177. Capitula on short, nodding peduncles **1012. *Ugamia***
– Capitula on elongated, straight peduncles **1011. *Trichanthemis***
178. Achenes with myxogenic cells 179
– Achenes without myxogenic cells 185
179. Achenes with 10–18 ribs, some with resin sacs **986. *Phymaspermum***
– Achenes with fewer than 10 ribs, always without resin sacs 180
180. Corolla tube swollen and with thick vascular strands; shrubs or subshrubs with ± ericoid leaves 181
– Corolla tube not or only slightly swollen and with thin vascular strands; perennial herbs or subshrubs with few-lobed, pinnatifid, or pinnatisect leaves 182
181. Achene apex with 7–10 elliptical, adaxially longer scales **979. *Marasmodes***
– Achene apex with an adaxial auricle, a corona of 3–5 adaxially longer scales, or marginally rounded and ecoronate **982. *Pentzia***
182. Achenes ecoronate 183
– Achenes with a corona of scales 184
183. Achenes narrowly cylindrical and somewhat arcuate; pericarp tuberculate; capitula in a dense corymb or a pseudo-umbel **1016. *Pseudohandelia***
– Achenes obovoid and ± straight; pericarp smooth; capitula solitary or in lax corymbs **993. *Brachanthemum***
184. Apex of achenes with an often oblique corona (adaxially larger than abaxially) formed by free or basally united scales; capitula usually in lax to dense corymbs, rarely solitary; involucre hemispherical, with phyllaries in 2–3 rows **1026. *Tanacetopsis***
– Apex of achenes with an adaxial auricle or 3–6 adaxial scales; capitula usually solitary, rarely in lax corymbs; involucre usually cylindrical to conical, with phyllaries in 4–5 rows, rarely hemispherical **1046. *Xylanthemum***
185. Anthers tailed 186
– Anthers not tailed 187
186. Achene apex with a corona of small, entire to toothed scales terminating each of the 8–10 ribs **971. *Inulanthera***
– Achene apex bordered by a ± distinct, rounded rim; achenes with 5–8 inconspicuous ribs; ribs sometimes with longitudinal resin canals **1018. *Hippolytia***
187. Pericarp conspicuously tuberculate or rugose **983. *Rennera***
– Pericarp with smooth longitudinal ribs 188
188. Achenes with longitudinal rows of resin sacs in ribs 189
– Achenes without any resin sacs or canals 190
189. Achene apex with a corona of basally united, fimbriate scales **963. *Hymenolepis***
– Achene apex marginally rounded or sometimes with a short, thickened rim **962. *Athanasia***
190. Leaves opposite **985. *Gymnopentzia***
– Leaves alternate or basally crowded 191
191. Capitula small and numerous, in a dense corymb; plant basally villous and with 3–4-pinnatisect leaves **1015. *Polychrysum***
– Capitula various in size, solitary, or in lax to dense corymbs; plants basally not densely villous; leaves entire, dentate, or 1–4-pinnatisect 192
192. Involucre cylindrical to conical; phyllaries in 4–7 rows **1020. *Lepidolopha***
– Involucre hemispherical; phyllaries in 1–4 rows 193
193. A compact, basally woody subshrub; indumentum of basifixed hairs; capitula solitary; phyllaries in 1–2 rows, all of almost the same length; receptacle sparsely hairy **1009. *Cancriniella***
– Perennial herbs; indumentum absent or of medifixed and/or basifixed hairs; capitula solitary or in lax to dense corymbs; phyllaries in 2–5 rows, of different lengths; receptacle glabrous or sparsely hairy 194
194. Apex of achenes with an adaxial auricle or with a crenate to dentate rim **1037. *Tanacetum***
– Apex of achenes with an often oblique (adaxially more developed) but abaxially developed corona formed by free or basally united scales **1026. *Tanacetopsis***

XVI. Group A [Southern Hemisphere Genera]

961. *Adenanthellum* B. Nord.

Adenanthellum B. Nord., Bot. Notiser 132: 160 (1979); Nordenstam, Bot. Notiser 129: 137–165 (1976), rev.
Adenanthemum B. Nord. (1976), non H. Conwentz (1886).

Perennial herb. Indumentum of basifixed hairs. Leaves alternate, serrate, glandular-punctuate. Capitula solitary or in lax corymbs, more or less distinctly pedunculate, radiate. Involucre broadly campanulate. Phyllaries in 3–4 rows, with scarious margins. Receptacle convex, glabrous, epaleate. Ray florets female, fertile; limb white, confluent with the achene, tube absent. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, confluent with the achene; tube not spongy; apical anther appendage ovate-elliptical. Achenes oblong, with 10 ribs, somewhat compressed; apex marginally rounded; pericarp without myxogenic cells, with 10 resin canals in the ribs. One species, *A. osmitoides* (Harv.) B. Nord. South Africa, Swaziland.

XVI.1. Athanasia Group (962–963)

962. *Athanasia* L. Fig. 69

Athanasia L., Sp. Pl., ed. 2: 1180 (1763); Källersjö, Opera Bot. 106: 1–75 (1991), rev.
Morysia Cass. (1824).
Holophyllum Less. (1832).
Stilpnophyton Less. (1832).
Pristocarpha E. Mey. ex DC. (1838).
Saintmorysia Endl. (1838).
Bembycodium Kunze (1842).

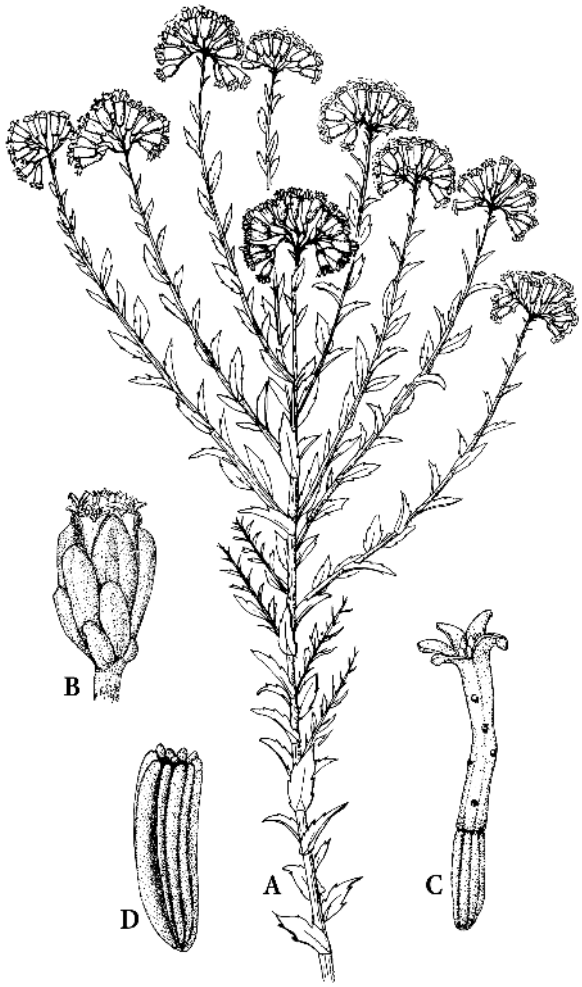

Fig. 69. Compositae-Anthemideae. *Athanasia dentata*. **A** Habit. **B** Capitulum. **C** Tubular floret. **D** Achene. (Drawings by Ch. Oberprieler)

Asaemia (Harv.) Harv. ex Benth. (1873).

Shrubs or shrublets. Indumentum absent or of stellate, rarely basifixed hairs. Leaves alternate, rarely opposite, entire to pinnatifid, sometimes succulent. Capitula in dense corymbs and pedunculate or solitary and sessile along branches, discoid. Involucre narrowly ellipsoid-cylindrical, hemispherical or spherical to urceolate. Phyllaries in 2–5 rows, often containing resin sacs. Receptacle flat to hemispherical, paleate, rarely epaleate; paleae flat or canaliculate, narrowly elliptical, rarely with a central resin duct. Florets hermaphrodite, fertile; corolla 5-lobed, yellow or whitish, tube with long-stalked glands, scattered or aggregated into a basal ring, rarely with short-stalked glands, or glabrous. Achenes obovoid or cylindrical, circular in cross-section and with 5–12(–18) sharply angled ribs, or dorsiventrally flattened and with two lateral and one adaxial rib; apex marginally rounded or with a short, thickened rim; pericarp with longitudinal rows of resin sacs in ribs. $x = 8$ (polyploidy). Thirty-nine species, South Africa, Namibia.

963. *Hymenolepis* Cass.

Hymenolepis Cass., Bull. Sci. Soc. Philom. Paris 1817: 138 (1817); Bremer & Källersjö, Nordic J. Bot. 5: 517–520 (1985), rev.
Oligodora DC. (1838).
Phaeocephalus S. Moore (1900).

Shrubs. Indumentum absent or of stellate hairs. Leaves alternate, entire, dentate or lobed. Capitula in dense corymbs, discoid, shortly pedunculate. Involucre narrowly ellipsoid-cylindrical to obconical. Phyllaries in 3–4 rows, without or with only narrow scarious margins. Receptacle flat, paleate, rarely epaleate; paleae flat, narrowly elliptical. Florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid, circular in cross-section, with 5–10 rounded ribs; apex with a corona of basally united, fimbriate scales; pericarp with longitudinal rows of resin sacs in ribs. Seven species, South Africa.

XVI.2. Cotula Group (964–966)

964. *Cotula* L.

Cotula L., Sp. Pl.: 891 (1753).
Cenia Comm. ex Juss. (1789).
Lancisia Lam. (1797).
Strongylosperma Less. (1832).
Machlis DC. (1837).
Otochlamys DC. (1838).
Pleiogyne Koch (1843).
Sphaeroclinium (DC.) Sch. Bip. (1844).
Gymnogyne Steetz (1845).
Ctenosperma Hook. f. (1847).

Annual or perennial herbs. Indumentum absent or of basifixed hairs. Leaves alternate, sometimes opposite or basally crowded, lobed or 1–3-pinnatisect, sometimes entire. Capitula solitary, discoid or disciform, sometimes shortly radiate, pedunculate; peduncles sometimes inflated. Involucre hemispherical or obconical. Phyllaries in 2–3 rows, with central resin ducts and pale or light to dark brown scarious margins. Receptacle flat to hemispherical, epaleate. Ray florets or outer disc florets female, fertile, stalked; limb (when present)

white. Inner disc florets hermaphrodite, fertile; corolla 3–4-lobed, yellow, basally sometimes adaxially saccate; lobes usually with central resin canals, one lobe occasionally forming a radiate limb. Achenes obovoid, dorsiventrally flattened and elliptical in cross-section, with 2 distinct, lateral, wing-like ribs; apex marginally rounded, ecoronate; pericarp rather thin, generally hairy, sometimes with myxogenic cells and/or 2 lateral resin canals. x = 8, 9, 10 (polyploidy). Fifty-five species, southern and eastern Africa, Australia, South America, Mexico, southern oceanic islands. Some species widespread and naturalised.

965. *Leptinella* Cass.

Leptinella Cass., Bull. Sci. Soc. Philom. Paris 1822: 127 (1822); Lloyd, N. Z. J. Bot. 10: 277–372 (1972), rev.
Symphyomera Hook. f. (1847).

Perennial or facultative annual herbs. Indumentum of basifixed hairs. Leaves alternate or opposite, pectinate or 1–2-pinnatisect. Capitula solitary, discoid or disciform, pedunculate. Involucre hemispherical, sometimes umbonate. Phyllaries in 2 rows, with rather narrow, pale scarious margins. Receptacle flat to conical, epaleate. Outer florets female, fertile, tubular, yellow, apically 4-lobed, inflated to form a hollow space between the outer and inner epidermis. Inner florets functionally male; corolla yellow, apically 4-lobed. Achenes obovoid to cylindrical, circular or dorsiventrally flattened and elliptic in cross-section, without distinct ribs; apex marginally rounded; pericarp glabrous or hairy, sometimes with myxogenic cells and/or minute resin canals. x = 13 (polyploidy). Thirty-three species, New Guinea, Australia, New Zealand, South America, Falkland Islands.

966. *Soliva* Ruiz & Pav.

Soliva Ruiz & Pav., Fl. Peruv. Prodr.: 113 (1794).
Gymnostyles Juss. (1804).

Annual herbs. Indumentum of basifixed hairs. Leaves alternate, 2–3-pinnatisect. Capitula solitary, sessile in leaf axils, disciform. Involucre hemispherical. Phyllaries in 2 rows, with narrow, pale or light brown scarious margins. Receptacle hemispherical to conical, epaleate. Outer florets female, fertile; tube and limb absent; style spinescent at maturity. Inner florets functionally male; corolla 3–4-lobed, yellow; style branches fused. Achenes obovoid, dorsiventrally flattened and narrowly elliptical in cross-section, with 2 lateral, wing-like ribs; ribs sometimes projecting into apical teeth; apex marginally rounded; pericarp glabrous, without myxogenic cells or resin sacs. x = 10 (polyploidy). Eight species, South America, North America, Australia. One species widespread as weed.

967. *Eriocephalus* L.

Eriocephalus L., Sp. Pl.: 926 (1753); Müller, Herman & Kolberg, Flora of Southern Africa 33, 4/1: 1–63 (2001), rev.
Cryptogyne Cass. (1827), non Hook. (1876).
Monochlaena Cass. (1827).

Shrubs. Indumentum of basifixed hairs. Leaves opposite, sometimes alternate, often fascicled on lateral brachyblasts, mostly ericoid, entire or lobed to pinnatisect. Capitula in dense corymbs, radiate or disciform. Involucre hemispherical or urceolate. Phyllaries in 2 unequal rows, the outer scarious, with very wide brown to reddish scarious margins, the inner (= paleae of marginal florets) connate and hairy. Receptacle flat, paleate; paleae elliptical to linear, canaliculate, villous. Ray florets or outer disc florets female, fertile; limb (when present) yellow, white or reddish. Inner disc florets functionally male, with fused style branches; corolla 5-lobed, yellow or mauve. Achenes obovoid, circular or dorsiventrally flattened and elliptical in cross-section, with 5 equally arranged or 2 lateral ribs; apex marginally rounded; pericarp lanate or pilose, without myxogenic cells or resin sacs. x = 9 (polyploidy). Thirty-two species, South Africa, Namibia, Botswana, Lesotho.

968. *Hilliardia* B. Nord.

Hilliardia B. Nord., Opera Bot. 92: 147 (1987).

Scrambling shrub. Indumentum of long and fine, basifixed hairs. Leaves alternate, 1–2-pinnatisect. Capitula in lax corymbs, pedunculate, radiate. Involucre hemispherical. Phyllaries in 2–3 rows, with broad, pale or light brown to reddish scarious margins. Receptacle conical to elongated, epaleate. Ray florets female, fertile; limb white, apically deeply bifid. Disc florets hermaphrodite, fertile; corolla 4-lobed, yellow. Achenes obovoid to subglobose, circular in cross-section, with 2–3 thin adaxial ribs; apex marginally rounded; pericarp very thin and translucent, glabrous, without myxogenic cells or resin sacs. x = 10. One species, *H. zuurbergensis* (Oliver) B. Nord., South Africa.

969. *Hippia* L.

Hippia L., Mant. Pl.: 158, 291 (1771).

Shrublets or subshrubs. Indumentum of basifixed hairs. Leaves alternate, entire, dentate to pinnatisect. Capitula in lax to dense corymbs, rarely solitary, disciform. Involucre hemispherical. Phyllaries in 3 rows, with narrow, pale scarious margins. Receptacle hemispherical to conical, epaleate. Outer florets female, fertile; limb absent; tube much reduced. Inner florets functionally male, with fused style branches; corolla 5-lobed, sometimes with 2 larger and 3 smaller lobes, white or yellow. Achenes obovoid, dorsiventrally flattened, narrowly elliptical in cross-section, with 2 lateral, wing-like ribs; apex marginally rounded; pericarp glabrous, papillose to sparsely pubescent, without myxogenic cells or resin sacs. Eight species, South Africa.

970. *Inezia* E. Phillips

Inezia E. Phillips, Bull. Misc. Inform. 1932: 297 (1932).

Perennial herbs. Indumentum of basifixed hairs. Leaves alternate, entire. Capitula solitary, pedunculate, radiate. Involucre obconical to hemispherical. Phyllaries in 3–5 rows, with narrow scarious margins. Receptacle conical, epaleate. Ray florets female, fertile or sterile; limb yellow or white, adaxially and basally laterally pilose, confluent with the achene, tube short or absent. Disc florets hermaphrodite, fertile; corolla 4-lobed, yellow. Achenes obovoid to cylindrical, dorsiventrally slightly flattened, 4-angled; apex marginally rounded or with minute scales; pericarp without myxogenic cells or resin sacs. $x = 10$. Two species, South Africa, Swaziland.

971. *Inulanthera* Källersjö

Inulanthera Källersjö, Nordic J. Bot. 5: 539 (1986).

Shrubs or subshrubs. Indumentum absent or of basifixed hairs. Leaves alternate, entire to lobed. Capitula in lax corymbs, discoid. Involucre hemispherical to spherical. Phyllaries in 3 rows, with narrow, pale to light brown scarious margins. Receptacle flat, paleate, rarely epaleate; paleae linear, flat to shallowly canaliculate, with a central resin duct. Florets hermaphrodite, fertile; corolla 5-lobed, yellow; anthers basally caudate. Achenes obovoid, circular in cross-section, with (8–)10 ribs; apex with a corona of small, entire to toothed scales terminating each rib; pericarp smooth, sometimes papillose, without myxogenic cells or resin sacs, but with protruding, light brown glands. Ten species, South Africa, Swaziland, Lesotho, Angola, Zimbabwe, Madagascar.

972. *Lasiospermum* Lag.

Lasiospermum Lag., Gen. Sp. Pl.: 31 (1816); Müller, Herman & Kolberg, Flora of Southern Africa 33, 4/1: 64–73 (2001), rev.

Annual or perennial herbs. Indumentum absent or of long basifixed hairs. Leaves alternate, 1–2-pinnatisect, rarely entire. Capitula solitary or in lax corymbs, radiate or discoid, pedunculate. Involucre hemispherical. Phyllaries in 2–4 rows, usually with several longitudinal resin ducts and light scarious margins. Receptacle flat to conical, paleate; paleae flat, elliptical to obovate, with a central resin duct. Ray florets (when present) female, fertile; limb white or reddish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow or reddish. Achenes obovoid, circular in cross-section, with 6 ribs; apex marginally rounded; pericarp densely villous, with longitudinal rows of resin sacs in ribs. $x = 9$, 10. Four species, South Africa, Namibia, Lesotho, Egypt.

973. *Lidbeckia* P.J. Bergius

Lidbeckia P.J. Bergius, Descr. Pl. Cap.: 306 (1767).

Subshrubs. Indumentum of basifixed hairs. Leaves alternate, glandular-punctate, pinnately to digitately lobed. Capitula solitary, pedunculate, radiate. Involucre hemispherical to cylindrical. Phyllaries in 3–4 rows, without scarious margins. Receptacle convex, hairy, epaleate. Ray florets female, sterile or neuter; limb white, sometimes dorsally pilose, tube sometimes laterally pilose, confluent with the achene. Disc florets hermaphrodite, fertile; corolla 4-lobed, yellow, sometimes pilose; stylopodium large and persistent in fruit. Achenes ellipsoid, laterally pilose, with 3–8 ribs; apex marginally rounded. Two species, South Africa.

974. *Osmitopsis* Cass.

Osmitopsis Cass., Bull. Sci. Soc. Philom. Paris 1817: 154 (1817); Bremer, Bot. Notiser 125: 9–48 (1971); Bremer, Bot. Notiser 129: 21–24 (1976), rev.

Shrubs or subshrubs. Indumentum absent or of basifixed hairs. Leaves alternate, entire to lobed. Capitula solitary or in lax corymbs, radiate. Involucre campanulate. Phyllaries in 2–4 rows, often with scarious margins. Receptacle flat to con-

ical, paleate; paleae narrowly elliptical to obovate, canaliculate and enclosing the florets. Ray florets female, fertile, sterile or neuter; limb white, occasionally pilose abaxially, tube occasionally pilose. Disc florets hermaphrodite and fertile or functionally male; corolla 5-lobed, yellow; anthers basally caudate; stylopodium sometimes large and persistent in fruit. Achenes obovoid, ellipsoid or obovate, 3–4-angled or -ribbed; apex with a corona of subulate to triangular, basally fused scales, or marginally rounded. $x = 10$. Nine species, South Africa.

XVI.3. Pentzia Group (975–983)

975. *Adenoglossa* B. Nord.

Adenoglossa B. Nord., Bot. Notiser 129: 137 (1976).

Annual herb. Indumentum absent, first stem internode with basifixed hairs. Leaves alternate or opposite, entire, succulent. Capitula solitary, pedunculate, radiate. Involucre hemispherical. Phyllaries in 2–3 rows, without scarious margins, with central resin canals. Receptacle conical, epaleate. Ray florets female, fertile; limb short, yellow. Disc florets hermaphrodite, fertile; corolla 5-lobed, slightly zygomorphic with 2 smaller adaxial and 3 larger abaxial lobes, yellow. Achenes obovate, dorsiventrally strongly flattened and laterally winged; apex with 5–6 scales; pericarp with myxogenic cells on abaxial surface and with 2 lateral resin canals. One species, *A. decurrens* (Hutch.) B. Nord., South Africa.

976. *Cymbopappus* B. Nord.

Cymbopappus B. Nord., Bot. Notiser 129: 150 (1976).

Shrubs or subshrubs. Indumentum woolly, of basifixed hairs. Leaves alternate, crowded, linear or pinnatisect. Capitula solitary, pedunculate, radiate. Involucre hemispherical to cylindrical. Phyllaries in 3–4 rows, with brownish scarious margins. Receptacle convex to subconical, epaleate. Ray florets female, fertile; limb white or pinkish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, tube swollen, with thick vascular strands. Achenes oblong, with 5 ribs; apex with an oblique, adaxially longer corona, or with a large adaxial and a smaller abaxial scale; pericarp with myxogenic cells on the ribs and on the abaxial surface, without resin sacs. Three species, South Africa.

977. *Foveolina* Källersjö

Foveolina Källersjö, Bot. J. Linn. Soc. 96: 316 (1988); Källersjö, Bot. J. Linn. Soc. 96: 299–322 (1988), rev.

Annual herbs. Indumentum of basifixed hairs. Leaves alternate, 2-pinnatisect. Capitula solitary, pedunculate, discoid, disciform or radiate. Involucre hemispherical. Phyllaries in 3–5 rows, with or without central resin canals. Receptacle flat-conical, epaleate. Ray florets (when present) female, fertile; limb white. Achenes inconspicuously 3-ribbed; apex with an adaxial auricle or a corona; pericarp abaxially covered with myxogenic cells, laterally with two rows of short-stalked glands immersed in small cavities, adaxially white and spongy with numerous druses, abaxially very thin and translucent. Outer florets (of disciform capitula) filiform, female. Achenes almost terete; apex marginally rounded; pericarp without myxogenic cells, spongy and wrinkled. (Inner) disc florets hermaphrodite, fertile; corolla 4–5-lobed, yellow, tube often basally saccate. Achenes as in ray florets or obovoid, with a marginally rounded apex and a thin pericarp, abaxially with myxogenic cells. Five species, South Africa, Namibia.

978. *Leucoptera* B. Nord.

Leucoptera B. Nord., Bot. Notiser 129: 140 (1976).

Glabrous shrublets. Leaves alternate or opposite, entire or lobed, somewhat succulent. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 2–3 rows, with wide scarious margins. Receptacle convex, epaleate. Ray florets female, fertile; limb white, often becoming pink-reddish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes dorsiventrally flattened, laterally winged; apex with 3 adaxial-lateral scales; pericarp abaxially covered with myxogenic cells, with 2 lateral resin canals. $x = 9$. Three species, South Africa.

979. *Marasmodes* DC.

Marasmodes DC., Prodr. 6: 136 (1838).

Glabrous shrubs. Leaves alternate, entire or occasionally lobed. Capitula small, closely aggregated, rarely solitary, discoid. Involucre hemispherical to urceolate. Phyllaries in 4–5 rows, with scarious margins. Receptacle flat, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow, tube swollen and with thick vascular strands. Achenes circular in cross-section, with 5 ribs; apex with a corona of 7–10 elliptical, adaxially longer scales; pericarp with myxogenic cells mainly abaxially and on the ribs. Four species, South Africa.

980. ***Myxopappus*** Källersjö

Myxopappus Källersjö, Bot. J. Linn. Soc. 96: 314 (1988); Källersjö, Bot. J. Linn. Soc. 96: 299–322 (1988), rev.

Annual herbs. Indumentum of basifixed hairs. Leaves alternate, variously pinnatisect. Capitula solitary, pedunculate, discoid. Involucre meniscoid to hemispherical. Phyllaries in 3–5 rows, very narrow and acute, without scarious margins, often with central resin canals. Receptacle convex to conical, epaleate. Florets hermaphrodite, fertile; corolla 4- or 5-lobed, yellow. Achenes obovoid to oblong, triquetrous in cross-section, with 1 adaxial and 2 lateral ribs; apex with a corona covered with myxogenic cells; pericarp spongy and containing numerous druses, with myxogenic cells abaxially and on the ribs. $x = 7$. Two species, South Africa, Namibia.

981. ***Oncosiphon*** Källersjö

Oncosiphon Källersjö, Bot. J. Linn. Soc. 96: 310 (1988); Källersjö, Bot. J. Linn. Soc. 96: 299–322 (1988), rev.

Annual herbs. Indumentum absent or of basifixed hairs. Leaves alternate, variously pinnatisect. Capitula solitary or in corymbs, pedunculate, radiate or discoid. Involucre hemispherical to cylindrical. Phyllaries in 3–4 rows, with scarious margins, with or without central resin canals. Receptacle flat to convex or conical, epaleate. Ray florets (when present) female, fertile; limb white. Disc florets hermaphrodite, fertile; corolla 4-lobed, yellow, tube conspicuously swollen and brittle. Achenes cylindrical, circular in cross-section, with 4 ribs; apex with a mainly abaxial entire or toothed rim; pericarp without myxogenic cells. $x = 6, 8$. Eight species, South Africa, Lesotho, Namibia.

982. ***Pentzia*** Thunb.

Pentzia Thunb., Prodr. Pl. Cap. 2: 145 (1800).

Shrubs or subshrubs. Indumentum absent or of medifixed hairs. Leaves alternate or rarely opposite, entire to pinnatisect. Capitula solitary or in corymbs, pedunculate, discoid. Involucre hemispherical. Phyllaries in 3–5 rows, with pale or brown scarious margins, sometimes with central resin canals. Receptacle convex to conical, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow, tube swollen and with thick vascular strands. Achenes narrowly obovoid, with 5 ribs; apex with an adaxial auricle, an adaxially longer corona of 3–5 scales, or marginally rounded; pericarp with myxogenic cells abaxially and along the ribs. $x = 6, 7, 8, 9$. Twenty-seven species, South Africa, Namibia, Morocco, Algeria, Chad, Somalia, Yemen.

983. ***Rennera*** Merxm.

Rennera Merxm., Mitt. Bot. Staatssamml. München 2: 335 (1957); Herman, Bot. J. Linn. Soc. 129: 367–377 (1999), rev.

Perennial herbs or shrublets. Indumentum absent or of basifixed hairs. Leaves alternate or opposite at base, entire to pinnatisect. Capitula solitary, pedunculate, discoid. Involucre hemispherical. Phyllaries in 3–4 rows, with central resin canals. Receptacle flat to convex, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow, tube narrow, limb wide. Achenes obovoid or ellipsoid, 5-angled; apex marginally rounded or with a thick, spreading to revolute rim; pericarp without myxogenic cells, conspicuously tuberculate to rugose. Four species, Namibia, South Africa, Botswana.

XVI.4. Phymaspermum Group (984–986)

984. ***Eumorphia*** DC.

Eumorphia DC., Prodr. 6: 2 (1838).

Shrubs or shrublets. Indumentum absent or of basifixed hairs. Leaves opposite, rarely alternate, entire or lobed. Capitula solitary or in lax corymbs, pedunculate, radiate. Involucre hemispherical. Phyllaries in 2–3 rows, usually with a central resin duct, with light to dark brown scarious margins. Receptacle flat to conical, paleate, rarely epaleate; paleae linear, canaliculate, with a central resin duct. Ray florets female, fertile; limb white, sometimes purplish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, sometimes purplish. Achenes cylindrical, circular in cross-section, with 10–12(–18) rounded ribs; apex with an entire or dentate, thickened rim; pericarp often minutely papillose, without myxogenic cells or resin sacs. Six species, South Africa, Lesotho, Swaziland.

985. ***Gymnopentzia*** Benth.

Gymnopentzia Benth. in Benth. & Hook. f., Gen. Pl. 2: 1235 (1876).

Shrub. Indumentum absent or of basifixed hairs. Leaves opposite, entire or lobed, connate and sheathing at base. Capitula in dense corymbs, pedunculate, discoid. Involucre hemispherical.

Phyllaries in few rows, with ciliate scarious margins. Receptacle flat to hemispherical, epaleate (occasionally paleate). Florets hermaphrodite, fertile; corolla 5-lobed, yellow, often purplish. Achenes ellipsoid, circular in cross-section, with 10 rounded ribs; apex truncate, without a corona or thickened rim; pericarp with very long papillae, without myxogenic cells or resin sacs. One species, *G. bifurcata* Benth., South Africa, Lesotho.

986. *Phymaspermum* Less.

Phymaspermum Less., Syn. Gen. Comp.: 253 (1832).
Brachymeris DC. (1837).
Adenachaena DC. '*Adenochaena*' (1838).
Iocaste E. Mey. ex Harv. (1865).

Shrubs or shrublets. Indumentum absent or of basifixed hairs. Leaves alternate, entire to lobed. Capitula solitary or in lax corymbs and pedunculate, rarely solitary and sessile along branches, radiate or discoid. Involucre hemispherical to spherical, rarely cylindrical to obconical. Phyllaries in 3–4 rows, often with longitudinal resin ducts. Receptacle flat-conical, epaleate. Ray florets female, fertile; limb white or yellow, sometimes purplish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, sometimes purplish; tube rarely pubescent with long hairs. Achenes obovoid or cylindrical, circular in cross-section, with 10–18 rounded ribs; apex with an entire or dentate rim or corona; pericarp often minutely papillose, with ovoid myxogenic trichomes and resin sacs in some of the ribs. Nineteen species, South Africa, Swaziland, Zimbabwe, Namibia.

987. *Schistostephium* Less.

Schistostephium Less., Syn. Gen. Comp.: 251 (1832).
Peyrousea DC. (1838).

Shrublets or subshrubs. Indumentum of basifixed hairs. Leaves alternate, entire to pinnatisect. Capitula in lax to dense corymbs, rarely solitary, disciform or discoid. Involucre hemispherical, sometimes obconical or urceolate. Phyllaries in 2–3 rows, with narrow, pale scarious margins. Receptacle hemispherical to conical, epaleate or with few marginal paleae. Outer florets female, fertile; limb absent. Inner florets hermaphrodite, fertile (innermost sometimes functionally male); corolla 4-lobed, yellow. Achenes obovoid, dorsiventrally flattened, elliptical in cross-section, with 2 lateral, wing-like ribs; apex truncate or marginally rounded; pericarp glabrous or papillose, sometimes with myxogenic cells, always without resin sacs. Twelve species, South Africa, Mozambique, Zimbabwe, Swaziland.

988. *Thaminophyllum* Harv.

Thaminophyllum Harv. in Harvey & Sonder, Fl. Cap. 3: 155 (1865); Bond, J. S. African Bot. 46: 157–166 (1980), rev.

Shrublets. Indumentum of basifixed hairs. Leaves alternate, crowded, entire, lanceolate to linear, ericoid. Capitula solitary or in lax corymbs, radiate. Involucre hemispherical. Phyllaries in 3–4 rows, with narrow, often reddish, scarious margins. Receptacle convex to conical, hairy, epaleate. Ray florets female, sterile; limb white to somewhat purple-pink, tube confluent with the achene. Disc florets hermaphrodite, fertile; corolla 4-lobed, yellow; stylopodium large and persistent in fruit. Achenes ellipsoid, 3–4-angled; apex marginally rounded; pericarp with large myxogenic cells in rounded, scattered groups. $x = 10$. Three species, South Africa.

989. *Ursinia* Gaertn.

Ursinia Gaertn., Fruct. Sem. Pl. 2: 462 (1791), nom. cons.; Prassler, Mitt. Bot. Staatssamml. München 6: 363–478 (1967), rev.
Sphenogyne R. Br. (1813).
Ursiniopsis E. Phillips (1951).

Annual or perennial herbs or shrublets. Indumentum absent or of basifixed hairs. Leaves alternate, entire to 2-pinnatisect, sometimes succulent. Capitula solitary or in lax corymbs, radiate or discoid, pedunculate. Involucre hemispherical. Phyllaries in 3–7 rows, with narrow to broad scarious margins. Receptacle hemispherical, paleate; paleae canaliculate, elliptical or narrowly linear with an apical limb. Ray florets usually neuter, sometimes female and fertile; limb yellow, orange, white or reddish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, purplish. Achenes cylindrical or obovoid, straight or curved, circular in cross-section, with 5 ribs and a basal tuft of hairs or glabrous; apex with a uniseriate pappus of 5–10 ovate or circular scales, or a biseriate pappus of 5 outer such scales and 5 inner subulate ones, or rarely epappose; pericarp rarely with myxogenic cells. $x = 5, 7, 8$. Thirty-nine species, South Africa, Namibia, Botswana, Ethiopia.

XVI. Group B [Asian Grade]

XVI.5. Ajania Group (990–998)

990. *Ajania* Poljakov

Ajania Poljakov, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 17: 419 (1955); Shih, Acta Phytotax. Sin. 32: 365–368 (1994), rev.

Perennial herbs or subshrubs. Indumentum of medifixed and basifixed hairs. Leaves alternate, serrate to pinnatisect, rarely entire. Capitula small, in corymbs or rarely solitary, disciform. Involucre hemispherical to cylindrical. Phyllaries in 3–4 rows, with rather wide, light to dark scarious margins. Receptacle convex to conical, epaleate. Outer row of florets female, fertile; corolla slender, 2–3-, rarely 4–5-lobed. Central florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid, with 4–6 ribs; apex marginally rounded; pericarp with myxogenic cells in rows, without resin sacs. $x = 9$ (polyploidy). Thirty-nine species, central Asia, China, Japan.

991. *Ajaniopsis* C. Shih

Ajaniopsis C. Shih, Acta Phytotax. Sin. 16: 86 (1978).

Annual herb. Leaves alternate, pinnatisect and few-lobed. Capitula small, in dense corymbs, disciform. Involucre hemispherical. Phyllaries in 2 rows, without or with narrow dark scarious margins. Receptacle convex, epaleate. Outer row of florets female, fertile; corolla 0–2-lobed, tapering above, apically densely pilose with erect, straight hairs. Central florets hermaphrodite, fertile; corolla 5-lobed, yellow, apically densely pilose with erect, straight hairs. Achenes obovoid, 3–6-ribbed; apex marginally rounded; pericarp thin, with 3–6 rows of myxogenic cells, without resin sacs. One species, *A. peniciliformis* C. Shih, China, Tibet.

992. *Arctanthemum* (Tzvelev) Tzvelev

Arctanthemum (Tzvelev) Tzvelev, Novosti Sist. Vyssh. Rast. 22: 274 (1985).

Perennial herbs. Indumentum absent or of basifixed hairs. Leaves rosulate to alternate, apically lobed-serrate. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 3–4 rows, with dark brown scarious margins. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes ellipsoid to obovoid, with 5–8 ribs; apex marginally rounded; pericarp without myxogenic cells or resin sacs. $x = 9$ (polyploidy). Three species, Arctic Eurasia, Siberia, Japan, Arctic North America.

993. *Brachanthemum* DC.

Brachanthemum DC., Prodr. 6: 44 (1838); Zhao, Acta Sci. Nat. Neimonggol 27: 805–807 (1996), rev.

Small shrublets, woody at base. Indumentum of basifixed, medifixed or stellate hairs. Leaves alternate, few-lobed. Capitula solitary or in lax corymbs, pedunculate, radiate or rarely discoid. Involucre hemispherical to cylindrical. Phyllaries in 4–5 rows, with pale to brownish membranous margins. Receptacle flat to convex or conical, glabrous or hairy, epaleate. Ray florets female, fertile; limb yellow, yellowish or white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid to oblong, with 5–7 ribs; apex marginally rounded; pericarp with myxogenic cells, without resin sacs. $x = 9$. Ten species, central Asia, Mongolia, China.

994. *Chrysanthemum* L.

Chrysanthemum L., Sp. Pl. 887 (1753); Gen. Pl., ed. 5: 379 (1754), nom. et typ. cons.
Dendranthema (DC.) Des Moul. (1860).

Perennial herbs or subshrubs. Indumentum absent or of medifixed or basifixed hairs. Leaves alternate, pinnatisect, lobed, serrate or rarely entire. Capitula in lax corymbs or solitary, pedunculate, radiate. Involucre meniscoid. Phyllaries in 2–4 rows, generally with brown scarious margins. Receptacle convex to conical, epaleate (paleate in some cultivars). Ray florets female, fertile; limb white, pink or yellowish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid, with 5–8 ribs; apex marginally rounded; pericarp thin, generally with myxogenic cells in rows, without resin sacs. $x = 9$ (polyploidy). Forty-one species, Asia (Mongolia, Russia, China, Japan, Korea), eastern Europe. Some species widely cultivated as ornamentals.

995. *Elachanthemum* Y. Ling & Y.R. Ling

Elachanthemum Y. Ling & Y.R. Ling, Acta Phytotax. Sin. 16: 62 (1978).

Annual herb. Leaves alternate, pinnatisect, few-lobed or entire. Capitula in lax corymbs, pedunculate, discoid. Involucre hemispherical to suborbicular. Phyllaries in 3–4 rows, with broad scarious margins. Receptacle subconical, epaleate. Florets

hermaphrodite, fertile (the inner sterile); corolla 5-lobed, yellow, tubular. Achenes obovoid, without ribs; apex oblique and marginally rounded; pericarp with longitudinal rows of myxogenic cells, without resin sacs. $x = 9$. One species, *E. intricatum* (Franchet) Y. Ling & Y.R. Ling, Mongolia, China.

996. *Hulteniella* Tzvelev

Hulteniella Tzvelev in B.A. Jurtzev, Arktich. Fl. S.S.S.R. 10: 117 (1987).

Perennial herb. Indumentum of basifixed hairs. Leaves rosulate to alternate, linear. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 3–4 rows, with dark brown scarious margins. Receptacle convex to conical, sparsely hairy, epaleate. Ray florets female, fertile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes ellipsoid to obovoid, with 5 ribs; apex truncate or with a rim; pericarp without myxogenic cells or resin sacs. $x = 9$. One species, *H. integrifolium* (Richardson) Tzvelev, Arctic Eurasia, Arctic North America.

997. *Phaeostigma* Muldashev

Phaeostigma Muldashev, Bot. Zhurn. (Moscow & Leningrad) 66: 586 (1981).

Perennial herbs or subshrubs. Indumentum of medifixed hairs. Leaves alternate, pinnatifid to shallowly lobed or entire. Capitula small, in dense corymbs, disciform. Involucre hemispherical. Phyllaries in 3–4 rows, with brown scarious margins. Receptacle convex, epaleate. Outer row of florets female, fertile; corolla slender, 2–4-lobed. Central florets hermaphrodite, fertile; corolla 5-lobed, yellow; style branches brownish. Achenes obovoid, with 4–6 ribs, apically ribs projected into minute teeth; pericarp without myxogenic cells or resin sacs. $x = 9$. Three species, China.

998. *Tridactylina* (DC.) Sch. Bip.

Tridactylina (DC.) Sch. Bip. in Webb & Berthelot, Hist. Nat. Iles Canaries 3 (2, 2): 245 (1844).

Annual herb. Indumentum of basifixed and medifixed hairs. Leaves alternate, few-lobed. Capitula in a lax corymb, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 3 rows, with dark brown scarious margins. Receptacle flat to convex, epaleate. Ray florets neuter; limb yellow or yellowish-white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid to cylindrical, with 5 ribs; apex marginally rounded or with a rim; pericarp with myxogenic cells, without resin sacs. One species, *T. kirilowii* (Turcz. ex DC.) Sch. Bip., eastern Siberia.

XVI.6. Artemisia Group (999–1005)

999. *Artemisia* L. Fig. 70

Artemisia L., Sp. Pl.: 845 (1753).
Oligosporus Cass. (1817).
Seriphidium Fourr. (1869).
Artanacetum (Rzazade) Rzazade (1956).

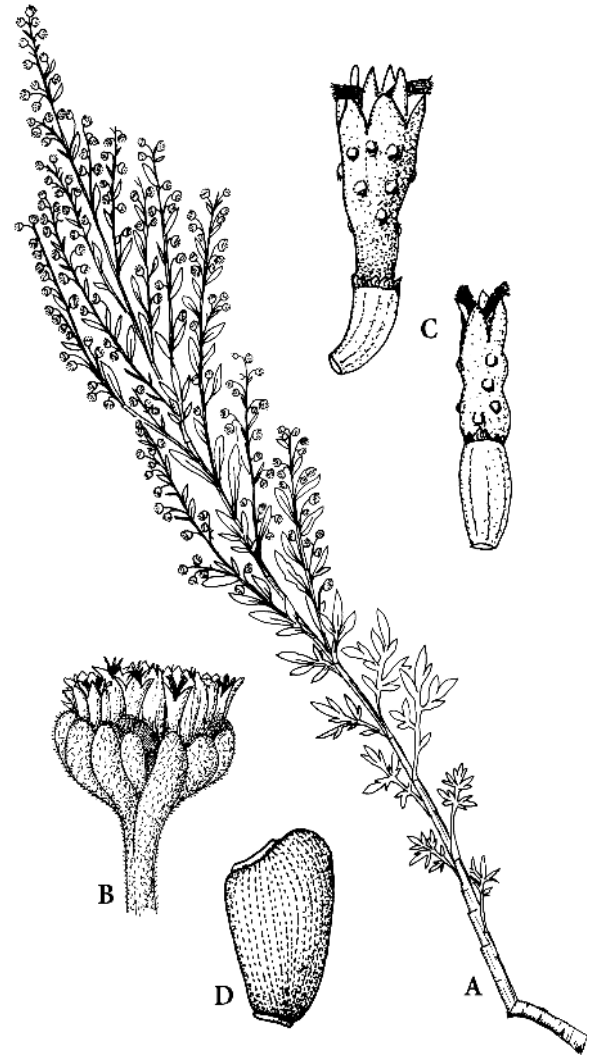

Fig. 70. Compositae-Anthemideae. *Artemisia absinthium*. **A** Habit. **B** Capitulum. **C** Hermaphrodite and tubular florets. **D** Achene. (Drawings by Ch. Oberprieler)

Annual or perennial herbs, subshrubs or shrubs. Indumentum absent or of basifixed, medifixed or stellate hairs. Leaves alternate, variously lobed or dissected, rarely entire. Capitula discoid or disciform, usually arranged in a long panicle but this sometimes much reduced and racemose, spiciform or subglobose. Involucrum hemispherical to cylindrical or urceolate. Phyllaries in 2–7 rows, with more or less scarious margins. Receptacle flat to conical, sometimes pilose, epaleate or occasionally paleate. Outer female florets usually tapering above, with 2–4 teeth, or truncate, commonly oblique at orifice. Central florets hermaphrodite and fertile or functionally male; corolla 5-lobed, yellow or sometimes reddish-violet or purple. Achenes obovoid to elliptical, cylindrical or flattened, usually glabrous but occasionally hairy; apex marginally rounded; pericarp with or without rows of myxogenic cells, without resin sacs. x = 7, 8, 9, 10, 11, 17 (polyploidy). Circa 522 species, Northern Hemisphere, South America, southern Africa, Pacific Islands.

1000. *Crossostephium* Less.

Crossostephium Less., Linnaea 6: 220 (1831).

Shrub. Indumentum tomentose, of medifixed hairs. Leaves alternate, narrowly spathulate, apically few-lobed or entire, succulent. Capitula rather small and rounded, paniculate, disciform. Involucre hemispherical. Phyllaries in 3 rows, outer bracts tomentose, inner bracts scarious. Receptacle hemispherical, epaleate. Outer female florets tubular, 2–3-lobed, yellow. Central florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid, weakly 5-ribbed; apex with a lacerate corona or with small scales. x = 9. One species, *C. chinense* (L.) Makino, Philippines, Taiwan, southern Japan, China. Widely cultivated in eastern Asia.

1001. *Filifolium* Kitam.

Filifolium Kitam., Acta Phytotax. Geobot. 9: 157 (1940).

Perennial herb, woody at base. Indumentum absent or of medifixed hairs. Leaves alternate, pinnatisect. Capitula in corymbs, disciform. Involucre hemispherical. Phyllaries in 3 rows, with scarious margins. Receptacle conical, epaleate. Outer row of florets female, fertile, tapering above, minutely 2–4-dentate. Central florets functionally male; corolla (4–)5-lobed, compressed in a resinous mass, yellowish. Achenes obliquely obovoid, without ribs; apex marginally rounded; pericarp consisting of large myxogenic cells in longitudinal rows, without resin sacs. x = 9. One species, *F. sibiricum* (L.) Kitam., Far East (Siberia, Mongolia, China, Korea).

1002. *Mausolea* Poljakov

Mausolea Poljakov, Trudy Inst. Bot. (Alma-Ata) 11: 170 (1961).

Shrub. Indumentum of medifixed hairs. Leaves alternate, few-lobed or entire. Capitula small, subglobose, few, more or less sessile in a reduced panicle, disciform. Involucre hemispherical. Phyllaries in 2 rows, with narrow scarious margins. Receptacle convex to hemispherical, epaleate. Outer florets female, fertile, without corolla; style branches dilated, lanceolate, flat, acute. Central florets functionally male; corolla 5-lobed, apically with medifixed hairs. Achenes obovoid; apex marginally rounded; pericarp densely pilose, without myxogenic cells or resin sacs. x = 9 (polyploidy). One species, *M. eriocarpa* (Bunge) Poljakov, Iran, Afghanistan, central Asia.

1003. *Neopallasia* Poljakov

Neopallasia Poljakov, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 17: 429 (1955).

Annual or biennial herbs. Indumentum of medifixed hairs. Leaves alternate, pectinate-pinnatisect. Capitula small and rounded in a narrow spiciform panicle, disciform. Involucre cylindrical to urceolate. Phyllaries in 2 rows, with broad scarious margins. Receptacle narrowly conical, epaleate. Outer florets female, fertile; corolla narrowly tubular, without apical lobes. Central florets of two kinds, outer hermaphrodite and fertile, inner completely sterile with reduced ovaries; corolla 5-lobed, bluish or pinkish. Achenes in one row at the base of the receptacle, oblong-obovoid, somewhat compressed or triquetrous; apex marginally rounded; pericarp with many rows of myxogenic cells, without resin sacs. x = 9. Three species, central Asia, southern Siberia, Mongolia, China.

1004. *Picrothamnus* Nutt.

Picrothamnus Nutt., Trans. Am. Philos. Soc., ser. II, 7: 417 (1841).

Shrublet, woody at base, with older branches forming long spines. Indumentum of medifixed hairs. Leaves alternate, few-lobed. Capitula small and subglobose, solitary or few together along

the branches, almost sessile, disciform. Involucre hemispherical. Phyllaries in 1–2 rows, with narrow hyaline scarious margins. Receptacle hemispherical, epaleate. Outer florets female, fertile; corolla tubular. Central florets functionally male; corolla 5-lobed, with long arachnoid hairs. Achenes obovoid; apex marginally rounded; pericarp densely arachnoid-pilose, without myxogenic cells or resin sacs. $x = 9$ (polyploidy). One species, *P. desertorum* Nutt., North America.

1005. *Sphaeromeria* Nutt.

Sphaeromeria Nutt., Trans. Am. Philos. Soc., ser. II, 7: 401 (1841); Holmgren, Shultz & Lowrey, Brittonia 28: 255–262 (1976), rev.
Chamartemisia Rydb. (1916).
Vesicarpa Rydb. (1916).

Perennial herbs or subshrubs. Indumentum of medifixed hairs. Leaves alternate to rosulate, pinnatisect and few-lobed or entire. Capitula apparently in corymbs but sometimes somewhat paniculate or capitate or solitary, disciform. Involucre hemispherical or obconical. Phyllaries in 2–3 rows, with light to dark scarious margins. Receptacle flat to conical, rarely pubescent, epaleate. Outer row of florets female, tapering above; corolla sometimes glandular, rarely with hairs at the apex. Central florets hermaphrodite, fertile; corolla 5-lobed, pale or bright yellow, rarely with hairs at the apex. Achenes obovoid-oblong, sometimes faintly 3–5-ribbed; apex marginally rounded or with a rim, a corona or with small scales; pericarp sometimes with myxogenic cells, without resin sacs. $x = 9$. Nine species, North America, Mexico.

1006. *Artemisiella* Ghafoor

Artemisiella Ghafoor, Candollea 47: 636 (1992).

Perennial herb, woody at base. Indumentum of medifixed hairs. Leaves alternate, basally crowded, 2–3-pinnatisect. Capitula in a simple raceme, pedunculate, disciform. Involucre hemispherical. Phyllaries in 3–4 rows, with rather broad, brown scarious margins. Receptacle hemispherical, pilose, epaleate. Outer florets female, fertile; corolla tubular, 4-lobed, densely hairy. Inner florets hermaphrodite, fertile; corolla 5-lobed, yellow, densely hairy. Achenes obovoid, quadrangular in cross-section; apex with a more or less distinct, rounded rim; pericarp sparsely or (in achenes of outer florets) densely hairy. $x = 9$. One species, *A. stracheyi* (Hook. f. & Thompson ex Clarke) Ghafoor, Ladakh, Tibet, Nepal, Bhutan, southern China.

XVI.7. Cancrinia Group (1007–1012)

1007. *Allardia* Decne

Allardia Decne in Jacquemont, Voy. Inde 4: 87 (1836).
Waldheimia Kar. & Kir. (1842).

Perennial herbs. Indumentum absent or of basifixed hairs. Leaves alternate, lobed to pinnatisect. Capitula solitary, pedunculate, radiate. Involucre hemispherical. Phyllaries in 3–4 rows, with broad, blackish-brown scarious margins. Receptacle hemispherical, epaleate. Ray florets female, fertile or sterile, or neuter; limb white, pink or bluish violet. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow or bluish violet. Achenes obconical, circular in cross-section, with 5–10 protruding ribs; apex with a corona formed by 25–50 bristle-like, apically brownish scales as long as or longer than the achene body; pericarp glabrous to densely hairy, without myxogenic cells or resin sacs. Eight species, Afghanistan, central Asia, Mongolia, China.

1008. *Cancrinia* Kar. & Kir.

Cancrinia Kar. & Kir., Bull. Soc. Imp. Naturalistes Moscou 15: 124 (1842).

Perennial herbs. Indumentum of basifixed hairs. Leaves alternate, 1–2-pinnatipartite to -pinnatisect. Capitula solitary, pedunculate, discoid. Involucre hemispherical. Phyllaries in 2–3 rows, with broad, pale to dark brown or blackish scarious margins. Receptacle hemispherical, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow, glabrous. Achenes obconical, circular in cross-section, with 5–6(–10) inconspicuous ribs; apex with a corona formed by 5–12 linear or narrowly elliptical, apically brownish scales as long as or longer than the achene body; pericarp glabrous to sparsely hairy, without myxogenic cells or resin sacs. Four species, central Asia, Mongolia, China.

1009. *Cancriniella* Tzvelev

Cancriniella Tzvelev in Komarov, Fl. U.R.S.S. 26: 292, 876 (1961).

Subshrub. Indumentum of long basifixed hairs. Leaves alternate, palmately lobed to pinnatipartite. Capitula solitary, pedunculate, discoid. Involucre

hemispherical. Phyllaries in 1–2 rows, all of nearly the same length, the outer with narrow, the inner with broad, pale scarious margins. Receptacle hemispherical, sparsely hairy, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow, glabrous. Achenes narrowly obconical, circular in cross-section, with 10 distinct ribs; apex with a corona formed by 6–10 rather short, apically rounded scales much shorter than the achene body; pericarp glabrous, without myxogenic cells or resin sacs. One species, *C. krascheninnikovii* (Rubtzov) Tzvelev, central Asia.

1010. *Richteria* Kar. & Kir.

Richteria Kar. & Kir., Bull. Soc. Imp. Naturalistes Moscou 15: 126 (1842).

Subshrubs. Indumentum absent or of long basifixed hairs. Leaves alternate, basally crowded, 2–3-pinnatisect. Capitula solitary, rarely 2–3 per shoot forming a lax corymb, pedunculate, radiate. Involucre hemispherical. Phyllaries in 2–3 rows, with broad, dark brown to blackish scarious margins. Receptacle hemispherical, epaleate. Ray florets female, fertile; limb white or pinkish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, glabrous. Achenes obconical, circular in cross-section, with 5–10 rather inconspicuous ribs; apex with a corona formed by 5–10 obovate to linear-elliptical, apically brownish scales shorter than the achene body; pericarp glabrous, without myxogenic cells or resin sacs. $x = 9$ (polyploidy). Six species, Iran, Afghanistan, central Asia, Mongolia, China, Himalaya.

1011. *Trichanthemis* Regel & Schmalh.

Trichanthemis Regel & Schmalh., Trudy Imp. S.-Peterburgsk. Bot. Sada 5: 617 (1877).
Glossanthis Poljakov (1959).

Subshrubs or perennial herbs. Indumentum of long basifixed hairs. Leaves alternate, apically trifid to 1–2-pinnatisect. Capitula solitary, pedunculate, radiate or discoid. Involucre hemispherical or obconical. Phyllaries in 3–5 rows, with narrow to broad, pale to brown scarious margins. Receptacle flat to hemispherical, glabrous or sparsely to densely hairy, epaleate. Ray florets (when present) female and fertile; limb white, yellow or pinkish; tube usually hairy. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, usually hairy. Achenes obconical, circular in cross-section, with 5–8(–10) distinct ribs; apex with a corona formed by (4–)5–10(–12) ovate to linear-elliptical scales as long as or adaxially distinctly longer than the achene body; pericarp densely hairy, sometimes with myxogenic cells, without resin sacs. Nine species, central Asia.

1012. *Ugamia* Pavlov

Ugamia Pavlov, Vestn. Akad. Nauk Kazakhsk. S.S.R. 8: 25 (1950).

Subshrub. Indumentum of basifixed hairs. Leaves alternate, 1–2-pinnatipartite to -pinnatisect. Capitula solitary, on very short, nodding peduncles, discoid. Involucre hemispherical. Phyllaries in 4–5 rows, with narrow to broad, light to dark brown scarious margins. Receptacle flat to hemispherical, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obconical, circular in cross-section, with 5 distinct and 5–10 inconspicuous ribs; apex with a corona of 10–20 narrow, linear-elliptical scales as long as or longer than the achene body; pericarp densely hairy, without myxogenic cells or resin sacs. One species, *U. angrenica* (Krasch.) Tzvelev, central Asia.

XVI.8. Handelia Group (1013–1017)

1013. *Handelia* Heimerl

Handelia Heimerl, Oesterr. Bot. Z. 71: 215 (1922).

Basally woody, hapaxanthic, biennial to perennial herb with one to few thick stems filled with soft pith. Indumentum of basifixed hairs. Leaves alternate, up to 3-pinnatisect. Capitula numerous, in dense corymbs, discoid. Involucre hemispherical to spherical. Phyllaries in 3 rows, with broad, pale scarious margins. Receptacle hemispherical, paleate; paleae narrowly elliptical to linear, moderately canaliculate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes cylindrical to narrowly obovoid, circular to elliptical in cross-section, with 5 inconspicuous ribs; apex with a short, abaxially more-developed rim; pericarp with myxogenic cells, without resin sacs. $x = 9$. One species, *H. trichophylla* (Schrenk) Heimerl, Afghanistan, Pakistan, central Asia, China.

1014. *Lepidolopsis* Poljakov

Lepidolopsis Poljakov, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 19: 374 (1956).

Basally woody, pollacanthic, perennial herb with one to few rather thick stems filled with soft pith. In-

dumentum of basifixed hairs. Leaves alternate, 2–3-pinnatisect. Capitula numerous, in a long panicle, shortly pedunculate, discoid. Involucre hemispherical. Phyllaries in 3–4 rows, the inner with broad, pale scarious margins. Receptacle hemispherical to conical, epaleate. Florets hermaphrodite, fertile; corolla (4–)5(–6)-lobed, yellow. Achenes narrowly obovoid, circular in cross-section, with 5 conspicuous ribs; apex with a slanted corona of abaxially prolonged, dentate to laciniate scales; pericarp without myxogenic cells or resin sacs. $x = 9$. One species, *L. turkestanica* (Regel & Schmalh.) Poljakov, Iran, Afghanistan, central Asia.

1015. *Polychrysum* (Tzvelev) Kovalevsk.

Polychrysum (Tzvelev) Kovalevsk. in Vvendensky, Fl. Uzbek. 6: 148 (1962).

Basally woody, monocarpic, perennial herb with usually one, rarely 2–3 rather thick stems filled with soft pith. Indumentum of basifixed hairs. Leaves alternate, 3–4-pinnatisect. Capitula numerous, in a large and dense corymb, discoid. Involucre hemispherical to spherical. Phyllaries in 2–3 rows, the inner with broad, pale scarious margins. Receptacle flat to hemispherical, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes narrowly cylindrical, circular in cross-section, with 5–7 ribs; apex with an irregularly dissected corona of many acute lobes; pericarp without myxogenic cells or resin sacs. $x = 9$. One species, *P. tadshikorum* (Kudr.) Kovalevsk., Afghanistan, central Asia.

1016. *Pseudohandelia* Tzvelev

Pseudohandelia Tzvelev in Komarov, Fl. U.R.S.S. 26: 878 (1961).

Basally woody, hapaxanthic, biennial to perennial herb with usually one, rarely 2–4 thick stems filled with soft pith. Indumentum of basifixed hairs. Leaves alternate, 2–3-pinnatisect. Capitula numerous, in a dense corymb or pseudo-umbel, discoid. Involucre hemispherical. Phyllaries in 2–3 rows, the outer and middle with broad, the inner with narrow, pale scarious margins. Receptacle hemispherical to conical, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes narrowly cylindrical, arcuate, circular in cross-section, with 4–5 inconspicuous ribs; apex ecoronate; pericarp tuberculate, with myxogenic cells, without resin sacs. One species, *P. umbellifera* (Boiss.) Tzvelev, Iran, Afghanistan, central Asia, China.

1017. *Sclerorhachis* (Rech. f.) Rech. f.

Sclerorhachis (Rech. f.) Rech. f., Anz. Österr. Akad. Wissensch., Math. Naturwissensch. Kl. 105: 242 (1969).

Monocarpic or pollacanthic, biennial to perennial herbs with one to few rather thick stems filled with soft pith. Indumentum of basifixed hairs. Leaves alternate, but often basally crowded, 3–4-pinnatisect, with a sclerified, persistent rhachis. Capitula in lax corymbs, discoid. Involucre hemispherical, umbonate. Phyllaries in 2–4 rows, with pale scarious margins. Receptacle flat to hemispherical, paleate; paleae persistent to readily deciduous, subulate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid, circular in cross-section, with 4–7 inconspicuous ribs; apex ecoronate; pericarp with myxogenic cells, without resin sacs. $x = 9$. Four species, Iran, Afghanistan.

1018. *Hippolytia* Poljakov

Hippolytia Poljakov, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 18: 288 (1957).

Perennial herbs. Indumentum of medifixed hairs. Leaves alternate, 2–3-pinnatipartite to -pinnatisect. Capitula rarely solitary, usually numerous (2–15), in lax to dense corymbs, shortly pedunculate to subsessile, discoid. Involucre hemispherical. Phyllaries in 2–3 rows, the outer with narrow, the inner with broad, pale to dark brown or blackish scarious margins. Receptacle flat to hemispherical, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow; anthers basally caudate. Achenes cylindrical to narrowly obovoid, circular in cross-section, with 5–8 inconspicuous ribs; apex with a more or less distinct, rounded rim; pericarp glabrous, without myxogenic cells, sometimes with longitudinal resin canals. $x = 9$. Nineteen species, central Asia, Mongolia, China, Himalaya.

1019. *Kaschgaria* Poljakov

Kaschgaria Poljakov, Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 18: 282 (1957).

Subshrubs. Indumentum of stellate hairs. Leaves alternate, entire or few-lobed. Capitula rather small and few in an elongated panicle, at the summit fasciculate, disciform. Involucre cylindrical. Phyllaries in 2–4 rows, with scarious margins. Receptacle conical, epaleate. Outer florets female,

tapering above; corolla 2–3-lobed, with stellate hairs. Central florets hermaphrodite, fertile; corolla 5-lobed, yellow, apically with stellate hairs. Achenes obovoid; apex marginally rounded; pericarp without myxogenic cells or resin sacs. $x = 9$. Two species, Mongolia, Kazakhstan, China.

1020. *Lepidolopha* C. Winkl.

Lepidolopha C. Winkl., Trudy Imp. S.-Peterburgsk. Bot. Sada 13: 236 (1894).

Shrublets with basally woody, virgate and sometimes leafless stems. Indumentum of medifixed hairs. Leaves alternate, sometimes crowded basally or fasciculate on brachyblasts, entire or 3-lobed. Capitula solitary or numerous in lax to dense corymbs, on short to long peduncules, discoid. Involucre cylindrical to obconical. Phyllaries in 4–7 rows, with narrow, pale scarious margins. Receptacle flat to hemispherical, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obconical, round in cross-section, with 6–10 ribs; apex with a corona formed by 8–10 linear-elliptical scales; pericarp glabrous, without myxogenic cells or resins sacs. $x = 6, 8$. Nine species, central Asia.

1021. *Leucanthemella* Tzvelev

Leucanthemella Tzvelev in Komarov, Fl. U.R.S.S. 26: 137 (1961).
Decaneurum Sch. Bip. (1844), non DC. (1833).

Perennial herbs. Indumentum absent or of basifixed and medifixed hairs. Leaves alternate, entire or serrate, glandular-punctate. Capitula solitary or in lax corymbs, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 2–3 rows, with brown scarious margins. Receptacle convex, epaleate. Ray florets female, sterile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes narrowly obovoid, slightly curved or straight, with 8–12 ribs; apex with a marginal rim; pericarp without myxogenic cells or resin sacs. $x = 9$. Two species, eastern Europe (Slovakia, Ukraine, Bulgaria, Romania, Yugoslavia, Hungary), Far East (Mongolia, China, Korea, Japan). Widely cultivated as ornamentals.

1022. *Microcephala* Pobed.

Microcephala Pobed., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 21: 356 (1961); Podlech, Mitt. Bot. Staatssamml. München 12: 655–682 (1976), rev.

Annual herbs. Indumentum of basifixed hairs. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, radiate or discoid. Involucre hemispherical. Phyllaries in 2–3 rows, with broad pale scarious margins. Receptacle conical, hollow, epaleate. Ray florets female, fertile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow or reddish. Achenes circular to slightly dorsiventrally flattened in cross-section, with 3–5 adaxially arranged ribs; apex with a lacerate or fimbriate, adaxially somewhat longer corona; pericarp with myxogenic cells abaxially and on the ribs, adaxially between the ribs with unbranched hairs of 3–8 cells with spiral cell wall thickenings. $x = 7$. Five species, central Asia, Afghanistan, Iran, Pakistan, Mongolia, China.

1023. *Nipponanthemum* Kitam.

Nipponanthemum Kitam., Acta Phytotax. Geobot. 29: 168 (1978).

Glabrous shrub. Leaves alternate, crowded at the end of the woody branches, serrate. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with pale brown scarious margins. Receptacle convex, epaleate. Ray florets female, fertile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes narrowly obovoid,slightly curved or straight, with c. 10 ribs; apex with a lacerate corona or with small scales; pericarp without myxogenic cells or resin sacs. $x = 9$. One species, *N. nipponicum* (Franchet ex Maxim.) Kitam., Japan.

1024. *Opisthopappus* C. Shih

Opisthopappus C. Shih, Acta Phytotax. Sin. 17: 110 (1979).

Perennial herbs with basally woody stems. Indumentum of basifixed hairs. Leaves alternate, 1–2-pinnatisect. Capitula solitary or 2–3 in lax corymbs, pedunculate, radiate. Involucre hemispherical. Phyllaries in 3–4 rows, with broad membranous margins. Receptacle hemispherical to conical, epaleate. Ray florets female, fertile; limb white or pinkish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid, with 3–5 ribs; apex with a corona of 4–6 separate, mainly abaxial subulate scales of unequal length; pericarp with myxogenic cells, without resin sacs. Two species, China.

1025. ***Stilpnolepis*** Krasch.

Stilpnolepis Krasch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 9: 207 (1946).

Annual herb. Indumentum of medifixed hairs. Leaves opposite or alternate, pinnatisect, few-lobed or entire. Capitula in lax corymbs, pedunculate, nodding, discoid. Involucre hemispherical to urceolate. Phyllaries in 4–5 rows, the outer ovate and with broad scarious margins, the inner broadly elliptical to obovate, completely scarious. Receptacle convex to subconical, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow, with a distinct tube and a broadened, crateriform limb. Achenes narrowly obovoid, without ribs; apex truncate to marginally rounded; pericarp thin, with longitudinal rows of myxogenic cells, without resin sacs. One species, *S. centiflora* (Maxim.) Krasch., Mongolia, China.

1026. ***Tanacetopsis*** (Tzvelev) Kovalevsk.

Tanacetopsis (Tzvelev) Kovalevsk. in Schreder, Fl. Uzbek. 6: 138 (1962).

Perennial herbs or subshrubs. Indumentum of basifixed and medifixed hairs. Leaves alternate, 1–4-pinnatsect. Capitula rarely solitary, usually numerous (2–40), in lax to dense corymbs, discoid, pedunculate. Involucre hemispherical. Phyllaries in 2–3 rows, the outer with narrow, the inner with broad, pale to dark brown or blackish scarious margins. Receptacle hemispherical, glabrous or sparsely hairy, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow, usually glabrous, rarely hairy. Achenes obconical, circular in cross-section, with 5–7 ribs; apex with an often oblique, adaxially more-developed corona formed by free or basally united scales of various shapes; pericarp glabrous, usually with myxogenic cells, without resin sacs. Twenty-three species, Iran, Afghanistan, central Asia.

1027. ***Turaniphytum*** Poljakov

Turaniphytum Poljakov in Komarov, Fl. U.R.S.S. 26: 880 (1961).

Perennial herbs, somewhat woody at base. Indumentum of basifixed and medifixed hairs. Leaves alternate or rosulate, pinnatisect. Capitula disciform; synflorescence a spike of glomerules with densely congested capitula, or rarely capitula solitary in interrupted, partly congested spikes. Involucre cylindrical. Phyllaries in 3 rows, with broad hyaline scarious margins. Receptacle convex to hemispherical, epaleate. Outer florets female, subtended by scaphoid inner involucral bracts; corolla unequally crenate at the apex. Central florets functionally male; corolla 5-lobed, apically with long rigid somewhat reddish hairs. Achenes obliquely oblong-obovoid; apex marginally rounded; pericarp with rows of myxogenic cells, without resin sacs. $x = 9$ (polyploidy). Two species, Turkmenistan, Iran, Afghanistan, Kazakhstan.

XVI. Group C [Eurasian Grade]

XVI.9. Achillea Group (1028–1032)

1028. ***Achillea*** L.

Achillea L., Sp. Pl.: 896 (1753).
Millefolium Mill. (1754).
Ptarmica Mill. (1754).
Arthrolepis Boiss. (1849).

Perennial herbs and subshrubs. Indumentum of basifixed, sometimes asymmetrically medifixed hairs. Leaves alternate, rarely entire, usually dentate to 4-pinnatisect, sometimes vermiform. Capitula usually in dense corymbs, rarely solitary, pedunculate to subsessile, radiate or rarely discoid. Involucre hemispherical to cylindrical. Phyllaries in 2–3 rows, with pale to black scarious margins. Receptacle flat, hemispherical or conical, rarely much elongated, paleate; paleae ± canaliculate, sometimes with a central resin duct. Ray florets female, fertile; limb white, yellow or pink; tube ± flattened. Disc florets hermaphrodite, fertile; corolla 5-lobed, white, yellow or pink, basally inconspicuously saccate, clasping top of achene. Achenes obovoid, dorsiventrally flattened, with 2 lateral and rarely with 1 additional adaxial rib; apex marginally rounded; pericarp with myxogenic cells on ribs, with or without longitudinal resin sacs. $x = 9$ (polyploidy). Circa 115 species, Europe, Asia, northern Africa. Some species naturalised in North America, Australia, New Zealand, South Africa.

1029. ***Anacyclus*** L.

Anacyclus L., Sp. Pl.: 892 (1753); Humphries, Bull. Brit. Mus. (Nat. Hist.), Bot. 7: 83–142 (1979), rev.
Cyrtolepis Less. (1831).

Annual or perennial herbs. Indumentum of basifixed hairs. Leaves alternate, 1–3-pinnatisect, flat to terete. Capitula solitary or in lax corymbs,

sometimes densely aggregated, discoid or radiate; peduncles sometimes inflated at maturity. Involucre hemispherical or obconical. Phyllaries in 3 rows, with narrow to broad, light to dark brown scarious margins. Receptacle flat to conical, paleate; paleae obcuneate to obovate, flat or canaliculate. Ray florets female, fertile; limb white or yellow, sometimes abaxially red; tube flattened, persistent on achenes. Disc florets hermaphrodite, fertile; corolla yellow, actinomorphic to zygomorphic with 2 larger, cucullate lobes, basally flattened and very slightly saccate. Achenes obconical, dorsiventrally flattened, with 2 lateral wing-like ribs; apex sometimes with a narrow marginal corona or a thin, lacerate appendage; pericarp with small myxogenic cells, without resin sacs. $x = 9$. Twelve species, northern Africa, southern Europe, Near East.

1030. *Heliocauta* Humphries

Heliocauta Humphries, Bot. Notiser 130: 155 (1977).

Perennial, creeping herb. Indumentum of basifixed hairs. Leaves in a basal rosette, 3-pinnatisect. Capitula solitary, pedunculate, discoid. Involucre hemispherical. Phyllaries in 3 rows, with laterally pale to light brown, apically dark brown scarious margins. Receptacle conical, paleate; paleae narrowly elliptical to narrowly obovate, moderately canaliculate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes narrowly obovoid, somewhat dorsiventrally flattened, circular to elliptical in cross-section, 4–5-ribbed with 2 distinct lateral ribs; apex with a minute corona formed by a dentate rim; pericarp without myxogenic cells, with elongated resin sacs. $x = 9$. One species, *H. atlantica* (Litard. & Maire) Humphries, northern Africa.

1031. *Leucocyclus* Boiss.

Leucocyclus Boiss., Diagn. Pl. Orient., ser. I, 11: 13 (1849).

Perennial herb. Indumentum of basifixed hairs. Leaves alternate, 2-pinnatisect, vermiform. Capitula solitary, long-pedunculate, radiate; peduncles slightly inflated at maturity. Involucre hemispherical. Phyllaries in 3 rows, sometimes with dark brown tips. Receptacle flat to convex, paleate; paleae linear-elliptical. Ray florets female, fertile; limb white, oblong to subrotund; tube flattened, basally saccate and both adaxially and abaxially clasping top of achene. Disc florets hermaphrodite, fertile; corolla yellow, basally clasping top of achene. Achenes dorsiventrally flattened, with two lateral wing-like ribs; apex marginally rounded; pericarp thin on faces, thick and sclerenchymatic in ribs. One species, *L. formosus* Boiss., Turkey.

1032. *Otanthus* Hoffmanns. & Link

Otanthus Hoffmanns. & Link, Fl. Portug. 2: 364 (1834).
Diotis Desf. (1799), non Schreber (1791).
Neesia Spreng. (1818), nom. rej., non Blume (1835), nom. cons.

Densely sericeous, greyish-white, suffruticose perennial. Indumentum of basifixed hairs. Leaves alternate, entire to dentate, ± succulent. Capitula in dense corymbs, pedunculate to subsessile, discoid. Involucre hemispherical. Phyllaries in 3 rows, almost without scarious margins. Receptacle convex, paleate; paleae ± canaliculate, with a central resin duct. Florets hermaphrodite, fertile; corolla 5-lobed, yellow, basally conspicuously swollen, laterally clasping upper half of achene or more; basal part persistent on achenes. Achenes obovoid, round to tetragonal, with 4–5 weak ribs; apex marginally rounded; pericarp without myxogenic cells or resin sacs. $x = 9$. One species, *O. maritimus* (L.) Hoffmanns. & Link, Europe, northern Africa, south-western Asia.

XVI.10. Anthemis Group (1033–1038)

1033. *Anthemis* L.

Anthemis L., Sp. Pl.: 893 (1753); Benedí I González, Thesis Barcelona (1987); Georgiou, Thesis Patras (1990); Ghafoor & Al Turki, Candollea 52: 457–474 (1997); Oberprieler, Bocconea 9: 1–328 (1998); Ghafoor & Ali, Comp. Newslett. 38: 1–41 (2002), rev.
Maruta (Cass.) Gray (1821).
Lyonnetia Cass. (1825).
Ammanthus Boiss. & Heldr. ex Boiss. (1849).

Annuals, biennials, or short- to long-lived perennial herbs and subshrubs. Indumentum of medifixed hairs. Leaves alternate, dentate to lobed or 1–3-pinnatisect. Capitula solitary or in lax corymbs, pedunculate, discoid or radiate; peduncles sometimes inflated or curved at maturity. Involucre hemispherical or obconical, sometimes umbonate. Phyllaries in 3–5 rows, with pale to brown or black scarious margins. Receptacle hemispherical or conical to narrowly conical, paleate or epaleate marginally or totally; paleae subulate or elliptical to obovate, flat. Ray florets (when present) female and fertile, or neuter; limb

white, yellow or pink; tube sometimes hairy. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, rarely pink, sometimes hairy. Achenes obovoid to obconical, circular or quadrangular in cross-section, usually with c. 10 smooth or tuberculate ribs, rarely without distinct ribs; apex with a shallow, often adaxially more-developed corona or auricle, or ecoronate; pericarp with small myxogenic cells; epicarpic cells with crystal sand. $x = 9$ (polyploidy). Circa 175 species, Europe, south-western Asia, northern and eastern Africa. Naturalised in North America, Australia, New Zealand, South Africa.

1034. *Cota* J. Gay

Cota J. Gay in Gussone, Fl. Sicul. Syn. 2: 866 (1845).

Annuals, biennials, or short- to long-lived perennial herbs. Indumentum of medifixed hairs, rarely of basifixed hairs. Leaves alternate, 1–3-pinnatisect; segments often pectinately divided. Capitula solitary or laxly corymbose, radiate or discoid, pedunculate; peduncles slender or inflated at maturity. Involucre hemispherical or obconical, sometimes umbonate. Phyllaries in 3–5 rows, with pale to dark scarious margins, often cartilaginous. Receptacle hemispherical, paleate; paleae elliptical to obovate, flat, often cartilaginous, persistent. Ray florets (when present) female, fertile; limb white, yellow or pinkish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow or pinkish. Achenes obconical, dorsiventrally flattened, with prominent lateral ribs, smooth or with 3–10 ribs on each face; apex with a rounded rim or a short corona; pericarp with small myxogenic cells; epicarpic cells without or with single, octahedral or prismatic crystals. $x = 9$ (polyploidy). Forty species, Europe, south-western Asia, northern Africa.

1035. *Gonospermum* Less.

Gonospermum Less., Syn. Gen. Comp.: 263 (1832).
Lugoa DC. (1838).

Basally woody perennial herbs and shrubs. Indumentum of medifixed hairs. Leaves alternate, 1–2-pinnatipartite to -pinnatisect. Capitula in lax to dense corymbs, pedunculate, discoid or radiate. Involucre obconical to hemispherical. Phyllaries in 2–4 rows, with rather narrow, pale to dark brown scarious margins. Receptacle hemispherical, paleate; paleae narrowly elliptical, moderately canaliculate. Ray florets (when present) female, fertile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes cylindrical to narrowly obovoid, circular in cross-section, with 5 conspicuous ribs; apex with a corona of 5 teeth projecting from the ribs; pericarp without myxogenic cells or resin sacs. $x = 9$. Five species, Canary Islands.

1036. *Nananthea* DC.

Nananthea DC., Prodr. 6: 45 (1838).

Small annual herb; glabrous, sometimes with some basifixed hairs. Leaves alternate, 3–5-lobed, with a long petiole, succulent. Capitula very small, solitary, pedunculate, radiate or disciform. Involucre hemispherical. Phyllaries in 1–2 rows, with broad, pale scarious margins. Receptacle conical, epaleate. Ray florets female, fertile; limb white or reduced. Disc florets hermaphrodite, fertile; corolla 4-lobed, yellow. Achenes obovoid, circular in cross-section, with c. 8 inconspicuous ribs; apex marginally rounded; pericarp with large myxogenic cells, without resin sacs. $x = 9$. One species, *N. perpusilla* (Loisel.) DC., southern Europe (Corsica, Sardinia).

1037. *Tanacetum* L.

Tanacetum L., Sp. Pl.: 843 (1753).
Balsamita Mill. (1754).
Pyrethrum Zinn (1757).
Gymnocline Cass. (1816).
Omalanthus Less. (1832), non Juss. (1824).
Omalotes DC. (1838).
Psanacetum (Necker ex Less.) Spach (1841).
Hemipappus K. Koch (1851).
Spathipappus Tzvelev (1961).
Poljakovia Grubov & Filat. (2001).

Perennial herbs, rarely annuals or subshrubs. Indumentum absent or of basifixed and/or medifixed, sometimes stellate hairs. Leaves alternate, rarely entire or dentate, usually 1–3-pinnatipartite to -pinnatisect. Capitula solitary or in lax to dense corymbs, pedunculate to subsessile, radiate, disciform or discoid. Involucre hemispherical. Phyllaries in 3–5 rows, with narrow to broad, pale to brown or blackish scarious margins. Receptacle flat to hemispherical, epaleate, rarely paleate. Ray florets female or neuter, fertile or sterile; limb yellow, white or pink. Disc florets all hermaphrodite or (in disciform capitula) the outer female, fertile; corolla 5-lobed, yellow. Achenes obconical or

cylindrical, circular in cross-section, with 5–10(–15) ribs; apex marginally rounded or with a short to well-developed, entire or dentate corona, rarely with an adaxial auricle; pericarp without myxogenic cells or resin sacs. $x = 9$ (polyploidy). Circa 160 species, Europe, Asia, northern Africa, North America. Some species widely cultivated.

1038. *Tripleurospermum* Sch. Bip.

Tripleurospermum Sch. Bip., Tanaceteen: 31 (1844).
Gastrosulum Sch. Bip. (1844).
Rhytidospermum Sch. Bip. (1844).
Dibothrospermum Knaf (1846).
Trallesia Zumag. (1849).

Annual or perennial herbs. Indumentum absent or of basifixed hairs. Leaves alternate, 1–3-pinnatisect. Capitula solitary or in corymbs, pedunculate, discoid, disciform or radiate. Involucre hemispherical to cup-shaped. Phyllaries in 2–5 rows, with narrow to broad pale to brown or black scarious margins. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb white or sometimes pale pink. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow or greenish, lobes usually with a resin sac. Achenes triquetrous with 1 adaxial and 2 lateral ribs and sometimes 1–2 abaxial ribs, often rugose or tuberculate abaxially and between ribs; apex with a corona, an adaxial auricle, or with few scales, sometimes marginally rounded; pericarp sometimes with myxogenic cells, with (1–)2(–3–5) abaxial-apical resin sacs. $x = 9$ (polyploidy). Forty species, Europe, northern Africa, temperate Asia, North America. One species widespread as a weed.

1039. *Brocchia* Vis.

Brocchia Vis. in Spongia, Comment. Med. 2: 218 (1836).

Annual herb. Indumentum of basifixed hairs. Leaves alternate, pinnatipartite to pinnatisect, sometimes entire to lobed. Capitula solitary or in lax corymbs, discoid, pedunculate. Involucre hemispherical. Phyllaries in 2 rows, with narrow, pale membranous margins. Receptacle hemispherical to conical, epaleate. Disc florets hermaphrodite, fertile; corolla yellow, apically 4-lobed. Achenes obovoid, circular in cross-section, with c. 4 inconspicuous lateral and adaxial ribs; apex slanting, marginally rounded; pericarp with large, elongated myxogenic cells, without resin sacs. $x = 9$. One species, *B. cinerea* (Del.) Vis., northern Africa, Near East.

XVI.11. Leucanthemopsis Group (1040–1043)

1040. *Castrilanthemum* Vogt & Oberprieler

Castrilanthemum Vogt & Oberprieler, Anales Jard. Bot. Madrid 54: 342 (1996).

Annual herb. Indumentum of medifixed hairs. Leaves alternate, 1–2-pinnatisect. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with broad brown scarious margins. Receptacle convex, epaleate. Ray florets female, fertile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow with reddish lobes. Achenes obovoid, with 10 ribs; apex marginally rounded; pericarp with myxogenic cells along the ribs, without resin sacs. $x = 9$. One species, *C. debeauxii* (Degen, Hervier & É. Rev.) Vogt & Oberprieler, south-western Europe (Spain).

1041. *Hymenostemma* Willk.

Hymenostemma Willk., Bot. Zeitung 22: 253 (1864).

Annual herb. Indumentum of medifixed hairs. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with light brown scarious margins. Receptacle convex, epaleate. Ray florets female, sterile; limb white, yellow at base. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid, with 5–7 ribs; apex with a scarious corona; pericarp with myxogenic cells along the ribs, without resin sacs. $x = 9$. One species, *H. pseudanthemis* (Kunze) Willk., south-western Europe (Spain).

1042. *Leucanthemopsis* (Giroux) Heywood

Leucanthemopsis (Giroux) Heywood, Anales Inst. Bot. Cavanilles 32: 181 (1975); Heywood, Anales Inst. Bot. Cavanilles 12: 313–374 (1954, under *Tanacetum* L.); Heywood, Anales Inst. Bot. Cavanilles 32: 175–187 (1975), rev.

Perennial herbs, sometimes woody at base. Indumentum of medifixed hairs. Leaves alternate, serrate-dentate to pinnatisect. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with pale to dark brown scarious margins. Receptacle convex, epaleate. Ray florets female, fertile; limb yellow, white, white with yellow base, or reddish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, lobes sometimes reddish. Achenes narrowly

obovoid, with (3–)5–10 ribs; apex with a scarious corona; pericarp with myxogenic cells along the ribs, without resin sacs. $x = 9$ (polyploidy). Nine species, central, southern and eastern Europe, north-western Africa (Morocco).

1043. *Prolongoa* Boiss.

Prolongoa Boiss., Voy. Bot. Espagne: 320 (1840), nom. cons.

Annual herb. Indumentum of medifixed hairs. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with broad whitish scarious margins. Receptacle convex, epaleate. Ray florets neuter, sterile; limb yellow. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid, slightly dorsiventrally compressed, with 1 adaxial and 2 lateral and 2 abaxial ribs; apex marginally rounded, in sterile ray achenes with a scarious corona; pericarp with myxogenic cells along the ribs, without resin sacs. $x = 9$. One species, *P. hispanica* G. López & C.E. Jarvis, south-western Europe (Spain).

1044. *Matricaria* L.

Matricaria L., Sp. Pl.: 890 (1753); Gen. Pl., ed. 5.: 380 (1754).
Chamomilla Gray (1821).
Lepidotheca Nutt. (1841).
Lepidanthus Nutt. (1841), non Nees (1830).
Cenocline Koch (1843).
Akylopsis Lehm. (1852).
Cotulina Pomel (1874).

Annual herbs. Indumentum absent or of basifixed hairs. Leaves alternate, pinnatisect. Capitula solitary or in lax corymbs, pedunculate, disciform or radiate. Involucre hemispherical to cup-shaped. Phyllaries in 2–3 rows, with broad pale or brown scarious margins. Receptacle conical, hollow, epaleate. Ray florets female, fertile; limb white, sometimes reduced. Disc florets hermaphrodite, fertile; corolla 4–5-lobed, yellow or greenish. Achenes obovoid-oblong, circular to slightly dorsiventrally flattened in cross-section, with 3–5 adaxially arranged ribs; apex marginally rounded or with a small corona, in ray achenes sometimes with adaxially longer corona; pericarp with myxogenic cells abaxially and on the ribs, lateral ribs sometimes with resin canals. $x = 9$ (polyploidy). Six species, Europe, northern Africa, Macaronesia, western, south-western and central Asia, western North America. Some species widespread as weeds.

1045. *Phalacrocarpum* (DC.) Willk.

Phalacrocarpum (DC.) Willk., Bot. Zeitung 22: 252 (1864); Nieto Feliner, Anales Jard. Bot. Madrid 39: 53–60 (1982), rev.

Perennial herb. Indumentum of medifixed hairs. Leaves opposite, sheathing at base, serrate-dentate to bipinnatisect. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with dark brown scarious margins. Receptacle convex, sometimes hairy, epaleate. Ray florets female, fertile, white or reddish. Disc florets hermaphrodite, fertile or functionally male; corolla 5-lobed, yellow. Achenes narrowly obovoid, slightly curved or straight, with 7–9 ribs; apex marginally rounded; pericarp without myxogenic cells or resin sacs. $x = 9$. Two species, south-western Europe (Spain, Portugal).

1046. *Xylanthemum* Tzvelev

Xylanthemum Tzvelev in Komarov, Fl. U.R.S.S. 26: 284, 877 (1961).

Shrublets with basally woody, virgate and sometimes leafless stems. Indumentum of medifixed and basifixed hairs. Leaves alternate, 1–2-pinnatipartite to -pinnatisect. Capitula solitary or numerous in lax corymbs, on long peduncles, discoid. Involucre hemispherical or cylindrical to obconical. Phyllaries in 4–5 rows, the outer with narrow, the inner with broad, dark brown scarious margins. Receptacle flat, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow, sometimes hairy. Achenes obconical, circular in cross-section, with 5–6 distinct ribs; apex with an adaxial auricle or a corona formed by 3–6 adaxial, elliptical scales shorter than the achene body; pericarp glabrous, with myxogenic cells, without resin sacs. $x = 9$ (polyploidy). Eight species, Iran, Afghanistan, central Asia.

rou

XVI. Group D [Mediterranean Clade]

1047. *Aaronsohnia* Warb. & Eig

Aaronsohnia Warb. & Eig, Bull. Agric. Exp. Stat. Tel-Aviv 6: 39 (1927).

Annual herbs. Indumentum of basifixed hairs. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, discoid, disciform or radiate. Involucre hemispherical. Phyllaries in 3–4 rows, with pale scarious margins. Receptacle convex to conical,

epaleate. Ray florets female, fertile or sterile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, lobes sometimes with a central resin sac. Achenes obovoid, circular to slightly dorsiventrally flattened in cross-section; apex with an adaxial, whitish auricle or sometimes marginally rounded; pericarp with myxogenic cells abaxially and sometimes with two lateral resin canals. $x = 9$. Two species, northern Africa, Near East.

XVI.12. Argyranthemum Group (1048–1051)

1048. *Argyranthemum* Webb Fig. 71

Argyranthemum Webb in Webb & Berthelot, Hist. Nat. Iles Canaries 3 (2, 2): 258 (1844); Humphries, Bull. Nat. Hist. Mus., ser. Bot. 5: 147–240 (1976), rev.
Monoptera Sch. Bip. (1844).
Preauxia Sch. Bip. (1844).
Stigmatotheca Sch. Bip. (1844).
Scyphopappus B. Nord. (1976).

Subshrubs. Indumentum absent or of basifixed hairs. Leaves alternate, serrate-dentate to variously dissected. Capitula solitary or in lax corymbs, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 3–4 rows, with broad pale to brown scarious margins. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb white, rarely yellow or reddish. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, rarely with reddish lobes. Achenes of ray florets triquetrous and generally strongly 3-winged, sometimes united into groups, wings sometimes reduced, often apically projected into a corona; achenes of disc florets generally laterally compressed and 2-winged, sometimes terete, sometimes united; apex often with a corona; pericarp without myxogenic cells or resin sacs. $x = 9$. Twenty-four species, Macaronesia (Madeira, Salvage Islands, Canary Islands). Some species widely cultivated as ornamentals.

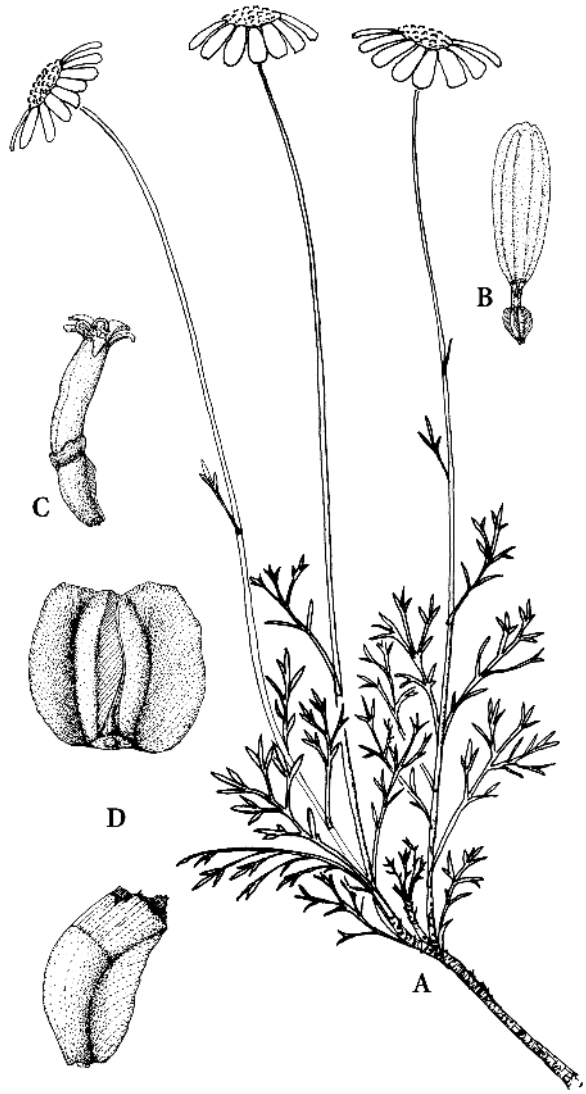

Fig. 71. Compositae-Anthemideae. *Argyranthemum foeniculaceum*. **A** Habit. **B** Ray floret. **C** Tubular floret. **D** Achenes of ray (*above*) and disc florets (*below*). (Drawings by Ch. Oberprieler)

1049. *Glebionis* Cass.

Glebionis Cass. in Cuvier, Dict. Sci. Nat. 41: 41 (1826).
Chrysanthemum sensu auct., non L. (1753) quoad typ. cons.
Xantophtalmum Sch. Bip. (1844).

Annual herbs. Indumentum absent or of basifixed hairs. Leaves alternate, serrate-dentate to 2-pinnatisect. Capitula solitary or in lax corymbs, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 3–4 rows, with broad pale or light brown scarious margins, with resin canals. Receptacle convex, epaleate. Ray florets female, fertile; limb yellow or white with yellow base. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes of ray florets triquetrous and 2–3-winged; achenes of disc florets cylindrical and 10-ribbed or adaxially 1-winged; apex marginally rounded; pericarp without myxogenic cells or resin sacs. $x = 9$. Two species, Europe, northern Africa, Caucasus, south-western Asia, Macaronesia. Widespread as weeds.

1050. *Heteranthemis* Schott

Heteranthemis Schott, Isis (Oken) 1818: 822 (1818).
Pinardia Cass. (1826).

Annual herb. Indumentum of viscid-glandular, basifixed hairs. Leaves alternate, serrate-dentate to pinnatisect. Capitula solitary or in lax corymbs, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with broad pale scarious margins, with resin canals. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb yellow. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes of ray florets triquetrous and 3-winged; achenes of disc florets laterally flattened and 1-winged, wings projected into apical spines; pericarp without myxogenic cells or resin sacs. $x = 9$. One species, *H. viscidehirta* Schott, south-western Europe, north-western Africa, introduced in Palestine.

1051. *Ismelia* Cass.

Ismelia Cass. in Cuvier, Dict. Sci. Nat. 41: 40 (1826).

Annual herb. Indumentum absent or of basifixed hairs. Leaves alternate, pinnatisect. Capitula solitary or in lax corymbs, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with broad whitish scarious margins, with resin canals. Receptacle convex, epaleate. Ray florets female, fertile; limb yellow or white with yellow base. Disc florets hermaphrodite, fertile; corolla 5-lobed, red or purple. Achenes of ray florets triquetrous and 3-winged; achenes of disc florets laterally flattened and 1–2-winged; apex marginally rounded or with a short lacerate corona; pericarp without myxogenic cells or resin sacs. $x = 9$. One species, *I. carinata* (Schousb.) Sch. Bip., north-western Africa (Morocco). Cultivated as an ornamental.

XVI.13. Chamaemelum Group (1052–1056)

1052. *Chamaemelum* Mill.

Chamaemelum Mill., Gard. Dict. Abr., ed. 4: 315 (1754).
Marcelia Cass. (1825).
Perideraea Webb (1838).

Perennial or annual herbs. Indumentum absent or of basifixed hairs. Leaves alternate, 2–3-pinnatisect. Capitula solitary or in lax corymbs, pedunculate, radiate, disciform or discoid. Involucre hemispherical. Phyllaries in 3 rows, flat, with narrow, light or broad, dark brown scarious margins, sometimes deflexed at maturity. Receptacle hemispherical to conical, paleate; paleae flat or slightly canaliculate. Ray florets female, fertile or sterile; limb white, sometimes strongly reduced and hidden by phyllaries. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, basally saccate, laterally clasping the top of achene. Achenes obovoid, round in cross-section, with 2 lateral and 1 adaxial, flimsy ridges; apex marginally rounded; pericarp consisting of large myxogenic cells in longitudinal rows, without resin sacs. $x = 9$. Two species, southern and western Europe, northern Africa.

1053. *Cladanthus* Cass.

Cladanthus Cass., Bull. Sci. Soc. Philom. Paris 1816: 199 (1816).
Ormenis (Cass.) Cass. (1823).

Perennial or annual herbs or subshrubs. Indumentum of basifixed hairs. Leaves alternate, dentate to 2-pinnatisect. Capitula solitary or in lax corymbs, sessile (and then plant branched immediately below capitula) or pedunculate, radiate. Involucre hemispherical. Phyllaries in 3 rows, flat to canaliculate, with broad, light scarious margins. Receptacle hemispherical to narrowly conical, paleate; paleae canaliculate and geniculate, with a central resin duct. Ray florets female, fertile or sterile; limb orange, yellow, or white with a yellow base. Disc florets hermaphrodite, fertile; corolla 5-lobed, orange or yellow, basally strongly saccate, adaxially clasping the upper half or more of achene. Achenes obovoid, round in cross-section, with 2 lateral and 1 adaxial, flimsy ridges; apex slanting, marginally rounded; pericarp consisting of large myxogenic cells in longitudinal rows, without resin sacs. $x = 9$. Five species, southern Europe, northern Africa, south-western Asia.

1054. *Mecomischus* Coss. ex Benth. & Hook. f.

Mecomischus Coss. ex Benth. & Hook. f., Gen. Pl. 2: 418 (1873).
Fradinia Pomel (1874).

Perennial or annual herbs. Indumentum of stellate hairs. Leaves alternate, sometimes basally opposite, entire to lobed. Capitula solitary, long-pedunculate, radiate. Involucre hemispherical, umbonate. Phyllaries in 3 rows, the outer with narrow, the inner with broad, light brown scarious margins. Receptacle hemispherical, paleate; paleae canaliculate, with a central resin duct. Ray flo-

rets neuter, sterile; limb white or yellow. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow, basally slightly saccate, hardly clasping the top of achene. Achenes obovoid, slightly dorsiventrally flattened, with 2 lateral and 1 adaxial, flimsy ridges; apex marginally rounded; pericarp with large myxogenic cells in longitudinal rows, without resin sacs. Two species, north-western Africa.

1055. *Rhetinolepis* Coss.

Rhetinolepis Coss., Bull. Soc. Bot. France 3: 707 (1856).

Annual herb. Indumentum of medifixed hairs. Leaves alternate, entire to palmately lobed. Capitula small, in few-headed corymbs, rarely solitary, shortly pedunculate, discoid. Involucre obconical to urceolate. Phyllaries in 3 rows, flat to canaliculate, with very narrow, light scarious margins; the inner with a central resin duct. Receptacle conical, paleate; paleae canaliculate, somewhat geniculate, with a central resin duct. Florets hermaphrodite, fertile; corolla 5-lobed, yellow, basally inconspicuously saccate, hardly clasping the top of achene. Achenes obovoid, slightly dorsiventrally flattened, with 2 lateral and 1 adaxial, flimsy ridges; apex marginally rounded; pericarp consisting of large myxogenic cells in longitudinal rows, without resin sacs. One species, *R. lonadioides* Coss., northern Africa.

1056. *Santolina* L.

Santolina L., Sp. Pl.: 842 (1753).

Shrublets. Indumentum of medifixed hairs. Leaves alternate, entire to dentate or pinnatisect, sometimes vermiform. Capitula solitary, pedunculate, discoid. Involucre hemispherical, sometimes umbonate. Phyllaries in 3–4 rows, flat to carinate, with light to dark brown or sometimes purple scarious margins. Receptacle hemispherical, paleate; paleae ± canaliculate, with a central resin duct. Florets hermaphrodite, fertile; corolla 5-lobed, yellow to whitish, basally saccate, clasping the apex of achene. Achenes obconical, 3–5-angled, sometimes slightly dorsiventrally flattened; apex marginally rounded; pericarp with or without myxogenic cells, without resin sacs. $x = 9$ (polyploidy). Circa thirteen species, southern Europe, northern Africa.

1057. *Daveaua* Willk. ex Mariz

Daveaua [*Daveana*] Willk. ex Mariz, Bol. Soc. Brot. 9: 206, 220, 243, 258 (1891).

Annual, glabrous herbs. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 3 rows, with dark brown scarious margins. Receptacle conical, epaleate. Ray florets female, fertile or sterile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes of ray florets dorsiventrally flattened, with 3 adaxial ribs, laterally winged, wings projected into apical teeth; apex with an adaxial auricle. Achenes of disc florets obovoid, circular in cross-section, with 5 ribs; apex marginally rounded; pericarp with myxogenic cells and with 3–5 resin sacs apically in the ribs. One species, *D. anthemoides* Mariz, south-western Europe, north-western Africa (Morocco).

1058. *Endopappus* Sch. Bip.

Endopappus Sch. Bip., Bonplandia 8: 369 (1860).

Glabrous annual herb. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 3–4 rows, with pale to brown scarious margins. Receptacle flat to convex, epaleate. Ray florets female, fertile; limb white or yellow. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes dorsiventrally flattened, 3-angled with one adaxial and two lateral ribs; apex with a corona; pericarp with myxogenic cells abaxially and along the ribs, without resin sacs. $x = 9$. One species, *E. macrocarpus* Sch. Bip., northern Africa (Morocco, Algeria, Tunisia, Libya).

1059. *Heteromera* Pomel

Heteromera Pomel, Bull. Soc. Sci. Phys. Algérie 11: 60 (1874).

Annual herbs. Indumentum of basifixed hairs. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 3–4 rows, with light brown to brown scarious margins. Receptacle convex to conical, epaleate. Ray florets female, fertile or sterile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow or basally reddish. Achenes cylindrical to obovoid, circular or dorsiventrally flattened in cross-section, with 3–5 ribs; apex with an adaxially longer scarious corona or auricle, with a short, basally callose corona, or with 5–9 obovate scales; pericarp with myxogenic cells along the ribs and on the abaxial surface, with 3–5 resin canals or apical sacs in the ribs. $x = 9$. Two species, northern Africa.

1060. *Lepidophorum* Neck. ex DC.

Lepidophorum Neck. ex DC., Prodr. 6: 19 (1838).

Annual, glabrous herb. Leaves alternate, serrate. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 3–4 rows, with narrow brown scarious margins. Receptacle convex, paleate; paleae flat to canaliculate, narrowly elliptical to obovate, with a central resin duct. Ray florets female or neuter, sterile; limb yellow. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes of ray florets flat; apex with c. 4 free or basally connate scales. Achenes of disc florets narrowly obovoid, 5-ribbed; apex marginally rounded; pericarp with myxogenic cells along the ribs, without resin sacs. $x = 9$. One species, *L. repandum* (L.) DC., south-western Europe.

XVI.14. Leucanthemum Group (1061–1068)

1061. *Chlamydophora* Ehrenb. ex Less.

Chlamydophora Ehrenb. ex Less., Syn. Gen. Comp.: 265, 448 (1832).

Glabrous annual herb. Leaves alternate or basally opposite, entire or lobed, somewhat succulent. Capitula solitary, pedunculate, discoid. Involucre meniscoid to hemispherical. Phyllaries in 3–4 rows, with light brown, sometimes red-tinged, scarious margins. Receptacle convex, epaleate. Florets hermaphrodite, fertile; corolla (4–)5-lobed, yellow or somewhat reddish. Achenes ellipsoid, with c. 10 ribs; apex with a large scarious and adaxially longer corona; pericarp with myxogenic cells along the ribs and with resin canals between the ribs. $x = 9$. One species, *C. tridentata* (Delile) Ehrenb. ex Less., northern Africa, eastern Mediterranean region.

1062. *Chrysanthoglossum* B.H. Wilcox, K. Bremer & Humphries

Chrysanthoglossum B.H. Wilcox, K. Bremer & Humphries, Bull. Brit. Mus. (Nat. Hist.), Bot. 23: 143 (1993).

Annual, biennial or perennial herbs. Indumentum absent or of basifixed hairs. Leaves alternate, pinnatisect. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with broad whitish to brown, scarious margins. Receptacle convex, epaleate. Ray florets female, sterile or sometimes fertile; limb yellow. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes of ray florets dorsiventrally compressed; apex with a scarious adaxial auricle or marginally rounded. Achenes of disc florets obovoid, with c. 10 conspicuous ribs; apex with a corona with myxogenic cells on the outside; pericarp with myxogenic cells along the ribs and with resin canals between the ribs. $x = 9$. Two species, northern Africa.

1063. *Coleostephus* Cass.

Coleostephus Cass. in Cuvier, Dict. Sci. Nat. 41: 43 (1826).
Myconia Neck. ex Sch. Bip. (1844).
Kremeria Durieu (1846).
Myconella Sprague (1928).

Annual herbs. Indumentum absent or of basifixed hairs. Leaves alternate, serrate-dentate. Capitula solitary or in lax corymbs, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with narrow to broad, whitish or pale brown, scarious margins. Receptacle convex to conical, epaleate. Ray florets female, fertile or sterile; limb yellow, sometimes white with yellow base. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes cylindrical, slightly curved to arcuate, with c. 10 ribs; base adaxially with a prominent whitish callus; apex with a scarious adaxial auricle, a scarious corona, or rarely marginally rounded; pericarp with myxogenic cells along the ribs and with resin canals between the ribs. $x = 9$. Three species, Mediterranean region, Macaronesia.

1064. *Glossopappus* Kunze

Glossopappus Kunze, Flora 29: 748 (1846).

Glabrous annual herb. Leaves alternate, entire to serrate-dentate. Capitula solitary, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 4 rows, with a fleshy central part and apically broad whitish to pale brown, scarious margins. Receptacle conical, epaleate. Ray florets female, fertile or sterile; limb yellow or rarely white with yellow base. Disc florets hermaphrodite, fertile; corolla 5-lobed, actinomorphic or slightly zygomorphic by two lobes having elongate appendages, yellow, basally abaxially saccate and clasping top of achene. Achenes cylindrical, with c. 10 ribs; base adaxially with a prominent, whitish callus; apex with a large scarious adaxial auricle, or rarely marginally rounded; pericarp with myxogenic cells along the ribs and with resin canals between the ribs. $x = 9$. One species, *G. macrotus* (Durieu) Briq. & Cavill., south-western Europe, northern Africa.

1065. *Leucanthemum* Mill.

Leucanthemum Mill., Gard. Dict. Abr., ed. 4: 769 (1754); Vogt, Ruizia 10: 1–261 (1991); Villard, Ber. Schweiz. Bot. Gesell. 80: 96–188 (1970); Horvatic, Acta Bot. Croat. 22: 203–218 (1963), rev.
Phalacrodiscus Less. (1832).

Perennial herbs, rarely subshrubs. Indumentum absent or of basifixed hairs. Leaves alternate, entire, dentate-serrate, lobed, or up to 3-pinnatisect. Capitula solitary or in lax corymbs, pedunculate, radiate or rarely discoid. Involucre meniscoid to hemispherical. Phyllaries in 4–5 rows, with pale to blackish scarious margins. Receptacle flat to convex, epaleate. Ray florets female, fertile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes obovoid to cylindrical, with c. 10 ribs; apex marginally rounded or with a scarious corona, or an adaxial auricle; pericarp with myxogenic cells along the ribs and with resin canals between the ribs. $x = 9$ (polyploidy). Forty-three species, Europe, Siberia. Some species widely cultivated as ornamentals or widespread as weeds.

1066. *Mauranthemum* Vogt & Oberprieler

Mauranthemum Vogt & Oberprieler, Taxon 44: 377 (1995).
Leucoglossum B.H. Wilcox, K. Bremer & Humphries (1993), nom. illegit.

Annual, rarely perennial, glabrous herbs. Leaves alternate, dentate-serrate to 2-pinnatisect. Capitula solitary, pedunculate, radiate. Involucre hemispherical. Phyllaries in 3–4 rows, with pale to dark brown or black scarious margins. Receptacle conical, epaleate. Ray florets female or neuter, fertile or sterile; limb white, rarely yellow at base. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes ellipsoid to obovoid, with c. 10 ribs; apex with a scarious corona, an adaxial auricle, or (in disc achenes) marginally rounded; pericarp with myxogenic cells along the ribs and with resin canals between the ribs. $x = 9$. Four species, south-western Europe, north-western Africa. One species widely cultivated as an ornamental.

1067. *Plagius* L'Hér. ex DC.

Plagius L'Hér. ex DC., Prodr. 6: 135 (1838); Vogt & Oberprieler, Willdenowia 36(Special Issue):47–68 (2006), rev.

Herbaceous or suffruticose perennials. Indumentum absent or of basifixed, sometimes glandular hairs. Leaves alternate, serrate-dentate. Capitula solitary or in lax corymbs, pedunculate, discoid. Involucre meniscoid to hemispherical. Phyllaries in 3–4 rows, with pale to brown scarious margins. Receptacle flat to convex, epaleate. Florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes cylindrical, slightly curved to arcuate, with c. 10 ribs; base adaxially with a prominent, whitish callus; apex with an oblique, adaxially longer corona or marginally rounded; pericarp with myxogenic cells along the ribs, and with resin canals between the ribs. $x = 9$ (polyploidy). Three species, southern Europe (Corsica, Sardinia), northern Africa.

1068. *Rhodanthemum* (Vogt) B.H. Wilcox, K. Bremer & Humphries

Rhodanthemum (Vogt) B.H. Wilcox, K. Bremer & Humphries, Bull. Brit. Mus. (Nat. Hist.), Bot. 23: 141 (1993).

Perennial herbs or subshrubs. Indumentum of basifixed or medifixed hairs. Leaves alternate, rosulate, 1–3-pinnatisect, long-petiolate. Capitula solitary, pedunculate, radiate. Involucre hemispherical. Phyllaries in 3–5 rows, with pale to dark brown scarious margins. Receptacle convex to hemispherical, epaleate. Ray florets female, fertile; limb white, red-violet or rarely yellow. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow or reddish. Achenes narrowly obovoid, straight or slightly curved, with 5–10 often strongly protruding ribs; apex with an often adaxially longer corona; pericarp with myxogenic cells along the ribs and with resin canals between the ribs. $x = 9$. Fourteen species, south-western Europe, north-western Africa.

1069. *Lonas* Adans.

Lonas Adans., Fam. Pl. 2: 118, 572 (1763).

Glabrous annual herb. Leaves alternate, pinnatisect. Capitula in a dense corymb, discoid. Involucre hemispherical to cylindrical. Phyllaries in 3–4 rows, with narrow pale scarious margins. Receptacle narrowly conical, paleate; paleae narrowly obovate, flat to slightly canaliculate, with a central resin canal. Florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes narrowly obovoid, round in cross-section or slightly dorsiventrally flattened, with 1 adaxial and 2 lateral ribs; apex with a scarious corona; pericarp with myxogenic cells abaxially and on the ribs and with a resin sac apically in the adaxial rib. $x = 9$. One species, *L. annua* (L.) Vines & Druce, southern Europe (Italy), northern Africa.

1070. ***Nivellea*** B.H. Wilcox, K. Bremer & Humphries

Nivellea B.H. Wilcox, K. Bremer & Humphries, Bull. Brit. Mus. (Nat. Hist.), Bot. 23: 140 (1993); Vogt & Oberprieler, Bot. J. Linn. Soc. 122: 123–135 (1996), rev.

Annual herb. Indumentum absent or of basifixed hairs. Leaves alternate, lobed and lacerate. Capitula solitary, pedunculate, radiate. Involucre meniscoid and hemispherical. Phyllaries in 4–5 rows, with broad pale brown to brown scarious margins. Receptacle convex, epaleate. Ray florets female, fertile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes narrowly obovoid, slightly curved or straight, with c. 10 ribs; apex marginally rounded; pericarp with myxogenic cells along the ribs, without resin sacs. $x = 9$. One species, *N. nivellei* (Braun-Blanq. & Maire) B.H. Wilcox, K. Bremer & Humphries, north-western Africa (Morocco).

1071. ***Otospermum*** Willk.

Otospermum Willk., Bot. Zeitung 22: 251 (1864).
Otocarpum Willk. (1892).

Glabrous annual herb. Leaves alternate, pinnatisect. Capitula solitary or in a lax corymb, pedunculate, radiate. Involucre meniscoid to hemispherical. Phyllaries in 3–4 rows, with brown scarious margins. Receptacle convex to conical, epaleate. Ray florets female, fertile; limb white. Disc florets hermaphrodite, fertile; corolla 5-lobed, yellow. Achenes basally connate with the receptacle, narrowly obovoid, circular to dorsiventrally flattened in cross-section, with one abaxial, two lateral, and 1–3 adaxial ribs; apex with an adaxial auricle; pericarp with myxogenic cells along the ribs, without resin canals. $x = 9$ (polyploidy). One species, *O. glabrum* (Lag.) Willk., south-western Europe, northern Africa.

XVII. Tribe Inuleae Cass. (1819).

Tribe Plucheeae (Benth.)
A. Anderb. (1989).

A.A. Anderberg and P. Eldenäs

Trees, shrubs, subshrubs, perennial or annual herbs. With elongated or tuberous (*Jasonia*) rhizome. Stems with (e.g. *Doellia*, *Laggera*, *Porphyrostemma*, *Limbarda*, *Rhanterium*, *Telekia* and *Tessaria*) or without resin ducts, generally without fibres in the phloem. Laticiferous tissue absent. Leaves alternate or subopposite, sometimes (*Cylindrocline*, *Monarrhenus*) clustered at branch tips, or confined to a basal rosette (*Rhodogeron*, *Sachsia*), simple or pinnatifid to pinnatisect, entire, serrate or dentate, sometimes fleshy (e.g. *Iphiona* p.p., *Limbarda*), often glandular and hairy with septate hairs (unseptate in *Pterocaulon*); leaf-base sometimes clasping, or conspicuously decurrent on the stem (*Calostephane*, *Geigeria*, *Laggera*, *Ondetia*, *Pterocaulon*). Capitula solitary, in corymbs, panicles, or in more or less pronounced spike-like to spherical secondary heads (*Caesulia*, *Neojeffreya*, *Pseudoblepharispermum*, *Pterocaulon*, *Sphaeranthus* and *Triplocephalum*), heterogamous or homogamous, radiate, disciform or discoid. Involucral bracts generally in many rows, herbaceous or cartilaginous; stereome undivided. Receptacle flat, convex or concave, epaleate or paleate. Female or rarely neuter marginal florets, when present, in one to several rows. Corolla radiate, minutely radiate, tubular or filiform, generally three-lobed, yellow, pink, mauve, purple or white. Cypselas and pappus generally similar to those of disc florets, sometimes flattened. Disc florets perfect or functionally male, 4- or 5-lobed, lobes generally short but sometimes long, yellow, pink, mauve, purple or sometimes white. Anthers ecalcarate or exceptionally calcarate; basally with long or short, branched or unbranched tails, rarely ecaudate; endothecial tissue radial or polarized. Cells of filament collar flattened or mammillose. Pollen caveate; sexine with one baculate layer between the spines and two baculate layers in the spine bases (Leins 1971). Style bifid or undivided; style branches most often with acute sweeping-hairs ending above the furcation or with obtuse sweeping-hairs reaching far below the furcation; stigmatic surface apically confluent and basally separated in two distinct lines, rarely covering the entire inner surface of the style branches. Cypselas generally with five vascular strands, ellipsoid, turbinate or triquetrous, often with sclerenchymatic ribs; sometimes with resiniferous ducts or cavities; glabrous or with glandular hairs and/or elongated non-myxogenic twin-hairs; twin-hairs straight, anchor-shaped or uncinate; epidermal cells with one large elongated oxalate crystal, with crystal sand, or without crystals. Cypselas often much reduced in functionally male florets. Pappus of capillary bristles, capillary bristles and small scales in combination, large scales only, sometimes rim-like or absent.

Inuleae are a mainly Eurasian and East and South African tribe, but some genera (e.g. *Pluchea*) have a worldwide distribution. About 66 genera and 687 species.

Inuleae (incl. Plucheeae) are a monophyletic group most closely related to Heliantheae s.lat., as evidenced by molecular data from the *ndh*F gene of the plastid genome (Kim and Jansen 1995; Eldenäs et al. 1999; Anderberg et al. 2005). The support for this is very robust, although data from morphology (Bremer 1987) and *trn*L/*trn*F (Bayer and Starr 1998) suggest that Inuleae s.lat. are basal in subfamily Asteroideae. The close relationship between Inuleae and Heliantheae is supported also by the fact that genera such as *Blepharispermum*, *Athroisma* and *Anisopappus*, which have always been placed in Inuleae, have been shown to belong to the Heliantheae clade, and not to the Inuleae-Plucheeae group. As they differ considerably from other Heliantheae, experts in that tribe have been reluctant to accept them, and consequently Panero and Funk (2002) placed them in the new tribe Athroismeae. The DNA sequence data from *ndh*F clearly support the separation of Inuleae-Gnaphaliinae into the separate tribe Gnaphalieae (Bremer 1987; Anderberg 1989, 1991a), but the distinction between Inuleae s.str. and Plucheeae as outlined by Anderberg (1989, 1991a, b, c) is more complex. Anderberg et al. (2005) found support for two major monophyletic lineages in the Inuleae-Plucheeae complex. One lineage corresponded to the core Inuleae s.str., with styles having acute sweeping-hairs ending above the furcation, and cypselas provided with one large oxalate crystal in each epidermis cell. The other lineage was Plucheeae, which included all genera placed there by Anderberg (1991c), but also five genera earlier included by him in Inuleae s.str. (Anderberg 1989, 1991b), viz. *Antiphiona*, *Calostephane* (incl. *Mollera*), *Geigeria*, *Ondetia* and *Pegolettia*. These five genera have style branches with acute sweeping-hairs, like the Inuleae s.str., but lack the characteristic, large elongated crystal in the cells of the cypsela epidermis. The monophyly of Inuleae s.str. is robust, but the support for the plucheoid lineage is weak. Since Inuleae and Plucheeae have been found to form a robustly supported clade together, but their interrelationships indicate that the core plucheoid group of genera has evolved from inuloid ancestors, there is little sense in treating them as two separate tribes. Several genera belonging to Inuleae s.lat. have been shown to be polyphyletic as presently circumscribed (Anderberg et al. 2005) but, since no formal reclassification has yet been presented, we have in the following maintained the traditional generic classification, adding notes on the generic status when relevant. The tribal position of some genera has not been confirmed by analysis of molecular data, but most of them are likely to be members of Inuleae as circumscribed here. Only *Nanothamnus* and *Feddea* have tentatively been treated here as members of Inuleae and of uncertain position.

Key to the Genera[10]

1. Cypsela epidermis cells each with one large calcium oxalate crystal. Flowers often yellow, rarely white. Capitula usually with long or short ray florets 2
– Cypsela epidermis cells without crystals or with many small crystals. Flowers often purple, sometimes yellow or whitish. Capitula with or without ray florets 29
2. Receptacle paleate 3
– Receptacle epaleate 12
3. Involucral bracts concrescent into a cupule. Receptacle strongly concave **1088. *Anvillea***
– Involucral bracts not forming a cupule. Receptacle flat or convex 4
4. Paleae villous. Cypselas villous with coiled hairs **1089. *Lifago***
– Paleae not villous. Cypselas glabrous or sparsely hairy 5
5. Leaves up to 50 cm long, petiolate with cordate lamina **1097. *Telekia***
– Leaves much smaller, neither distinctly petiolate nor with cordate lamina 6
6. Inner involucral bracts enclosing outer florets. Pappus of very broad flattened bristles or absent **1079. *Rhanterium***
– Inner involucral bracts not enclosing outer florets 7
7. Leaves with raised reticulate venation. Pappus of flattened bristles **1078. *Rhanteriopsis***
– Leaves not with raised reticulate venation. Pappus of scales or absent 8
8. Capitula homogamous or minutely radiate. Cypselas ellipsoid **1098. *Chrysophthalmum***
– Capitula with well-developed ray florets. Cypselas more or less triquetrous 9
9. Cypselas with chambered secretory cavities along the margins **1091. *Asteriscus***
– Cypselas without chambered secretory cavities along the margins 10
10. Shrub. Leaves needle-shaped, or somewhat dentate **1090. *Ighermia***
– Herbs. Leaves flat, not needle-shaped 11
11. Capitula subtended by a row of leaf-like bracts **1092. *Pallenis***
– Capitula not subtended by leaf-like bracts **1093. *Buphthalmum***

[10] With the exception of genera 1136. *Nanothamnus* Thoms. and 1137. *Feddea* Urb.

12. Pappus of bristles, or of capillary bristles and short scales 13
– Pappus absent 28
13. Pappus of bristles only 14
– Pappus of bristles and short scales 23
14. Pappus bristles of unequal length, in many rows 15
– Pappus bristles more or less equal in length, in one to several rows 16
15. Leaves trifid, pinnatifid, needle-shaped or terete. Disc floret corolla epidermis with long needle-shaped crystals; cell walls sinuous **1085. *Iphiona*** p.p.
– Leaves simple, flat and elliptic. Disc floret corolla epidermis cells without long needle-shaped crystals; cell walls straight **1077. *Vieraea***
16. Leaves conspicuously fleshy, semiterete, sometimes apically tridentate. Cypselas with five secretory ducts **1087. *Limbarda***
– Leaves neither fleshy nor apically tridentate 17
17. Capitula with filiform female florets **1074. *Blumea*** s.str.
– Capitula with only perfect florets, or with radiate female florets 18
18. Anthers with distinctly polarized endothecial tissue 19
– Anthers with radial endothecial tissue 20
19. Cypselas contracted, pappus bristles basally connate into a cupule **1086. *Dittrichia***
– Cypselas not contracted, pappus bristles not forming a cupule **1072. *Duhaldea***
20. Capitula small, few-flowered. Pappus bristles generally few 21
– Capitula larger, many-flowered. Pappus bristles many **1094. *Inula***
21. Leaves terete or almost so, somewhat fleshy **1076. *Schizogyne***
– Leaves flat, not fleshy 22
22. Capitula homogamous, florets perfect. Plants erect with divaricate branches. Leaves lanceolate to narrowly oblong **1100. *Varthemia***
– Capitula generally heterogamous, outer female florets radiate to almost tubular. When all florets perfect, then plants compact and leaves elliptic **1099. *Pentanema***
23. Disc floret epidermis cells with long needle-shaped crystals 24
– Disc floret epidermis cells without long needle-shaped crystals 25
24. Corolla epidermis cell walls sinuous **1085. *Iphiona*** p.p.
– Corolla epidermis cell walls straight **1084. *Perralderia***
25. Shrubs with dichotomously branched stem **1083. *Allagopappus***
– Herbs or normally branched shrubs 26
26. Anthers with radial endothecial tissue **1080. *Pulicaria***
– Anthers with polarized endothecial tissue 27
27. Capitula radiate. Inner involucral bracts not scarious nor ciliate at apex **1081. *Jasonia***
– Capitula discoid. Inner involucral bracts scarious and ciliate at apex **1082. *Chiliadenus***
28. Capitula with short ray florets. Cypselas not contracted into a beak **1095. *Amblyocarpum***
– Capitula with tubular female florets. Cypselas contracted into a beak **1096. *Carpesium***
29. Receptacle paleate 30
– Receptacle epaleate 33
30. Capitula radiate, with yellow, radiate female florets **1106. *Ondetia***
– Capitula discoid, with whitish or pink filiform female florets 31
31. Capitula arranged in spherical secondary heads 32
– Capitula in dense corymbs but not in spherical secondary heads **1112. *Cylindrocline***
32. Pappus of capillary bristles **1124. *Neojeffreya***
– Pappus absent **1127. *Pseudoblepharispermum***
33. Capitula arranged in spherical or spike- or raceme-like secondary heads (many *Pterocaulon* with dense raceme-like or spike-like arrangement of capitula) 34
– Capitula solitary or more or less congested but never arranged in spherical or spike-like secondary heads or dense raceme-like capitulescences 37
34. Pappus of capillary bristles. Secondary heads spike-like or spherical **1111. *Pterocaulon***
– Pappus absent, or a short scale-like rim 35
35. All secondary heads sessile in leaf axils **1073. *Caesulia***
– Secondary heads terminal 36
36. Herbs or subshrubs. Leaves decurrent **1126. *Sphaeranthus***
– Shrub. Leaves not decurrent **1125. *Triplocephalum***
37. Involucral bracts straw-coloured with a dark longitudinal midstripe **1109. *Iphionopsis***
– Involucral bracts not with a dark contrasting longitudinal midstripe 38
38. Delicate perennial herbs with a basal leaf-rosette and a leafless scape with capitula in a terminal corymb 39
– Stems not scapose and with leaves not in a basal rosette 40
39. Capitula discoid **1108. *Sachsia***
– Capitula radiate **1107. *Rhodogeron***
40. Styles with acute sweeping-hairs ending at or above the furcation 41
– Styles with obtuse sweeping-hairs extending down the shaft below the furcation 48
41. Capitula with well-developed yellow ray florets 42
– Capitula without ray florets 43
42. Receptacle with numerous bristles **1105. *Geigeria***
– Receptacle naked, without bristles **1103. *Calostephane***
43. Capitula heterogamous, with filiform outer florets and bisexual or functionally male disc florets 44
– Capitula homogamous with only one kind of functional floret 46
44. Leaves entire. Florets purple **1115. *Pechuel-loeschea***
– Leaves dentate to lobed 45
45. Leaves large and deeply lobed. Disc florets functionally male **1075. *Merrittia***
– Leaves dentate or entire, rarely lobed. Disc florets generally perfect **1074. *Blumea*** p.p.
46. Functionally dioecious shrubs **1110. *Cratystylis***
– Herbs or shrublets with perfect florets 47
47. Leaves pinnatifid or pinnatisect, pappus of barbellate bristles **1102. *Antiphiona***
– Leaves entire or dentate, or if leaves pinnatifid, then pappus plumose **1104. *Pegolettia***
48. Cypselas with conspicuous red resiniferous ducts or cavities 49
– Cypselas without red resiniferous ducts or cavities 50
49. Cypselas with longitudinal resiniferous ducts. Pappus of capillary bristles **1132. *Doellia***

– Cypselas with 2- or 3-celled resiniferous cavities arranged in rows. Pappus absent or a short rim **1133. *Porphyrostemma***
50. Capitula radiate or disciform with minutely radiate or almost tubular female florets 51
– Capitula disciform with filiform female florets 52
51. Leaves broad, florets purple **1134. *Streptoglossa***
– Leaves filiform, florets whitish **1135. *Allopterigeron***
52. Pappus absent, a short rim, or a few scale-like bristles 53
– Pappus of capillary bristles 57
53. Receptacle deeply concave. Pappus absent **1114. *Litogyne***
– Receptacle flat or slightly convex. Pappus absent or of scale-like bristles 54
54. Capitula axillary near the base of the stem. Cypselas with uncinate hairs **1121. *Thespidium***
– Capitula not axillary near the base of the stem. Cypselas not with uncinate hairs 55
55. Pappus absent, or exceptionally of free scale-like bristles **1113. *Epaltes***
– Pappus of scale-like bristles which are connate into tube at base 56
56. Capitula large. Involucral bracts very broad, obtuse **1122. *Coleocoma***
– Capitula small. Involucral bracts not very broad, acute **1123. *Delamerea***
57. Shrubs. Capitula congested into dense corymbs. Leaves confined to the distal part of the branches **1120. *Monarrhenus***
– Trees, shrubs or herbs. Capitula not congested into dense corymbs. Leaves scattered along the stem or branches 58
58. Tree. Capitula heterogamous, with only one functionally male floret. **1119. *Tessaria***
– Shrubs or herbs. Male florets, if present, more than one 59
59. Perennial herbs with decurrent leaves. Anther tails long and branched. Cypselas more than 3 mm long **1101. *Stenachaenium***
– Shrubs or herbs. Cypselas less than 3 mm. Anther tails short or inconspicuous 60
60. Leaves bipinnatifid, anthers ecaudate **1116. *Adelostigma***
– Leaves not pinnatifid, or anthers caudate 61
61. Disc florets functionally male with reduced cypselas. Pappus bristles generally with erecto-patent teeth 62
– Disc florets perfect with developing cypselas. Bristles often with adpressed teeth 63
62. Capitula solitary, terminal and > 1 cm long **1118. *Karelinia***
– Capitula in corymbs, or seldom solitary but then < 1 cm long **1117. *Pluchea***
63. Anthers ecaudate 64
– Anthers caudate **1128. *Pseudoconyza*** and **1074. *Blumea*** p.p.
64. Flowers yellow. Leaves sharply dentate, not decurrent **1129. *Blumeopsis***
– Flowers purple. Leaves often decurrent 65
65. Pappus with numerous bristles **1130. *Laggera***
– Pappus with few bristles **1131. *Nicolasia***

Genera of Inuleae

1072. *Duhaldea* DC.

Duhaldea DC., Prodr. 5: 366 (1836).
Inula L. sect. *Cappa* DC. (1836).

Shrubs or perennial herbs. Leaves alternate, simple, hairy. Capitula heterogamous, radiate or disciform, solitary or in terminal corymbs. Receptacle epaleate, with scale-like ridges. Marginal florets female. Corolla yellow to white, radiate to miutely radiate. Disc florets perfect. Corolla yellow or whitish. Anthers ecalcarate, with branched tails; apical appendix truncate and almost emarginate; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, hairy; epidermis with elongated crystals. Pappus of barbellate, capillary bristles in one row. $2n$ = 18, 20, 40. Fourteen species, Asia, possibly one species in Africa.

1073. *Caesulia* Roxb.

Caesulia Roxb., Pl. Corom. 1: 64. t. 93 (1759).

Annual herb. Leaves alternate, linear-lanceolate, serrate, glabrous. Capitula in dense axillary secondary heads, homogamous, discoid, one-flowered. Involucral bracts two, enclosing the fruit, bracts with resiniferous ducts. Receptacle epaleate. Florets perfect. Corolla whitish, deeply lobed. Anthers ecalcarate, with branched tails; endothecial tissue polarized. Style branches with semi-acute sweeping-hairs not reaching the furcation. Stigmatic area covering almost the entire inner surface. Cypselas dorsiventrally flattened; pericarp one-layered, epidermis crystals missing. Pappus missing (but with two awns formed by the enclosing bracts). One species, *C. axillaris* Roxb., India.

1074. *Blumea* DC.

Blumea DC., Prodr. 5: 447 (1836), nom. cons.; Randeria, Blumea 10: 176–317 (1960), rev.

Shrubs or herbs. Leaves alternate, simple, dentate, serrate or lobed, hairy. Capitula heterogamous, disciform, in loose or dense corymbs or panicles, or more or less solitary. Receptacle epaleate, with scale-like ridges. Marginal florets female, in several rows. Corolla yellow or purple, filiform. Disc florets perfect. Corolla yellow, white or purple. Anthers minutely calcarate, tailed; endothecial tissue radial or polarized. Style branches with acute

sweeping-hairs not reaching the furcation (type) or obtuse sweeping-hairs reaching below the furcation. Cypselas narrowly oblong, hairy, shorter than the corolla; epidermis with elongated crystals (type) or not. Pappus of barbellate, capillary bristles in one row, with patent (type) or adpressed teeth. $2n$ = 16, 18, 20, 22, 30, 32, 36, 44, 48, 54. About 100 species, mainly subtropical and tropical Asia.

Blumea is a heterogeneous assemblage with considerable variation in micromorphological characters. The type of the genus, *B. balsamifera* (L.) DC., shares its characteristics with *Duhaldea* DC. of Inuleae s.str., and the overall similarity between *Blumea balsamifera* and *Duhaldea cappa* (Buch.-Ham. ex D. Don) Pruski & Anderb. is also striking. Molecular data have shown that many other *Blumea* species belong to the same clade as the type and *Duhaldea*, but also that some species belong to other clades than the type. Two former *Blumea* species (now in *Doellia* Sch. Bip.) have obtuse sweeping-hairs reaching below the furcation, and pappus bristles with adpressed teeth, and their floral features more resemble plucheoid genera such as *Pseudoconyza* Cuatr. (*Blumea aurita* (L. f.) DC.). *Blumea gariepina* DC. has acute sweeping-hairs and is closely related to *Antiphiona* Merxm. The relationships with *Merrittia* Merr. are still unclear.

1075. *Merrittia* Merr.

Merrittia Merr., Philip. J. Sci. Bot. 5: 396 (1910).

Herb. Leaves alternate, deeply and acutely lobed, sparsely hairy. Capitula heterogamous, disciform, small, several in loose corymbs. Receptacle epaleate. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers tailed; endothecial tissue radial. Style branches with acute sweeping-hairs reaching below the furcation. Cypselas sparsely hairy. Pappus of free, barbellate, capillary bristles in one row; each bristle with patent teeth. One species, *M. benguetensis* Merr., Philippines.

1076. *Schizogyne* Cass.

Schizogyne Cass., Dict. Sci. Nat. 56: 23 (1828).

Shrubs. Leaves alternate, linear, somewhat fleshy, glabrous or sericeous. Capitula heterogamous, disciform, in dense terminal corymbs. Receptacle epaleate. Marginal florets female. Corolla yellow, minutely radiate to almost tubular. Disc florets perfect. Corolla yellow. Anthers minutely calcarate, with branched tails; endothecial tissue radial. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid; epidermis imbricate, with elongated crystals. Pappus of barbellate, capillary bristles in one row. $2n$ = 18. Two species, Canary Islands.

1077. *Vieraea* Webb & Berth.

Vieraea Webb & Berth., Hist. Nat. Isles Canar. 3, 2: t. 84 (1839).

Shrub. Leaves alternate, coarsely serrate, glabrous, glaucous, fleshy. Capitula heterogamous, radiate, solitary. Receptacle epaleate, smooth. Marginal florets female. Corolla yellow, radiate. Disc florets perfect. Corolla yellow. Anthers ecalcarate, with branched tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid; epidermis with elongated crystals. Pappus of unequal, barbellate, capillary bristles in more than one row. $2n$ = 16. One species, *V. laevigata* Webb & Berth., Canary Islands.

1078. *Rhanteriopsis* S. Rauschert

Rhanteriopsis S. Rauschert, Taxon 31: 557 (1982); Wiklund, Bot. J. Linn. Soc. 95: 27–42 (1987), rev., phylog.
Postia Boiss. & Blanche (1875), nom. illegit.

Subshrubs. Leaves alternate, elliptic, with alveolate surface, hairy. Capitula solitary, heterogamous, radiate or homogamous, discoid. Receptacle paleate; paleae folded. Marginal female florets present or often absent. Corolla yellow, radiate. Disc florets perfect. Corolla yellow. Anthers minutely calcarate, with short tails; endothecial tissue radial. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas subcylindrical; epidermis with elongated crystals. Pappus of few, very broad, flattened bristles in one row. Four species, Middle East.

1079. *Rhanterium* Desf.

Rhanterium Desf., Fl. Atl. 2: 291 (1799); Wiklund, Bot. J. Linn. Soc. 93: 213–246 (1986), rev., phylog.

Shrublets. Leaves alternate, lanceolate, hairy. Capitula solitary, terminal, heterogamous, radiate. Receptacle smooth, paleate; paleae folded. Involucre hemispherical; inner involucral bracts enclosing the outer florets. Marginal florets female.

Corolla yellow, radiate. Disc florets perfect. Corolla yellow. Anthers minutely calcarate, with short tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ribbed; epidermis with elongated crystals. Pappus of very broad, flattened bristles in one row, or absent. $2n = 24$. Three species, North Africa to Middle East.

1080. *Pulicaria* Gaertn.

Pulicaria Gaertn., Fruct. 2: 461 (1791); Gamal-Eldin, Phanerog. Monogr. 14 (1981), reg. rev.; Wagenitz & Gamal-Eldin, Bot. Jahrb. Syst. 104: 91–113 (1983), rev.
Francoeuria Cass. (1825).
Platychaete Boiss. (1845).
Sclerostephane Chiov. (1929).

Shrubs, shrublets, perennial or annual herbs. Leaves alternate, simple, entire to dentate, hairy. Capitula solitary or in more or less dense corymbs, heterogamous, radiate or disciform or homogamous, discoid. Receptacle epaleate, often with with scale-like ridges. Marginal female florets present or absent. Corolla yellow, radiate or minutely radiate. Disc florets perfect. Corolla yellow. Anthers minutely calcarate, with branched tails; endothecial tissue radial. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid to cylindrical, in a few species with a tube-shaped distal outgrowth surrounding the base of the corolla, often apically contracted and glandular, hairy; epidermis cells with elongated crystals. Pappus of barbellate, capillary to more or less flattened bristles in one row with an outer cup of connate scales (one species with bristles only). $2n = 12, 14, 16, 18, 20, 36$. About 85 species, Europe, Africa, Arabia, Asia.

Pulicaria is heterogeneous and not monophyletic as presently circumscribed. Genera such as *Jasonia* Cass. and *Dittrichia* Greuter have been shown to have their closest relatives within *Pulicaria* (Anderberg et al. 2005). The status of *Francoeuria* Cass. also needs to be clarified.

1081. *Jasonia* Cass.

Jasonia Cass., Dict. Sci. Nat. 24: 200 (1822); Brullo, Webbia 34: 289–308 (1979), rev.

Perennial herb with tuberous rhizome. Leaves alternate, simple, lanceolate to linear-lanceolate, hairy. Capitula heterogamous, radiate. Receptacle epaleate, with scale-like ridges. Marginal florets neuter. Corolla yellow, radiate. Disc florets perfect. Corolla yellow. Anthers minutely calcarate, with branched tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, hairy; epidermis with elongated crystals. Pappus of barbellate, capillary bristles in one row with an outer row of small scales. $2n = 18$. One species, *J. tuberosa* DC., Spain.

1082. *Chiliadenus* Cass.

Chiliadenus Cass., Dict. Sci. Nat. 34: 34 (1825); Brullo, Webbia 34: 289–308 (1979), rev.

Perennial herbs or shrublets. Leaves alternate, sessile, ovate to lanceolate, glandular, hairy. Capitula homogamous, discoid, solitary or in dense raceme-like corymbs. Receptacle with scale-like ridges, epaleate. Florets perfect. Corolla yellow. Anthers long, minutely calcarate, with very short tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, hairy, apically constricted and glandular; epidermis with elongated crystals. Pappus of barbellate, capillary bristles in one row with an outer row of narrow scales. $2n = 16, 18$. Ten species, Mediterranean region.

1083. *Allagopappus* Cass.

Allagopappus Cass., Dict. Sci. Nat. 56: 21 (1828).

Shrubs, stem subdichotomously branched. Leaves confined to tips of branches, alternate, glabrous, dentate, viscid. Capitula small, homogamous, discoid, in umbel-like corymbs. Receptacle smooth, epaleate. Florets perfect. Corolla yellow. Anthers minutely calcarate with short tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas elliptic, hairy and apically glandular; epidermis with elongated crystals. Pappus of barbellate capillary bristles in one row with an outer row of narrow scales. $2n = 20$. Two species, Canary Islands.

1084. *Perralderia* Coss.

Perralderia Coss., Bull. Soc. Bot. France 6: 394 (1859); Eldenäs, Bot. J. Linn. Soc. 102: 157–173 (1990), rev., phylog.
Fontquera Maire (1931).

Shrublets or subshrubs. Leaves alternate, somewhat fleshy, pinnatisect to bi- or tripinnatisect; axils with hair tufts. Capitula heterogamous, radiate or homogamous, discoid. Receptacle

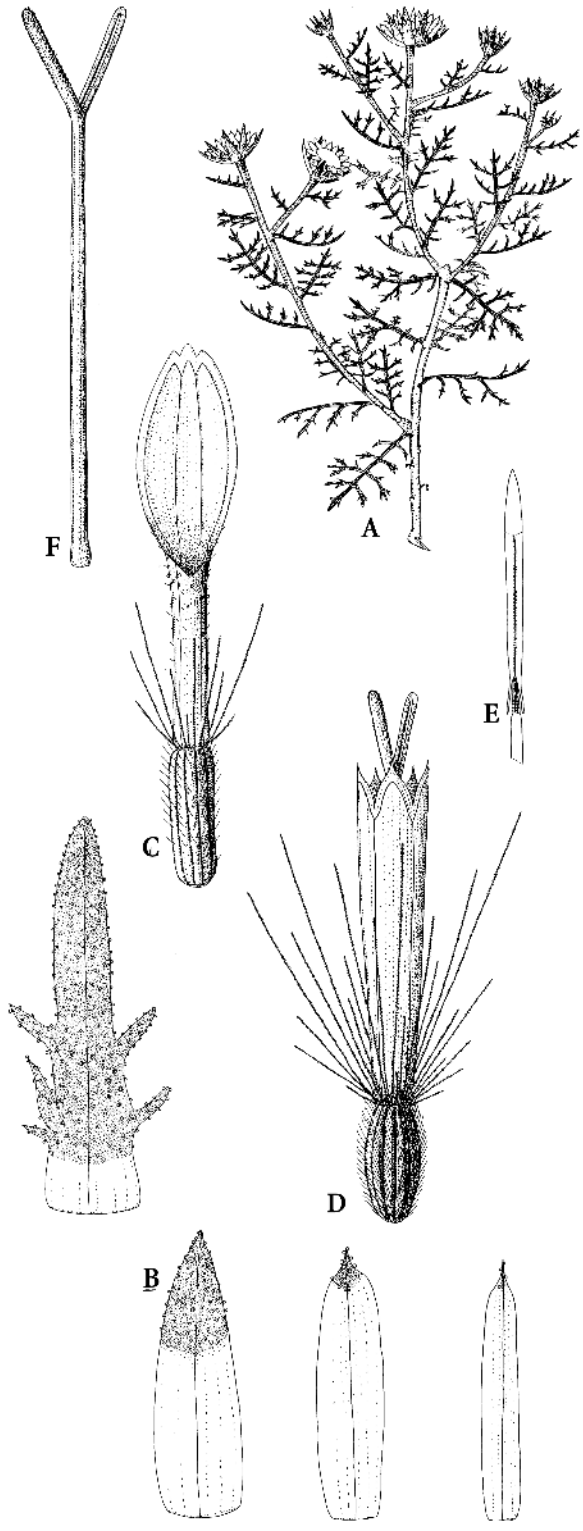

Fig. 72. Compositae-Inuleae. *Iphiona anthemidifolia*. **A** Habit. **B** Involucral bracts. **C** Ray floret. **D** Disc floret. **E** Stamen. **F** Style. (Anderberg 1985)

epaleate, with scale-like ridges. Neuter marginal florets present or absent. Corolla yellow, radiate; epidermal cells papillose. Disc florets perfect. Corolla yellow or purple-tinged. Anthers minutely calcarate, with short tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, hairy; epidermis with elongated crystals. Pappus of barbellate, capillary bristles in one row with an outer row of short scales. $2n = 18$. Three species, North Africa.

1085. *Iphiona* Cass. Fig. 72

Iphiona Cass., Bull. Sci. Soc. Philom. Paris 1817: 153 (1817), nom. cons.; Anderberg, Nordic J. Bot. 5: 169–194 (1985), rev., phylog.
Grantia Boiss. (1845).
Hirschia Baker (1895).
Perralderiopsis S. Rauschert (1982).

Shrubs or perennial herbs. Leaves alternate, sessile, entire, lobed or pinnatisect, often fleshy, sometimes spiny, hairy or glabrous. Capitula solitary or few, heterogamous, radiate to minutely radiate or homogamous, discoid. Receptacle epaleate, with scale-like ridges. Neuter marginal florets present or absent. Corolla yellow, radiate. Disc florets perfect. Corolla yellow; epidermis with sinuous cell walls, with needle-like crystals. Anthers minutely calcarate, with short tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, conspicuously ribbed; epidermis with elongated crystals. Pappus of unequal, spreading, barbellate, capillary bristles in several rows, or equally long capillary bristles in one row with an outer row of small scales. $2n = 18, 20$. Twelve species, north-eastern Africa, Arabia to Pakistan.

1086. *Dittrichia* Greuter

Dittrichia Greuter, Exsiccat. Genavensium fasc. 4: 71 (1973).

Annual or perennial herbs. Leaves alternate, lanceolate to linear, glandular, viscid, dentate, hairy. Capitula heterogamous, radiate, many in terminal racemes. Receptacle epaleate, with scale-like ridges. Marginal florets female. Corolla yellow, radiate or minutely radiate. Disc florets perfect. Corolla yellow. Anthers ecalcarate, with branched tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, hairy, apically

somewhat constricted, glandular; epidermis with elongated crystals. Pappus of barbellate, capillary bristles in one row, basally connate and concrescent into a cupule. $2n$ = 16, 18, 20. Two species, Mediterranean, introduced in America and Australia.

1087. *Limbarda* Adans.

Limbarda Adans., Fam. 2: 125, 570 (1763).

Shrublet. Leaves alternate, fleshy, glabrous, subterete, sessile, entire or apically three-lobed. Capitula heterogamous, radiate, solitary or in loose corymbs. Receptacle epaleate. Marginal florets female. Corolla yellow, radiate. Disc florets perfect. Corolla yellow. Anthers ecalcarate, with branched tails; endothecial tissue radial. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, with five secretory ducts; epidermis with elongated crystals. Pappus of barbellate, capillary bristles in several rows. $2n$ = 18. One species, *L. crithmoides* (L.) Dumort., Mediterranean region.

1088. *Anvillea* DC. Fig. 73

Anvillea DC., Prodr. 5: 487 (1836); Anderberg, Nordic J. Bot. 2: 297–305 (1982), rev.
Anvilleina Maire (1940).

Shrublets. Leaves alternate, lanceolate to cuneate or spathulate, hairy. Capitula heterogamous, radiate or homogamous, discoid, solitary. Involucre concrescent into hard spiny cup with age. Receptacle concave, smooth, paleate, paleae subtending the florets, basally folded with elongated apical appendix. Neuter marginal florets present or absent. Corolla yellow, radiate. Cypselas flattened, subcordate, with anchor-shaped hairs. Pappus absent. Disc florets perfect. Corolla yellow. Anthers minutely calcarate, with long tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas quadrangular, ribbed, with anchor-shaped hairs; epidermis with elongated crystals. Pappus absent. $2n$ = 14. Two species, Morocco to Iran.

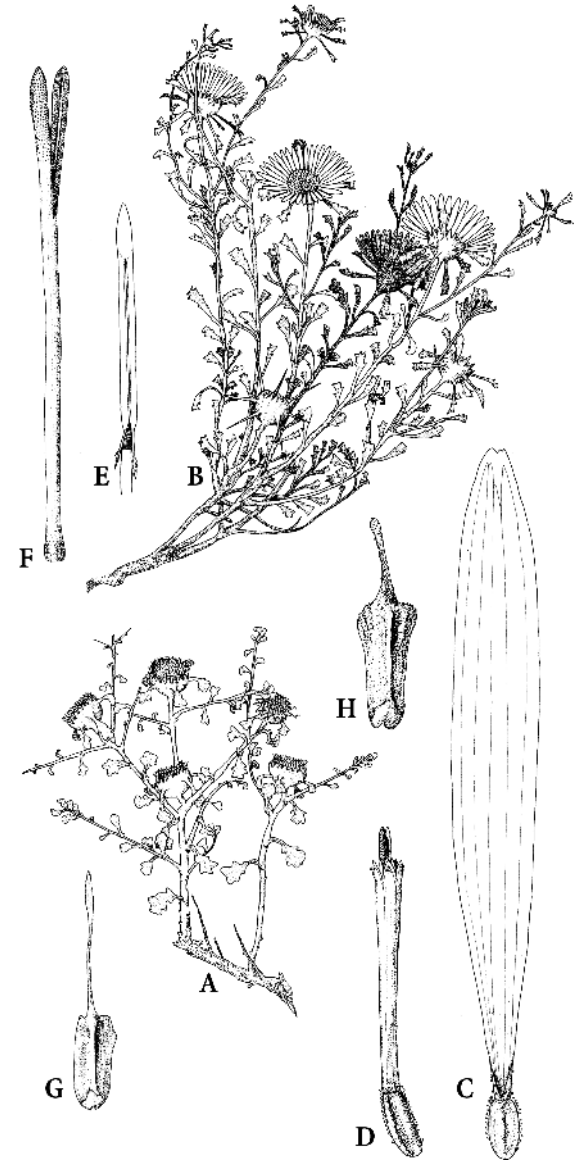

Fig. 73. Compositae-Inuleae. *Anvillea garcinii*. **A** Habit, subsp. *garcinii*. **B** Habit, subsp. *radiata*. **C** Ray floret. **D** Disc floret. **E** Stamen. **F** Style. **G** Palea, subsp. *garcinii*. **H** Palea, subsp. *radiata*. (Anderberg 1982)

1089. *Lifago* Schweinf. & Muschl.

Lifago Schweinf. & Muschl., Bot. Jahrb. 45: 429 (1911).
Niclouxia Battand. (1915).

Annual herb. Leaves spathulate, white-woolly. Capitula heterogamous, radiate, falling as a unit. Receptacle paleate; paleae subulate, villous. Marginal florets female. Corolla yellow, radiate. Cypselas triquetrous, villous. Pappus absent. Disc florets perfect. Corolla yellow. Anthers minutely calcarate, with branched tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas flattened or tetragonous, glabrous but distally with long, brown hairs; epidermis with elongated crystals. Pappus absent. One species, *L. dielsii* Schweinf. & Muschl., Algeria and Morocco.

1090. *Ighermia* Wikl.

Ighermia Wikl., Nordic J. Bot. 3: 445 (1983).

Shrub. Leaves alternate, simple, narrowly linear, needle-like. Capitula solitary, heterogamous, radiate. Receptacle smooth, paleate; paleae folded. Involucre hemispherical; involucral bracts hard and cartilaginous. Marginal florets female. Corolla yellow, radiate. Disc florets perfect. Corolla yellow. Anthers long-calcarate, with short tails; endothecial tissue polarized. Style branches short, blunt with subacute sweeping-hairs not reaching the furcation. Cypselas triquetrous, glabrous; sclerenchymatic tissue more or less confluent; epidermis with elongated crystals. Pappus of large hard scales. $2n = 14$. One species, *I. pinifolia* (Maire & Wilczek) Wikl., Morocco.

1091. *Asteriscus* Tourn. ex Mill.

Asteriscus Tourn. ex Mill., Gard. Dict. 1, ed. 4 (1754); Wiklund (as *Nauplius*), Nordic J. Bot. 7: 1–23. (1987), rev.; Halvorsen & Borgen, Sommerfeltia 3: 1–103 (1986), rev.; Greuter, Flora Mediterranea 7: 41–48 (1997) nomencl.; Francisco-Ortega et al., Biol. J. Linn. Soc. 72: 77–97 (2001), phylog.
Bubonium J. Hill (1761).
Nauplius Cass. (1822).
Odontospermum Necker ex Schultz-Bip. (1844).

Shrublets, perennial or annual herbs. Leaves alternate, sessile, sometimes fleshy, generally entire to somewhat lobed, hairy. Capitula solitary, heterogamous, radiate. Receptacle convex to flat, paleate; paleae subtending the florets, folded and crested with secretory cavities under the crest. Marginal florets female. Corolla yellow, radiate; epidermis crested. Disc florets perfect, yellow. Corolla yellow. Anthers long-calcarate, with short tails; endothecial tissue polarized. Style branches with subacute sweeping-hairs not reaching the furcation. Cypselas more or less triquetrous, with confluent sclerenchymatic tissue and chambered secretory cavities; epidermis with elongated crystals. Pappus of broad scales in c. two rows. $2n = 14, 16, 18$. Eight species, southern Europe, North Africa, Middle East, Macaronesia.

1092. *Pallenis* (Cass.) Cass.

Pallenis (Cass.) Cass. in Cuvier, Dict. Hist. Nat. 23: 566 (1822), nom. cons.; Wiklund (as *Asteriscus*), Nordic J. Bot. 5: 299–314 (1985), rev.; Greuter, Flora Mediterranea 7: 41–48 (1997), nomencl.; Francisco-Ortega et al., Biol. J. Linn. Soc. 72: 77–97 (2001), phylog.

Subshrubs, perennial or annual herbs. Leaves alternate, simple, not lobed, hairy. Capitula heterogamous, radiate, solitary, hygrochastic or not. Receptacle smooth, paleate, paleae folded and crested. Involucre broadly campanulate with subtending leaves. Marginal florets female. Corolla yellow, radiate; epidermis crested. Cypselas oblong-obovate, terete or dorsiventrally compressed and winged; epidermis with elongated crystals. Pappus of large scales or absent. Disc florets perfect. Corolla yellow. Anthers long-calcarate, with short tails; endothecial tissue polarized. Style branches short with subacute sweeping-hairs not reaching the furcation. Cypselas somewhat triquetrous; sclerenchymatic ribs few and inconspicuous; epidermis with elongated crystals. Pappus of large scales. $2n = 10, 12$. Three species, Mediterranean region, Middle East, one species introduced elsewhere.

1093. *Buphthalmum* L.

Buphthalmum L., Sp. Pl.: 903 (1753).
Xerolekia A. Anderb. (1991).

Perennial herbs. Leaves alternate, entire or dentate, hairy. Capitula heterogamous, radiate, solitary. Receptacle paleate, paleae folded, subtending the florets. Involucre hemispherical, phyllaries linear, herbaceous. Marginal florets female. Corolla yellow, radiate. Cypselas triquetrous to flattened. Pappus absent or a rim of scales. Disc florets perfect. Corolla yellow. Anthers long- or minutely calcarate, with very short tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas flattened to triquetrous, glabrous or hairy along the edges; epidermis with elongated crystals. Pappus a rim of irregularly incised scales. $2n = 20$. Three species, southern and central Europe, Sardinia.

1094. *Inula* L.

Inula L., Sp. Pl.: 881 (1753).
Bojeria DC. (1836).
Codonocephalum Fenzl (1843).

Perennial or annual herbs. Leaves alternate, simple, hairy or glabrous. Capitula solitary or few in corymb, heterogamous radiate to minutely radiate, heterogamous disciform, or homogamous discoid. Receptacle smooth, epaleate. Marginal florets female. Corolla yellow, radiate, minutely radiate or rarely tubular. Disc florets perfect. Corolla yellow. Anthers ecalcarate, with branched tails; endothecial tissue radial. Style branches with acute

sweeping-hairs not reaching the furcation. Cypselas ellipsoid, cylindrical or angled, ribbed; epidermis with elongated crystals. Pappus of barbellate, capillary bristles in one or several rows. $2n$ = 16, 18, 24, 32, 36. About 100 species, Old World.

Inula is heterogeneous and not monophyletic as now circumscribed. Genera such as *Telekia* Baumg., *Pentanema* Cass., *Amblyocarpum* Fisch. & Mey. and *Chrysophthalmum* Sch. Bip. have their closest relatives within *Inula* (Anderberg et al. 2005).

1095. *Amblyocarpum* Fisch. & Mey.

Amblyocarpum Fisch. & Mey., Index Sem. Hort. Bot. Petrop. 3 (1837).

Annual herb. Leaves alternate, simple, entire, hairy. Capitula heterogamous, disciform, subtended by radiating leaves. Receptacle smooth, epaleate. Marginal florets female. Corolla yellow, minutely radiate. Disc florets perfect. Corolla yellow. Anthers ecalcarate with long tails; endothecial tissue radial. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas cylindrical, longer than the florets, glandular; epidermis with elongated crystals. Pappus absent. One species, *A. inuloides* Fisch. & Mey., Caspian Sea region.

1096. *Carpesium* L.

Carpesium L., Sp. Pl.: 859 (1753).

Perennial or annual herbs. Leaves alternate, often in a rosette, hairy, serrate. Capitula heterogamous, disciform, solitary or few, or many in spiciform racemes. Receptacle smooth, epaleate. Marginal florets female, tubular to minutely radiate, in many rows. Corolla yellow. Disc florets perfect. Corolla yellow. Anthers ecalcarate, with branched tails; endothecial tissue radial. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, bottle-necked with conspicuous glands, longer than the corolla, ribbed; epidermis cells with elongated crystals. Pappus absent. $2n$ = 20, 36, 40. Twenty-five species, mainly Asia but extending into Europe and Australia.

1097. *Telekia* Baumg.

Telekia Baumg., Enum. Stirp. Transsilv. 3: 149 (1816).

Perennial herb. Leaves large, alternate, cordate, dentate, hairy. Capitula heterogamous, radiate, large, in loose corymbs. Receptacle paleate; paleae subulate with a widened base, persistent after flowering. Involucral bracts herbaceous, cordate. Marginal florets female. Corolla yellow, radiate; ray very long, linear. Disc florets perfect. Corolla yellow. Anthers minutely calcarate, with branched tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas linear, flattened; epidermis with elongate crystals. Pappus a rim of minute scales, or absent. $2n$ = 20. One species, *T. speciosa* Baumg., Europe, Caucasus, Asia Minor.

1098. *Chrysophthalmum* Sch. Bip.

Chrysophthalmum Sch. Bip., Walpers Repert. 2: 955 (1843) [as *Chrysophtalmum*]; Aytec & Anderberg, Bot. J. Linn. Soc. 137: 211–214 (2001).

Perennial herbs or subshrubs. Leaves simple, alternate, hairy. Capitula heterogamous, disciform. Receptacle smooth, paleate; paleae linear, somewhat canaliculate. Marginal florets female. Corolla yellow, minutely radiate. Disc florets perfect. Corolla yellow. Anthers ecalcarate, with branched tails; endothecial tissue radial. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas elongated; epidermis with elongated crystals. Pappus a short rim of scales, or absent. Three species, Turkey, Syria, Iraq.

1099. *Pentanema* Cass.

Pentanema Cass., Bull. Sci. Soc. Philom. Paris 1818: 74 (1818).
Vicoa Cass. (1825).

Shrublets or annual herbs. Leaves alternate, oblong to lanceolate, entire to serrate, often villous. Capitula generally heterogamous, radiate, but in some species heterogamous, disciform or homogamous discoid. Overwintering young capitula often present. Receptacle epaleate, smooth. Marginal florets female. Corolla yellow, radiate, minutely radiate or more or less tubular. Disc florets perfect. Corolla yellow. Anthers ecalcarate, with branched tails; endothecial tissue radial. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, shorter than the corolla; epidermis with elongated crystals. Pappus of barbellate, capillary bristles in one row. $2n$ = 18, 27. About 20 species, Turkey through central Asia, India and Sri Lanka to Africa.

Pentanema is heterogeneous and it seems doubtful that it is monophyletic with its present circumscription.

1100. *Varthemia* DC.

Varthemia DC., Prodr. 5: 473 (1836).

Shrublet. Leaves alternate, lanceolate to narrowly oblong, sparsely hairy. Capitula homogamous, discoid, in loose corymbs. Receptacle epaleate, smooth. Florets perfect. Corolla yellow. Anthers ecalcarate, with branched tails; endothecial tissue radial. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas shorter than the corolla, ellipsoid, hairy; epidermis with elongated crystals. Pappus of barbellate, capillary bristles in one row. $2n = 16$. One species, *V. persica* DC., Afghanistan, Iran, Pakistan.

1101. *Stenachaenium* Benth.

Stenachaenium Benth. in Benth. & Hook. f., Gen. Pl. 2: 289 (1873).

Herbs. Leaves alternate, dentate to serrate, decurrent, tomentose. Capitula heterogamous, disciform, terminal, solitary or few. Receptacle epaleate. Involucral bracts in several rows. Florets white, yellow or purple. Marginal florets female; corolla filiform. Disc florets perfect. Anthers tailed; endothecial tissue polarized. Style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas ellipsoid, either dark brown, smooth, glossy, laterally compressed, or pale brown, terete, ribbed, with straight hairs. Pappus of numerous free, stiff, barbellate, capillary bristles in one row; each bristle with patent teeth. Five species, South America (Brazil, Uruguay, Paraguay, Argentina).

1102. *Antiphiona* Merxm.

Antiphiona Merxm., Mitt. Bot. Staatssamml. München 9–10: 432 (1954).

Shrubs or subshrubs. Leaves alternate, pinnatisect or bi- to tripinnatisect. Capitula homogamous, discoid, solitary or few. Receptacle smooth, epaleate. Florets perfect. Corolla purple, corolla lobes with acute one-celled hairs. Anthers minutely calcarate with long tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, hairy; epidermis without elongated crystals. Pappus of barbellate, capillary bristles. Two species, Namibia.

1103. *Calostephane* Benth.

Calostephane Benth., Hooker's Ic. Pl. 12: 1111 (1872).
Mollera O. Hoffm. (1890).

Herbs. Stem winged or not. Leaves alternate, simple, with scattered hairs. Capitula heterogamous, radiate. Receptacle smooth, epaleate. Marginal florets female. Corolla yellow, radiate. Disc florets perfect. Corolla yellow. Anthers minutely calcarate, tailed; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas broadly elliptic, with glands alternating with ribs; epidermis without elongated crystals. Pappus of short obtuse scales in two rows often with protruding, bristle-like mid-portion, or absent. Six species, tropical Africa, Madagascar.

1104. *Pegolettia* Cass.

Pegolettia Cass., Dict. Sci. Nat. 38: 230 (1825); Anderberg, Cladistics 2: 158–186 (1986), rev., phylog.

Shrubs or herbs. Leaves alternate, simple, dentate or entire, or pinnatifid, glandular, hairy. Capitula homogamous, discoid. Receptacle epaleate. Florets perfect. Corolla yellow or purple-tinged; corolla lobes with acute hairs. Anthers minutely calcarate, with branched tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas cylindrical, with sclerenchymatous ribs; epidermis with crystal sand. Pappus of barbellate or plumose capillary bristles in one row, with an outer row of small narrow, entire to lacerate or almost bristle-like scales. $2n = 20$. Nine species, southern Africa, one species extending into North Africa and Middle East.

1105. *Geigeria* Griess.

Geigeria Griess., Linnaea 5: 411 (1830); Merxmüller, Mitt. Bot. Staatssamml. München 1: 239–316 (1953), rev.

Herbs or shrublets. Stem winged. Leaves alternate, sessile, simple, linear to lanceolate, sometimes decurrent, hairy. Capitula heterogamous, radiate (sometimes homogamous, discoid). Receptacle epaleate but with numerous bristles. Marginal female florets present or absent. Corolla yellow, radiate. Disc florets perfect. Corolla yellow; corolla deeply lobed. Anthers long-calcarate, with short tails; endothecial tissue polarized. Style branches with acute sweeping-hairs reaching below the furcation. Cypselas ellipsoid or turbinate, villous; epidermis without crystals. Pappus of large scales in two rows, often with a long bristle-shaped mid-portion. $2n = 20$. Twenty-eight species, Africa, mainly in the southern part.

1106. *Ondetia* Benth.

Ondetia Benth., Hooker's Ic. Pl. 12: t. 1112 (1872).

Perennial herb. Stem winged. Leaves alternate, linear. Capitula solitary, heterogamous, radiate. Receptacle paleate; paleae flattened. Marginal florets female. Corolla yellow, radiate. Disc florets perfect. Corolla yellow; corolla deeply lobed. Anthers long-calcarate, with short tails; endothecial tissue polarized. Style branches with acute sweeping-hairs not reaching below the furcation. Cypselas villous; epidermis without crystals. Pappus of short bristle-like scales. One species, *O. linearis* Benth., Namibia.

1107. *Rhodogeron* Griseb.

Rhodogeron Griseb., Cat. Pl. Cuba 151 (1866); Liu et al., Intl J. Pl. Sci. 165: 209–217 (2004), phylog.

Perennial herb. Stem scapose. Leaves rosulate, dentate or pinnatifid, hairy. Capitula few in a corymb, heterogamous, radiate. Receptacle epaleate. Florets purple. Marginal florets female; corolla radiate. Disc florets functionally male. Anthers tailed; endothecial tissue polarized. Style undivided, with acute sweeping-hairs reaching below the furcation. Cypselas ellipsoid. Pappus of free, barbellate, capillary bristles in one row. One species, *R. coronopifolius* Griseb., Cuba.

1108. *Sachsia* Griseb.

Sachsia Griseb., Cat. Pl. Cuba 150 (1866); Liu et al., Intl J. Pl. Sci. 165: 209–217 (2004), phylog.

Perennial herbs. Stem scapose. Leaves rosulate, dentate, hairy. Capitula few in a corymb, heterogamous, disciform. Receptacle epaleate. Florets white. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers tailed; endothecial tissue polarized. Style undivided, with acute sweeping-hairs reaching below the furcation. Cypselas ellipsoid. Pappus of free, barbellate, capillary bristles in one row. $2n = 20$. Four species, West Indies, southern USA.

1109. *Iphionopsis* A. Anderb.

Iphionopsis A. Anderb., Nordic J. Bot. 5: 52 (1985), rev.

Shrubs. Leaves alternate, entire or dentate, sparsely hairy. Capitula homogamous, discoid, in corymbs. Receptacle epaleate. Involucral bracts broad with conspicuous median secretory duct. Florets perfect. Corolla white to yellowish, sometimes with red tinge, with conspicuous longitudinal secretory ducts. Anthers minutely calcarate, with short tails; endothecial tissue radial. Style branches with subacute to obtuse sweeping-hairs not reaching the furcation. Cypselas hairy, without sclerenchymatic tissue; epidermis without crystals. Pappus of barbellate capillary bristles in several rows. Three species, East Africa, Madagascar.

1110. *Cratystylis* S. Moore

Cratystylis S. Moore, J. Bot. 43: 138 (1905).
Stera Ewart (1912).

Dioecious shrubs. Leaves alternate, entire, hairy or glabrous. Capitula solitary, narrowly cylindrical, heterogamous but functionally homogamous, discoid. Receptacle epaleate. Florets white. Anthers ecalcarate, shortly tailed; endothecial tissue polarized. Style branches almost smooth, with minute acute sweeping-hairs reaching the furcation. Cypselas ellipsoid, glabrous. Pappus of barbellate, capillary bristles. $2n = 20$. Four species, Australia.

1111. *Pterocaulon* Ell. Fig. 74

Pterocaulon Ell., Sketch Bot. S.-Carolina Georgia 2: 323 (1823); Cabrera & Ragonese, Darwiniana 21: 185–257 (1978), rev.
Monenteles Labill. (1825).

Herbs. Leaves alternate, dentate to serrate, decurrent into long wings. Capitula heterogamous, disciform, terminal, forming dense glomerules or long, more or less dense spikes or racemes of capitula. Receptacle epaleate. Florets purplish. Marginal florets female; corolla filiform. Disc florets perfect, purple. Anthers tailed with radial endothecial tissue. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas hairy. Pappus of free, barbellate, capillary bristles, in one to several rows; each bristle with patent teeth. $2n = 20$. Eighteen species, North and South America, Australia and adjacent areas.

1112. *Cylindrocline* Cass.

Cylindrocline Cass., Bull. Sci. Soc. Philom. Paris 1817: 11 (1817).

Shrubs or small trees. Leaves elliptic, on tips of branches, not decurrent, marginally dentate, white-woolly below. Capitula heterogamous, disciform, in dense terminal corymbs. Florets mauve. Receptacle paleate; paleae hairy. Involucral bracts with a tuft of hairs. Marginal florets female; corolla filiform. Disc florets perfect. Anthers tailed; endothecial tissue

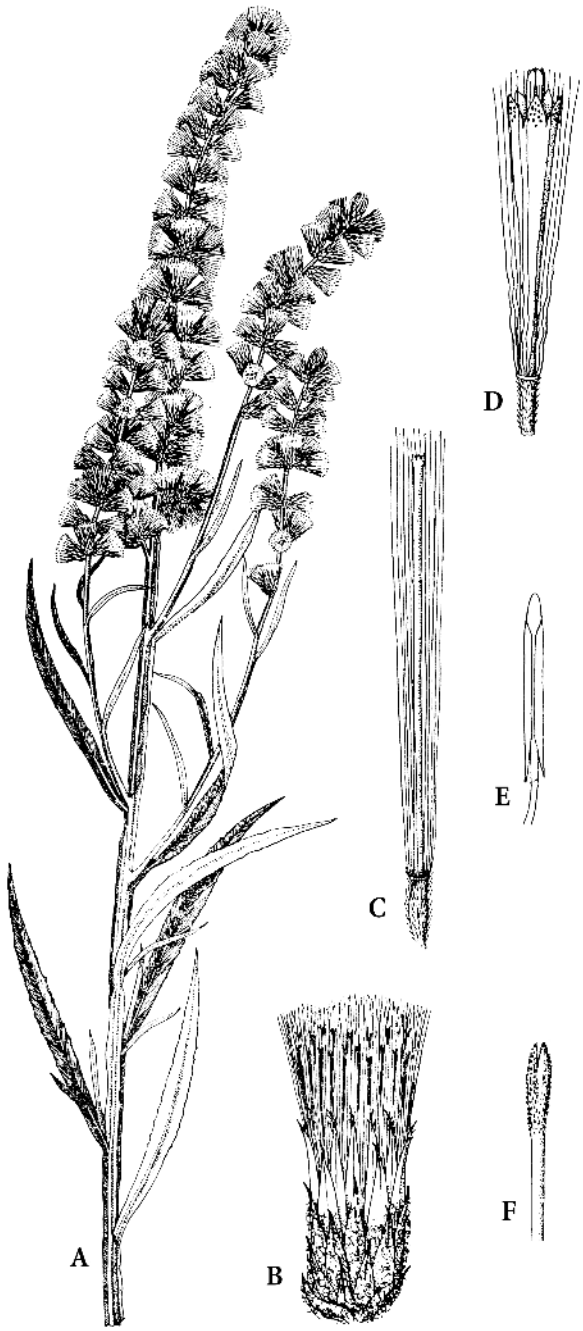

Fig. 74. Compositae-Inuleae. *Pterocaulon virgatum*. **A** Flowering branch. **B** Capitulum. **C** Female floret. **D** Hermaphrodite floret. **E** Stamen. **F** Style. (Cabrera 1978)

radial. Style branches with acute sweeping-hairs reaching below the furcation. Cypselas terete to triquetrous, sparsely hairy on the edges. Pappus of a few free, stiff, scale-like bristles; each bristle with patent teeth. Two species, Mauritius.

1113. *Epaltes* Cass.

Epaltes Cass., Bull. Sci. Soc. Philom. Paris 1818: 139 (1818).
Sphaeromorphaea DC. (1837).
Ethuliopsis F. Muell. (1861).

Herbs. Leaves alternate or subopposite, dentate, sparsely hairy or glabrous. Capitula heterogamous, solitary or few in terminal clusters. Receptacle epaleate. Florets white or purple. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers tailed; cells of filament collar mammillose; endothecial tissue radial. Style undivided, with obtuse sweeping-hairs reaching far down the shaft. Cypselas glandular, or sparsely hairy. Pappus absent or present as a short rim or, as in *E. cunninghamii* Benth., a few elongated, flattened scale-like bristles. $2n = 20$. Fourteen species, pantropical.

Epaltes is heterogeneous and likely to be polyphyletic. The genus is diagnosed only by reduction or loss of pappus.

1114. *Litogyne* Harv.

Litogyne Harv., Fl. Cap. 3: 48 (1865).

Subshrub. Leaves alternate, entire, decurrent, hairy. Capitula heterogamous, disciform, few in terminal clusters. Receptacle epaleate, dome-shaped and centrally depressed with a marginal ridge. Florets purple. Marginal florets female, situated on the vertical outer face of the marginal receptacle ridge; corolla filiform. Disc florets functionally male, in the central depression of the receptacle. Anthers tailed; endothecial tissue radial. Style undivided, with obtuse sweeping-hairs reaching far down the shaft. Cypselas hairy. Pappus absent. One species, *L. gariepina* (DC.) Anderb., tropical Africa, Namibia.

1115. *Pechuel*-loeschea O. Hoffm.

Pechuel-loeschea O. Hoffm., Bot. Jahrb. Syst. 10: 274 (1888).

Shrub. Leaves alternate, lanceolate, sericeous. Capitula heterogamous, disciform, in loose corymbs. Receptacle epaleate. Marginal florets female. Corolla purple, filiform. Disc florets perfect. Corolla purple. Anthers minutely calcarate, with branched tails; endothecial tissue polarized; cells of filament collar longer than wide. Style branches with acute sweeping-hairs not reaching the furcation. Cypselas ellipsoid, hairy; epidermis without crystals. Pappus of one row of basally

connate, barbellate, capillary bristles. One species, *P. leubnitziae* O. Hoffm., Namibia.

1116. *Adelostigma* Steetz

Adelostigma Steetz in Peters, Naturwissensch. Reise Mossambique 6, Bot.: 428 (1864).

Herbs. Leaves alternate, bipinnatifid. Capitula heterogamous, disciform, solitary. Receptacle epaleate. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers very shortly tailed; endothecial tissue radial. Style almost undivided, with obtuse sweeping-hairs reaching far down the shaft. Cypselas sparsely hairy. Pappus of free, barbellate, capillary bristles in one row; each bristle with adpressed teeth. Two species, tropical Africa.

This description is based on *A. senegalensis* Benth., one of two species of the genus. The identity of the generic type (*A. athrixioides* Steetz, destroyed in Berlin) is unclear and its description differs from that above. Possibly the two taxa represent different genera, in which case *A. senegalensis* should be treated under a new generic name.

1117. *Pluchea* Cass. Fig. 75

Pluchea Cass., Bull. Sci. Soc. Philom. Paris 1817: 31 (1817); King-Jones, Englera 23: 1–136 (2001), rev., phylog.
Berthelotia DC. (1836).
Tecmarsis DC. (1836).
Eyrea F. Muell. (1852).
Eremohylema A. Nels. (1924).

Shrubs or herbs. Leaves alternate or subopposite, dentate to serrate or entire, generally not decurrent, hairy. Capitula heterogamous, disciform, solitary or few to many in corymbs. Receptacle epaleate. Florets purple. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers tailed; cells of filament collar mammillose or flattened; endothecial tissue radial. Style entirely or almost undivided or sometimes divided; style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas sometimes indistinct or entirely reduced to a small carpopodium, hairy. Pappus of free, barbellate, capillary bristles in one row; each bristle with patent or sometimes with adpressed teeth. $2n = 20, 30$. About 80 species, pantropical.

Pluchea is heterogeneous and not monophyletic. It is composed of several entities which have been given generic status. Genera such as *Coleocoma* F. Muell. and *Streptoglossa* Steetz have their closest relatives within *Pluchea* (Anderberg et al. 2005). Other genera may also prove to be part of the *Pluchea* complex, e.g. *Monarrhenus* Cass., *Karelinia* Less. and *Tessaria* Ruiz & Pavon.

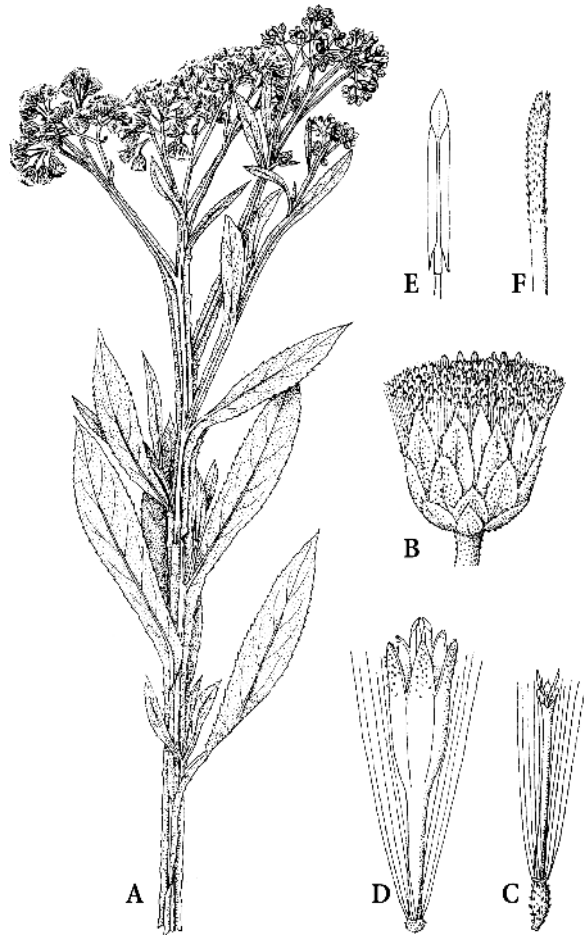

Fig. 75. Compositae-Inuleae. *Pluchea microcephala*.**A** Flowering branch. **B** Capitulum. **C** Marginal floret. **D** Disc floret. **E** Stamen. **F** Style. (Cabrera 1978)

1118. *Karelinia* Less.

Karelinia Less., Linnaea 9: 187 (1834).

Perennial herb. Leaves alternate, elliptic-oblong, entire, sparsely hairy. Capitula heterogamous, disciform, solitary. Receptacle epaleate. Involucral bracts broadly oblong. Florets purple. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers tailed; cells of filament collar mammillose; endothecial tissue radial. Style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas hairy. Pappus of free, barbellate, capillary bristles, in one row; each

bristle with patent teeth. $2n = 20$. One species, *K. caspia* Less., Caspian Sea region.

1119. *Tessaria* Ruiz & Pavon

Tessaria Ruiz & Pavon, Prod. Fl. Peruv. Chil. (1794).

Trees. Leaves alternate, entire, glabrous or sparsely hairy. Capitula heterogamous, disciform, few in loose corymbs. Receptacle epaleate. Florets pink. Marginal florets female; corolla filiform. Disc florets functionally male, usually one; corolla lobes longer than tube. Anthers tailed, conspicuously calcarate; cells of filament collar mammillose; endothecial tissue radial. Style undivided, with obtuse sweeping-hairs reaching far down the shaft. Cypselas of marginal female florets small, ellipsoid, glabrous. Pappus of free, barbellate, capillary bristles in one row; each bristle with patent teeth. $2n = 20$. One species, *T. integrifolia* Ruiz & Pavon, South America.

1120. *Monarrhenus* Cass.

Monarrhenus Cass., Bull. Soc. Philom. Paris 1817: 31 (1817).

Shrubs. Leaves on the distal portion of the branches, ovate-lanceolate, subentire, hairy. Capitula heterogamous, disciform, small, in dense terminal clusters. Receptacle epaleate. Florets purplish. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers tailed; endothecial tissue radial. Style branches with obtuse sweeping-hairs reaching the furcation. Cypselas of marginal florets small, ellipsoid, distally hairy. Pappus of free, barbellate capillary bristles, in one row; each bristle with patent teeth. Two species, Mauritius, La Réunion.

1121. *Thespidium* F. Muell. ex Benth.

Thespidium F. Muell. ex Benth., Fl. Austral. 3: 534 (1867).

Perennial herb, often densely tufted. Leaves alternate, marginally dentate, hirsute. Capitula heterogamous, disciform, small, more or less sessile at the base of the stems. Receptacle epaleate. Involucral bracts few, acute. Marginal florets female; corolla filiform. Disc florets perfect. Anthers tailed; endothecial tissue radial. Style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas obconical, ribbed, hairs uncinate. Pappus of a few, free, rather stiff, scale-like bristles in one row; each bristle with patent teeth. One species, *T. basiflorum* F. Muell., Australia.

1122. *Coleocoma* F. Muell.

Coleocoma F. Muell., Hooker's J. Bot. Kew Gard. Misc. 9: 19 (1857).

Small rigid herb. Leaves alternate, glabrous, dentate. Capitula heterogamous, disciform, solitary, subsessile, subterminal, ovoid. Receptacle epaleate. Involucral bracts broadly ovate, obtuse. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers tailed; endothecial tissue radial. Style undivided, with obtuse sweeping-hairs reaching far down on the shaft. Cypselas quadrangular with several narrow ribs. Pappus of scale-like bristles forming a narrow tube surrounding the corolla base; each bristle with patent teeth. One species, *C. centaurea* F. Muell., Australia.

1123. *Delamerea* S. Moore

Delamerea S. Moore, J. Bot. 38: 457 (1900).

Procumbent herb. Leaves alternate, spathulate, shallowly dentate, not decurrent, greyish-tomentose. Capitula heterogamous, disciform, solitary, subsessile, subterminal. Receptacle epaleate. Involucral bracts acute, slightly squarrose. Florets purple. Marginal florets female; corolla filiform. Disc florets perfect. Style branches with obtuse sweeping-hairs reaching below the furcation. Anthers tailed; endothecial tissue radial. Cypselas terete or angled. Pappus of a few scale-like bristles connate into a tube surrounding the corolla; each bristle with patent teeth. One species, *D. procumbens* S. Moore, East Africa.

1124. *Neojeffreya* Cabr.

Neojeffreya Cabr., Hickenia 1: 160 (1978).

Annual herb. Leaves alternate, denticulate to sinuate, decurrent into long wings, woolly-hairy. Capitula heterogamous, disciform, small, aggregated in dense terminal glomerules. Receptacle paleate; paleae marginally plumose. Marginal florets female; corolla filiform. Disc florets perfect. Anthers tailed; endothecial tissue radial. Style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas laterally compressed. Pappus of free, barbellate, capillary bristles in one row; each bristle with patent teeth. One species, *N. decurrens* (L.) A. L. Cabrera, Madagascar, East Africa.

1125. *Triplocephalum* O. Hoffm.

Triplocephalum O. Hoffm., Engler & Prantl, Nat. Pflanzenfam. 4, 5: 389 (1894).

Shrub. Leaves alternate, shallowly dentate, hairy. Capitula heterogamous, disciform, small, in globose, terminal secondary heads. Receptacle epaleate. Florets purplish. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers tailed; endothecial tissue radial. Style undivided, with obtuse sweeping-hairs reaching far down on the shaft. Cypselas hairy. Pappus absent, or a minute rim of scales. One species, *T. holstii* O. Hoffm., East Africa.

1126. *Sphaeranthus* L.

Sphaeranthus L., Sp. Pl.: 927 (1753); Ross-Craig, Hooker's Ic. Pl. 6: 1–117 (1955), rev.
Tisserantia Humbert (1927).

Herbs. Leaves alternate, dentate, decurrent into wings. Capitula heterogamous, disciform, small, congested in globose or ovoid to cylindrical, terminal secondary heads. Receptacle epaleate. Florets purple. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers tailed; endothecial tissue radial. Style undivided, with obtuse sweeping-hairs reaching far down on the shaft. Cypselas often reduced, often with uncinate or anchor-shaped hairs. Pappus absent. $2n = 20$. Forty-one species, Old World tropics.

1127. *Pseudoblepharispermum* Lebrun & Stork

Pseudoblepharispermum Lebrun & Stork, Adansonia 4: 419 (1981); Beentje & Hind, Kew Bull. 57: 214 (2002), key.

Shrubs. Leaves alternate, entire, densely white-tomentose, ovate or subglabrous, linear. Capitula heterogamous, disciform, small, congested into terminal secondary heads. Receptacle paleate; paleae hairy. Marginal florets female; corolla filiform. Disc florets functionally male. Anthers without tails or with short tails; endothecial tissue radial (type). Style undivided, with obtuse sweeping-hairs reaching far down on the shaft. Cypselas with straight or uncinate hairs. Pappus absent. Two species, East Africa.

Pseudoblepharispermum is heterogeneous, and the tribal position for the two rare and little-known species placed in this genus remains to be tested.

1128. *Pseudoconyza* Cuatr.

Pseudoconyza Cuatr., Ci. Mexico 21: 30 (1961).

Herb. Leaves alternate, dentate and sometimes basally shallowly lobed, slightly stem-clasping. Capitula heterogamous, disciform, terminal, solitary or few together. Receptacle epaleate. Florets greenish-white. Marginal florets female; corolla filiform. Disc florets perfect. Anthers tailed; endothecial tissue radial. Style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas hairy. Pappus of free, barbellate, capillary bristles in one row; each bristle with adpressed teeth. One species, *P. viscosa* (Mill.) D'Arcy, Central America, Africa, Asia.

1129. *Blumeopsis* Gagnep.

Blumeopsis Gagnep., Bull. Mus. Hist. Nat. Paris 26: 75 (1929).

Herb. Leaves alternate, sharply dentate, sparsely hairy. Capitula heterogamous, disciform, rather small, few, in terminal corymb. Receptacle epaleate. Florets yellow. Marginal florets female; corolla filiform. Disc florets perfect. Anthers without tails; endothecial tissue radial. Style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas hairy. Pappus of free, barbellate, capillary bristles in one row; each bristle with adpressed teeth. One species, *B. falcata* (D. Don) Merr., eastern Asia.

1130. *Laggera* Sch. Bip. ex Koch

Laggera Sch. Bip. ex Koch, Linnaea 19: 391 (1847).

Herbs. Leaves alternate, dentate, decurrent, hairy. Capitula heterogamous, disciform, terminal, few to many. Receptacle epaleate. Florets purple. Marginal florets female; corolla filiform. Disc florets perfect. Anthers without tails; endothecial tissue radial. Style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas hairy. Pappus of free, barbellate, capillary bristles in one row; each bristle with adpressed teeth. $2n = 20$. Seventeen species, tropical Africa, Arabia, Asia.

1131. *Nicolasia* S. Moore

Nicolasia S. Moore, J. Bot. 38: 458 (1900); Merxmüller, Mitt. Bot. Staatssamml. München 2: 1–10 (1954), rev.

Herbs or subshrubs. Leaves alternate, entire to dentate, generally decurrent, sparsely hairy. Capitula heterogamous, disciform, solitary or few together. Receptacle epaleate. Florets purple. Marginal florets female; corolla filiform. Disc florets perfect. Anthers without tails; endothecial tissue radial.

Style branches with obtuse or sometimes acute sweeping-hairs reaching below the furcation. Cypselas hairy. Pappus of few, free, barbellate, capillary bristles in one row; each bristle with adpressed teeth. Seven species, southern tropical Africa.

1132. *Doellia* Sch. Bip.

Doellia Sch. Bip., Walpers Repert. 2: 953 (1843); Anderberg, Willdenowia 25: 19–24 (1995).

Herbs. Leaves alternate, dentate, hairy. Capitula heterogamous, disciform, solitary or few together. Receptacle epaleate. Florets purple. Marginal florets female; corolla filiform. Disc florets perfect. Anthers tailed; endothecial tissue radial. Style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas with conspicuous red longitudinal resin ducts, hairy. Pappus of free, barbellate, capillary bristles in one row; each bristle generally with adpressed teeth. Two species, Arabia, Africa.

1133. *Porphyrostemma* Benth. ex Oliv.

Porphyrostemma Benth. ex Oliv., Trans. Linn. Soc. London 29: 96 (1873).

Herbs. Leaves alternate, narrowly linear, entire, glabrous. Capitula heterogamous, radiate or disciform, solitary. Receptacle epaleate. Involucral bracts in many rows. Florets purple. Marginal florets female; corolla minutely radiate. Disc florets perfect; corolla with conspicuous secretory canals. Anthers tailed; endothecial tissue radial. Style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas with conspicuous, red, two- or three-celled secretory cavities in longitudinal rows, hairy. Pappus of free, barbellate, capillary bristles in one row each with adpressed teeth, and a short rim of connate scales, sometimes rim-shaped or absent. Four species, tropical Africa.

1134. *Streptoglossa* Steetz

Streptoglossa Steetz, Trans. Proc. Bot. Soc. Edinburgh 7: 491 (1863); Dunlop, Adelaide Bot. Gard. 3: 167–182 (1981), rev. *Pterigeron* (DC.) Benth. (1867).

Herbs or subshrubs. Leaves alternate, dentate, often decurrent, hairy. Capitula heterogamous, radiate to disciform, solitary or few. Receptacle epaleate. Florets purple. Marginal florets female, radiate or minutely radiate to almost tubular. Disc florets perfect or functionally male. Anthers tailed; cells of filament collar mammillose; endothecial tissue radial. Style branches with obtuse sweeping-hairs reaching below the furcation. Cypselas villous. Pappus of free, rather stiff, barbellate bristles in one row; each bristle with patent teeth. $2n = 20$. Eight species, Australia.

1135. *Allopterigeron* Dunlop

Allopterigeron Dunlop, J. Adelaide Bot. Gard. 3, 2: 183 (1981).

Annual herb. Leaves alternate, fleshy, entire. Capitula heterogamous, minutely radiate or disciform, solitary. Receptacle epaleate. Florets white. Marginal florets female; corolla minutely radiate. Disc florets functionally male, three-lobed. Anthers three, without tails. Style undivided, with obtuse sweeping-hairs reaching far down the shaft. Cypselas ellipsoid, hairy. Pappus of several free, stiff, barbellate, capillary bristles. One species, *A. filifolius* (F. Muell.) Dunlop, Australia.

Genera Incertae Sedis

1136. *Nanothamnus* Thoms.

Nanothamnus Thomson, J. Linn. Soc. 9: 342, t. 3 (1867).

Annual herb. Leaves lanceolate, serrate, sericeous. Capitula heterogamous, disciform, few-flowered, in dense terminal clusters. Receptacle epaleate. Involucre narrowly cyathiform, bracts cartilaginous, acute, in few rows. Florets yellow. Outer florets functionally female, with vestigial stamens, pseudobilabiate (1/4). Disc florets perfect, bilabiate. Anthers long-calcarate, with short tails, apical appendage soft. Endothecial tissue radial. Style branches with semi-acute sweeping-hairs reaching below the furcation. Cypselas ellipsoid, ribbed; epidermis with elongated crystals. Pappus absent. One species, *N. sericeus* Thoms., India.

The large crystals in the cypsela epidermis would indicate a position in Inuleae s.str., possibly near *Blumea* DC., but the tribal position for this genus is uncertain. Its bilabiate corolla, calcarate anthers and soft anther appendage are character states that poorly match the other taxa of the tribe.

1137. *Feddea* Urb.

Feddea Urb., Repert. Spec. Nov. Regni Veg. 21: 73 (1925).

Scandent shrub. Leaves alternate, elliptic, glabrous, coriaceous. Capitula homogamous, discoid.

Involucral bracts in several rows, imbricate, cartilaginous, rather broad with a median secretory duct. Receptacle flat, epaleate. Florets deeply lobed, perfect. Anthers ecalcarate, caudate. Style branches obtuse-rounded, dorsally and apically with obtuse sweeping-hairs; stigmatic area in two marginal bands, confluent apically. Cypselas oblong, glabrous. Pappus of barbellate capillary bristles in several rows. One species, *F. cubensis* Urb., Cuba.

A stigmatic area with two lateral bands confluent at the apex is a typical character state in Inuleae. The median secretory ducts resemble those of *Iphionopsis* A. Anderb. If it belongs in Inuleae, then *Feddea* may be another odd member of the *Pluchea* Cass. complex.

Key to the Tribes of the Heliantheae Alliance

J.L. Panero

The common denominator in the history of the classification of the Heliantheae alliance has been the subjective delimitation and selective recognition of the classical tribes Heliantheae and Helenieae. Cassini (1819) erected tribe Heliantheae to accommodate most New World sunflowers with key characters including yellow corollas, opposite leaves, and uniseriate or biseriate involucres. He placed Eupatorieae in the proximity of Vernonieae but drew attention to their connection to Heliantheae. In his final classification of the family (Cassini 1829), he recognized Helenieae as a group within Heliantheae and separated Heliantheae-Ambrosiinae and Tageteae-Pectidinae as tribes (Ambrosieae and Tageteae respectively). Bentham (1873b) recognized Helenieae at the tribal level, in which he placed most helianthoid genera with epaleate receptacles. This implied that the paraphyletic nature of Helenieae was a necessary condition to have a monophyletic (paleate) Heliantheae. These decisions were to dominate the classification of the genera of these tribes for more than a century. Robinson (1981) published a revolutionary classification of the group in which he placed Helenieae in the synonymy of Heliantheae, as done earlier by Cronquist (1955), and recognized 35 subtribes. His system benefited from the use of floret morphological features previously not used in classification and termed microcharacters, most being visible only with the aid of a light microscope. Subsequent classifications (Karis and Ryding 1994a, b), although accepting some of the findings reported by Robinson (1981), reverted to a bipolar system in which Heliantheae were deemed as probably monophyletic and Helenieae as paraphyletic. Eupatorieae was seen as sister tribe to these. The advent of molecular comparative studies of these groups of sunflowers has clarified the phylogenetic position of Eupatorieae and, if Eupatorieae are to be maintained at tribal rank, forces the recognition of several tribes as hypothesized by some previous authors.

Readers will notice that the tribal classification outlined in the Introduction to Compositae in this volume differs from that of the authors of tribes XVIII–XXX of the so-called Heliantheae alliance (cf. below). This discrepancy centres on the recognition of Eupatorieae, a tribe of more than 2,000 species and 190+ genera, well-defined by both morphological and molecular features, and long established in the taxonomic literature (Cassini 1819; King and Robinson 1987; Bremer et al. 1994b). To maintain recognition and use of Eupatorieae, and at the same time a classification which recognizes only monophyletic groups, Heliantheae can no longer be recognized in the traditional, broad sense of Robinson (1981). This is because all molecular evidence to date (Kim and Jansen 1995; Baldwin et al. 2002; Panero and Funk 2002) indicates that Eupatorieae are not a basal member of subfamily Asteroideae (King and Robinson 1987), and not sister to the classical Heliantheae-Helenieae as previously thought (Karis and Ryding 1994a, b) but rather embedded within that lineage (Fig. 76). Eupatorieae are now identified as one of at least 13 major lineages (Panero and Funk 2002) recognized at tribal rank by the authors of tribal accounts XVIII–XXX. These 13 groups are accepted in the Introduction to Compositae but recognized at the rank of supersubtribe (Jeffrey 2004), with Eupatorieae included in an expanded Heliantheae of more than 5,200 species. For ease of discussion, these 13 tribes (Heliantheae s.l. of the Introduction) hereafter are referred to as the Heliantheae alliance (Fig. 76). Comparative molecular studies provided the phylogenetic hypotheses adopted in tribes XVIII–XXX (Baldwin et al. 2002; Panero and Funk 2002; Panero, unpubl. data). Among the most important conclusions from these studies is the recognition of a more exclusive tribe Heliantheae

s.s., the elucidation of the phylogenetic position of tribe Helenieae, and the sister-group relationship of Eupatorieae and Perityleae within the clade containing tribes Millerieae and Madieae (Fig. 76). An equally interesting, if not perplexing, result is the relatively basal position of Coreopsideae and the sister-group relationship of Neurolaeneae to the epaleate tribes Tageteae, Bahieae and Chaenactideae (Fig. 76). Equally exciting is the realization that the tremendous diversity of the Heliantheae alliance in the New World is the result of a single introduction from the southern hemisphere, most probably Africa. This assertion is supported by the fact that the mostly African tribe Athroismeae was found to be sister to the rest of the Heliantheae alliance. In addition, the genus *Callilepis*, also from southern Africa and traditionally classified in Gnaphalieae, is sister to the Heliantheae alliance (Anderberg et al. 2005; Panero, unpublished chloroplast data). Apparently, the only unifying feature of the Heliantheae alliance within Asteraceae is the presence of a phytomelanin layer in the cypselae. This layer renders the fruit black or dark brown, hence the term carbonized cypselae or cypselae with carbonized walls. This character is sometimes difficult to observe because some cypselae are either densely pubescent, covered by epidermal outgrowths in the form of wings (Heliantheae-Ecliptinae), or phyllaries are fused to the fertile cypselae (Millerieae-Melampodiinae). Tribe Helenieae and subtribes Anisopappinae and Centipedinae of Athroismeae lack phyomelanin in their cypselae, and could be confused with other groups of Asteraceae. Most members of tribe Helenieae are distinctive by having crystals in each of the epidermal cells of the cypsela, and lacking a phytomelanin layer. Elsewhere in Asteraceae, this character is seen only in some 30 genera of tribe Inuleae. Helenieae are endemic to the New World and, for the most part, have a scaly pappus whereas those Inuleae with crystals in their cypselae are found only in the Old World and tend to have a pappus of bristles. Subtribe Anisopappinae contains taxa with an Old World distribution which differ from most Inuleae in having a scaly pappus and obtuse style papillae. Subtribe Centipedinae is distinctive for having mostly disciform capitula with several rows of tubular florets, central florets with tetramerous corollas, and anthers with very reduced or obsolete appendages.

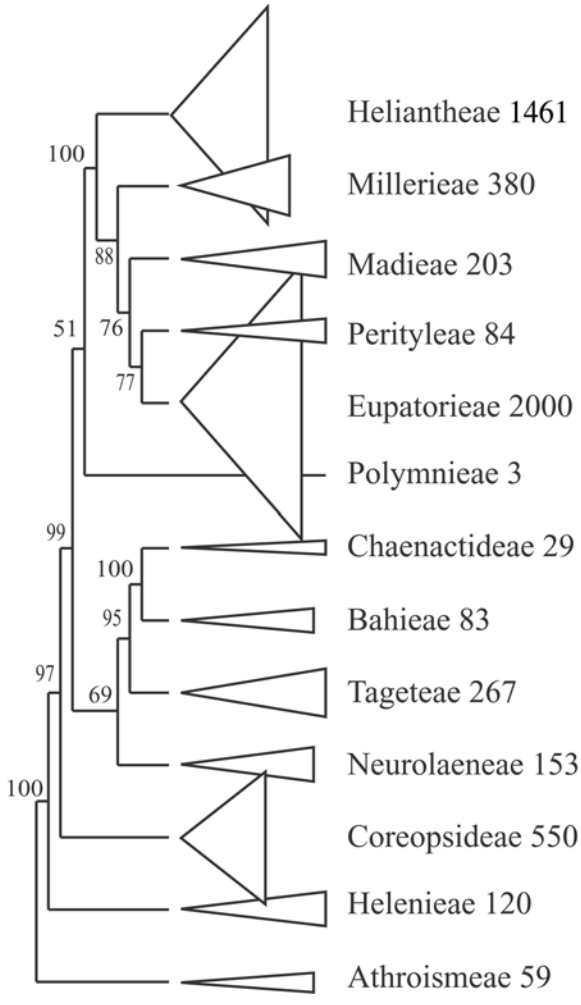

Fig. 76. Summary of phylogenetic relationships among tribes recognized in the Heliantheae alliance, based on chloroplast DNA sequence analysis. *Numbers along branches* indicate bootstrap support. *Numbers after tribal names* indicate approximate number of species. (Modified from Panero and Funk 2002)

The key below facilitates identification of the tribes and distinctive genera of the Heliantheae alliance. Most members of this group are endemic to the American continent where they constitute approximately 40–50% of its sunflower diversity. The key uses characteristics which sometimes are not included in the descriptions. My aim in constructing this key has been to use characters which can be readily observed in the field and in herbarium specimens. Nevertheless, a number of leads are based on characters which require the use of a microscope.

Key to the Tribes

1. Cypsela walls with 1–3 crystals per cell, rarely none, not carbonized; plants from the New World
XIX. Helenieae (p. 400)
– Cypsela walls without crystals, carbonized, rarely not carbonized; plants mostly from America, rarely fromq the Old World 2
2. Capitula with 1, rarely 2 florets and fused phyllaries, central ribs of phyllaries swollen and wing-like; shrubs with opposite, glaucous leaves, growing at the edge of saline marshes surrounding La Paz, Baja California, Mexico **XXII. Tageteae-Coulterellinae** (p. 422)
– Capitula otherwise, if with 1–2 florets, then phyllaries without wing-like central ribs; plants various, if from La Paz, Baja California, then capitula with more than 2 florets 3
3. Cypselae not carbonized 4
– Cypselae carbonized 5
4. Capitula radiate; corollas yellow; receptacles mostly paleate; cypselae mostly pappose
XVIII. Athroismeae-Anisopappinae (p. 397)
– Capitula disciform, rarely radiate; corollas mostly white or greenish white, rarely yellow; receptacles epaleate; cypselae epappose
XVIII. Athroismeae-Centipedinae (p. 399)
5. Capitula arranged in compact, glomerule-like, compound cymes; plants of Africa and Asia, with white corollas and alternate leaves
XVIII. Athroismeae-Athroisminae (p. 398)
– Capitula otherwise, if arranged in glomerule-like compound cymes, then female florets enclosed in perigynia; plants mostly from America, if from Africa or Asia, then corolla colour various and leaves opposite 6
6. Capitula paleate 7
– Capitula epaleate, sometimes paleae present as a single row between ray florets and first row of disc florets or in discoid capitula paleae fused and resembling an involucre 26
7. Anther appendages linear, flat, without basal constrictions, reduced or lacking; capitula always discoid; corollas white, pink, blue or purple; style arm appendages longer than stigmatic lines
XXX. Eupatorieae (p. 510)
– Anther appendages lanceolate to oval, rarely linear, shallowly to strongly concave, constricted at base; capitula discoid, disciform or radiate; corollas mostly yellow or yellow-orange, sometimes white, rarely pink or purple; style arm appendages usually as long as or shorter than stigmatic lines 8
8. Capitula with dimorphic involucres, innermost phyllaries translucent, chartaceous, normally dull orange or yellow, outer herbaceous, green, mostly reflexed, rarely capitula ligulate and all phyllaries herbaceous, gradate (*Fitchia*); cypselae obcompressed with resin canals; anther appendages mostly with resin canals and without glandular trichomes
XX. Coreopsideae-Chrysanthellinae (p. 407), **Coreopsidinae** (p. 409)
– Capitula without dimorphic involucres or, if dimorphic, innermost series of phyllaries rarely chartaceous and translucent; cypselae various, rarely with resin canals; anther appendages without resin canals, either glabrous or with glandular trichomes 9
9. Capitula with 4 deeply trilobed yellow florets subtended by 4 scarious phyllaries enclosed by two, broad suborbicular phyllaries
XX. Coreopsideae 1186. *Staurochlamys*
– Capitula and phyllaries otherwise 10
10. Phyllaries of innermost series fused to ray cypselae
XXVII. Millerieae-Melampodiinae (p. 487)
– Phyllaries of innermost series not fused to ray cypselae 11
11. Innermost phyllaries partially or fully covering ray floret cypselae; ray corollas trilobed; plants of the Pacific coast of the USA and extreme north-western Mexico, Hawaii **XXVIII. Madieae-Madiinae** in part (p. 497)
– Innermost phyllaries rarely covering ray cypselae; if covering ray cypselae, then edge of phyllaries translucent or ray corollas reduced to a tube; plants of tropical America 12
12. Anther filaments papillose, thecae green
XXVII. Millerieae-Guardiolinae (p. 486)
– Anther filaments glabrous, if papillose, then thecae black or brown, never green 13
13. Leaves with expanded leaf bases or more commonly forming a cupule (invaginated) around stem; plants forming persistent rosettes with woody stems (acauli- or caulirosulae) or sometimes shrub- or tree-like with leaves aggregated at distal ends of stems
XXVII. Millerieae-Espeletiinae (p. 482)
– Leaves without expanded bases; plants otherwise, if forming rosettes, then stems not woody, if shrubs or trees, then leaves evenly spaced along branches 14
14. Capitula with functionally staminate disc florets; cypselae without wings, epappose, broadly biconvex or trigonal; phyllaries and herbage with long stipitate glandular trichomes 15
– Capitula mostly with bisexual disc florets, if with functionally staminate disc florets, then either cypselae strongly flattened, mostly winged and pappose or cypselae broadly biconvex and peripheral floret corollas tubular with very reduced limbs and corollas white or light yellow; phyllaries and herbage rarely with long stipitate glandular trichomes 16
15. Anther thecae hyaline or pale yellow; phyllaries subequal, outermost series never reflexed nor patent
XXV. Polymnieae (p. 439)
– Anther thecae brown or black; phyllaries gradate with outermost series much larger than inner series, sometimes reflexed **XXVII. Millerieae-Milleriinae** (p. 487)
16. Plants aquatic with fistulose stems and axillary capitula **XXI. Neurolaeneae-Enydrinae** (p. 418)
– Plants otherwise 17
17. Disc florets with very reduced or undivided styles and functionally staminate 18
– Disc florets bisexual 20
18. Ray corollas conspicuous, yellow or greenish yellow
XXVI. Heliantheae-Dugesiinae (p. 446), **Engelmanniinae** in part (p. 461), **Ecliptinae** in part (p. 446), **1360. *Zinnia*** in part
– Ray corollas inconspicuous, mostly reduced to a tubular corolla or ring, sometimes missing, if protruding beyond phyllaries, then these white and clearly trilobed 19
19. Anthers mostly light yellow or hyaline, if light brown, then paleae of adjacent disc florets fused to ray cypsela;

styles of disc florets absent or with 1 (rarely 2) vascular traces; anthers normally free and with numerous minute thickenings surrounding endothecial cells
XXVI. Heliantheae-Ambrosiinae (p. 443)

– Anthers black or brown; styles with 2 vascular traces, anthers normally fused, endothecial thickenings 1–4, polar **XXVI. Heliantheae-Ecliptinae** (p. 446) **1261. *Clibadium*, 1275. *Lantanopsis*, XXVII. Millerieae-Milleriinae** (p. 487) **1386. *Ichthyothere***

20. Disc floret cypselae moderately to strongly compressed, rarely quadrate or the exocarp juicy and cypselae drupe-like; pappus elements, when present, mostly disposed in a narrowly oval to linear arrangement on cypsela neck; cypselae sometimes winged; ray cypselae never enclosed in perigynia **XXVI. Heliantheae** (p. 440)

– Disc floret cypselae mostly terete or subterete, if quadrate, then cypselae either with 4 small horns (*Greenmaniella*) or prismatic (*Lycapsus*), without juicy exocarps; pappus elements mostly present and in radial arrangement on cypsela neck; cypselae never winged; ray cypselae sometimes tightly wrapped by phyllaries or enclosed in perigynia 21

21. Disc corolla throats with resinous areas between vascular strands just below lobe sinuses; style arms canaliculate on adaxial surface; carpopodia missing, base of cypsela appearing invaginated **XXII. Tageteae-Varillinae** (p. 430)

– Disc corolla throats otherwise; style arms not canaliculate; carpopodia present 22

22. Leaves alternate; ray florets fertile 23

– Leaves opposite, if alternate, then ray florets neuter or plants shrubby and leaves linear (*Dyscritothamnus*) 25

23. Capitula discoid; corollas tetramerous **XXIX. Perityleae-Lycapsinae** (p. 509)

– Capitula radiate, rarely discoid; disc corollas pentamerous 24

24. Leaves entire or lobed, never bipinnate **XXI. Neurolaeneae-Neurolaeninae** (p. 419) **1189. *Calea*** in part, **1190. *Greenmaniella*, 1191. *Neurolaena***

– Leaves bipinnate, segments linear or filiform **XXIV. Bahieae 1237. *Hymenopappus*** in part

25. Corollas with reddish resin in resin ducts **XXI. Neurolaeneae-Neurolaeninae** (p. 419) **1189. *Calea*** in part

– Corollas with yellow resin in resin ducts or these colourless, if with reddish resin in resin ducts, then plants endemic to Africa (*Guizotia*) **XXVII. Millerieae-Galinsoginae** (p. 483), **Desmanthodiinae** (p. 479), **Dyscritothamninae** (p. 480), **Jaegeriinae** (p. 487), **Milleriinae** (p. 488)

26. Leaves and/or phyllaries with embedded or marginal, pellucid secretory cavities/glands or pustules, aromatic **XXII. Tageteae-Pectidinae** (p. 423)

– Leaves and phyllaries without embedded or marginal, pellucid secretory cavities/glands or pustules, rarely aromatic 27

27. Capitula with one row of paleae between ray florets and first row of disc florets; in discoid capitula phyllaries reduced, wanting or missing and these paleae connate and appearing as an involucre **XXVIII. Madieae-Madiinae** in part (p. 497)

– Capitula otherwise 28

28. Capitula with 1 broadly biconvex, obcompressed cypsela **XXVI. Heliantheae-Ecliptinae** (p. 446) **1275. *Lantanopsis*, 1292. *Riencourtia***

– Capitula otherwise 29

29. Anther appendages linear, flat, without basal constrictions, reduced or lacking; capitula always discoid; corollas white, pink or purple; style arm appendages longer than stigmatic lines **XXX. Eupatorieae** (p. 510)

– Anther appendages lanceolate to oval, rarely linear, shallowly to strongly concave, constricted at base; capitula discoid, disciform or radiate; corollas mostly yellow or yellow-orange, sometimes white, rarely pink or purple; style arm appendages usually as long as or shorter than stigmatic lines 30

30. Disc corollas tetramerous; cypselae strongly compressed or prismatic with 4 ribs usually ciliate on margins; styles subulate; herbage of most species densely glandular, sticky **XXIX. Perityleae-Peritylinae** (p. 509)

– Disc corollas mostly pentamerous; cypselae various, rarely strongly compressed or with 4 ribs, pubescence various; styles various, sometimes subulate, herbage glabrous or pubescent, rarely glandular 31

31. Plants forming small rosettes with axillary, solitary capitula on long peduncles; plants from Cuba 32

– Plants otherwise, if forming small rosettes, then capitula terminal in corymbiform inflorescences, rarely solitary (*Chamaechaenactis*), if appearing axillary, then capitula nearly sessile; plants from America, rarely Cuba 33

32. Ray florets without corollas; pappus of 4 accrescent scales **XX. Coreopsideae-Pinillosiinae 1185. *Tetraperone***

– Ray florets with corollas; pappus of several accrescent, ciliate scales **XXI. Neurolaeneae-Heptanthinae** (p. 418)

33. Decumbent perennial herbs with ovate to reniform, opposite leaves; capitula with 4 phyllaries and 4 florets; ray florets either without corollas or corollas, when present, deeply bilobed; plants from the Caribbean **XX. Coreopsideae-Pinillosiinae** (p. 416)

– Plants otherwise; capitula otherwise; ray florets, when present, always corollate, limbs various, never deeply bilobed; plants from America, rarely the Caribbean 34

34. Phyllaries of capitula with black striae; receptacles setose **XXII. Tageteae-Clappinae** (p. 421)

– Phyllaries without black striae; receptacles rarely setose 35

35. Leaves glabrous, linear to acicular, glaucous, succulent; plants of saline environments 36

– Leaves otherwise; plants rarely from saline environments 37

36. Leaves opposite **XXII. Tageteae-Jaumeinae** (p. 423)

– Leaves alternate **XXII. Tageteae 1223. *Pseudoclappia***

37. Cypselae terete with multiple ribs (8–11) **XXII. Tageteae-Flaveriinae** (p. 422)

– Cypselae compressed or obcompressed, sometimes prismatic to terete with 5 or fewer ribs 38

38. Weak shrubs with alternate, entire, petiolate, ovate to deltate leaves; phyllaries fused at base forming a bowl-

shaped involucre
XXVIII. Madieae-Venegasiinae (p. 507)
– Annual or perennial herbs, if shrubs, then leaves mostly sessile and linear, if petiolate, then blades dissected 39
39. Corollas with long, stipitate, biseriate, glandular trichomes, trichome stalk approximately 20+ times as long as diameter of glandular terminal group of cells or head, head slightly depressed in centre and appearing obcordate in cross-section **XXII. Tageteae** **1220. *Arnicastrum*, 1221. *Jamesianthus***
– Corollas glabrous or pubescent, if with glandular trichomes, then these with shorter stalks, approximately 1–5 times as long as diameter of glandular head; head round, never depressed in centre nor obcordate in cross-section 40
40. Ray cypsela with 3 and disc cypselae with 5 triangular, subulate scales **XXII. Tageteae** **1222. *Oxypappus***
– Ray and disc cypselae otherwise 41
41. Cypselae epappose, mostly trigonal with abaxial face broader than other two faces, glabrous; plants with mostly glandular herbage, viscid **XXIX. Perityleae-Galeaninae** (p. 401)
– Cypselae pappose, rarely epappose, cypselae compressed or obcompressed, subterete to terete, sometimes pyramidal, if trigonal, then all faces of equal size; plants glabrous to sparsely to densely pubescent, sometimes lanate-white, herbage rarely glandular and sticky 42
42. Capitula disciform, minute; pappus a lacerate crown; plants of the northern Caribbean **XXIV. Bahieae 1246. *Thymopsis***
– Capitula discoid or radiate, pappus various, rarely a lacerate crown; plants mostly from North America, some from South America, few from Africa, rarely from the Caribbean 43
43. Pappus of scales with a thickened median rib sometimes protruding beyond scales as an awn **XXIV. Bahieae** in part (p. 433)
– Pappus various, if of scales, then scales without a median midrib, rarely absent 44
44. Pappus of bristles 45
– Pappus otherwise or absent 46
45. Cauline leaves mostly opposite **XXVIII. Madieae-Arnicinae** (p. 493)
– Cauline leaves alternate **XXIV. Bahieae** **1231. *Bartlettia*, 1242. *Peucephyllum*, 1244. *Psathyrotopsis***
46. Shrubs with petiolate leaves 47
– Annual or perennial herbs 48
47. Capitula discoid; corollas white **XXIV. Bahieae** (p. 433) **1229. *Apostates*, 1240. *Loxothysanus***
– Capitula radiate; corollas yellow **XVIII. Madieae-Baeriinae** **1398. *Constancea***
48. Pappus deciduous as a unit **XIII. Chaenactideae** **1224. *Dimeresia*, 1226. *Orochaenactis***
– Pappus persistent or absent 49
49. Plants aquatic, glabrous, with fistulose stems; capitula solitary, axillary on long peduncles; ray florets white with black veins on abaxial surfaces; plants of vernal pools of western Durango state, Mexico **XVI. Heliantheae-Zinniinae** **1359. *Trichocoryne***
– Plants not aquatic, mostly pubescent; capitula terminal, if appearing axillary, then capitula sessile; ray florets mostly yellow or absent, if white, then inconspicuous and without black veins on abaxial surfaces; plants from western USA and extreme north-western Mexico 50
50. Capitula radiate, sometimes discoid; leaves mostly sessile; phyllaries in 1–3 series, mostly broadly ovate, sometimes with a thickened rib **XXVIII. Madieae-Baeriinae** (p. 494), **Hulseinae** (p. 497)
– Capitula discoid; leaves petiolate; phyllaries in 1 series, linear to lanceolate **XXIII. Chaenactideae** **1225. *Chaenactis***

XVIII. Tribe Athroismeae Panero (2002).

J.L. Panero

Annual or perennial herbs, shrubs or small trees, sometimes aromatic. Leaves simple, alternate or fasciculate on brachyblasts, petiolate or sessile, abaxial surfaces with or without sessile glandular trichomes. Capitula terminal, rarely appearing axillary, in congested, glomerule-like or open, paniculiform cymes, or solitary, pedunculate, sometimes sessile, radiate, disciform or discoid; phyllaries in 1 to 4 series, sometimes absent, herbaceous, subequal or gradate. Receptacles convex to conic, sometimes subglobose to globose, paleate or epaleate. Ray florets pistillate or absent, corollas yellow. Peripheral and disc florets pistillate, bisexual or functionally staminate, rarely shallowly zygomorphic, peripheral pistillate florets absent to several, corollas tubular, disc florets bisexual or functionally staminate, 2 to many, corollas campanulate, glabrous or pubescent mostly with twin trichome glands, lobes 4–5, corollas white, greenish white, white-yellow, rarely purplish; anthers 4–5, usually ecalcarate, shortly caudate or ecaudate, rarely the tails well-developed and branched, endothecium with polarized thickenings, sometimes radial or both, rarely evenly thickened, appendages shallowly constricted above thecae or lacking, sometimes with apical gland; style arms with parallel stigmatic areas sometimes meeting at style apices, or style filiform and undivided. Cypselae black or brown, obcompressed to subterete, sometimes with thickened striations or ribs, sometimes with a proliferation of spongy

cells at apical portions of cypselae, glabrous or with ciliate lateral ridges and glandular trichomes, sometimes with apically arcuate twin trichomes. Pappus of fertile floret cypselae a crown of twin trichomes, sometimes with recurved apices or of deeply lacerate fused squamellae, sometimes with two awns at angles of cypselae, a variously lacerate crown or of a few, free, lacerate scales, or absent.

Six genera in three subtribes and about 59 species mostly in eastern Africa, a few species in western Africa, India, Madagascar, south-eastern Asia and Indonesia. *Centipeda* also occurs in Australia, New Zealand, south-eastern Asia, Madagascar and southern South America. Most members of Athroismeae are found in a variety of habitats ranging from dry open grassland and thickets to dense woodland (Eriksson 1992, 1993). *Centipeda* is unusual in the tribe by growing in habitats prone to inundation, such as the edges of irrigation canals or of intermittent ponds or on brackish, muddy tidal flats.

Eriksson (1991) placed *Athroisma*, *Blepharispermum* and *Leucoblepharis* (as the *Blepharispermum* group, here subtribe Athroisminae) in tribe Heliantheae, away from their original placement in Inuleae, because of their carbonized cypselae and paleate receptacles. Molecular studies (Kim and Jansen 1995; Baldwin et al. 2002) do not support the inclusion of the group in any of the lineages of the Heliantheae alliance but rather support its status as their sister taxon. The recognition of the group as a tribe of Asteraceae is based primarily on evidence from molecular phylogenetic studies of the family (Panero and Funk 2002). *Centipeda* has been placed in several tribes including Anthemideae and Astereae. Bremer (1994) considered the genus difficult to place but maintained it in Asteroideae unassigned to tribe. Nesom (1994c) considered the genus a member of Astereae. An ITS analysis aimed at identifying the phylogenetic relationships of endemic New Zealand Asteraceae by Wagstaff and Breitwieser (2002) found strong support for the exclusion of the genus from Astereae and its close relationship to Athroismeae and the Heliantheae alliance. These results were recently confirmed using several coding regions of chloroplast DNA (Panero 2005, and unpubl. data). In consequence, *Centipeda* is here included in an expanded tribe Athroismeae. The monotypic *Symphyllocarpus* of eastern Asia may prove to be sister to *Centipeda*. *Symphyllocarpus* shares with *Centipeda* a similar habit, alternate phyllotaxy, sessile leaves, terminal capitula with marginally scarious, subequal phyllaries, several rows of peripheral, tubular female florets and central bisexual florets with tetramerous corollas. The main difference between *Symphyllocarpus* and *Centipeda* lies in their cypsela morphology. The cypselae of *Symphyllocarpus* are subterete and smooth and lack the deep grooves and ribs found in the cypselae of *Centipeda*. In addition, *Symphyllocarpus* is reported to have paleate receptacles (epaleate in *Centipeda*), although the paleae may represent asymmetrical growth of the cypsela exocarp. Molecular studies of Inuleae by Eldenäs et al. (1999) revealed that the genus *Anisopappus* is more closely related to Heliantheae and relatives than to Inuleae. Additional molecular evidence (Panero et al., unpubl. data) supports the placement of *Anisopappus* in tribe Athroismeae. *Welwitschiella* has been traditionally viewed as a member of Helenieae (Karis and Ryding 1994b). Based on my interpretation of the morphology of the genus, I believe *Welwitschiella* is not a member of the Heliantheae alliance of tribes. For the purposes of this publication, I have decided to include the genus in Athroismeae, as *Anisopappus* appears to share more characteristics with *Welwitschiella* than any other genus of the Heliantheae alliance. *Welwitschiella* shares with some or all species of *Anisopappus* an involucre of several series of phyllaries, strongly ribbed cypselae, a pappus of scales fused at the base and forming a lacerate corona, alternate phyllotaxy, yellow corollas, and with *A. athanasioides*, also from Angola, irregularly lobed, peripheral corollas. *Welwitschiella* lacks paleate receptacles present in *Anisopappus*, although lacking in *A. latifolius*. The three original genera of Athroismeae are now included in subtribe Athroisminae, *Centipeda* in subtribe Centipedinae, and *Anisopappus* and *Welwitschiella* in subtribe Anisopappinae (Panero 2005). The three subtribes are quite distinctive morphologically, and their genera have never been grouped together in the past or even hypothesized to be closely related. Recent molecular studies of Inuleae and related genera by Anderberg et al. (2005) support, albeit weakly, a close relationship of the southern African *Callilepis* to either Athroismeae or the rest of the tribes of the Heliantheae alliance. Molecular studies based on several genes of chloroplast DNA (Panero et al., unpubl. data) clearly show that *Callilepis* is neither a member of Gnaphalieae, Inuleae or Athroismeae nor is it closely related to other tribes of the Heliantheae alliance.

Key to the Subtribes

1. Cypselae black, carbonized, obcompressed **2. Athroisminae**
– Cypselae brown or dark brown to black, never carbonized, subterete to compressed 2
2. Capitula disciform; receptacles epaleate; innermost corollas tetramerous, leaves sessile **3. Centipedinae**
– Capitula radiate, very rarely discoid; receptacles paleate, very rarely epaleate; innermost corollas pentalobed; leaves mostly petiolate, rarely sessile **1. Anisopappinae**

XVIII.1. Subtribe Anisopappinae Panero (2005).

Annual or perennial herbs. Leaves alternate, petiolate or subsessile, blades linear to ovate, sometimes subcordate, entire to pinnatifid, triplinerved, sometimes pinnate. Capitula terminal, in open paniculiform or rarely subumbelliform cymes, radiate, rarely discoid or disciform. Involucres campanulate to mostly hemispheric. Receptacles convex, rarely shallowly conic, usually paleate. Ray florets pistillate, sometimes with staminodes, corollas yellow. Peripheral florets in disciform capitula with zygomorphic corollas, penta- or tetramerous. Disc florets bisexual, rarely functionally staminate, corollas 5-lobed, golden-yellow; stamens 5, anthers shallowly calcarate or ecalcarate, shallowly to sometimes strongly tailed, tails sometimes branched, appendages ovate; style with divided stigmatic surfaces, with obtuse to subacute papillae or sweeping trichomes. Cypselae subterete, narrowly obovate in outline, ribbed, epidermis without crystals. Pappus of small scales fused at the base and forming a lacerate cup or absent.

Key to the Genera

1. Capitula radiate; receptacles paleate, rarely epaleate **1138. *Anisopappus***
– Capitula disciform; receptacles epaleate **1139. *Welwitschiella***

1138. *Anisopappus* Hook. & Arn. Fig. 77

Anisopappus Hook. & Arn., Bot. Beech. Voy. 196 (1837); Humbert, Fl. Madag. 189, 2: 595–611 (1962), part. rev. as *Epallage*; Wild, Kirkia 4: 45–76. (1964), rev.; Eldenäs & Anderberg, Pl. Syst. Evol. 199: 167–192 (1996), phylog.; Ortiz et al., Anales Jard. Bot. Madrid 54: 378–391 (1996), rev.

Epallage DC. (1837).

Sphacophyllum Benth. (1873).

Astephania Oliver (1886).

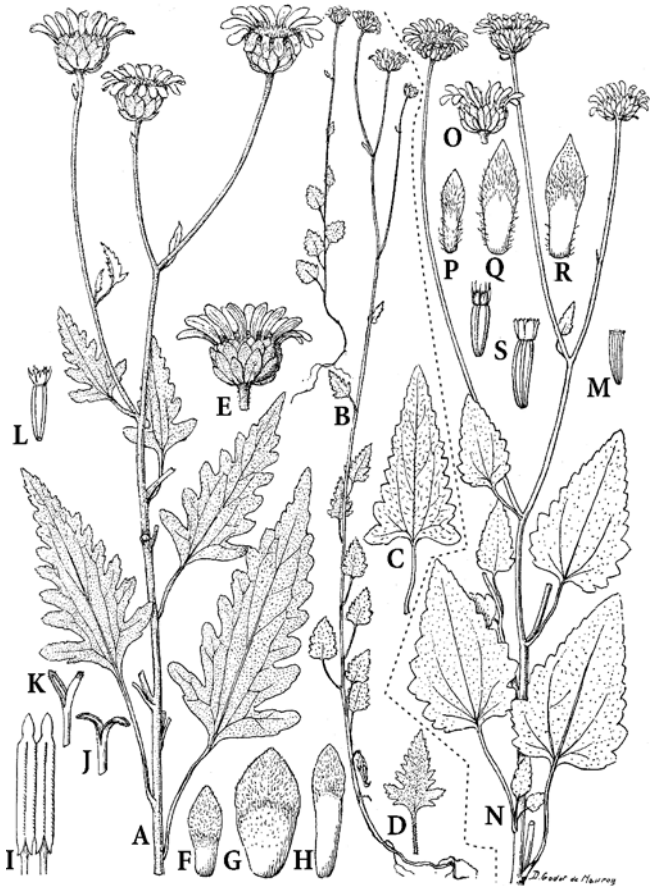

Fig. 77. Compositae-Athroismeae. **A–M** *Anisopappus chinensis* subsp. *chinensis*. **A** Flowering branch. **B** Different habits. **C, D** Leaves. **E** Capitulum. **F–H** Involucral bracts (external, middle, internal). **I** Anthers. **J** Style arms of female floret. **K** Style arms of bisexual floret. **L, M** Cypselae. **N–S** *Anisopappus chinensis* subsp. *buchwaldii*. **N** Flowering branch. **O** Capitulum. **P–R** Involucral bracts (external, middle, internal). **S** Two forms of cypselae. (Humbert 1962, with permission from the Muséum National d'Histoire Naturelle, Paris; taxon names according to Ortiz et al. 1996)

Temnolepis Baker (1887).

Eenia Hiern & S. Moore (1899).

Annual or perennial herbs. Leaves alternate, blades linear to ovate, sometimes subcordate, entire to pinnatifid, triplinerved, sometimes pinnate. Capitula terminal, in open paniculiform or corymbiform, rarely subumbelliform cymes, radiate, rarely discoid or disciform. Involucres campanulate to mostly hemispherical. Receptacles convex, rarely shallowly conic, usually paleate. Ray florets pistillate, sometimes with staminodes, corollas yellow. Disc florets bisexual, corollas 5-lobed, golden-yellow; stamens 5, anthers shallowly calcarate or

ecalcarate, tailed, tails rarely branched, appendages ovate; styles with divided stigmatic surfaces, with obtuse papillae. Cypselae subterete, ribbed, pappus of small scales or absent. $x = 7$. Approximately 20 species, tropical Africa, Madagascar, one species in south-eastern Asia.

1139. *Welwitschiella* O. Hoffm.

Welwitschiella O. Hoffm. Nat. Pflanzenfam. IV, 5: 390 (1894).

Perennial herbs, stems ridged. Leaves alternate, sessile, blades narrowly oblong, pinnately veined. Capitula disciform, terminal, in small paniculiform cymes. Involucres campanulate, phyllaries in 3–4 series, slightly gradate, innermost longer and somewhat chartaceous, otherwise herbaceous. Receptacles convex, epaleate. Peripheral florets tetramerous, rarely pentamerous, fertile, corollas yellow, some zygomorphic, inner florets functionally staminate(?), corollas yellow, edge of lobes thickened, cells slightly sclerified; anthers hyaline or white/yellow(?), ecalcarate, without tails, appendages narrowly ovate, glabrous; style arm apices of peripheral florets acute to acuminate, with divided stigmatic surfaces, glabrous on abaxial surface, style arms of disc florets densely papillose, acuminate. Cypselae obcompressed, mostly 4-ribbed, brown, sparsely pubescent. Pappus an erose crown or multiple erose scales fused at base. One species, *W. neriifolia* O. Hoffm., south-central tropical Africa.

XVIII.2. Subtribe Athroisminae Panero (2005).

Perennial herbs, shrubs or small trees. Leaves alternate or fasciculate on brachyblasts, petioles sometimes with a basal spine; blades linear, lanceolate to ovate or obovate. Capitula disciform or discoid, homogamous or heterogamous, in congested glomerule-like cymes; glomerules solitary or arranged in open to compact, paniculiform cymes. Involucres narrowly campanulate, phyllaries 0–2. Receptacles paleate. Florets all actinomorphic, rarely zygomorphic, female florets 2 to several or absent, corollas tubular, bisexual florets 2–25, corollas campanulate, lobes (4–)5; anthers (4–)5, ecalcarate, caudate; styles divided or filiform and undivided in functionally staminate florets, stigmatic area divided and confluent at style apices, sweeping hairs present. Cypselae obcompressed, black, lateral ridges ciliate. Pappus of fertile floret cypselae a crown of twin trichomes, or of deeply lacerate and fused squamellae, sometimes with two awns at angles of cypsela. Pappus of functionally staminate floret ovaries a variously lacerate crown or of a few, free, lacerate scales.

Key to the Genera

1. Florets with campanulate corollas functionally staminate, styles filiform **1141. *Blepharispermum***
– Florets with campanulate corollas perfect, styles divided 2
2. Herbaceous bracts subtending capitula longer than capitula; apices of twin trichomes on cypselae straight **1142. *Leucoblepharis***
– Herbaceous bracts subtending capitula shorter than capitula; apices of twin trichomes on cypselae diverging or recurved **1143. *Athroisma***

Genera of Athroisminae

1140. *Athroisma* DC. Fig. 78

Athroisma DC., Guill. Arch. Bot. 2: 516 (1833); Eriksson, Bot. J. Linn. Soc. 119: 101–184 (1993), rev.

Perennial herbs or shrubs. Leaves petiolate or sessile, blades linear to ovate or obovate, margins entire to pinnatifid. Capitula heterogamous or homogamous with 0–2 female florets and 4–45 perfect florets. Florets with white to pinkish, glabrous or glandular corollas, anthers 5, rarely 4, styles divided. Cypselae elliptic to obovate. Pappus a corona of twin trichomes. Twelve species, Africa, India, Indonesia, Madagascar, south-eastern Asia.

1141. *Blepharispermum* Wight ex DC.

Blepharispermum Wight ex DC. in Wight, Contrib.: 11 (1834); Eriksson, Pl. Syst. Evol. 182: 149–227 (1992), rev.

Shrubs or small trees. Leaves sometimes on brachyblasts, petiolate to sessile, petiole sometimes with a spine or spine-like protuberance, blades linear to ovate or obovate, rarely spathulate, entire to serrate. Capitula heterogamous with 2 female florets and 2–4 functionally staminate florets. Functionally staminate florets with greenish-white, creamy white or yellowish-white corollas, anthers 5, style undivided or dividing late in anthesis. Cypselae elliptic to obcordate, margins ciliate to scaly. Pappus of female floret cypselae of 2–15 scales of equal length or with two lateral scales or awns longer, pappus of functionally staminate floret ovaries a lacerate crown or of few, free, lacerate scales or awns. Fifteen species,

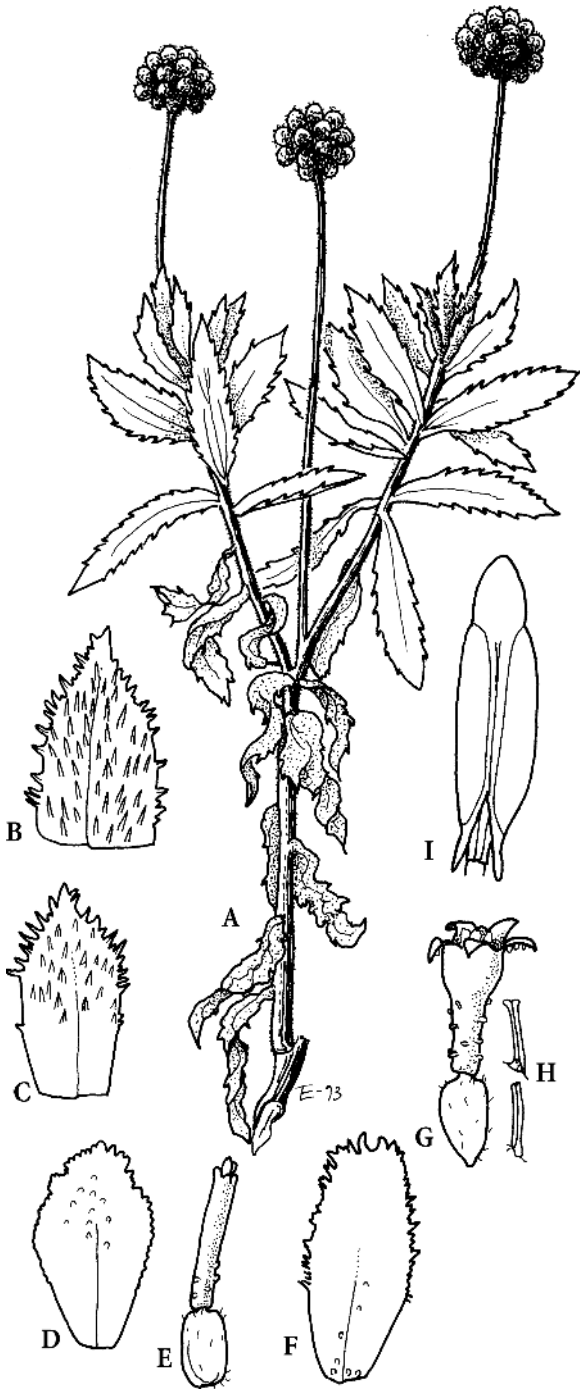

Fig. 78. Compositae-Athroismeae. *Athroisma boranense*. **A** Flowering branch. **B** Basal subtending bract. **C** Median subtending bract. **D** Involucral bract. **E** Female floret. **F** Palea. **G** Hermaphrodite floret. **H** Twin trichomes. **I** Anther. (Eriksson 1993, with permission from Botanical Journal of the Linnean Society; artist T. Eriksson)

Africa, Arabian Peninsula, India, Madagascar, Sri Lanka.

1142. *Leucoblepharis* Arnott

Leucoblepharis Arnott, Mag. Zool. Bot. 2: 422 (1838); Eriksson, Bot. Jahrb. Syst. 112: 167–191 (1990), rev.

Shrubs. Leaves petiolate, blades lanceolate to obovate, entire to shallowly serrate. Capitula heterogamous with 2 female florets and 10–15 perfect florets. Florets with greenish-white corollas, anthers 5, styles divided. Cypselae elliptic to obcordate, margins ciliate, twin hairs with straight apical cells. Pappus of 10–15 flat scales. One species, *L. subsessilis* (DC.) Arnott, south-western India

XVIII.3. Subtribe Centipedinae Panero (2005).

Annual or perennial herbs. Leaves alternate, sessile, blades linear to obovate, variously toothed, rarely entire. Capitula sessile to shortly pedunculate, terminal, appearing axillary, solitary or in simple monochasial cymes, disciform or radiate. Involucres campanulate to hemispherical, phyllaries in 1–2 series, subequal, herbaceous, margins scarious. Receptacles shallowly concave to convex, subglobose, epaleate. Peripheral/radiate florets in several series, sometimes lobes (3) extremely reduced and corolla tubular, pistillate, corollas creamy-white, green, light yellow or purplish. Disc florets bisexual, corollas tetramerous, creamy-white, green, light yellow or purplish, glabrous with a few glandular trichomes; stamens 4, anthers hyaline, tailed, ecalcarate, appendages, when present, ovate; style arms with divided stigmatic surfaces, concave, urceolate in outline, apices papillose. Cypselae clavate to subterete, broadly ribbed, glabrescent on basal end, cells of distal end with raised apical tips, elongating and forming biseriate trichomes, increasing in density at apical end and forming a short, dentate, spongy corona ("pappus") around corolla tube, glandular trichomes normally found between ribs. Pappus absent.

Only one genus:

1143. *Centipeda* Lour. Fig. 79

Centipeda Lour., Fl. Cochinchin. 492 (1790); Walsh, Muelleria 15: 33–64 (2001), reg. rev.
Myriogyne Less. (1831).

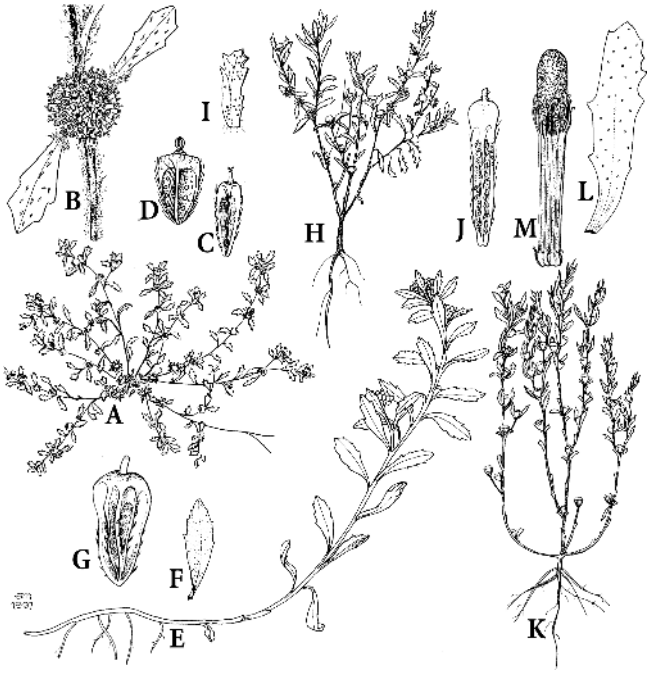

Fig. 79. Compositae-Athroismeae. **A–C** *Centipeda minima*. **A** Habit. **B** Capitulum. **C** Cypsela. **D** *Centipeda nidiformis*, cypsela. **E–G** *Centipeda elatinoides*. **E** Habit. **F** Leaf. **G** Cypsela. **H–J** *Centipeda cunninghamii*. **H** Habit. **I** Leaf. **J** Cypsela. **K–M** *Centipeda thespidioides*. **K** Habit. **L** Leaf. **M** Cypsela. (Walsh 1999, with permission from the author; artist Enid Mayfield; species names according to N.G. Walsh, pers. comm.)

Characters of the subtribe. $x = 10$. Ten species, Australia, New Zealand, south-eastern Asia, Madagascar, Papua New Guinea, southern South America.

XIX. Tribe Helenieae Lindl. (1829).

J.L. Panero

Annual, biennial, perennial herbs, rarely shrubs. Leaves alternate, rarely opposite, petiolate, subsessile or sessile, blades entire to pinnatifid, linear to lanceolate, rarely ovate, glabrous to densely white lanate-floccose. Capitula radiate or discoid, terminal, solitary and scapose or in open, rarely congested paniculiform or corymbiform cymes. Involucres cylindrical, campanulate or hemispheric, phyllaries subequal to gradate, in 2 to several series, sometimes reflexed at anthesis. Receptacles flat to convex or globose, usually epaleate. Ray florets fertile or neuter, obscurely but most commonly conspicuously 3–5-lobed, limbs mostly attenuate to oblique into tube, rarely obtuse to truncate. Disc florets bisexual, rarely functionally staminate, corollas tubular to campanulate, glabrescent to densely pubescent, veins meeting at apices of corolla lobes (except in *Plateilema*); anthers shortly caudate to ecaudate, appendages narrowly ovate to round and strongly carinate, cells of appendages mostly sclerified, filaments and endothecium with or without crystals, median endothecial cells quadratic to fusiform with 1–5 polar bridges, rarely with radial thickenings confined to distal ends of thecae; style arms with two stigmatic surfaces parallel to the edges of the style arm, rarely meeting apically, mostly truncate with a tuft of papillae, sometimes with a tapered, vascularized appendage (*Balduina*, *Gaillardia*), or with a proliferation of cells producing an obtuse apex. Ray and disc cypselae essentially homomorphic, clavate to subterete, walls not carbonized, mostly with large quadratic or isodiametric crystals, glabrous to densely sericeous, sometimes pubescence confined to ridges and alternating with glandular trichomes. Pappus of several ovate to quadratic, rarely triangular scales with aristate, acuminate or obtuse apices, or of multiple bristles either free or coalescing into scales, rarely absent.

The tribe contains 13 genera and approximately 120 species in North and South America, with most species in the south-western USA and northern Mexico. Many species grow in desert or dry regions and produce small rosettes through the wetter winter months, from which flowering shoots arise rapidly as temperatures increase in the drier spring months. Species of *Balduina*, *Helenium* and *Marshallia* are adapted to wetter habitats of eastern North America. Several species of *Helenium* and *Gaillardia* are horticulturally important.

Helenieae were characterized by Cassini (1819) as having cypselae with scaly pappi. The concept was modified by Bentham (1873b) to include all taxa of Heliantheae affinity lacking paleae. Turner and Powell (1977) concluded that Helenieae were a paraphyletic assemblage and disposed of the genera in several tribes including Senecioneae and Heliantheae. Robinson (1981) placed Helenieae into a large Heliantheae containing 35 subtribes. His subtribes Gaillardiinae and Marshalliinae correspond to the concept of Helenieae subtribe Gaillardiinae of Karis and Ryding (1994b). Molecular studies of Helenieae by Baldwin and Wessa (2000b) and Baldwin et al. (2002) support a narrower interpretation of Helenieae to include only 13 genera, which corresponds to the composition of Robinson's

subtribes Gaillardiinae and Marshallinae, showing that Helenieae is the basalmost lineage of the classical Helenieae-Heliantheae complex. Most Heleniae can be distinguished from any other group in the Heliantheae alliance by their non-carbonized cypselae which rather contain crystals in the cypsela wall (similarly to some Inuleae). Additional characters which collectively can be useful in recognizing Helenieae include mostly truncate style arms, conspicuously trilobed ray limb apices, a scaly pappus and mostly alternate leaves. Baldwin and Wessa (2000b) recognize five subtribes in tribe Helenieae, namely Gaillardiinae, Marshallinae, Plateileminae, Psathyrotinae and Tetraneurinae (as Riddelliinae; see Bierner 2001).

Key to the Subtribes

1. Pappus of bristles sometimes fused at base **4. Psathyrotinae** (p. 403)
– Pappus of erose, quadratic to ovate, aristate or acuminate scales or absent 2
2. Receptacles paleate throughout **2. Marshalliinae** (p. 402)
– Receptacles epaleate or paleate near margins 3
3. Veins of corolla lobe margins not merging at corolla lobe apices **3. Plateileminae** (p. 403)
– Veins of corolla lobe margins merging at corolla lobe apices 4
4. Phyllaries reflexed at anthesis, if erect, then anther appendages with glandular trichomes on abaxial surface **1. Gaillardiinae** (p. 401)
– Phyllaries erect (not reflexed) at anthesis **5. Tetraneuriinae** (p. 404)

XIX.1. Subtribe Gaillardiinae Less. (1831).

Subtribe Heleniinae Less. (1832).

Annual or perennial herbs, sometimes caespitose, rhizomatous and producing a thickened root caudex or short stem. Leaves alternate, entire or pinnatifid. Capitula scapose, solitary or in open paniculiform or corymbiform cymes. Ray florets fertile, rarely neuter. Disc florets bisexual. Cypselae with a pappus of ovate, acuminate, aristate, rarely linear scales.

Key to the Genera

1. Leaves without decurrent bases; styles with conic to linear, conspicuous vascularized appendages, style papillae with minute mucronate tips 2
– Leaves usually with decurrent bases; styles without vascularized appendages, normally truncate with papillose tips; style papillae without mucronate tips **1146. *Helenium***
2. Anther appendages and style arms with glandular trichomes; pappus of scales without midrib extending as an awn or bristle **1144. *Balduina***
– Anther appendages and style arms without glandular trichomes; pappus of scales with midribs extending as an awn or bristle **1145. *Gaillardia***

Genera of Gaillardiinae

1144. *Balduina* Nutt.

Balduina Nutt., Gen. N. Amer. Pl. 2: 175 (1818), nom. cons.; Parker & Jones, Brittonia 27: 355–361 (1975), rev.

Annual or perennial herbs (?). Leaves sessile to shortly petiolate, entire, linear to oblanceolate. Capitula radiate, terminal, solitary or in open corymbiform cymes. Involucres hemispheric, phyllaries gradate. Receptacles strongly alveolate, with multiple aristae, growing after anthesis and forming an aristate basket or cup around cypselae. Ray florets neuter, 3-lobed, corollas bright to golden yellow. Disc corollas bright yellow to purple or yellow with purple lobes, sparsely glandular, without sclerified cells, lobes densely pubescent on abaxial surfaces; anthers ecaudate, appendages ovate, with glandular trichomes, cells sclerified; style arms with tapered, papillose apices and glandular trichomes, style appendages vascularized. Cypselae obconic, glabrous to densely sericeous, sometimes glandular. Pappus of several ovate scales with acuminate apices and erose margins. $x = 18$. Three species, south-eastern USA.

1145. *Gaillardia* Foug.

Gaillardia Foug., Obs. Phys. 29: 55 (1786); Biddulph, Res. Stud. State College Wash. 12: 195–256 (1944), rev.

Annual or perennial herbs, rarely caespitose, low shrubs with xylopodia, sometimes forming rosettes, rarely strongly aromatic. Leaves petiolate or sessile, entire to pinnatifid sometimes semisucculent. Capitula terminal or axillary, solitary, sometimes on long peduncles, radiate or discoid. Involucres hemispheric to broadly hemispheric, phyllaries subequal, herbaceous or chartaceous. Receptacles convex to hemispheric, densely setose. Ray florets neuter, rarely fertile, corollas yellow to red or purple, often bicoloured with deeply trilobed apices. Disc corollas yellow or greenish yellow, often red or deep purple distally, or purple throughout, glabrous or sparsely pubescent, without sclerified cells, lobes densely pubescent on abaxial surfaces; anthers caudate, appendages ovate to narrowly ovate, cells sclerified, especially

distally and on margins; style arms with tapered papillose apices, style appendages vascularized. Cypselae obpyramidal to obconic, glabrous to densely sericeous, sometimes with ridges. Pappus of 6–12 aristate, rarely linear scales with erose margins. x = 9, 15, 17, 19. Twenty species, south-eastern Canada, northern Mexico, south-western USA, temperate eastern South America.

1146. ***Helenium*** L. Fig. 80

Helenium L., Sp. Pl. 2: 886 (1753).

Annual or perennial herbs. Leaves alternate, usually sessile, mostly decurrent, blades linear to lanceolate, elliptic. Capitula terminal, solitary or in open paniculiform cymes, sometimes on swollen peduncles, radiate or discoid. Involucres rotate to reflexed at anthesis, phyllaries subequal, herbaceous. Receptacles convex to globose, rarely with paleae on outermost rows of florets. Ray florets neuter or pistillate and fertile, corollas yellow or orange, sometimes brownish orange. Disc corollas yellow, sometimes obscured by red or purple pilose lobes, glabrous to sparsely pubescent, without sclerified cells, lobes densely pubescent on abaxial surface; anthers ecaudate, appendages ovate to deltate, cells sclerified; style arms with truncate papillose apices. Cypselae obpyramidal to cylindric, sometimes ridged, glabrous or variously pubescent, sometimes glandular. Pappus absent or of a few scales with obtuse, acuminate or aristate tips. x = 17. Thirty species, North and South America, most species in northern Mexico and southern USA.

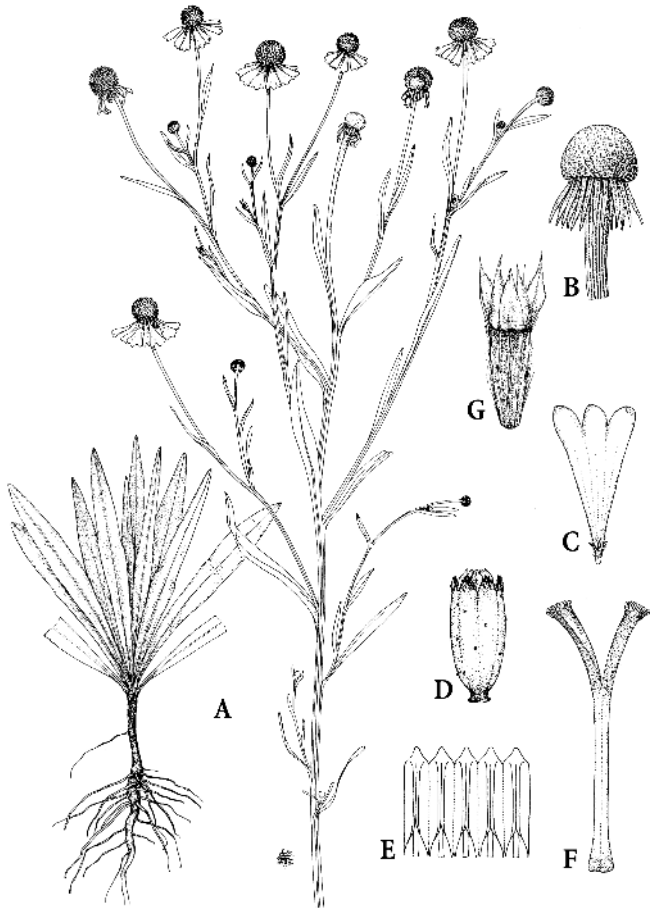

Fig. 80. Compositae-Helenieae. *Helenium mexicanum*. **A** Flowering branch and young plant. **B** Capitulum with denuded receptacle. **C** Ray floret. **D** Disc corolla. **E** Anthers. **F** Style. **G** Cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

XIX.2. Subtribe Marshalliinae H. Rob. (1978).

Perennial, mostly glabrous herbs, sometimes rhizomatous and producing a thickened root caudex. Leaves alternate, petiolate to subsessile, blades linear to narrowly ovate to oval, triplinerved or with a single midvein. Capitula solitary or in open paniculiform cymes, discoid, paleate throughout. Involucres campanulate to hemispheric, phyllaries herbaceous in 2 series. Receptacles flat to shallowly convex. Florets bisexual, corollas deeply dissected, white to cream, purplish or pale lavender, without sclerified cells, lobes sparsely pubescent with a few large, round glandular trichomes; anthers caudate, appendages ovate to round, cells sclerified only on upper margins; style arms with obtuse papillose apices, papillae extending down to bifurcation. Cypselae obpyramidal, weakly 5-angled, with tapered trichomes on ridges interspersed with glandular trichomes. Pappus of 5–6 hyaline to ferrugineous acuminate scales. x = 9.

Only one genus:

1147. ***Marshallia*** Schreb.

Marshallia Schreb., Gen. Pl. 2: 810 (1791), nom. cons.; Channell, Contr. Gray Herb. 181: 41–132, (1957), rev.; Watson & Estes, Syst. Bot. 15: 403–414, (1990), phylog.

Characters of the subtribe. Seven species, north-eastern Mexico (*M. caespitosa* Nutt. ex DC., pers. obs.), south-western and eastern USA.

XIX.3. Subtribe Plateileminae B.G. Baldwin (2000).

Perennial herbs, rosulate. Leaves alternate, oblanceolate in outline, pinnatifid. Capitula radiate, terminal, scapose, solitary. Involucres campanulate. Receptacles flat, epaleate. Ray florets fertile, corollas 3-lobed, yellow on adaxial surface, pink to purple on abaxial surface. Disc florets bisexual, corollas variously yellow, glabrous, without sclerified cells, lobes sparsely pubescent on abaxial surfaces, trichomes with mucronate tips; anthers ecaudate, appendages ovate to round, cells sclerified; style arms with obtuse apices, papillae with short mucronate tips. Ray cypselae shallowly obcompressed to obconic, triquetrous, essentially glabrous. Disc cypselae clavate, quadrate, essentially glabrous. Pappus of 5–8 quadratic or ovate scales with obtuse, bifid or erose apices.

Only one genus:

1148. *Plateilema* (A. Gray) Cockerell

Plateilema (A. Gray) Cockerell, Bull. Torrey Bot. Club 31: 462 (1904).

Characters of the subtribe. One species, *P. palmeri* (A. Gray) Cockerell, north-western Mexico, Texas, USA.

XIX.4. Subtribe Psathyrotinae B.G. Baldwin (2000).

Annual or perennial herbs, rarely shrubs. Leaves alternate or opposite. Capitula in dichasial cymes, discoid, sometimes with peripheral florets with two lobes expanded. Receptacles epaleate. Pappus of multiple bristles, either free or connate into 5 scales.

Key to the Genera

1. Style arms with tapered apices and with papillae on abaxial surfaces extending approximately halfway down from apices; capitula in corymbiform cymes; leaves linear, trilobed. Shrubs endemic to Isla San Pedro Mártir, Sea of Cortes, Mexico **1149. *Pelucha***
– Style arms with obtuse to rounded apices with papillae on abaxial surfaces confined to distalmost end; capitula solitary in centres of dichotomously branched cymes, the lateral shoots of which are vegetative; leaves deltate, ovate or rhombic, variously lobed, never trilobed. Annuals of the western USA and Mexico 2
2. Pappus of free bristles **1150. *Psathyrotes***
– Pappus of bristles fused into 5 distinctive scales at base **1151. *Trichoptilium***

Genera of Psathyrotinae

1149. *Pelucha* S. Wats.

Pelucha S. Wats., Proc. Amer. Acad. Arts 24: 55 (1889).

Shrubs. Leaves alternate, sessile, blades oblanceolate in outline, pinnatifid with 1–2 pairs of linear lobes. Capitula in terminal, corymbiform cymes, discoid. Involucres campanulate. Receptacles flat. Florets bisexual, corollas yellow, densely pubescent, without sclerified cells, lobes densely pubescent on abaxial surfaces; anthers caudate, appendages narrowly ovate, cells sclerified; style arm apices tapered, papillae confined to distal half of style arm. Cypselae cylindric, densely sericeous. Pappus of multiple bristles. $x = 19$. One species, *P. trifida* S. Wats., island in Sea of Cortes, Mexico.

1150. *Psathyrotes* (Nutt.) A. Gray

Psathyrotes (Nutt.) A. Gray, Smithsonian Contr. Knowl. 5: 100 (1853); Strother & Pilz, Madroño 23: 24–40, (1975), rev.

Annual herbs, dichotomously branched, leaves of first nodes opposite, soon thereafter producing three leaves with very short internodes and appearing whorled with a capitulum terminating the main axis of the shoot, with three shoots alternating with the leaves becoming the three main branches of the plant. Leaves subalternate or opposite, petiolate, blades ovate to deltate, margins dentate to crenulate, densely pubescent, glaucous, semisucculent. Inflorescence a terminal, solitary, vegetative dichasium in which the central shoot is a solitary capitulum and the lateral shoots are vegetative. Capitula discoid. Involucres cylindric to campanulate. Receptacles flat to convex. Florets bisexual, corollas golden yellow, becoming purplish with age, glabrescent to sparsely pubescent, without sclerified cells, lobes densely pubescent on abaxial surfaces; anthers shallowly caudate, appendages narrowly ovate, cells sclerified; style arm apices obtuse, vascular strands conspicuously expanded at style arm apices. Cypselae cylindric to obpyramidal, sparsely to densely sericeous, trichomes on ridges. Pappus of multiple bristles. $x = 17$. Three species, north-western Mexico, western USA.

1151. *Trichoptilium* A. Gray

Trichoptilium A. Gray, Rep. U.S. Boundary Bot.: 97 (1859).

Annual herbs, dichotomously branched. Leaves subalternate or opposite, shortly petiolate or ses-

sile, blades oblanceolate, bases attenuate, margins dentate distally, white-floccose to lanate on abaxial surface. Capitula arranged in dichasia in which the central shoot is a solitary capitulum and the lateral shoots are vegetative. Capitula discoid. Involucres campanulate to hemispheric. Receptacles flat to convex. Florets bisexual, corollas yellow, glabrescent, without sclerified cells, lobes moderately pubescent on abaxial surfaces; anthers caudate, appendages ovate, cells sclerified; style arm apices obtuse. Cypselae cylindric to obpyramidal, densely sericeous. Pappus of multiple bristles coalesced into 5(–6) discrete scales. $x = 13$. One species, *T. incisum* (A. Gray) A. Gray, north-western Mexico, western USA.

XIX.5. Subtribe Tetraneuriinae Rydb. (1915).

Subtribe Riddelliinae A. Gray (1884), nom illegit.

Subtribe Psilostrophinae B.L. Turner & A.M. Powell (1978).

Annual or perennial herbs, caespitose shrubs. Leaves alternate, entire or dissected, sometimes pinnatifid.Capitula scapose, solitary or in open to congested paniculiform or corymbiform cymes, radiate or discoid. Receptacles epaleate. Cypselae epappose or with a pappus of ovate, acuminate or aristate scales.

Key to the Genera

1. Lobes of disc corollas narrowly deltate, thickened and without multicellular trichomes on abaxial surfaces; cypselae prominently ribbed **1152. *Amblyolepis***
– Lobes of disc corollas deltate with variously shaped multicellular trichomes on abaxial surfaces; cypselae not prominently ribbed 2
2. Pappus absent 3
– Pappus present 4
3. Disc florets perfect **1153. *Baileya***
– Disc florets functionally staminate **1154. *Hymenoxys***
4. Throats (excluding lobes) of disc corollas with strongly sclerified cells; rays with obtuse to truncate bases; plants usually with floccose, whitish stems **1155. *Psilostrophe***
– Throats of disc corollas without sclerified cells; rays with attenuate to oblique bases; plants usually without floccose whitish stems 5
5. Plants caespitose with scapose, solitary capitula; plants with mostly entire leaves **1156. *Tetraneuris***
– Plants various and with leaves associated with solitary or cymose capitula; plants with variously dissected leaves, when entire, ovate, sessile and evenly distributed along flowering scape **1154. *Hymenoxys***

Genera of Tetraneuriinae

1152. *Amblyolepis* DC.

Amblyolepis DC., Prodr. 5: 667 (1836); Bierner, Madroño 37: 133–140 (1990), rev.

Annual herbs. Leaves petiolate to sessile, basal spathulate, blades elliptic to ovate, bluish green when live, drying green. Capitula terminal, solitary or loosely corymbiform, radiate. Involucres campanulate to hemispheric, phyllaries subequal. Receptacles convex to slightly globose with age. Ray florets fertile, 3-lobed, corollas yellow-orange. Disc corollas yellow-orange, essentially glabrous, without sclerified cells; anthers ecaudate, appendages narrowly ovate, cells sclerified; style arms with truncate papillose apices. Cypselae obconic, strongly ribbed, densely pubescent, glandular between ribs. Pappus of 5–6 quadrate, hyaline scales with obtuse, rarely acuminate apices. $x = 19$. One species, *A. setigera* DC., north-eastern Mexico, Texas, USA.

1153. *Baileya* Harv. & A. Gray ex A. Gray Fig. 81

Baileya Harv. & A. Gray ex A. Gray, Not. Milit. Recon. 01.144 (1848).

Annual or perennial herbs, stems conspicuously floccose. Leaves sessile, basal producing a rosette, pinnatifid, cauline entire, linear to oblanceolate, white-floccose especially on abaxial surfaces. Capitula terminal, solitary and scapose or in open corymbiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries subequal. Receptacles shallowly convex. Ray florets fertile, entire to mostly 3-lobed, in 2–3 series, corollas bright yellow, ray erect to patent during anthesis, then reflexed, persistent. Disc florets bisexual, corollas bright yellow, sparsely glandular, without sclerified cells, lobes densely pubescent on abaxial surfaces; anthers ecaudate, appendages ovate, cells sclerified; style arms with truncate to slightly obtuse papillose apices. Cypselae obconic to oblong, conspicuously ribbed, glabrescent with a few, scattered glandular trichomes and short double trichomes. Pappus absent. $x = 16$. Three species, northern Mexico, western USA.

1154. *Hymenoxys* Cass.

Hymenoxys Cass., Dict. Sci. Nat., ed. 2, 55: 278 (1828); Parker, Leaflets W. Bot. 9: 197–224 (1962), part. rev.; Bierner, Brittonia 26: 385–392 (1974), part. rev.; Bierner,

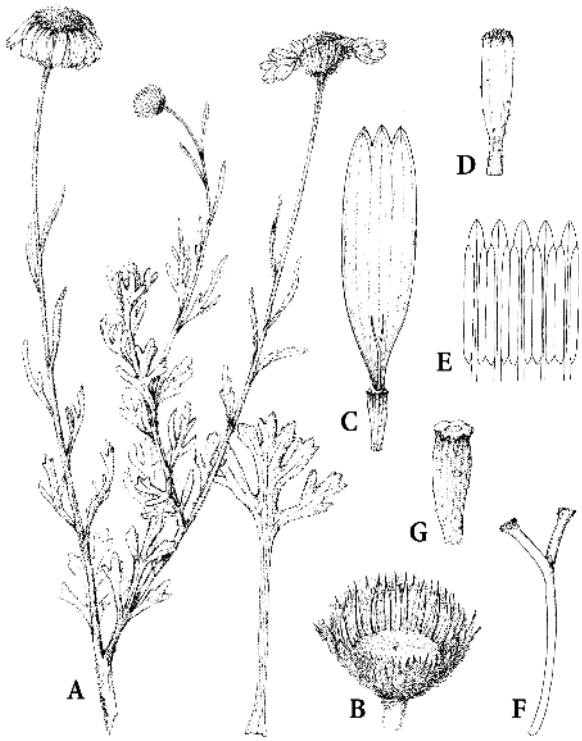

Fig. 81. Compositae-Helenieae. *Baileya multiradiata*. **A** Flowering branch and leaf. **B** Capitulum past flower, to show naked receptacle. **C** Ray floret. **D** Disc corolla. **E** Anthers. **F** Style arms. **G** Cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

Sida 16: 1–8 (1994), part. rev.; Bierner & Jansen, Lundellia 1: 17–26 (1998), phylog.; Bierner, Lundellia 4: 37–63 (2001), part. rev.

Annual or perennial herbs, sometimes with a thickened caudex. Leaves sessile or petiolate, entire or mostly trilobed or bipinnate, blades mostly linear or lanceolate, rarely ovate. Capitula terminal, solitary or in open to congested corymbiform cymes, radiate, rarely discoid. Involucres campanulate to hemispheric, phyllaries mostly in two series, outer phyllaries fused at base. Receptacles flat to shallowly convex. Ray florets fertile, conspicuously to obscurely 3-lobed, corollas yellow. Disc florets bisexual or rarely functionally staminate, corollas yellow, glabrescent to densely pubescent, sometimes with a few sclerified cells, lobes densely pubescent on abaxial surfaces; anthers ecaudate, appendages ovate to round, cells sclerified; style arms with truncate, rarely obtuse papillose apices. Cypselae obconic, moderately to densely sericeous with glandular trichomes. Pappus of ovate, acuminate or caudate to aristate scales, rarely absent. $x = 15$. Twenty-eight species (Bierner 2001), eastern and central Mexico, western USA, temperate South America.

1155. *Psilostrophe* DC.

Psilostrophe DC., Prodr. 7: 261 (1838); Heiser, Ann. Missouri Bot. Gard. 32: 265–278 (1944), rev.

Perennial, rarely biennial herbs, stems conspicuously floccose. Leaves petiolate to sessile, entire to pinnatifid, pinnatifid leaves mostly in basal rosette, blades linear, lanceolate to oblanceolate or spathulate, floccose especially on abaxial surfaces. Capitula in compact to open corymbiform cymes, radiate. Involucres cylindric to campanulate, innermost phyllaries with membranaceous margins. Receptacles flat to convex. Ray florets fertile, 3–5-lobed, corollas yellow, persistent and turning white-stramineous with age. Disc florets bisexual, corollas yellow, glabrous to sparsely pubescent, with sclerified cells throughout except lobes, lobes moderately pubescent on abaxial surfaces; anthers ecaudate, appendages ovate, cells sclerified; style arms with truncate apices. Cypselae obconic, essentially glabrous to densely villous/sericeous, trichomes uniseriate. Pappus of 4–6 hyaline quadratic scales with obtuse, erose or laciniate apices. $x = 16$. Seven species, northern Mexico, western USA.

1156. *Tetraneuris* Greene

Tetraneuris Greene, Pittonia 3: 265 (1898); Bierner & Jansen, Lundellia 1: 17–26 (1998), phylog.; Bierner & Turner, Lundellia 6: 44–96 (2003), rev.

Annual or perennial herbs, sometimes caespitose, rarely shrubs. Leaves alternate, mostly tightly clustered on short nodes forming rosettes. Capitula terminal, solitary on long scapes, rarely in open paniculiform cymes, radiate. Involucres campanulate to hemispheric. Receptacles flat to convex. Ray florets fertile, 3-lobed, persistent, corollas yellow. Disc florets bisexual, corollas yellow, glabrescent to sparsely pubescent, with a few sclerified cells on throat, lobes moderately to densely pubescent; anthers ecaudate, appendages ovate, cells sclerified; style arms with truncate apices. Cypselae obconic, moderately to densely sericeous especially on ridges. Pappus of several acuminate to aristate scales. $x = 14, 15$. Nine species, northern Mexico, western USA.

XX. Tribe Coreopsideae Lindl. (1829).

Family Coreopsidaceae Link (1829).
Tribe Bidentideae Godr. (1850).
Tribe Coreopsideae B.L. Turner & A.M. Powell (1977), isonym.

J.L. Panero

Annual or perennial herbs, shrubs, sometimes aquatic, rarely trees. Leaves alternate or opposite, petiolate or sessile, blades mostly ovate or trullate, commonly dissected, 1–3-pinnatifid, segments lanceolate or linear sometimes filiform. Capitula terminal, rarely axillary, solitary or more commonly in open paniculiform, sometimes congested corymbiform, cymes, discoid or mostly radiate, rarely disciform or ligulate. Involucres cylindric to hemispheric, phyllaries mostly dimorphic and gradate, rarely isomorphic, in 1–6 series, outermost herbaceous, green, mostly reflexed, innermost membranaceous, sometimes with scarious margins. Receptacles flat to conic, usually paleate. Ray florets with or rarely without corollas, pistillate or sterile. Disc florets bisexual or functionally staminate, corollas usually pentamerous, peripheral sometimes zygomorphic; anthers yellow, brown, black or deep purple, appendages lanceolate to round, sometimes wanting, glabrous, rarely with glands, sometimes with prominent resin canals, endothecial cells mostly quadrate or oblong, sometimes fusiform with 1–3 polar thickenings, sometimes with multiple radial and polar thickenings; style arm apices broadly deltate or acuminate to subulate, appendages short or very well developed, appendages penicillate, papillose and vascularized, papillae apically round, rarely tapered. Cypselae usually isomorphic, sometimes with resin canals, rarely striate, walls carbonized, sometimes corky on edges, sometimes winged. Pappus of 1–8 awns or absent, rarely of 4–6 round, lanceolate or obovate scales, awns smooth or with retrorse or antrorse barbs.

The tribe contains 30 genera and approximately 550 species with a worldwide distribution. Most species are found in America, especially North America. The tribe, as opposed to other helianthoid tribes, has a fair number of genera endemic to the palaeotropics, Oceania and Polynesia. Several members of the tribe are valued for their horticultural potential; wild species of *Coreopsis*, *Cosmos* and *Dahlia* and their hybrids are now important components of gardens worldwide. Mexico contains the highest generic diversity of Coreopsideae.

Molecular studies of Heliantheae and related tribes (Panero and Funk 2002) support the recognition of Coreopsideae at the tribal level. Similar studies (Panero et al., unpubl. data) support, albeit tentatively, the inclusion of the genera *Staurochlamys* and *Pinillosia* in Coreopsideae. Pinillosiinae, as circumscribed by Robinson (1981) and including *Pinillosia* and *Koehneola*, are transferred here to Coreopsideae. The other Cuban endemic genus *Tetraperone* (in Heptanthinae sensu Robinson 1981) is also included in Coreopsideae on the basis of its involucre morphology. Generic relationships within Coreopsideae until recently have been very difficult to ascertain. The difficulty in separating *Coreopsis* from *Bidens*, and the apparent close relationship of certain lineages of *Coreopsis* to other genera in the tribe have increased uncertainty about the monophyly of several genera of Coreopsideae (Tadesse et al. 2001). Molecular studies using the ITS region of the nuclear ribosomal DNA by Kimball and Crawford (2004) show that the traditional morphological features used to circumscribe genera and infer generic relationships (Ryding and Bremer 1992) are labile. Kimball and Crawford (2004) show that *Ericentrodea* appears to be the basal lineage of the tribe, followed by a large polytomy including all genera of Coreopsideae sampled to date. *Bidens* and *Coreopsis* are revealed as polyphyletic or paraphyletic assemblages, because distinctive genera such as *Coreocarpus*, *Cosmos* and *Thelesperma* are derived from within them. Based on the results by Kimball and Crawford (2004), the relative position of Chrysanthellinae within Coreopsideae is impossible to ascertain but the distinctive morphology and photosynthesis of this group provide support for its recognition. Their data also support the close relationship of *Oparanthus* to *Fitchia*. *Selleophytum* clearly is a distinctive genus sister to *Narvalina*, also endemic to Hispaniola. *Coreopsis cyclocarpa* is here included in *Heterosperma*. The genus *Henricksonia* is not placed in the synonymy of *Heterosperma*, as it has a series of distinctive morphological features. Future studies of the *Heterosperma* complex may support the recognition of *Coreopsis mutica* as a distinctive genus. The polyphyletic nature of *Coreopsis*, as revealed by molecular studies, supports the views of Tadesse et al. (1995) that the genus may be treated as a smaller assemblage of species essentially endemic to the USA, with the other sections of the genus recognized as closely related genera. My circumscrip-

tion of *Coreopsis* follows scenario 3 of Tadesse et al. (1995), in which the genus is viewed as endemic to the New World. I include the African species of *Coreopsis* in *Bidens*. The inclusion of *Diodontium* in Coreopsideae is tentative because the original description states the herbage to be aromatic. Most species of Coreopsideae have a particular odour when the herbage is crushed, although this can hardly be considered aromatic. Therefore, it is possible that *Diodontium* does not belong in Coreopsideae but rather in another tribe of Asteroideae, possibly Astereae or Anthemideae. The relationship of *Staurochlamys* to Coreopsideae is difficult to ascertain. The genus has a series of morphological features which are unique in the helianthoid alliance. My decision to include this genus in Coreopsideae is based solely on very limited molecular evidence; further analysis may support the inclusion of *Staurochlamys* in Neurolaeneae, as suggested by Robinson (1981), or its recognition as a distinctive lineage. Future molecular studies of Coreopsideae should focus on including *Staurochlamys*, Pinillosiinae and members of related tribes such as Helenieae, Tageteae and Neurolaeneae in an attempt to elucidate the relationships of this complex lineage of the Heliantheae alliance. Furthermore, it should be noted that Coreopsideae may be of hybrid origin, as molecular studies based on chloroplast DNA (Panero and Funk 2002) and nuclear DNA (Goertzen et al. 2003) show widely different but well-supported phylogenetic positions for the tribe. Finally, it should be kept in mind that molecular studies and morphological evidence support the recognition of subtribes Chrysanthellinae and Pinillosiinae, with the residuum as a large subtribe Coreopsidinae. It is very probable that Coreopsidinae, as circumscribed here, are not monophyletic.

Key to the Subtribes and Unplaced Genera

1. Plants without glandular trichomes on anther appendages, if glandular, then appendages hyaline, ray corollas never deeply trilobed 2
– Plants with glandular, black anther appendages; ray corollas deeply trilobed **1186. *Staurochlamys***
2. Receptacles paleate 3
– Receptacles epaleate 4
3. Leaves alternate, sometimes on short internodes and restricted to the base of the plant; stigmatic branches with prominent, penicillate appendages either as long as or several times longer than stigmatic area; plants with C4 photosynthesis and Kranz anatomy syndrome **1. Chrysanthellinae** (p. 407)
– Leaves opposite, sometimes those associated with the capitulescences alternate, stigmatic branch appendages present normally shorter than length of stigmatic area; plants without Kranz anatomy **2. Coreopsidinae** (p. 409)
4. Plants small rosettes or trailing, forming mats; plants of the Caribbean **3. Pinillosiinae** (p. 416)
– Plants bushy; northern Australia **1. Chrysanthellinae** (**1158. *Diodontium***)

XX.1. Subtribe Chrysanthellinae Ryding & K. Bremer (1992).

Annual or perennial herbs, sometimes forming rosettes, rarely shrubs. Leaves usually alternate, blades entire or dissected, 1–2-pinnatifid. Capitula terminal, solitary, mostly on long peduncles appearing scapose or in open paniculiform cymes, radiate, sometimes discoid. Involucre turbinate or campanulate, sometimes hemispheric, phyllaries in 2–5 series, dimorphic, outermost herbaceous, normally much smaller than innermost, inner erect, scarious. Receptacles paleate. Ray florets pistillate or sterile, corollas sometimes lacking, apices bilobed or trilobed. Disc florets bisexual, sometimes functionally staminate, corollas tetramerous or pentamerous, mostly yellow; anthers yellow to brown or yellow-purple, appendages ovate, rarely wanting, glabrous, with or without resin canals; style arm apices subulate, appendages normally as long as or several times longer than stigmatic surfaces, densely papillose and vascularized. Ray cypselae coiled or straight, clavate to terete, sometimes narrowly obconic. Disc cypselae obcompressed, rarely compressed, quadrate, straight or sometimes concave. Pappus of 2–4 erect or reflexed, smooth or retrorsely barbed awns, sometimes absent.

Key to the Genera

1. Anther appendages with a prominent resin canal; capitula solitary on long peduncles; corollas mostly deep purple or yellow-purple, sometimes pink; plants of South America **1161. *Isostigma***
– Anther appendages without resin canals or these very reduced; corollas yellow, white, pink or purple; plants of North America, Oceania and palaeotropics, if in South America, then corollas yellow and capitula not scapose 2
2. Cypselae with a pappus of 3 or 4 awns **1162. *Trioncinia***
– Cypselae with a pappus of 2 awns or absent 3
3. Capitula epaleate **1158. *Diodontium***
– Capitula paleate 4
4. Ray florets with mostly bifid apices; tubes of disc corollas shorter than the throats 5

– Ray florets with mostly trifid apices; tubes of disc corollas as long as throats **1160. *Glossocardia***
5. Plants perennial and forming a woody, bulbous root or base; leaves ampliated at base **1159. *Eryngiophyllum***
– Plants annual, if perennial, then with a narrow, woody root, not a bulbous base **1157. *Chrysanthellum***

Genera of Chrysanthellinae

1157. *Chrysanthellum* Rich. Fig. 82

Chrysanthellum Rich., Syn. Pl. 2: 471 (1807); Turner, Phytologia 64: 410–444 (1988), rev.

Annual or perennial herbs, sometimes with a woody caudex. Leaves basal in a loose rosette, cauline mostly alternate, pinnatifid. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres turbinate to campanulate, phyllaries in 2–3 series, outermost very reduced, innermost membranaceous, oval to ovate. Receptacles flat to convex. Ray florets pistillate, corollas yellow, golden yellow or yellow-white, narrowly lanceolate to oblong, apices bilobed. Disc florets bisexual or functionally staminate, corollas yellow to reddish orange, tetramerous or pentamerous, sometimes innermost twice as large as those surrounding them; anther appendages round to ovate, acuminate or bilobed, without resin canals; style arm apices subulate, appendages penicillate, mostly longer than stigmatic surfaces. Ray cypselae coiled or straight, clavate to terete, sometimes narrowly obconic, sometimes with prominent ridges, brown or blackish, glabrescent, not winged. Disc cypselae like those of the ray florets or biconvex, compressed or obcompressed, sometimes winged, black or brown, glabrescent. Pappus absent or of two obsolete awns on some cypselae of the disc florets. $x = 8, 9, 12$. Eleven species, pantropical, apparently not in Oceania, most species in Mexico.

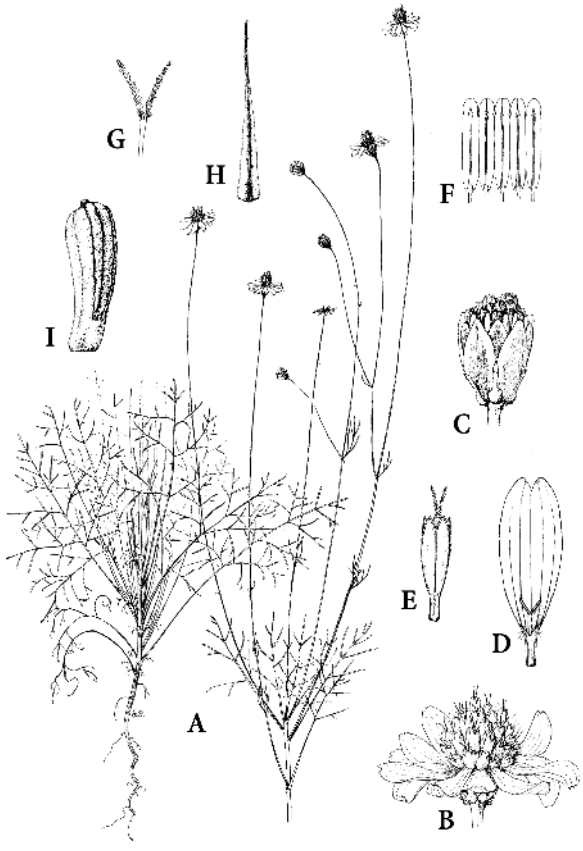

Fig. 82. Compositae-Coreopsideae. *Chrysanthellum filiforme*. **A** Habit. **B** Flowering capitulum. **C** Capitulum in bud showing involucre. **D** Ray corolla. **E** Disc corolla. **F** Anthers. **G** Style arms. **H** Palea. **I** Cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

1158. *Diodontium* F. Muell.

Diodontium F. Muell., Hooker's J. Bot. Kew Gard. Misc. 9: 19 (1857); Veldkamp & Kreffer, Blumea 35: 459–482 (1991), rev.

Perennial herbs, shrubs (?), aromatic (?). Leaves opposite (?), basal in tufts, sessile, blades linear. Capitula terminal in subscapose paniculiform cymes, discoid. Receptacles flat, paleate, (epaleate?). Disc florets bisexual, corollas yellow, tubular, pentameous; anthers brownish, appendiculate. Cypselae obcompressed (?), narrowly winged, concave. Pappus of 2 smooth or barbed awns. One species, *D. filifolium* F. Muell., northern Australia.

1159. *Eryngiophyllum* Greenm.

Eryngiophyllum Greenm., Proc. Amer. Acad. Arts 39: 113 (1903).

Perennial herbs forming a small rosette. Leaves alternate, sessile, blades linear, sometimes dissected. Capitula terminal, subscapose, solitary or in open paniculiform cymes, radiate. Involucres campanulate, phyllaries in 3–4 series, dimorphic, outermost as long as innermost, innermost membranaceous. Receptacles flat. Ray florets pistillate, corollas yellow, apices mostly trifid, rarely bifid. Disc florets bisexual, functionally staminate (?), corollas yellow; anthers yellow, appendages broadly ovate, without resin canals; style arm apices round to acuminate,

appendages penicillate, very conspicuous, approximately 7–10 times as long as stigmatic surfaces, papillose. Cypselae obcompressed, those of the ray perhaps obpyramidal. Pappus absent. Two species, western Mexico.

1160. *Glossocardia* Cass.

Glossocardia Cass., Bull. Sci. Soc. Philom. Paris 1817: 138 (1817); Veldkamp & Kreffer, Blumea 35: 459–482 (1991), rev.

Annual or perennial herbs. Leaves alternate, uppermost sometimes opposite, sometimes forming a loose rosette, sessile or petiolate, trullate or ovate in outline, simple with trilobed apices or 1–2-pinnatifid. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres cylindric to campanulate, phyllaries in 2–3 series, outermost filiform, herbaceous, innermost several times longer, broader, membranaceous. Receptacles flat. Ray florets pistillate or sterile, corollas yellow, white, pink or purple, apices trilobed, rarely bilobed. Disc florets bisexual, sometimes functionally staminate, corollas pentamerous, sometimes tetramerous, yellow, white or brownish; anther appendages ovate, sometimes wanting, without resin canals; style arm apices filiform, appendages papillose, 2–5 times as long as stigmatic surfaces. Cypselae obcompressed, sometimes triquetrous, oblong to linear-lanceolate, black to brown, glabrous to densely pubescent. Pappus absent or of two awns. $x = 12$. Eleven species, eastern Africa, south-eastern Asia, Australia and Pacific islands.

1161. *Isostigma* Less.

Isostigma Less., Linnaea 6: 513 (1831); Sherff, Bot. Gaz. 81: 241–257 (1926), rev.; Peter & Katinas, Austral. J. Bot. 51: 217–226 (2003), anat.

Perennial herbs, sometimes forming rosettes with well-developed xylopodia or large subterranean tuber-like roots. Leaves alternate, petiolate or sessile, blades linear to obovate in outline, entire or variously dissected, deeply dentate to twice trifoliolate, segments linear to filiform. Capitula terminal, solitary, scapose, radiate, rarely discoid. Involucres campanulate or hemispheric, phyllaries in 2–5 series, outermost reflexed, innermost membranaceous to scarious, erect. Receptacles flat. Ray florets pistillate, corollas dull red-purple, pink, sometimes yellow on adaxial surface, limb oval, sometimes conspicuously trilobed. Disk florets bisexual, corollas yellow-red or deep purple, pentamerous, rarely tetramerous; anther appendages broadly ovate, glabrous, with a central resin canal; style arm apices subulate, strongly arcuate, appendages as long as or longer than stigmatic surfaces, cylindric. Cypselae obcompressed, rarely quadrate, rectangular to obpyramidal, black, glabrous to sparsely pubescent. Pappus of 2 erect to reflexed, smooth or barbellate awns, sometimes with a few minute scales in between, sometimes wanting. Approximately 15 species, Argentina, Bolivia, Brazil, Paraguay and Uruguay.

1162. *Trioncinia* (F. Muell.) Veldkamp

Trioncinia (F. Muell.) Veldkamp, Blumea 35: 480 (1991).

Perennial herbs. Leaves alternate, mainly basal, blades trullate in outline, simple or 1–2-pinnatifid. Capitula in terminal, open paniculiform cymes, radiate. Involucres campanulate (?), phyllaries in 2–3 series. Receptacles flat. Ray florets sterile (?), corollas yellow (?). Disc florets bisexual, tetramerous. Cypselae obcompressed, brown or black, tuberculate. Pappus of 3–4 strongly reflexed awns. One species, *T. retroflexa* (F. Muell) Veldkamp, north-eastern Australia.

XX.2. Subtribe Coreopsidinae Cass. ex Dumort. (1829).

Subtribe Petrobiinae Benth. in Benth. & Hook. f. (1873).
Subtribe Fitchiinae Carlquist (1957).

Annual or perennial herbs, shrubs, sometimes aquatic, rarely trees. Leaves alternate or opposite, blades mostly ovate or trullate, commonly dissected, 1–3-pinnatifid, segments lanceolate or linear. Capitula in terminal, rarely axillary, open paniculiform or sometimes congested corymbiform cymes, discoid or mostly radiate, rarely ligulate. Involucres cylindric to hemispheric, phyllaries mostly dimorphic and gradate, rarely isomorphic, in 1–6 series, outermost herbaceous, green, innermost membranaceous. Receptacles paleate. Ray florets pistillate. Disc florets bisexual or functionally staminate, corollas pentamerous, sometimes tetramerous rarely hexamerous, peripheral sometimes zygomorphic, mostly yellow or purple; anther appendages lanceolate to round, sometimes wanting, glabrous, sometimes with glands, sometimes with prominent resin canals; style arm apices broadly deltate or acuminate to subulate, appendages short or very well developed

and sometimes several times longer than stigmatic surfaces, penicillate, papillose and vascularized. Cypselae isomorphic or sometimes those of the ray or the innermost disc florets different in shape from the other cypselae, sometimes growing after anthesis, sometimes corky on edges or winged. Pappus of 1–8 awns or absent, rarely of 4–6 round, lanceolate or obovate scales, awns smooth or with retrorse or antrorse barbs.

Key to the Genera

1. Anther filaments papillose or pubescent **1166. *Cosmos***
– Anther filaments not papillose nor pubescent 2
2. Abaxial surface of disc corollas with a ring of broad trichomes at base of throat; cypselae with corky sinuate or pectinate margins **1164. *Coreocarpus***
– Abaxial surface of disc corollas glabrous or variously pubescent, pubescence not restricted to a ring at base of throat; cypselae with or without wings, wings entire, very rarely sinuate or pectinate 3
3. Phyllaries of innermost series variously fused at base up to mid-length **1182. *Thelesperma***
– Phyllaries free 4
4. Capitula with dimorphic cypselae, normally those of the ray floret obcompressed, broadly oblong and winged, those of the disc florets or innermost disc florets obpyramidal to terete, fusiform 5
– Capitula with isomorphic cypselae 8
5. Disc cypselae terete to obpyramidal, striate; pappus of scales; anther appendages glandular **1173. *Henricksonia***
– Disc cypselae obcompressed to weakly terete, not striate; pappus absent or of two diverging awns; anther appendages not glandular 6
6. Involucres with gradate phyllaries, not dimorphic; leaf bases oblique **1172. *Goldmanella***
– Involucres with dimorphic phyllaries, outermost herbaceous, green, reflexed, innermost erect, membranaceous 7
7. Shrubs or small trees with corymbiform inflorescences **1165. *Coreopsis***
– Annual or perennial herbs, rarely woody with capitula solitary or in open paniculiform inflorescences **1174. *Heterosperma***
8. Leaf bases oblique; capitula in umbelliform cymes **1172. *Goldmanella***
– Leaf bases various, never oblique; inflorescences various, never umbelliform cymes 9
9. Capitula ligulate, pendulous; shrubs or small trees of Polynesia **1171. *Fitchia***
– Capitula various, never ligulate, erect; worldwide, if shrubs or trees from Polynesia, then capitula not ligulate 10
10. Plants aquatic with dimorphic leaves; capitula solitary **1176. *Megalodonta***
– Plants terrestrial, if aquatic without dimorphic leaves; capitula variously arranged 11
11. Cypselae urceolate in outline; pappus of several (3 or more) retrorsely barbed awns arising from shoulders of cypsela; vines of tropical Andean South America **1170. *Ericentrodea***
– Cypselae various, pappus absent or, if retrorsely barbed, then awns mostly 2, one on each side of cypsela; annual or perennial herbs, shrubs or trees, if vines, then not from Andean South America 12
12. Shrubs or trees with broadly ovate to round, very thick, coriaceous leaves and densely pectinate foliar venation; style branches with continuous stigmatic surfaces, disc corollas tetramerous; plants of Rapa Island, French Polynesia **1179. *Oparanthus***
– Plants various, without thick, broadly ovate or round leathery leaves; style branches with parallel stigmatic surfaces; disc corollas mostly pentamerous, rarely tetramerous; worldwide, not from Rapa Island 13
13. Small, dioecious trees; disc corollas tetramerous, lobes narrowly lanceolate; plants from St. Helena island **1180. *Petrobium***
– Annual, perennial herbs or shrubs, never trees; disc corollas pentamerous, if tetramerous, then mostly yellow and without narrowly lanceolate lobes; worldwide, not from St. Helena island 14
14. Capitula with winged cypselae, wings corky, stramineous 15
– Capitula rarely with winged cypselae, wings, if present, very narrow, not corky 16
15. Leaves simple; cypselae with a pappus of two awns; plants from Hispaniola **1178. *Narvalina***
– Leaves compound; cypselae with a pappus of two awns arising from a cup or corona; plants of Ecuador **1167. *Cyathomone***
16. Capitula with all disc florets functionally staminate 17
– Capitula with bisexual disc florets, sometimes a few of the innermost florets functionally staminate 19
17. Disc florets 3–4; limbs of ray florets very reduced and mostly covered by phyllaries; cypselae with a pappus of broadly divergent awns **1169. *Dicranocarpus***
– Disc florets 10–many; limbs of ray florets conspicuous, protruding and spreading beyond phyllaries; cypselae epappose or with two broad awns 18
18. Perennial herbs or shrubs; ray florets with conspicuous trilobed apices; cypselae oval and plump, broadly convex in cross-section; plants of southern India and Sri Lanka **1177. *Moonia***
– Vines; ray florets with minute and inconspicuous bilobed or trilobed apices; cypselae broadly oval, flattened, lenticular in cross-section; plants of Mexico and Central America **1175. *Hidalgoa***
19. Style branches with large, conspicuous papillose appendages, appearing plumose to the naked eye; capitula nodding **1168. *Dahlia***
– Style branches without large, conspicuous, papillose appendages, capitula erect 20
20. Cypselae with antrorsely barbed awns; plants of America and surrounding islands 21
– Cypselae with retrorsely barbed awns, when plants from Africa, cypselae may be antrorsely awned **1163. *Bidens***
21. Shrubs with sessile, subcoriaceous, lanceolate to ovate leaves; plants from Hispaniola **1181. *Selleophytum***
– Annual or perennial herbs, if shrubs, then leaves otherwise; plants mostly from continental America **1165. *Coreopsis***

Genera of Coreopsidinae

1163. *Bidens* L.

Bidens L., Sp. Pl. 2: 831 (1753); Sherff, Field Mus. Nat. Hist., Bot. 16: 1–709 (1937), rev.; Tadesse, Kew Bull. 48: 437–516 (1993), part. rev.

Annual or perennial herbs, vines or shrubs, sometimes aquatic. Leaves opposite, sometimes alternate towards inflorescence, rarely whorled, simple to pinnately compound, blades deltate to ovate in outline. Capitula in terminal, open to congested corymbiform to paniculiform cymes, radiate or discoid. Involucres campanulate to hemispheric, phyllaries dimorphic, outer herbaceous, inner membranaceous. Receptacles flat to convex. Ray florets sterile, rarely pistillate, corollas yellow, orange, white with black nerves on abaxial surface, rarely purple or pink. Disc florets bisexual, corollas mostly yellow to orange, rarely greenish, pink, white or purple; anther appendages ovate, glabrous, with or without resin canals; style arm apices deltate, densely papillose, appendages cylindric, sometimes not vascularized. Cypselae obcompressed, triquetrous, quadrate, obovoid to oblong, linear or fusiform in outline, black to reddish brown, glabrous to densely pubescent, sometimes tuberculate, rarely winged. Pappus absent or mostly 2 to few awns or scales, awns usually retrorsely barbed, antrorsely barbed in some African species, rarely glabrous. $x = 10, 11$ 12, 17, 18. Approximately 280 species, worldwide, most species in America.

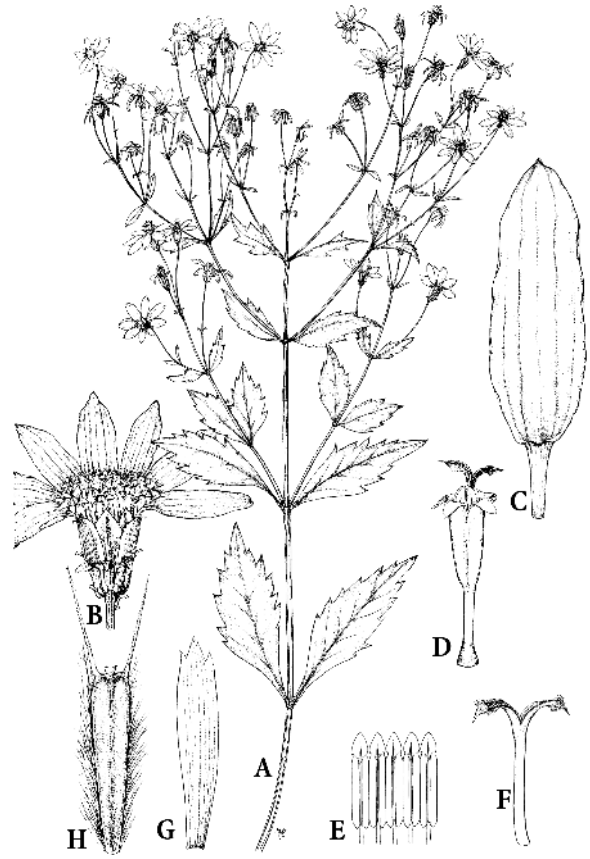

Fig. 83. Compositae-Coreopsideae. *Coreopsis petrophiloides*. **A** Flowering branch. **B** Flowering capitulum with some ray florets removed. **C** Ray corolla. **D** Disc corolla. **E** Anthers. **F** Style arms. **G** Palea. **H** Cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

1164. *Coreocarpus* Benth.

Coreocarpus Benth., Bot. Voy. Sulphur 28, pl. 16 (1844); Smith, Syst. Bot. 14: 448–472 (1989), rev.; Kimball et al., Evolution 57: 52–61 (2003), syst.

Annual or perennial herbs or weak shrubs. Leaves opposite, blades ovate to trullate in outline, 1–2-pinnate, segments linear to lanceolate. Capitula in open paniculiform, rarely congested corymbiform cymes, radiate, rarely discoid. Involucre campanulate to hemispheric, phyllaries in 2–3 series, dimorphic, outer 1–3 very reduced, linear, herbaceous, membranaceous, appressed. Receptacles flat to convex. Ray florets sterile, rarely pistillate, corollas yellow or white with pink or purple veins. Disc florets bisexual or sometimes functionally staminate, sometimes only 1 floret fertile, corollas yellow, with a ring of broadly lanceolate, glandular trichomes on abaxial surface at junction of tube and throat; anther appendages ovate to suborbicular, glabrous, resin canals poorly developed or wanting; style arm apices subulate, appendages as long as or longer than stigmatic lines, subulate to cylindric. Cypselae obcompressed, somewhat concave or cucullate, black, margins corky, stramineous, wings sinuate or tuberculate to shallowly crenate, essentially glabrous. Pappus of 1–2 retrorsely barbed awns or absent. $x = 12$. Approximately eight species, western North America.

1165. *Coreopsis* L. Fig. 83

Coreopsis L., Sp. Pl. 2: 907 (1753); Sherff, Field Mus. Nat. Hist., Bot. (1936), rev.; Crawford, Amer. J. Bot. 58: 361–367 (1971), part. rev.; Smith, Brittonia 25: 200–208 (1973), part. rev.; Crawford, Brittonia 28: 329–336 (1976), part. rev.;

Smith, Sida 123–215 (1976), part. rev.; Jansen et al., Pl. Syst. Evol. 157: 73–84 (1987) phylog.; Tadesse et al., Brittonia 47: 61–91 (1995), anat., phylog.

Annual or perennial herbs, shrubs or small trees. Leaves opposite to alternate towards inflorescence, blades simple or 1–3 pinnately compound, triplinerved, pinnate. Capitula solitary or in open paniculiform or corymbiform cymes, discoid or radiate. Involucres cylindric to campanulate, phyllaries in 2–3 series, dimorphic, outer herbaceous, spreading, inner membranaceous to scarious, erect. Receptacles flat to convex. Ray florets sterile, rarely pistillate, corollas yellow to orange, sometimes bicoloured with purplish bases. Disc florets bisexual, sometimes innermost functionally staminate, corollas pentamerous, rarely tetramerous, yellow, orange to purplish brown; anther appendages ovate, glabrous, with or without resin canals; style arm apices deltate, densely papillose, appendages cylindric, sometimes not vascularized. Cypselae obcompressed, oblong, elliptic, fusiform, sometimes with corky, entire or pectinate margins or wings, glabrous to moderately pubescent. Pappus absent or of two awns, sometimes a short crown of scales, awns antrorsely barbed. $x = 12, 13, 14$. Approximately 70 species, America.

1166. *Cosmos* Cav.

Cosmos Cav., Icon. 1: 9, pl. 14 (1791).

Annual or tuberous perennial herbs. Leaves opposite, blades deltate, sagittate or ovate in outline, 1–3-pinnatifid or pinnate, rarely simple. Capitula terminal, solitary or in very open paniculiform cymes, discoid or radiate. Involucres cylindric to hemispheric, phyllaries dimorphic, outermost herbaceous, shortly fused, inner membranaceous or scarious. Receptacles flat. Ray florets neuter, corollas pink, magenta, maroon to black-purple, white, rarely red or orange. Disc florets bisexual, corollas yellow, green, white, brownish yellow, purple or bicoloured; anther filaments pubescent, appendages broadly ovate, with a prominent resin canal; style arm apices deltate-aristate, appendages prominent, as long as or longer than stigmatic surfaces, deltate/aristate. Cypselae fusiform to linear or narrowly lanceolate, apices conspicuously tapered, usually quadrate in cross-section, black to dark brown, glabrescent to hispid, curved outwards with age. Pappus of 1–8 retrorsely barbed and either erect or divergent awns, sometimes absent. $x = 12, 17$. Approximately 28 species, Mexico, Central America and Andean South America.

1167. *Cyathomone* S.F. Blake

Cyathomone S.F. Blake, J. Wash. Acad. Sci. 13: 105 (1923).

Shrubs (?). Leaves opposite, ternate, biternate or pinnate-ternate. Capitula in terminal, paniculiform cymes. Involucre campanulate (?), phyllaries in 2–3 series, outermost about 5, herbaceous, innermost longer and membranaceous. Receptacles convex. Cypselae obcompressed, obovate in outline, black, wings stramineous, erose and fused to two fragile awns, squamellae around neck fused to awns and forming a cup. Pappus of two fragile awns fused to a ciliolate cup. One species, *C. sodiroi* (Hieron.) S.F. Blake, Ecuador.

1168. *Dahlia* Cav.

Dahlia Cav., Icon. 1: 56 (1791); Sorensen, Rhodora 71: 309–365, 367–416 (1969), rev.; Gatt, Hammett & Murray, Bot. J. Linn. Soc. 133: 229–239 (2000), phylog.; Saar et al., Syst. Bot. 28: 627–639. (2003), phylog.

Tuberous perennial herbs or shrubs, one species epiphytic, sometimes rupicolous. Leaves opposite, sometimes whorled, sometimes semisucculent, blades simple to 1–3-pinnatifid, ovate to deltate in outline, rarely cordate. Capitula solitary or loosely aggregated in paniculiform cymes, radiate, nodding. Involucres cylindric to campanulate, hemispheric, phyllaries in 2–3 series, strongly dimorphic, outermost herbaceous, reflexed at anthesis, innermost broad, scarious, translucent. Receptacles flat. Ray florets sterile, corollas in a wide variety of shades of pink and lavender, yellow, orange, red or dark maroon sometimes appearing black, white. Disc florets bisexual, innermost often functionally staminate, corollas yellow to orange, red or purple, sometimes bicoloured; anther appendages ovate to deltate, glabrous or sometimes with a few short trichomes or papillae; style arms densely papillose abaxially, apices narrowly deltate, subulate, as long as or longer than stigmatic surfaces, cylindric, densely papillose. Cypselae obcompressed, linear to spathulate, sometimes shallowly tuberculate, glabrous to sparsely pubescent, black or greyish black. Pappus absent or of 2(5) small teeth or of two weak, filiform, caducous bristles. $x = 12, 16, 17, 18$. Approximately 40 species, Mexico, Central America, Colombia, widely cultivated.

1169. *Dicranocarpus* A. Gray

Dicranocarpus A. Gray, Mem. Amer. Acad. Arts n.s. 5: 322 (1854).

Annuals. Leaves opposite, blades ovate in outline, 1–2-pinnatifid, segments linear. Capitula terminal, solitary, sometimes nodding and appearing axillary, radiate. Involucre turbinate to campanulate, phyllaries in 2–3 series, dimorphic, outer narrowly lanceolate to linear, herbaceous, innermost scarious. Receptacle flat. Ray florets pistillate, corollas very reduced and covered by phyllaries, yellow. Disc florets functionally staminate, style undivided, papillose, corollas yellow, throat abruptly narrowed into tube; anther appendages translucent, sometimes suffused with black, glabrous, without resin canals; style arm apices of disc corollas deltate to acuminate, of ray corollas rounded to subulate. Cypselae obcompressed to shallowly terete, linear, moderately pubescent, growing after anthesis and sometimes up to 2–3 times length of capitulum. Pappus of two diverging, arcuate, very conspicuous, smooth awns, growing after anthesis. $n = 10$. One species, *D. parviflorus* A. Gray, Mexico, USA.

1170. *Ericentrodea* S.F. Blake

Ericentrodea S.F. Blake, J. Wash. Acad. Sci. 13: 104 (1923).

Weak shrubs or vines. Leaves opposite, blades ovate to deltate in outline, 2–3-pinnate, segments linear to lanceolate. Capitula in terminal, corymbiform cymes, discoid, rarely radiate. Involucres campanulate to hemispheric, phyllaries in 2–4 series, dimorphic, outermost 2 series reflexed, green, herbaceous, innermost series erect, membranaceous. Receptacles convex. Ray florets pistillate, corollas white (?) or yellow. Disc florets bisexual, corollas yellow or white, throats broad and abruptly narrowed into tube; anther appendages black, glabrous, with a prominent central resin canal; style arm apices deltate, stigmatic surfaces very broad, dense, touching and appearing continuous, confluent at apices, stigmatic papillae sometimes black. Cypselae obcompressed, flatly biconvex, obovate, with two minute or well-developed shoulders flanking neck, ciliate, brown. Pappus of 3 to numerous, retrorsely barbed awns on each shoulder of cypselae, awns spreading, reflexed or arched inwards. Six species, Andes, Colombia to Bolivia.

1171. *Fitchia* Hook. f.

Fitchia Hook. f., London J. Bot. 4: 640 (1845).

Shrubs or small trees. Leaves opposite, blades entire, broadly ovate to cordate, sometimes elliptic, entire to crenulate. Capitula axillary, pendulous on lax or recurved peduncles, ligulate. Involucres hemispheric, phyllaries in 5–6 series, outermost woody, innermost with scarious margins. Receptacles flat to shallowly convex. Florets bisexual, corollas yellow-orange, inrolled forming a navicular structure; anthers with prominent, lanceolate appendages, without resin canals; style arms reduced, acute to round, stigmatic surfaces continuous. Cypselae obcompresed, oblong, densely pubescent. Pappus of 2 barbellate awns. Seven species, Polynesia.

1172. *Goldmanella* Greenm.

Goldmanella Greenm., Bot. Gaz. 45: 198 (1908).
Goldmania Greenm. (1907), nom. illegit.

Prostrate, perennial herbs rooting at nodes. Leaves alternate, blades asymmetrically ovate to elliptic, bases oblique. Capitula terminal in umbelliform cymes, radiate. Involucres campanulate, phyllaries in 3–4 series, gradate with conspicuous brown striae, membranaceous. Receptacles conic, paleate. Ray florets pistillate, corollas white to pale yellow. Disc florets bisexual, corollas yellow-orange, pentamerous, rarely hexamerous; anther appendages deltate, sides involute, glabrous, without resin canals; style arm apices subulate, tapered, papillae sometimes extending below bifurcation point, appendages long, cylindric, papillose. Cypselae shallowly obcompressed, innermost subterete, cylindric, brown or reddish brown, corky. Pappus absent or of 2–4 minute protuberances. One species, *G. sarmentosa* Greenm., Mexico, Belize, Guatemala.

1173. *Henricksonia* B.L. Turner

Henricksonia B.L. Turner, Amer. J. Bot. 64: 78 (1977).

Weak, rupicolous shrubs. Leaves opposite, blades twice tripinnate, segments lanceolate. Capitula terminal, solitary on long peduncles, radiate. Involucres campanulate to hemispheric, phyllaries in 2 series, dimorphic, outer herbaceous, patent to reflexed, inner chartaceous, striate, each subtending a ray floret. Receptacles shallowly convex. Ray florets pistillate, corollas yellow with conspicuous reddish veins. Disc florets bisexual, corollas yellow; anther appendages ovate, glandular abaxially, glands also on distal part of connective, without resin canals; style arm apices

acuminate, appendages cylindric. Ray cypselae obcompressed, oval, broadly winged, wings smooth, corky, of even width throughout circumference of cypsela, glabrous, black, wings stramineous. Disc cypselae obpyramidal, 3–5-sided, brown, striate, some striae thickened (carinate), brown, sparsely pubescent. Pappus of ray cypselae of two small projections or awns, disc cypselae with 3–5 obovate squamellae. One species, *H. mexicana* B.L. Turner, northern Mexico.

1174. *Heterosperma* Cav. Fig. 84

Heterosperma Cav., Icon. 3: 34 (1795/1796).

Annual or perennial herbs, weak shrubs. Leaves opposite, blades simple to 1–2-pinnatifid, segments linear. Capitula terminal, solitary, radiate. Involucres cylindric to campanulate or hemispheric, phyllaries in 2–3 series, dimorphic, outer herbaceous, linear, inner membranaceous to chartaceous, ovate. Receptacles flat to convex. Ray florets pistillate, corollas yellow to orange, sometimes conspicuously trilobed. Disc florets bisexual, fertile, corollas yellow to orange; anther appendages ovate to deltate with shallowly to strongly developed resin canals; style arm apices deltate, papillose, appendages cylindrical. Cypselae obcompressed, those of the ray and sometimes some or nearly all except for two to four of the innermost disc florets broad, oval, with corky wide margins, flatly biconvex, the innermost growing after anthesis, terete, protruding above the capitula, and slightly arched. Pappus absent or of 2–4 retrorsely barbed awns, mostly perpendicular to the cypsela, mostly restricted to innermost cypselae. x = 11, 12, 13. Approximately seven species, neotropical, introduced elsewhere.

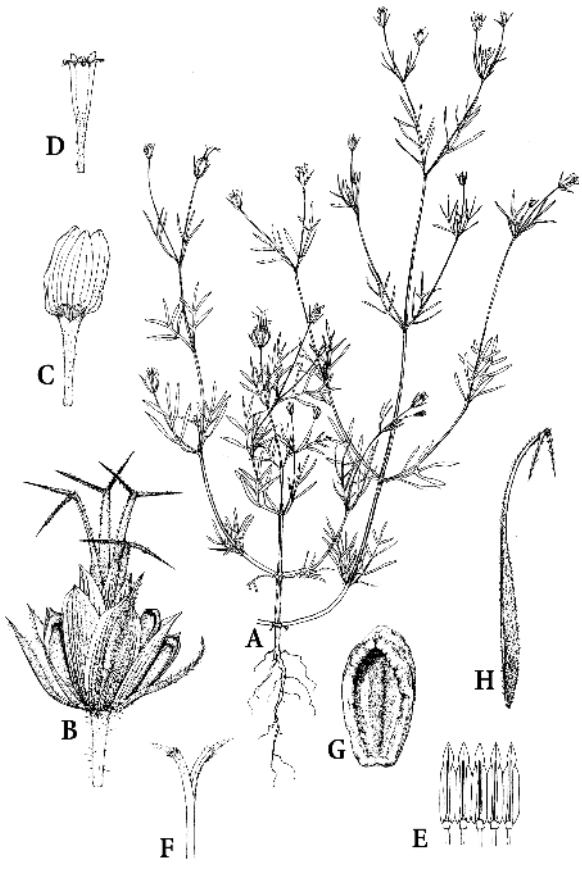

Fig. 84. Compositae-Coreopsideae. *Heterosperma pinnatum*. **A** Habit. **B** Fruiting capitulum. **C** Ray corolla. **D** Disc corolla. **E** Anthers. **F** Style arms. **G** Ray cypsela. **H** Inner disc cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

1175. *Hidalgoa* La Llave & Lex.

Hidalgoa La Llave & Lex., Nov. Veg. Descr. 1: 15 (1824).

Vines or lianas. Leaves opposite, petioles twining at their bases, blades suborbicular in outline, pedate or pinnate with 3–5 or more leaflets. Capitula terminal or axillary, solitary or in simple cymes on long peduncles, radiate. Involucres campanulate, phyllaries dimorphic, outer fleshy, herbaceous, spreading, inner membranaceous. Receptacles flat. Ray florets pistillate, corollas bright yellow to orange or red. Disc florets functionally staminate, corollas yellow to orange; anther appendages shortly acute, brown, glabrous, sometimes with one gland, without resin canals; style arms of disc florets fused, penicillate, of ray florets slender, subulate, spreading, stigmatic surfaces parallel, confluent at apices. Cypselae obcompressed, biconvex, fusiform, brown to black. Pappus absent, wings projecting as thickened, lacerate awns above neck. x = 15, 16. Five species, Mexico, Central America.

1176. *Megalodonta* Greene

Megalodonta Greene, Pittonia 4: 271 (1901).

Aquatic annual or perennial herbs. Leaves opposite, submerged leaves finely dissected, filiform, those above water simple, lanceolate, serrate. Capitula terminal, solitary, radiate. Involucres hemispheric, phyllaries in 2–3 series, shallowly gradate, outermost few, herbaceous, reflexed, innermost scarious. Receptacles flat. Ray florets neuter, corollas yellow. Disc florets bisexual, corollas yellow; anther

appendages hyaline to yellow, glabrous; style arm apices deltate, densely papillose. Cypselae obcompressed, linear to narrowly fusiform, brown, essentially glabrous. Pappus of approximately 6, easily caducous, retrorsely barbed awns, sometimes one of the awns reflexed. One species, *M. beckii* (Torr. ex Spreng.) Greene, northern USA, Canada.

1177. *Moonia* Arn.

Moonia Arn., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 18: 348 (1836); Stuessy, Brittonia 27: 97–102 (1975), rev.

Perennial herbs, shrubs (?). Leaves opposite, blades trilobed, lobes ovate to elliptical, serrate, terminal lobe deeply to strongly trilobed. Capitula terminal, solitary on long peduncles, radiate. Involucres campanulate to hemispheric, phyllaries in 4 series, outermost 2 series lanceolate, herbaceous, reflexed, innermost series appressed, densely and minutely striate. Receptacles flat. Ray florets pistillate, corollas yellow with conspicuous reddish veins, deeply trilobed, outer lobes wider than central and overlapping it. Disk florets functionally staminate, corollas yellow; anther appendages short, ovate, black or sometimes basal half black, distal half stramineous, with a weak resin canal in the centre; styles of disc florets undivided, apices deltate, papillose, styles of ray florets subulate, spreading. Cypselae obcompressed, broadly biconvex, slightly concave with abaxial surface larger than adaxial surface, apices with a short annular neck, greenish black, glabrous. Pappus absent. One species, *M. heterophylla* Arn., south-eastern India, Sri Lanka.

1178. *Narvalina* Cass.

Narvalina Cass., Dict. Sci. Nat. 38: 17 (1825).

Shrubs. Leaves opposite, blades obovate or elliptic, semisucculent, with a few, evenly spaced, conspicuous teeth on each side of lamina. Capitula in terminal, open paniculiform cymes, radiate. Involucres turbinate to campanulate, phyllaries in 3 series, gradate, outermost herbaceous, spreading, innermost membranaceous to coriaceous. Receptacles flat. Ray florets pistillate, corollas yellow. Disc florets functionally staminate, corollas yellow; anther appendages ovate, glabrous with a conspicuous resin canal; style arm apices deltate, densely papillose. Cypselae obcompressed, oval in outline, black, glabrous, with a thick, stramineous, corky wing all around cypsela. Pappus of diverging, retrorsely barbed awns, stramineous, fragile. One species, *N. domingensis* Cass., Hispaniola.

1179. *Oparanthus* Sherff

Oparanthus Sherff, Occas. Pap. Bernice P. Bishop. Mus. 12: 9 (1937); Stuessy, Fieldiana, Bot. 38: 63–70 (1977), rev.; Shannon & Wagner, Allertonia 7: 273–295 (1997), rev.

Shrubs or trees. Leaves opposite, blades oval to round, entire, pinnately veined, sometimes very thick, leathery. Capitula in terminal, solitary, simple, open or congested cymes, radiate. Involucres cupuliform, campanulate, phyllaries in 2–3 series, coriaceous, striate. Receptacles convex. Ray florets pistillate, corollas white, yellow to yellow-green, apices trilobed, rarely bilobed or tetralobed, style arms with continuous stigmatic surfaces. Disc florets functionally staminate, corollas white or yellow; anthers black, styles of disc florets undivided, penicillate. Cypselae obcompressed, linear to narrowly fusiform, narrowly winged on one or both sides, wings extending as awns, glabrous. Pappus of 2–3 smooth awns. Approximately six species, Rapa Island, Marquesas Islands, French Polynesia.

1180. *Petrobium* R. Br.

Petrobium R. Br., Trans. Linn. Soc. London 12: 113 (1817).

Shrubs or small trees, dioecious. Leaves opposite, blades ovate to elliptic, dentate. Capitula terminal in simple cymes, discoid. Involucres campanulate, phyllaries dimorphic in 2–4 series, outermost herbaceous in 1–2 series, green, innermost membranaceous. Receptacles flat. Florets bisexual or functionally staminate or functionally pistillate, corollas tetramerous, white or brownish white; anther appendages ovate. Cypselae obcompressed to triquetrous, linear, shallowly winged, margins ciliate. Pappus of 2–3 awns. One species, *P. arboreum* R. Br., St. Helena island.

1181. *Selleophytum* Urb.

Selleophytum Urb., Repert. Spec. Nov. Regni Veg. 13: 483 (1915).

Shrubs. Leaves opposite, blades lanceolate to narrowly ovate, coriaceous, apparently semisucculent. Capitula terminal, solitary or in simple cymes, radiate. Involucres hemispheric, phyllaries in 2–3 series, dimorphic, outermost herbaceous, reflexed, innermost erect, membranaceous to coriaceous. Receptacles flat. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas

yellow; anther appendages ovate, yellow, glabrous, with a resin canal in the centre; style arm apices deltate, densely papillose. Cypselae obcompressed to shallowly quadrate, edges flattened (wings wanting), black, sparsely to moderately pubescent. Pappus of 2 antrorsely barbed awns. One species, *S. buchii* Urb., Hispaniola.

1182. *Thelesperma* Less.

Thelesperma Less., Linnaea 6: 511 (1831); Blake, Proc. Biol. Soc. Wash. 41: 145–150 (1928), syn.; Shinners, Field Lab. 18: 14–24 (1950), part. rev.

Perennial herbs or weak shrubs. Leaves opposite, blades linear or ovate to trullate in outline, 1–2-pinnatifid, segments linear. Capitula terminal, solitary on long peduncles or in open paniculiform cymes, radiate or discoid. Involucres campanulate to hemispheric, phyllaries dimorphic in 2 series, outer herbaceous, free, linear, inner fused in basal half, membranaceous. Receptacles convex to conic. Ray florets neuter, corollas yellow or sometimes bicoloured with distal half yellow and basal half brown or deep purple. Disc florets bisexual, corollas yellow, in discoid capitula outermost disc corollas zygomorphic, with one or two lobes shorter than other 3; anther appendages ovate, glabrous, resin canals prominent or wanting; style arm apices deltate to aristate, appendages aristate. Cypselae terete to slightly obpyramidal, quadrate, strongly incurved, brown, tuberculate, glabrescent. Pappus of 2–3 retrorsely barbed awns or absent. $x = 9$, 10, 11, 12. Approximately 15 species, south-western USA, north-eastern Mexico, Argentina, southern Brazil, Uruguay.

XX.3. Subtribe Pinillosiinae H. Rob. (1978).

Prostrate perennial or small rosette herbs, sometimes forming dense mats and appearing caespitose. Leaves opposite or alternate, blades sometimes semisucculent. Capitula axillary, solitary, radiate or disciform. Involucres turbinate to hemispheric, phyllaries either 4 in 1 series, subequal, free, herbaceous or more than 4 in 3 series and gradate, shortly fused at base, outermost filiform, herbaceous, innermost lanceolate to oval, membranaceous. Receptacles flat to convex, epaleate. Ray florets with or without corollas, 2–10, pistillate, corollas when present yellow. Disc florets 2, or 9–11, bisexual, fertile or functionally staminate, corollas tetramerous or pentamerous, lobes long, lanceolate and spreading or very short and erect; anthers hyaline to white or black, sometimes broadly quadrate or oval, appendages present or wanting and reduced to a tuft of trichomes; style arm apices broadly deltoid or subulate, sometimes broadly expanded and densely papillose, sometimes appendages tapered, penicillate. Cypselae obconic, terete, sometimes triquetrous, essentially glabrous. Pappus of either 4 short, distally retrorsely barbed awns or 4 scales which grow after anthesis, sometimes absent.

Key to the Genera

1. Phyllaries 4, subequal; prostrate herbs, sometimes forming mats or growing in between short vegetation; capitula with 4 florets 2
– Phyllaries 6–9, dimorphic; plants forming small rosettes, caespitose with age; capitula with more than 4 florets **1185. *Tetraperone***
2. Capitula radiate **1183. *Koehneola***
– Capitula disciform, outermost florets without corollas **1184. *Pinillosia***

Genera of Pinillosiinae

1183. *Koehneola* Urb.

Koehneola Urb., Symb. Antill. 2: 463 (1901); Liogier, Fl. Cuba 5: 184–185 (1962), rev.

Prostrate perennial herbs. Leaves opposite, blades cordate to deltate. Capitula radiate. Involucres turbinate to campanulate, phyllaries 4 in 1 series, lanceolate to elliptic. Receptacles flat. Ray florets 2, pistillate, corolla apices deeply bilobed. Disc florets 2, bisexual, corollas yellow (?), tetramerous, throat short, abruptly narrowed into tube, as long as lobes, lobes spreading, lanceolate; anther appendages black, glabrous; style arm apices subulate, with a small papillose, tapered appendage. Cypselae obpyramidal to obconic, triquetrous, brownish black, densely pubescent. Pappus absent. One species, *K. repens* Urb., Cuba.

1184. *Pinillosia* Ossa ex DC.

Pinillosia Ossa ex DC., Prodr. 5: 528 (1836); Liogier, Fl. Cuba 5: 184 (1962), rev.

Prostrate perennial herbs, sometimes forming mats. Leaves opposite, blades cordate to deltate, sometimes reniform or elliptic. Capitula disciform. Involucres turbinate to campanulate, phyllaries 4 in 1 series, obtuse, somewhat connate at base. Receptacles flat. Florets 4, outermost 2 without corollas, pistillate, inner 2 functionally

staminate, corollas white or greenish yellow, pentamerous, rarely hexamerous, throat short, as long as lobes, abruptly narrowed into tube, lobes spreading, lanceolate; anthers broadly quadrate to oval, appendages brown, reduced to a tuft of cells, glabrous; style arms of inner florets broadly deltoid, very conspicuous, styles of ecorollate florets slender, subulate. Cypselae obconic with mostly 4 retrorsely barbed awns when young, which develop into short knobs or protuberances in fully developed cypselae, brown, slightly tuberculate. Pappus of 4 very short, distally retrorsely barbed awns, the awns soon absorbed by developing cypsela. One species, *P. berteri* Urb., Cuba, Hispaniola.

1185. *Tetraperone* Urb.

Tetraperone Urb., Symb. Antill. 2: 462 (1901); Liogier, Fl. Cuba 5: 184 (1962), rev.

Small rosulate herbs with rhizomes, becoming caespitose with age. Leaves alternate, blades elliptic to reniform, semisucculent. Capitula disciform. Involucre campanulate to hemispheric, phyllaries in 3 series, gradate, outermost filiform, herbaceous, innermost lanceolate to oval, membranaceous. Receptacles convex. Outer florets without corollas, approximately 8–10, pistillate. Disc florets 9–11, functionally staminate, corollas white, greenish white, tetramerous, lobes short; anther appendages wanting; style arm apices subulate. Cypselae terete, tuberculate, brownish black, glabrous. Pappus of 4 triangular, thickened stramineous scales, growing after anthesis. One species, *T. bellioides* Urb., Cuba.

Genus Unassigned to Subtribe

1186. *Staurochlamys* Baker

Staurochlamys Baker, Hooker's Icon. Pl. t. 1825 (1889).

Annual herbs. Leaves opposite, blades entire, lanceolate. Capitula in terminal, open paniculiform cymes, radiate. Involucres hemispheric, globose, phyllaries 8 in 3 series, phyllaries of first series 2, broadly ovate, flat, of second series 2, erect, round, herbaceous, opposite, striate, of third series enclosed by outer phyllaries, 4, scarious, ovate, each subtending a ray floret. Receptacles conic, paleate. Ray florets 4, pistillate, corollas yellow, apices deeply trilobed. Disc florets bisexual, corollas yellow, lobes conspicuously rimmed by orange-red resin canals, throat extremely short, lobes long, spreading; anthers black, glandular; style arms short, apices acute, papillose. Cypselae terete, slightly concave, with a brownish, glandular epidermis, black underneath, glabrous. Pappus absent. One species, *S. burchellii* Baker, north-central Brazil.

XXI. Tribe Neurolaeneae Rydb. (1927).

J.L. Panero

Annual or perennial herbs sometimes forming rosettes, shrubs, rarely trees. Leaves alternate or opposite, rarely whorled, blades various, most commonly linear, ovate or trullate. Capitula terminal or axillary, solitary on long peduncles or more commonly in paniculiform or corymbiform cymes, discoid or radiate. Involucres cylindric, campanulate or hemispheric, 4 or 6 to many in 1–8 series, subequal to gradate, rarely dimorphic. Receptacles flat to conic, usually paleate, pales chartaceous or sometimes indurate and wrapping tightly around cypselae. Ray florets pistillate, limbs conspicuous or sometimes barely protruding beyond paleae, rarely corolla tubular. Disc florets bisexual or sometimes functionally staminate, (4–)5(–6)-lobed, corollas with conspicuous reddish or orange resin canals; anthers ecalcarate, without tails, appendages deltate to ovate, rarely broadly ovate, abaxially glandular, endothecium of 1–3 polar bridges; styles with two vascular strands with parallel stigmatic areas, usually not confluent at apex, apices acute to acuminate with a short tuft of papillae. Cypselae obconic to obpyramidal, sometimes obcompressed, rarely quadrate, walls carbonized, glabrous to densely pubescent, sometimes glandular. Pappus present or absent, persistent, of multiple bristles or scales of subequal or uneven length, scales sometimes fused at the base forming a cup, rarely a shallow crown with 4 minute awns, sometimes growing after anthesis. $x = 11, 19$.

The tribe contains five genera and approximately 150 species, with most species in tropical areas of Mexico and South America, *Heptanthus* endemic to Cuba, and a few species of *Enydra* endemic to the Old World tropics.

Molecular studies of Heliantheae and relatives (Panero et al. 2001c; Panero and Funk 2002) support recognition of the group as a tribe of the He-

liantheae alliance sister to Bahieae, Chaenactideae and Tageteae. Neurolaeneae include only five genera with *Neurolaena* sister to *Greenmaniella*, and these two sister to *Calea*. The genus *Enydra* of Enydrinae is sister to the latter three genera. Preliminary molecular studies of the genus *Heptanthus* (Panero et al., unpubl. data) support, albeit weakly, the inclusion of *Heptanthus* in Neurolaeneae. The genus *Tetraperone*, the second member of Heptanthinae (Robinson 1981), is treated as part of Coreopsideae. The genera *Tetrachyron*, *Staurochlamys* and *Unxia*, included in Neurolaeninae by Robinson (1981), are treated under Heliantheae, Coreopsideae and Millerieae respectively. The limits of the tribe are preliminary, and will probably change as future molecular phylogenetic studies of members of the Heliantheae alliance include broader sampling and more characters.

Key to the Subtribes

1. Pales wrapping tightly around cypselae; limbs of ray floret very reduced or wanting and barely protruding beyond paleae or phyllaries; capitula solitary, axillary and sessile to subsessile; cypselae epappose; stems fistulose, rooting at nodes; plants of aquatic or marshy areas **1187. Enydrinae** (p. 418)
– Pales never wrapping around cypselae, sometimes lacking; limbs of ray florets, when present, conspicuous; capitula mostly in paniculiform or corymbiform cymes, if solitary and axillary, then capitula on long peduncles; cypselae with a pappus of multiple bristles or scales, rarely wanting or reduced to a shallow crown; stems not fistulose nor plants rooting at nodes; plants of various habitats, rarely aquatic or of marshy areas 2
2. Plants forming a small rosette; disc florets functionally staminate, style arms densely covered with broadly acute to round papillae; capitula axillary on long peduncles; endothecium of numerous radial and polar, minute thickenings **1188. Heptanthinae** (p. 418)
– Plants various, never forming a rosette, disc florets bisexual; style arms sparsely to moderately papillose, papillae tapered and confined to distal half and abaxial surface, capitula terminal, solitary or in compound thyrsoid, corymbiform or paniculiform cymes; endothecium of 1–3 polar thickenings **3. Neurolaeninae** (p. 419)

XXI.1. Subtribe Enydrinae H. Rob. (1979).

Perennial herbs, aquatic or of very wet areas, with fistulose stems, rooting at nodes. Leaves opposite, blades lanceolate to ovate or obovate, entire to broadly serrate. Capitula axillary, solitary, sessile, radiate or disciform. Involucres campanulate to hemispherical, phyllaries 4–6 in 2–3 series, the outermost larger, herbaceous, striate. Receptacles convex to minutely conical, paleate, pales wrapping tightly around florets. Ray florets pistillate, corollas white, yellow, rarely brownish, limbs minute or wanting, trilobed. Disc florets bisexual or functionally staminate, corollas pentamerous, white, yellow or pale brown, corollas barely protruding beyond paleae, with a few large, glandular trichomes; style arm apices acute. Cypselae obcompressed to subterete, shallowly stipitate, black, essentially glabrous. Pappus absent.

Only one genus:

1187. *Enydra* Lour.

Enydra Lour., Fl. Cochinchin. 510 (1790); Lack, Willdenowia 10: 3–12 (1980), part. rev.

Characters of the subtribe. Ten species, pantropical.

XXI.2. Subtribe Heptanthinae H. Rob. (1978).

Perennial herbs, forming rosettes, sometimes persistent on a thickened single caudex. Leaves alternate, blades lanceolate to ovate or cordiform on long petioles, entire or deeply lobed, sometimes trilobed. Capitula axillary, solitary on long peduncles, radiate. Involucres campanulate, phyllaries in 1–2 series, subequal, herbaceous to chartaceous. Receptacles convex, epaleate. Ray florets pistillate, corollas yellow or creamy yellow, limbs trilobed. Disc florets functionally staminate, (4–)5(–6)-lobed, corollas yellow with conspicuous reddish resin canals; disc floret style arms densely papillose, glandular (?), style of ray florets with divided stigmatic surfaces, tapered, essentially without papillae. Ray cypselae obconical, terete, black or dark brown, with a few glandular trichomes, otherwise glabrous, rugose, especially on basal half. Pappus of several, subequal, ciliate scales, shorter than disc corollas, growing after anthesis.

Only one genus:

1188. *Heptanthus* Griseb.

Heptanthus Griseb., Cat. Pl. Cub. 148 (1866); Liogier, Fl. Cuba 5: 187–189 (1962), reg. rev.

Characters of the subtribe. Seven species, Cuba.

XXI.3. Subtribe Neurolaeninae (Rydb.) Stuessy, B.L. Turner & A.M. Powell (1977); Robinson, Smithsonian Contrib. Bot. 51: 58–60 (1981), rev.

Annual or perennial herbs, shrubs or small trees. Leaves alternate or opposite, sometimes whorled. Capitula in terminal, paniculiform to corymbiform cymes, discoid or radiate. Involucres cylindrical to hemispherical, phyllaries in 2–8 series, subequal to gradate, rarely dimorphic. Receptacles flat to conical, paleate, rarely epaleate. Ray florets pistillate. Disc florets bisexual, corollas with prominent resin canals along veins of throat and lobes; anthers ecalcarate, without tails, appendages deltate or ovate, with glandular trichomes on abaxial surface, sometimes glabrous, endothecium of 1–3 polar thickenings; style arms with parallel stigmatic areas, not confluent, acute to acuminate, apices in ray florets tapered, resin canals outside the vascular traces. Cypselae obconical to obpyramidal, rarely quadrate or urceolate in outline. Pappus persistent, of numerous bristles or scales of unequal or equal size, rarely a shallow crown. $x = 11, 19$.

Key to the Genera

1. Leaves alternate, blades ovate, trullate, or weakly trilobed, never linear 2
– Leaves opposite, if alternate, then blades linear **1189. *Calea***
2. Cypselae with a pappus reduced to a shallow crown with 4 minute awns at angles of cypsela **1190. *Greenmaniella***
– Cypelae with a pappus of multiple bristles **1191. *Neurolaena***

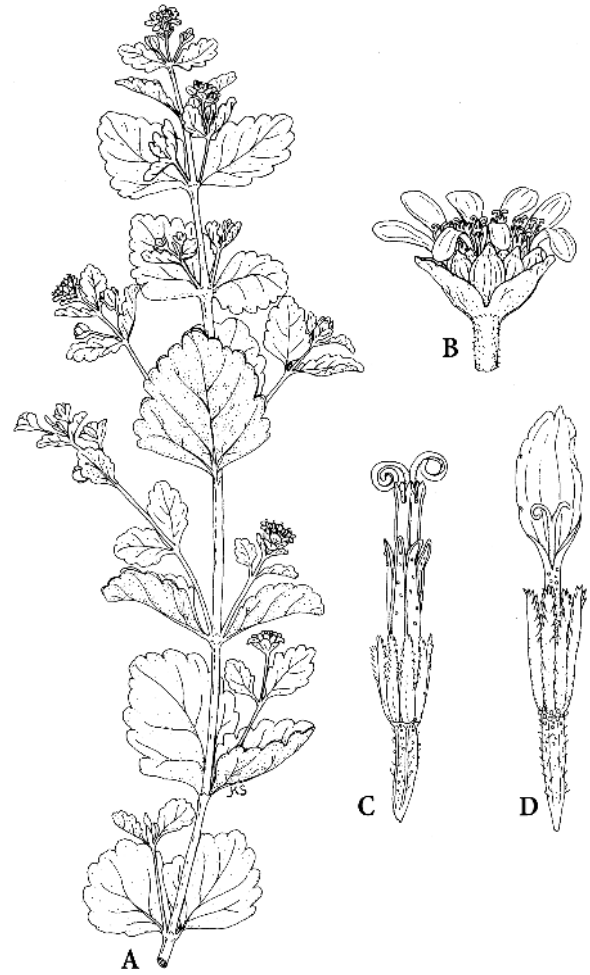

Fig. 85. Compositae-Neurolaeneae. *Calea crocinervosa*. **A** Habit. **B** Capitulum. **C** Disc floret. **D** Ray floret. (Wussow et al. 1985, with permission from Systematic Botany; artist J.K. Sullivan)

Genera of Neurolaeninae

1189. *Calea* L. Fig. 85

Calea L., Sp. Pl., ed. 2, 1179 (1763); Wussow et al., Syst. Bot. 10: 241–267 (1985); Urbatsch et al., Syst. Bot. 11: 501–504 (1986), reg. rev.
Tyleropappus Greenm. (1931).
Brasilia G.M. Barroso (1962).

Perennial herbs sometimes with woody xylopodia and tuberous roots, shrubs, sometimes scandent to vine-like or small trees. Leaves opposite, rarely alternate, whorled or basal, blades linear to ovate. Capitula solitary or in variously thyrsoid, paniculiform or corymbiform cymes, discoid or radiate. Involucres cylindrical to hemispherical, phyllaries in 2–8 series, subequal to gradate, sometimes dimorphic. Receptacles flat to conical, usually paleate. Ray florets pistillate, corollas yellow, rarely whitish. Disc florets bisexual, corollas yellow, less commonly white or purplish; style arm apices acute. Cypselae obconical or obpyramidal, black or brown, glabrous to densely pubescent, sometimes glandular. Pappus of multiple unequal or subequal, linear or tapered, rarely obovate, ciliate or erose scales, much shorter than or as long as the disc corolla, sometimes an erose crown. $x = 19$. Approximately 125 species, neotropical.

1190. *Greenmaniella* W.M. Sharp.

Greenmaniella W.M. Sharp, Ann. Missouri Bot. Gard. 22: 141 (1935).

Perennial herbs or weak shrubs. Leaves alternate, blades ovate. Capitula in terminal, paniculiform cymes, radiate. Involucres hemispherical, phyllaries in 2–3 series, dimorphic. Receptacles shallowly to conspicuously conical with age. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow to yellow-orange; style arm apices acute. Cypselae quadrate, with minute wings on each angle, black, sometimes with a greenish tinge, glabrous. Pappus a shallow crown with 4 minute awns at angles of cypselae, the crown enveloping corolla tube when young and expanding outwards as cypsela develops. One species, *G. resinosa* W.M. Sharp, north-eastern Mexico.

1191. *Neurolaena* R. Br.

Neurolaena R. Br., Trans. Linn. Soc. London 12: 120 (1817); Turner, Pl. Syst. Evol. 140: 119–139. (1982), reg. rev.

Annual or perennial herbs, shrubs or small trees. Leaves alternate, blades lanceolate to ovate, trullate, sometimes shallowly trilobed. Capitula in terminal, paniculiform, monochasial cymes, discoid or radiate. Involucres cylindrical to hemispherical, phyllaries in 2–5 series, subequal. Receptacles convex to conical. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow or greenish white; style arm apices acute to acuminate. Cypselae obconical to urceolate in outline, terete to obscurely obpyramidal with 4–5 shallow ribs, black, glabrous or pubescent especially on apices, sometimes with glandular trichomes, apices flat, bases tapered. Pappus of numerous bristles in 1–2 series, sometimes sigmoid at base. $x = 11$. Eleven species, neotropical.

XXII. Tribe Tageteae Cass. (1819).

J.L. Panero

Annual or perennial, sometimes aquatic herbs, shrubs, rarely small trees, sometimes with C_4 photosynthesis(*Flareria, Pectis*). Leaves alternate or opposite, blades filiform to broadly ovate, simple, pinnate or bipinnate, often with marginal and scattered pellucid glands. Capitula in open, terminal, paniculiform cymes, sometimes solitary and scapose, peduncles sometimes fistulose, capitula radiate, rarely discoid. Involucres cylindric, turbinate, campanulate or hemispheric, sometimes with a calyculus, phyllaries in 1–5 series, subequal to gradate, free or variously fused, with pellucid, oval glands or inflated pustules, sometimes with linear glands, sometimes eglandular. Receptacles flat to conical, mostly epaleate, sometimes with minute scales or bristles, sometimes foveolate. Ray florets pistillate. Disc florets bisexual, rarely functionally staminate, corollas actinomorphic, rarely zygomorphic, pentamerous, rarely tetramerous or hexamerous; anther appendages usually without glandular trichomes, usually strongly sclerified rarely without sclerification, endothecium cells with 1–2, sometimes with 2–4 polar thickenings, rarely evenly thickened or with radial thickenings; style arms acute to narrowly tapered, with narrow to broad (sometimes touching) stigmatic surfaces, usually not confluent at apices, appendages wanting or well developed, rarely style arms short and round and essentially fused except for distalmost apices and style shaft papillose. Cypselae cylindric to narrowly fusiform or obpyramidal, rarely compressed and narrowly convex, walls carbonized, black, rarely brown, striate, sparsely to densely pubescent, most commonly with trichomes concentrated on distal and basal ends, carpopodium usually well developed and conspicuous. Pappus of few to multiple scales or bristles or sometimes reduced to a crown of scales, rarely absent, persistent, rarely caducous, scales variously dissected into sometimes slightly flattened bristles, sometimes pappus of alternating scales and bristles.

The tribe contains 32 genera and approximately 270 species found mostly in the south-western USA and Mexico. Temperate and tropical South America contain an important number of species; *Schizotrichia* is the only genus of Tageteae endemic to South America. A few species occur in the Caribbean, with the monotypic genera *Harnackia* and *Lescaillea* being endemic to Cuba. One species of *Flaveria* is native to Australia. Members of the genus *Tagetes* (marigolds) are widely used in horticulture as well as a source of edible orange pigments. Some species of *Tagetes* are important components in the religious rituals of the peoples of Mesoamerica.

Tribe Tageteae was named by Cassini (1819) to accommodate a group of plants, previously placed in his Heliantheae. Strother (1977) provided the first modern account of the tribe. He viewed Tageteae as having two main phyletic lines, subtribe Pectidinae containing the distinctive genus *Pectis*, and subtribe Tagetinae containing the other 15 genera he recognized. Robinson (1981) viewed Tageteae as another subtribe of Heliantheae, and

placed Tagetinae in the synonymy of Pectidinae. A similar interpretation of Pectidinae was provided by Karis and Ryding (1994a). Molecular studies of Heliantheae and related tribes (Baldwin et al. 2002; Panero and Funk 2002) support the recognition of Pectidinae at the tribal level as tribe Tageteae. In addition, Baldwin's studies support, albeit weakly, a broader circumscription of Tageteae which 'dilutes' the convenient original circumscription of the tribe including only those taxa with glandular leaves and/or phyllaries. My decision to include the eglandular taxa in Tageteae follows Baldwin et al. (2002) and morphological considerations. The eglandular genera of Tagetae, for the most part, have glabrous, strongly sclerified anther appendages, striate cypselae with well-developed carpopodia, and a tendency to have cypselae with a pappus of bristles or dissected scales. These morphological characteristics are shared by most members of the traditional Tageteae (herein subtribe Pectidinae), and are unusual among the epaleate tribes with carbonized cypselae. The traditional view of two main phyletic lines within tribe Tageteae-Pectidinae has been recently challenged by results from molecular studies (Loockerman et al. 2003). These data support the monophyly of the subtribe and the dismemberment of *Dyssodia* into seven genera, as proposed by Strother (1986). The endemic Cuban genera *Harnackia* and *Lescaillea* are sister to *Boeberastrum* and, along with *Chrsyactinia*, they represent the basal lineages of the tribe. The other genera of the subtribe are placed in two clades, each with an equivalent number of genera. The findings of Loockerman et al. (2003) support the redefinition of the genus *Porophyllum*, by removing *Porophyllum tridentatum* and related species from Baja California and placing these in the new genus *Bajacalia*. *Poropyllum* is sister to *Pectis* and collectively to *Nicolletia*, *Bajacalia*, *Urbinella* and *Leucactinia*. The other clade contains *Dyssodia* and segregates, sister to *Strotheria* and *Gymnolaena* and collectively sister to the clade containing *Tagetes* and *Hydropectis*. Their findings also support the placement of *Vilobia* and *Adenopappus* in *Tagetes*.

Key to the Subtribes and Genera Unassigned to Subtribe

1. Capitula with 1(2) florets and fused phyllaries **2. Coulterellinae** (p. 422)
– Capitula normally with 3 or more florets, if fewer than 3, then phyllaries free 2
2. Receptacles paleate **6. Varillinae** (p. 430)
– Receptacles epaleate , sometimes with minute scales or bristles 3
3. Leaves and/or phyllaries with pellucid glands or pustules, aromatic **5. Pectidinae** (p. 423)
– Leaves and phyllaries without glands 4
4. Leaves alternate, filiform to acicular, succulent 5
– Leaves opposite, if alternate towards the inflorescences, then leaves not succulent 6
5. Receptacles setose **1. Clappiinae** (p. 421)
– Receptacles not setose **1223. *Pseudoclappia***
6. Leaves on stem and inflorescences alternate **1222. *Oxypappus***
– Leaves opposite throughout 7
7. Plants stoloniferous, rooting at the nodes, forming mats; phyllaries succulent; plants of brackish, coastal environments **4. Jaumeinae** (p. 423)
– Plants not stoloniferous, nor forming mats nor rooting at the nodes; phyllaries not succulent, plants found mostly in the interior of continents 8
8. Corolla tubes with long, stipitate, glandular trichomes; anther endothecial cells with 1–2 polar thickenings; style arms acute to deltate; pappus of disc florets easily caducous 9
– Corolla tubes glabrous or with a few scattered, short glandular trichomes; anther endothecial cells with 2–4 polar thickenings; style arms truncate; pappus of disc florets, when present, persistent **3. Flaveriinae** (p. 422)
9. Capitula solitary or in simple cymes; disc cypselae with a pappus of numerous bristles; plants of western and southern Mexico **1220. *Arnicastrum***
– Capitula in open paniculiform cymes; disc cypselae with a pappus of 6–12 bristles; plants of the SE USA **1221. *Jamesianthus***

XXII.1. Subtribe Clappiinae H. Rob. (1978).

Compact, perennial herbs or weak shrubs. Leaves alternate, sessile, blades linear, rarely shallowly lobed at base, succulent, mucronate, not aromatic. Capitula terminal, solitary, on long, distally fistulose peduncles, radiate. Involucres hemispheric, phyllaries in 3 series, subequal. Receptacles convex, epaleate, setose. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow, slightly zygomorphic, lobes acuminate, edges thickened, shallowly sclerified, with two resin canals along edges; anther appendages deltate, glabrous; style arms tapered, with broad, parallel stigmatic surfaces, appendages papillose, not vascularized. Cypselae cylindric, 10-ribbed, glabrous, slightly stipitate. Pappus of multiple, flattened, scabrid bristles, stramineous. $x = 16$.

Only one genus:

1192. ***Clappia*** A. Gray

Clappia A. Gray, Rep. U.S. Mex. Bound.2:93 (1859).

Characters of the subtribe. One species, *C. suaedifolia* Wooton & Standl., south-western USA, north-eastern Mexico.

XXII.2. Subtribe Coulterellinae H. Rob. (1978).

Brittle shrubs with whitish stems. Leaves opposite, sessile, blades ovate, dentate, concave, succulent, glaucous. Capitula with 1(2) florets, aggregated in terminal, umbelliform cymes, discoid. Involucres cylindric to rhombic, phyllaries 2–4, fused, subtended by a bract, ribs of each phyllary thickened after anthesis. Receptacles flat. Florets bisexual, corollas deep golden yellow, lobes as long as or longer than throat, corollas sometimes zygomorphic with 2 lobes fused; anther appendages ovate, with abaxial glandular trichomes; style arms acute to deltate, without appendages, with very broad, parallel stigmatic surfaces confluent at apices, papillae covering completely their abaxial surfaces. Cypselae cylindric to narrowly obconic, striate, black, distal end stramineous, indurate, glabrous. Pappus absent.

Only one genus:

1193. ***Coulterella*** Vasey & Rose

Coulterella Vasey & Rose, Contr. U.S. Natl Herb. 1: 71, pl. 1 (1890).

Characters of the subtribe. One species, *C. capitata* Vasey & Rose, southernmost Baja California, Mexico.

XXII.3. Subtribe Flaveriinae Less. (1832).

Annual or perennial herbs, shrubs, rarely trees. Leaves opposite, blades linear to elliptic, sometimes semisucculent. Capitula in terminal, open to congested corymbiform cymes, radiate or discoid. Involucres cylindric to hemispheric, phyllaries in 1–3 series, normally 5–6, subequal. Receptacles flat to conic, epaleate, sometimes with setae. Ray florets pistillate, corollas yellow, apices shallowly bilobed or trilobed. Disc florets bisexual, corollas yellow; anther appendages linear to ovate or deltate, glabrous; style arms truncate, with narrow, parallel stigmatic surfaces, appendages very short or wanting, not vascularized. Cypselae cylindric to narrowly obovate, rarely shallowly compressed, 8–11-ribbed, black, glabrous to sparsely pubescent, sometimes with a prominent, conic carpopodium. Pappus absent or of a few to numerous scales or bristles. $x = 18$.

Key to the Genera

1. Heads discoid, if radiate, then with only one or two ray florets **1194.** ***Flaveria***
– Heads radiate, with 3 or more ray florets 2
2. Disc cypselae with a pappus of numerous bristles **1195.** ***Haploësthes***
– Disc cypselae with a pappus of 4–6 scales alternating with 4–6 bristles **1196.** ***Sartwellia***

Genera of Flaveriinae

1194. ***Flaveria*** Juss.

Flaveria Juss., Gen. Pl. 186 (1789); Powell, Ann. Missouri Bot. Gard. 65: 590–636 (1978), rev.

Annual or perennial herbs, shrubs, rarely small trees. Leaf blades linear to elliptic. Capitula in terminal or axillary congested corymbiform cymes, tightly aggregated into glomerules with peripheral heads having one ray floret, radiate or discoid. Involucres cylindric, phyllaries in 1–2 series, subequal, navicular, herbaceous to corky. Receptacles flat to convex, paleae sometimes present as setae. Ray florets 1–2 per capitulum, corollas yellow. Disc floret anther appendages ovate to deltate. Cypselae shallowly compressed, obovate, 8–11-ribbed, glabrous, carpopodium wanting, base of cypsela sometimes invaginated. Pappus absent or rarely either a crown of minute scales, or 2–4 minute, free squamellae. $x = 18$. Twenty-two species, America, one species in Australia; introduced elsewhere.

1195. ***Haploësthes*** A. Gray

Haploësthes A. Gray, Mem. Amer. Acad. Arts n.s. 4: 109 (1849); Turner, Wrightia 5: 108–115 (1975), rev.

Multistemmed, annual or perennial herbs or weak shrubs. Leaf blades linear, semisucculent. Capitula in terminal, corymbiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries 5–6, in 2–3 series, subequal, broadly ovate to suborbicular. Receptacles convex to conic, epaleate. Disc floret anther appendages lanceolate. Cypselae cylindric, 9–15-ribbed, sparsely to densely pubescent. Pappus of multiple bristles. $x = 18$. Three species, south-western USA, north-eastern Mexico.

1196. *Sartwellia* A. Gray

Sartwellia A. Gray, Smithsonian Contr. Knowl. 3: 122 (1852); Turner, Sida 4: 265–273 (1971), rev.

Annual herbs. Leaf blades filiform, flat to terete, semisucculent, glabrous. Capitula in terminal, congested corymbiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries 5 in 2 series, subequal, herbaceous, yellowish. Receptacles conic, epaleate. Ray floret apices shallowly bilobed or trilobed. Disc floret anther appendages narrowly ovate to linear. Cypselae narrowly elliptic, 9–11-ribbed, glabrous, with a conic carpopodium. Pappus of (4–)5(–6) erose, isodiametric scales alternating with (4–)5(–6) capillary bristles, sometimes united into a shallow crown, rarely united to corolla and deciduous with it, ray florets sometimes with a pappus of erose, minute, obovate scales, rarely pappus absent. $x = 18$. Four species, south-western USA, north-eastern Mexico.

XXII.4. Subtribe Jaumeinae Benth. & Hook. f. (1873).

Perennial herbs or prostrate shrubs of estuarine sandy areas or salty mud flats. Leaves opposite, blades linear to terete, succulent. Capitula terminal, appearing axillary, solitary, radiate or discoid. Involucres cylindrical to campanulate, rarely hemispheric, phyllaries in 3–4 series, gradate, herbaceous, succulent. Receptacles conic, epaleate. Ray florets pistillate, corolla apices shallowly trilobed. Disc florets bisexual, corollas yellow, glabrous, edge of lobes thickened; anther appendages narrowly ovate/deltate, glabrous; style arms with parallel, broad stigmatic surfaces, apices deltate, appendages short, papillose, not vascularized. Cypselae cylindric, conspicuously striate, abruptly narrowed into a short cylindric carpopodium, black to brown, glabrous. Pappus persistent, of multiple awns, stramineous, or absent. $x = 19$.

Only one genus:

1197. *Jaumea* Pers.

Jaumea Pers., Syn. Pl. 2: 397 (1807).

Characters of the subtribe. Two species, coastal western USA, north-western Mexico, coastal, central Argentina, Uruguay.

XXII.5. Subtribe Pectidinae Less. (1830).

Subtribe Tagetinae Less. (1831).

Annual or perennial herbs, sometimes shrubs, rarely vines, sometimes aquatic herbs, aromatic. Leaves opposite or alternate, entire or dissected, with pustules or pellucid glands, either embedded in the leaf, marginal or terminal on the tips of lobes, sometimes with conspicuous setose bristles at ends of lobes or scattered along margins of leaves, sometimes bristles restricted to basal portions of leaves. Capitula terminal, solitary or in open paniculiform cymes, rarely congested corymbiform cymes, radiate or discoid. Involucres cylindric, turbinate, campanulate or hemispheric, phyllaries normally in 1–5 series, sometimes with a calyculus, free, partially or completely fused, usually with oval or linear glands. Receptacles flat to conic, epaleate, sometimes setose, scaly or with minute projections, sometimes foveolate. Ray florets pistillate. Disc florets bisexual, rarely functionally staminate, corollas sparsely to moderately covered with glandular trichomes, actinomorphic or zygomorphic, sometimes with one lobe or two either smaller or longer than rest; anther appendages ovate to lanceolate or very reduced, without glandular trichomes, normally densely sclerified; style arms acute to narrowly tapered, with narrow to broad, parallel stigmatic surfaces never confluent at apices, appendages wanting to well developed and sometimes as long as length of stigmatic arms, acute to deltate, sometimes cylindric and densely papillose, rarely arms very reduced, knob-like and style shaft densely papillose (*Pectis*). Cypselae cylindric to narrowly fusiform or obpyramidal, rarely compressed and narrowly biconvex, black or brown, sparsely to densely pubescent, with well-developed carpopodia. Pappus of a few to many scales or bristles, scales normally dissected into many bristles, bristles barbellulate, stramineous, rarely purple or red, sometimes scales alternating with bristles.

Key to the Genera

1. Vines or scandent shrubs; genera endemic to Cuba 2
– Annual or perennial herbs, erect or wiry shrubs, never scandent; genera endemic to America, some species in Cuba 3
2. Leaves reduced to minute scales, eglandular; capitula discoid **1209. *Lescaillea***
– Leaves twice trilobed, lobes glandular; capitula radiate **1207. *Harnackia***

3. Styles with minute, erect, rounded, style arms, papillae densely covering distal 1/2–2/3 of style **1212. *Pectis***
– Styles with spreading or arcuate style arms, papillae rarely found below style bifurcation point 4
4. Capitula with 4 or 5 disc florets **1215. *Strotheria***
– Capitula with more than 5 disc florets 5
5. Ray corollas white or pink, rarely white with a yellow base 6
– Ray corollas yellow, greenish-yellow, orange, red, if white, then phyllaries connate 9
6. Plants perennial, rhizomatous; leaves tightly clustered and forming a loose, rosette-like structure; capitula solitary, on long peduncles, scapose; plants of north-eastern Mexico **1210. *Leucactinia***
– Plants annuals, leaves evenly spaced and never forming rosette-like structures; capitula in open paniculiform cymes, rarely solitary, plants of the south-western USA and north-western Mexico 7
7. Pappus of numerous bristles, sometimes fused at base **1217. *Thymophylla***
– Pappus of entire or dissected scales 8
8. Style arms long, acuminate, appendages well developed, nearly as long as length of stigmatic surface, cylindric; pappus of dissected scales nearly as long as disc corollas **1211. *Nicolletia***
– Style arms short, appendages very short, acute to deltate; pappus of 5–6 obovate scales, much shorter than disc corolla tube **1218. *Urbinella***
9. Plants aquatic, stems fistulose **1208. *Hydropectis***
– Plants not aquatic, if in marshy areas, then stems not fistulose, sometimes along rivers and stems shallowly fistulose, then capitula with prominent, orange ray corollas 10
10. Receptacles with scales or setae, scales or setae as long as or longer than the cypselae **1203. *Comaclinium***
– Receptacles without scales or setae or if setose, then setae minute and much shorter than cypselae 11
11. Phyllaries free 12
– Phyllaries or innermost series of phyllaries partially to nearly completely connate 16
12. Calyculus of 5–8 bracts, herbaceous not scarious, normally narrower than phyllaries, reflexed 13
– Calyculus absent or reduced to 1 bract, sometimes phyllaries in several series with outermost ending in an inflated pustule 14
13. Annual or perennial herbs; plants of North America **1205. *Dyssodia***
– Shrubs, plants of Andean Peru **1214. *Schizotrichia***
14. Annuals **1200. *Boeberastrum***
– Shrubs 15
15. Phyllaries in 1–3 series, outermost phyllaries ending in an inflated pustule; plants of Baja California, Mexico **1199. *Bajacalia***
– Phyllaries in 1 series, phyllaries with a pellucid gland, gland not inflated nor at the very tips of the phyllaries; plants of Mexico and the south-western USA, not in Baja California **1202. *Chrysactinia***
16. Phyllaries in 4–5 series (or calyculus of several gradate, acute bracts), innermost series fused at base **1201. *Boeberoides***
– Phyllaries in one series, variously fused, calyculus, if present, of bracts or bracteoles with setose apices 17
17. Calyculus of 5 to many setose bracts, sometimes as long as phyllaries 18
– Involucres without a calyculus, sometimes with 1–3 bracts 19
18. Leaves linear; style arm apices deltate with a narrow, cylindric appendage **13. *Dysodiopsis***
– Leaves lanceolate or compound; style arm apices long, acuminate or subulate, if deltate, then without cylindric appendages **1198. *Adenophyllum***
19. Capitula discoid 20
– Capitula radiate 21
20. Pappus of multiple bristles **1213. *Porophyllum***
– Pappus of 5 scales alternating with 5 bristles **1217. *Thymophylla***
21. Capitula solitary, on peduncles held above foliage, if not above foliage, then herbage densely pubescent, lanate; leaves opposite below, alternate above; capitula with 1–3 bracts **1217. *Thymophylla***
– Capitula in open paniculiform or corymbiform cymes, rarely solitary, herbage never densely pubescent so as to appear lanate, leaves opposite; capitula without bracts 22
22. Pappus of scales dissected into multiple bristles **1206. *Gymnolaena***
– Pappus of a few scales, apices acute to acuminate, never dissected into multiple bristles **1216. *Tagetes***

Genera of Pectidinae

1198. *Adenophyllum* Pers.

Adenophyllum Pers., Syn. Pl. 2: 458 (1807); Strother, Sida 11: 371–378 (1986), rev.

Annual or perennial herbs, shrubs. Leaves opposite, sometimes alternate distally, blades pinnatifid, deltate to lanceolate-ovate in outline with ovate, obovate, linear or filiform lobes, teeth usually setose or bristly, glands marginal, on bases of lobes and subterminal in lobe tips. Capitula terminal, solitary, or in open paniculiform cymes, discoid or radiate. Involucres cylindric-campanulate to hemispheric, phyllaries in 1–2 series, weakly connate 1/3–2/3 of their length. Receptacles flat to shallowly convex, setose. Ray floret corollas yellow, orange, vermillion or bright scarlet. Disc floret corollas yellow to orange, sometimes zygomorphic, lobes lanceolate to subulate; anther appendages lanceolate to ovate; style arms either narrowly lanceolate, tapered with a prominent, partly vascularized, papillose, cylindric appendage, or acute to deltate with a reduced appendage. Cypselae linear to narrowly obpyramidal, dark brown, glabrous to moderately pubescent. Pappus of multiple squamellae, aristate or dissected into multiple bristles. $x = 7$, 13. Approximately 10 species, USA, Mexico, Central America, Cuba.

1199. ***Bajacalia*** Loockerman, B.L. Turner & R.K. Jansen

Bajacalia Loockerman, B.L. Turner & R.K. Jansen, Syst. Bot. 28: 204 (2003).

Shrubs. Leaves alternate, blades broadly acicular to linear, sometimes apices tridentate, in the shape of a T, semisucculent or succulent, each lobe terminated by a gland. Capitula terminal, solitary or in simple cymes, discoid. Involucres campanulate, phyllaries in 1–3 series, subequal, herbaceous, semisucculent, apices of outermost ending in a gland, innermost with a gland embedded in central region. Receptacles convex. Corollas light yellow with conspicuous brown or dark orange resin canals along vascular strands; anther appendages ovate; style arms acuminate, with vascularized, tapered, papillose appendages, papillae confined to distal half of style arms. Cypselae terete to narrowly obconic, black, sparsely to moderately pubescent. Pappus of multiple, unequal, capillary bristles, stramineous. $x = 15$. Three species, Baja California, Mexico.

1200. ***Boeberastrum*** (A. Gray) Rydb.

Boeberastrum (A. Gray) Rydb., N. Amer. Fl. 34: 161 (1915); Strother, Sida 11: 371–378 (1986), rev.
Dyssodia Cav. sect. *Boeberastrum* A. Gray (1883).

Annual herbs. Leaves alternate, blades oblong in outline, pinnatifid, leaflets linear, semisucculent, with a few, oval glands scattered throughout. Capitula terminal, solitary or in open paniculiform cymes, on fistulose peduncles, radiate. Involucres hemispheric, phyllaries free, in 2 series, membranaceous, suborbicular, with a few scattered, oval glands. Receptacles convex to conic, minutely scaly. Ray floret corollas yellow. Disc floret corollas yellow, zygomorphic, one lobe shorter than other 4, lobe apices thickened, with a mucronate projection; anther appendages ovate; style arms acute to deltate, appendages acuminate, papillose, not vascularized. Cypselae narrowly obconic, black, sparsely pubescent, pubescence denser on the base. Pappus of multiple scales each dissected into multiple bristles. $x = 7$. Two species, Baja California, Mexico.

1201. ***Boeberoides*** (DC.) Strother

Boeberoides (DC.) Strother, Sida 11: 373 (1986); Strother, Sida 11: 371–378 (1986), rev.
Dyssodia Cav. sect. *Boeberoides* DC. (1836).

Stout, perennial herbs or weak shrubs. Leaves opposite, blades shallowly trullate to elliptic, or obovate, minutely serrate, with numerous small glands, scattered throughout. Capitula terminal, solitary or a few in decussate, long-pedunculate paniculiform cymes, radiate. Involucres broadly cylindric to campanulate, bracts of calyculus free, phyllaries connate, in 4–5 series, last series connate from base to mid section, without glands. Receptacles convex. Ray floret corollas orange to vermillion. Disc floret corollas yellow, zygomorphic with two lobes appearing longer than others because of deeper sinuses; anther appendages lanceolate, glabrous; style arms long, acuminate, appendages acuminate, papillose, not vascularized, appendages approximately 1/4–1/5 the length of the stigmatic surfaces. Cypselae obpyramidal, sparsely pubescent. Pappus of multiple scales each dissected into multiple bristles. One species, *B. grandiflora* (DC.) Strother, Mexico.

1202. ***Chrysactinia*** A. Gray

Chrysactinia A. Gray, Mem. Amer. Acad. Arts n.s. 4: 93 (1849); Strother, Madroño 24: 129–139 (1977), rev.

Compact, erect or weak trailing shrubs, sometimes hanging from crevices in rocky canyons. Leaves alternate, simple or compound, blades simple, acicular to linear or compound and ovate in outline, 1-pinnate, segments filiform to linear, sometimes cuneate. Capitula terminal, solitary, on long peduncles, radiate. Involucres campanulate, phyllaries in 1 series, subequal, with a single gland on central, apical region. Receptacles flat to convex. Ray floret corollas lemon yellow to golden yellow, drying greenish or cherry red. Disc floret corollas yellow; anther appendages narrowly ovate; style arms acuminate, with narrow, parallel stigmatic surfaces, appendages acute. Cypselae cylindric, black, glabrous except for distalmost end, carpopodium broad, conic. Pappus of multiple bristles, white to stramineous. $x = 15$. Six species, south-western USA, northern Mexico.

1203. ***Comaclinium*** Scheidw. & Planch.

Comaclinium Scheidw. & Planch., Fl. Serres Jard. Eur. 8: 19, t. 756 (1852); Strother, Sida 11: 371–378 (1986), rev.

Perennial herbs. Leaves opposite, alternate along peduncles, blades simple, rarely trifoliolate, lanceolate, glands scattered between secondary veins and in a single row along edge of leaf. Capitula solitary, on long peduncles, radiate. Involucres cam-

panulate, phyllaries in 2 series, subequal, herbaceous with pellucid glands. Receptacles conic, scaly with 3–4 caducous scales surrounding each cypsela, scales as long as or longer than cypselae. Ray floret corollas orange. Disc floret corollas yellow to orange, lobes lanceolate to linear, subulate with oval, slightly expanded apices; anther appendages lanceolate, glabrous; style arms acute to deltate, appendages shortly deltate, not vascularized. Cypselae obpyramidal, weakly 4–5-angled, pubescent. Pappus of approximately 20 scales in 2 series, the outer shorter with each scale dissected into 5–10 bristles. $x = 13$. One species, *C. montanum* (Benth.) Strother, Mexico to Panama.

1204. *Dysodiopsis* (A. Gray) Rydb.

Dysodiopsis (A. Gray) Rydb., N. Amer. Fl. 34: 170 (1915); Strother, Sida 11: 371–378 (1986), rev.

Annual or perennial herbs. Leaves alternate, with a few, randomly spaced, filiform or setaceous serrations, setaceous at base, with scattered glands. Capitula terminal, in open paniculiform cymes, radiate. Involucres cylindric to turbinate, phyllaries in 2 series, connate with a reflexed calyculus of a few, deeply serrate bracts, phyllaries and bracts with several oval glands. Receptacles flat to convex, minutely setose. Ray floret corollas yellow. Disc floret corollas yellow; anther appendages lanceolate; style arms acute, appendages acuminate, vascularized only at the base. Cypselae obpyramidal, black, sparsely pubescent. Pappus of several scales, scale apices sometimes trifid. $x = 13$. One species, *D. tagetoides* Rydb., south-central USA.

1205. *Dyssodia* Cav. Fig. 86

Dyssodia Cav., Descr. Pl. 202 (1801) [1802]; Strother, Univ. Calif. Publ. Bot. 48: 1–88 (1969), rev.; Strother, Sida 11: 371–378 (1986), rev.

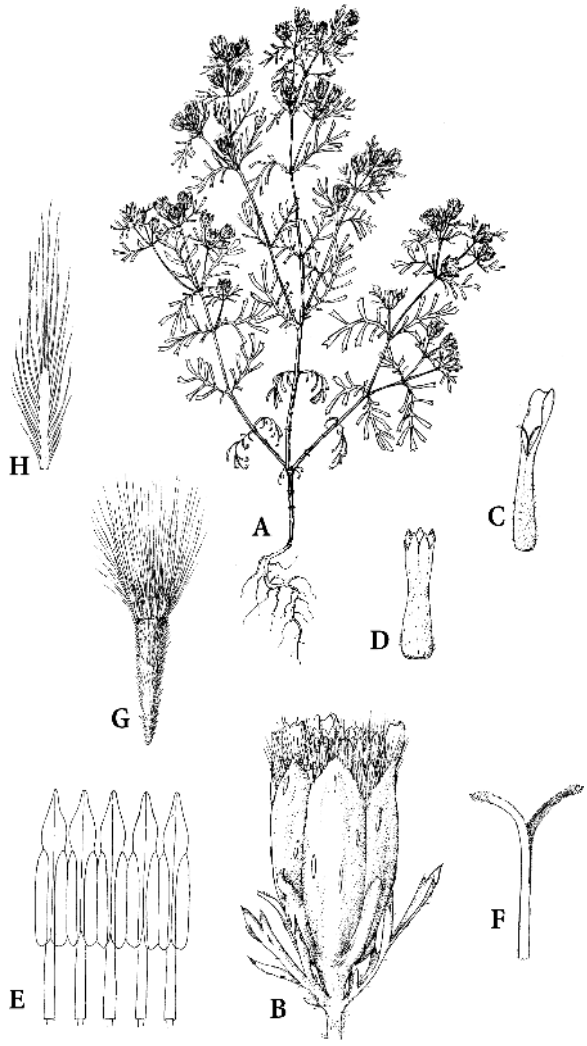

Fig. 86. Compositae-Tageteae. *Dyssodia papposa*. **A** Habit. **B** Flowering capitulum. **C** Ray corolla. **D** Disc corolla. **E** Anthers. **F** Style arms. **G** Cypsela. **H** Pappus scale. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

Annual or perennial herbs. Leaves opposite or alternate above, blades pinnatifid, segments linear to oblanceolate with scattered, pellucid glands. Capitula terminal, solitary, or in open paniculiform cymes, sometimes syncephalous and the syncephalia resembling single, radiate capitula, discoid or radiate. Involucres cylindric to hemispheric, phyllaries dimorphic in 1–3 series, outer herbaceous (calyculus), inner herbaceous to membranaceous, with pellucid oval or narrowly oblong glands. Receptacles flat to conic. Ray floret corollas yellow to orange. Disc floret corollas yellow to dull orange, sometimes with purple tips; anther appendages ovate to lanceolate; style arms acute to deltate, appendages deltate, not vascularized. Cypselae obpyramidal to obconical, black, glabrous to moderately pubescent. Pappus of 15–20 squamellae of various lengths, each squamella composed of 5–10 basally connate bristles, stramineous to burgundy. $x = 13$. Approximately five species, USA, Mexico, Guatemala.

1206. *Gymnolaena* (DC.) Rydb.

Gymnolaena (DC.) Rydb., N. Amer. Fl. 34: 160 (1915); Strother, Sida 3: 110–114 (1967), rev.

Shrubs. Leaves opposite, blades lanceolate to ovate, conspicuously serrate, pinnately nerved, with small, round glands scattered throughout. Capitula terminal, solitary or in simple cymes, radiate. Involucres cylindric, phyllaries uniseriate, connate to tips, with pellucid glands. Receptacles convex, epaleate. Ray floret corollas yellow to red. Disc floret corollas yellow to red, sometimes bicoloured; anther appendages lanceolate; style arms strongly acuminate, with broad, parallel stigmatic surfaces, nearly touching at apices, appendages filiform, papillose, partly vascularized. Cypselae obpyramidal, moderately pubescent. Pappus of multiple scales, each comprised of several connate bristles. $x = 13$. Three species, Mexico.

1207. *Harnackia* Urb.

Harnackia Urb., Repert. Spec. Nov. Regni Veg. 21: 72 (1925); Liogier, Fl. Cuba 5, 224 (1962), rev; Strother, Madroño 24: 129–139 (1977), rev.

Scandent shrubs or vines. Leaves opposite, trilobed, lobes cuneate to acuminate, apices entire to trilobed, each lobe with an oval, inflated gland at its apex, sometimes central lobe without glands. Capitula in terminal, simple to compound cymes, each on a long peduncle, radiate. Involucres turbinate, sometimes with a calyculus of 2 bracts, phyllaries few, free, in one series. Receptacles flat to slightly convex. Ray floret corollas yellow. Disc floret corollas yellow, with 8–9 vascular traces; anther appendages ovate, glabrous; style arms tapered, with narrow, parallel stigmatic surfaces, appendages lanceolate, papillose, not vascularized. Cypselae cylindric, black-striate, glabrous with a few apical trichomes. Pappus of multiple, barbellulate, subequal bristles, weakly united at base. One species, *H. bisecta* Urb., eastern Cuba.

1208. *Hydropectis* Rydb.

Hydropectis Rydb., N. Amer. Fl. 34: 216 (1914); Turner, Phytologia 78: 211–213 (1995), rev.
Hydrodyssodia B.L. Turner (1988).

Aquatic annuals. Leaves opposite, blades linear, entire or pinnate, sometimes with pellucid, oval glands. Capitula terminal, sometimes appearing axillary, solitary or in open simple cymes, discoid or radiate. Involucres turbinate or hemispheric, phyllaries in 1–2 series, herbaceous to membranaceous, sometimes with linear glands. Receptacles convex to conic, epaleate. Ray floret corollas brownish, limbs very reduced. Disc floret corollas tetramerous or pentamerous, yellow or brownish; anther appendages lanceolate; style arms acute, without appendages. Cypselae cylindric or shallowly obpyramidal, sparsely pubescent, pubescence denser on basal area and around carpopodium. Pappus of multiple scales or bristles, scales sometimes trifid or divided into a few bristles. $x = 9$. Three species, western Mexico.

1209. *Lescaillea* Griseb.

Lescaillea Griseb., Cat. Pl. Cub. 156 (1866); Liogier, Fl. Cuba 5, 224 (1962), rev.; Strother, Madroño 24: 129–139 (1977), rev.

Scandent shrubs or vines. Leaves opposite, blades reduced to minute scales. Capitula in terminal, simple cymes, discoid. Involucres turbinate, phyllaries few, in one series, each with an oval gland at the apex. Receptacles flat. Corollas yellow, with 8–9 vascular traces; anther appendages ovate, glabrous; style arms tapered, with narrow, parallel stigmatic surfaces, appendages lanceolate, papillose, not vascularized. Cypselae cylindric, black, glabrous with a few apical trichomes. Pappus of multiple, barbellulate, subequal bristles, weakly united at base. One species, *L. equisetiformis* Griseb., western Cuba.

1210. *Leucactinia* Rydb.

Leucactinia Rydb., N. Amer. Fl. 34: 180 (1915).

Perennial herbs, rhizomatous, each shoot forming a small tuft of leaves. Leaves alternate, on short internodes, blades filiform with a few, scattered, oval glands. Capitula terminal, solitary on long peduncles well above foliage, radiate. Involucres campanulate, phyllaries in 1 series, subequal, herbaceous with a few, oval glands, edges and distal apices scarious. Receptacles convex, with a few golden, caducous trichomes surrounding bases of cypselae. Ray floret corollas white, apices shallowly trilobed. Disc floret corollas yellow with the base turning purplish after anthesis, with conspicuous brown or dark orange resin canals along vascular strands; anther appendages narrowly ovate, glabrous; style arms acute to deltate, appendages short, papillose, not vascularized. Cypselae subterete to narrowly obconic, black, sparsely pubescent, pubescence denser on distal and basalmost areas. Pappus of multiple, slender, unequal, capillary bristles, stramineous. $x = 16$. One species, *L. bracteata* Rydb., north-eastern Mexico.

1211. *Nicolletia* A. Gray

Nicolletia A. Gray, Rep. Exped. Rocky Mts 315 (1845); Strother, Sida 7: 369–374 (1978), rev.

Annual herbs. Leaves alternate, blades linear or filiform, trilobed or with several, filiform projections on each side. Capitula terminal, solitary on essentially all branches of the plant, radiate. Involucres turbinate to campanulate, phyllaries in 2 series, free, subequal, with a few smaller, phyllaries/bracts on peduncle just below capitula. Receptacles flat to convex. Ray floret corollas white suffused with pink or deep pink. Disc floret corollas yellow; anther appendages ovate, strongly sclerified, glabrous; style arms long-acuminate, with densely papillose, vascularized, filiform appendages nearly as long as the stigmatic surfaces. Cypselae cylindric, moderately to densely pubescent. Pappus of a few broad scales, edges soon dissected into multiple bristles, stramineous. $x = 10$. Three species, south-western USA, north-western Mexico.

1212. *Pectis* L. Fig. 87

Pectis L., Syst. Nat., ed. 10: 1189, 1221, 1376 (1759); Keil, Madroño 23: 181–191 (1975), part. rev.; Keil, Rhodora 79: 32–78 (1977), part. rev.; Keil, Rhodora 80: 135–146 (1978), part. rev.

Annual or perennial herbs, sometimes stoloniferous. Leaves opposite, with pairs of setaceous bristles, blades linear to narrowly ovate, abaxial surfaces with large glands. Capitula terminal, solitary or in paniculiform cymes, radiate. Involucres cylindric to campanulate, phyllaries in 1 series, free, calyculus absent. Receptacles flat to convex. Ray florets rarely functionally staminate, corollas yellow or reddish yellow. Disc floret corollas actinomorphic or zygomorphic with one lobe shorter and more deeply cut, yellow; anther appendages ovate to round, sometimes reduced and shallowly obcordate, not sclerified; style arms very short, knob-like or rounded, sometimes fusiform, densely papillose, papillae extending well below bifurcation, appendages in most species reduced to an aggregation of minute papillae. Cypselae cylindric to clavate, sometimes obpyramidal, black or brown, sparsely to moderately pubescent, sometimes densely pubescent on angles. Pappus of few to multiple scales or bristles or sometimes reduced to a crown of scales, stramineous to burgundy red. $x = 12$. Approximately 85 species, tropical and subtropical America.

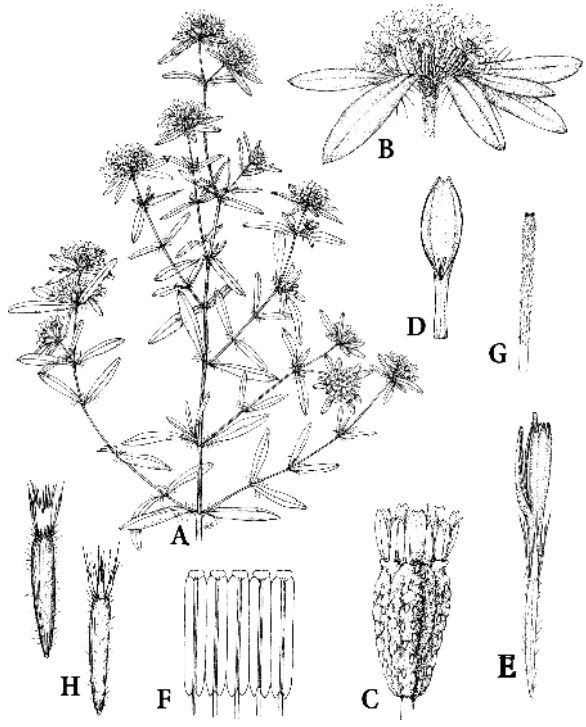

Fig. 87. Compositae-Tageteae. *Pectis decemcarinata*. **A** Flowering branch. **B** Involucrate cluster of capitula. **C** Flowering capitulum. **D** Ray corolla. **E** Disc floret. **F** Anthers. **G** Style. **H** Ray cypselae. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

1213. *Porophyllum* Adans.

Porophyllum Adans., Hist. Acad. Roy. Sci. Mem. Math. Phys. (Amsterdam) 1750: 377 (1754); Johnson, Univ. Kansas Sci. Bull. 48: 225–267 (1969), rev.

Annual or perennial herbs or densely branched shrubs, sometimes weak stoloniferous shrubs. Leaves opposite or alternate, blades linear to ovate, with embedded, pellucid glands, herbage strongly aromatic. Capitula in terminal, open corymbiform to paniculiform cymes, discoid. Involucres cylindric to campanulate, phyllaries in 1 series, free, calyculus absent. Receptacles flat or slightly convex. Corollas actinomorphic to slightly zygomorphic, green-brown, purple-brown, purple, green, white-yellow or yellow; style arms long, tapered, appendages cylindric, papillose. Cypselae fusiform or narrowly cylindric, brown or black, sparsely to moderately pubescent. Pappus of numerous bristles. $x = 11, 12$. Thirty species, tropical and subtropical America.

1214. ***Schizotrichia*** Benth. in Benth. & Hook. f.

Schizotrichia Benth. in Benth. & Hook. f., Gen. Pl. 2: 202, 410 (1873).

Shrubs. Leaves opposite, blades narrowly ovate to ovate or elliptic, entire to deeply serrate, with scattered orange glands. Capitula in terminal, simple or open paniculiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries in 3 series, gradate, outermost reflexed. Receptacles flat to convex, epaleate. Ray floret corollas yellow, apices shallowly trilobed. Disc floret corollas yellow; anther appendages ovate, glabrous; style arms acuminate to deltate, with parallel, broad stigmatic surfaces, appendages short, not vascularized. Cypselae subterete, black to silvery black, moderately pubescent. Pappus of multiple, soft scales soon divided into several bristles of unequal length, stramineous. Two (to five?) species, Peru.

1215. ***Strotheria*** B.L. Turner

Strotheria B.L. Turner, Amer. J. Bot. 59: 180 (1972).
Graciela Rzed. (1975).

Low shrubs forming small mounds. Leaves alternate, few nodes below capitula with opposite leaves, blades linear, navicular, succulent, not glandular. Inflorescences terminal, solitary, subtended by two bracts, neighbouring capitula tightly clustered into small congested, corymbiform to umbelliform cymes, capitula discoid. Involucres cylindric to narrowly campanulate, phyllaries 4–6, fused except for acute apices, subequal, with one to several glands on apices. Receptacles flat. Florets 4 or 5, corollas yellow to greenish yellow, pentalobed or hexalobed; anther appendages ovate, strongly sclerified, glabrous; style arms acute to deltate, with narrow, parallel stigmatic surfaces, appendages short, acuminate, not vascularized. Cypselae obpyramidal, obscurely 3- or 4-angled, black, shiny, moderately sericeous. Pappus of multiple lanceolate, erose, overlapping scales with a thickened midrib, sometimes protruding as a short, erose awn. $x = 8$. One species, *S. gypsophila* B.L. Turner, north-eastern Mexico.

1216. ***Tagetes*** L.

Tagetes L., Sp. Pl. 2: 887 (1753); Soule, Ph.D. Dissertation, University of Texas, Austin (1993), rev.
Adenopappus Benth. (1840).
Vilobia Strother (1968).

Annual or perennial herbs, sometimes shrubs. Leaves opposite, simple or pinnately dissected, blades linear to lanceolate or ovate in outline, segments sometimes reduced to bristles, glands scattered throughout blade. Capitula terminal, solitary or more commonly in open (rarely congested) paniculiform cymes, sometimes on long, fistulose peduncles, radiate, rarely discoid. Involucres cylindric, fusiform or campanulate, phyllaries in 1 series, fused except for apices, with 2 or more rows of glands, calyculus absent. Receptacles flat to conic. Ray floret corollas white, yellow, orange or sometimes bicoloured. Disc floret corollas yellow, orange, purplish or white, sometimes zygomorphic with one lobe longer than the rest; anther appendages narrowly lanceolate to ovate; style arms acute to deltate, appendages short, acuminate to deltate, sometimes fully vascularized. Cypselae clavate, linear or narrowly oblanceolate, sometimes compressed, biconvex or obpyramidal, black, sparsely pubescent. Pappus of a few, acute, acuminate or subulate scales or a combination thereof, sometimes of 1 or 2 very narrow awns and a few very short scales in between, rarely of scales subdivided into bristles, rarely absent. $x = 11, 12$. Approximately 50 species, tropical and subtropical America, a few species adventive and widespread in temperate and tropical regions of the Old World.

1217. ***Thymophylla*** Lag.

Thymophylla Lag., Gen. Sp. Pl. 25 (1816); Strother, Sida 11: 371–378 (1986), rev.
Dyssodia Cav. sect. *Acyphyllaea* DC. (1836).
Dyssodia Cav. sect. *Aurantiacae* Strother (1969).

Annual or perennial herbs, sometimes persisting as weak shrubs. Leaves opposite below or alternate throughout, blades linear or filiform, spathulate, entire or pinnatisect, segments linear or filiform, essentially without setae, glands scattered. Capitula terminal, pedunculate or sessile, solitary or in open paniculiform cymes, usually radiate, rarely discoid. Involucres turbinate to hemispheric, phyllaries in 1 series, membranaceous, connate 1/2–2/3 of their length, glands small, round, scattered, calyculus mostly of 1–3 bracts. Receptacles flat to convex, epaleate. Ray floret corollas yellow, golden yellow, rarely white. Disc floret corollas yellow to yellow-orange; anther appendages ovate, glabrous; style arms acute to deltate, appendages short, not vascularized. Cypselae narrowly obconic, cylindric or obpyramidal, black. Pappus of multiple scales, aristate or dissected into several bristles, sometimes obovate scales alternating with bristles. $x = 8$. Ap-

proximately 18 species, south-western USA, Mexico and north-western Argentina.

1218. *Urbinella* Greenm.

Urbinella Greenm., Proc. Amer. Acad. 39: 117 (1903).

Small, dainty annual herbs. Leaves opposite below, alternate distally, blades filiform, with a few, scattered, oval glands. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres campanulate, phyllaries in 1 series, subequal, medial area with a few oval glands. Receptacles convex to conic, epaleate. Ray floret corollas bicoloured, white, base of limb yellow. Disc floret corollas yellow, with a very narrow tube; anther appendages reduced to a minute deltate tip or wanting; style arms acute to deltate, appendages deltate, papillose, not vascularized. Cypselae subterete to terete, black, glabrous with a few trichomes on distal and basalmost areas. Pappus of a few, broadly obovate, minute scales, hyaline. $x = 8$. One species, *U. palmeri* Greenm., north-western Mexico.

XXII.6. Subtribe Varillinae B.L. Turner & A.M. Powell (1978).

Shrubs. Leaves opposite, sometimes alternate along peduncles, blades lanceolate or linear, sometimes succulent. Capitula terminal, in corymbiform cymes or solitary on long peduncles, discoid. Involucres campanulate to hemispheric, phyllaries in 2–3 series, subequal. Receptacles conic, paleate. Disc floret corollas yellow, pubescent with glandular trichomes and dense resinous areas between vascular strands; anther appendages ovate, glabrous or sometimes with minute glandular trichomes abaxially; style arms truncate to broadly acute, short and canaliculate, appendages acute, with numerous, minute papillae, not vascularized. Cypselae cylindric, 9–11-ribbed, without carpopodia, black, glabrous to sparsely pubescent. Pappus mostly absent, sometimes pappus of a few awns.

Only one genus:

1219. *Varilla* A. Gray

Varilla A. Gray, Mem. Amer. Acad. Arts n.s. 4: 106 (1849); Turner, Phytologia 68: 4–13 (1990), rev.

Characters of the subtribe. $x = 18$. Two species, south-western USA, northern Mexico.

Genera Unassigned to Subtribe

1220. *Arnicastrum* Greenm.

Arnicastrum Greenm., Proc. Amer. Acad. 39: 115 (1903).

Perennial herbs or weak, trailing subshrubs. Leaves opposite, blades broadly lanceolate to ovate. Capitula solitary or few capitula in open, paniculiform cymes, radiate. Involucres hemispheric, phyllaries in 3 series, subequal to gradate, ovate with attenuate tips. Receptacles flat to convex, epaleate. Ray floret corollas yellow. Disc florets fertile (?), corollas yellow, with long, stipitate glandular trichomes; style arms acuminate to deltate, without appendages, with broad, parallel stigmatic surfaces. Cypselae narrowly obconic, striate, black, sparsely pubescent. Pappus of multiple barbellulate bristles, fragile, easily caducous, absent in ray cypselae. Two species, northern and southern Mexico.

1221. *Jamesianthus* S.F. Blake & Sherff

Jamesianthus S.F. Blake & Sherff, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 399 (1940).

Perennial herbs. Leaves opposite, blades narrowly ovate to trullate, acuminate. Capitula terminal, in open paniculiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries in 2–3 series, gradate. Receptacles flat to convex, epaleate. Ray floret corollas yellow, apices shallowly trilobed, with distinctive, stipitate, glandular trichomes. Outermost disc florets (those alternating with ray florets) bisexual, otherwise functionally staminate, corollas yellow, with long, stipitate glandular trichomes; anther appendages ovate, glabrous; style arms long, arcuate, curling, acute to deltate, with narrow, parallel stigmatic surfaces, appendages wanting. Cypselae elliptic, black to brown, sparsely pubescent, the trichome bases broad and appearing as glands with age, ray cypselae slightly curved inwards, carpopodium broad, bowl-shaped. Pappus a shallow crown or ring with 6–12 caducous, slender bristles, ray cypselae apparently lacking bristles and the ring slightly more thickened. One species, *J. alabamensis* S.F. Blake & Sherff, south-eastern USA.

1222. *Oxypappus* Benth.

Oxypappus Benth., Bot. Voy. Sulphur 118 (1845).

Annual or perennial herbs. Leaves opposite below, alternate above, those at the base ovate and much larger than the linear, cauline blades, herbage

with stipitate glands. Capitula terminal, in open paniculiform cymes, radiate. Involucres campanulate, phyllaries in 1 series, subequal. Receptacles flat to convex, epaleate. Ray floret corollas yellow, apices shallowly trilobed. Disc floret corollas yellow; anther appendages ovate, glabrous; style arms long-acuminate, with an apical short tuft of papillae, without appendages. Cypselae subterete, black, glabrous, carpopodium conspicuous, bowl-shaped. Pappus of narrowly triangular scales prolonged into barbellate awns, 3 in the ray cypselae, 5 in the disc cypselae. One species, *O. scaber* Benth., western and southern Mexico.

1223. *Pseudoclappia* Rydb.

Pseudoclappia Rydb., J. Wash. Acad. Sci. 13: 288 (1923).

Low, open shrubs. Leaves alternate, blades terete to subacicular, succulent. Capitula terminal, solitary on long peduncles, radiate. Involucres cylindric to turbinate, phyllaries in 2–3 series, without glands. Receptacles flat to shallowly convex, epaleate. Ray floret corollas yellow. Disc floret corollas yellow; anther appendages lanceolate to narrowly lanceolate; style arms acute to tapered, with parallel, broad stigmatic surfaces, confluent at very apex, appendages short, papillose. Cypselae cylindric, black, moderately pubescent. Pappus of multiple, barbellulate bristles, white to stramineous. x = 18. Two species, south-western USA, north-eastern Mexico.

XXIII. Tribe Chaenactideae B.G. Baldwin (2002).

J.L. Panero

Annual, often ephemeral, or perennial herbs, rarely alpine subshrubs. Leaves alternate, sometimes subopposite or opposite, in some species the basal leaves forming a rosette, petiolate or sessile, blades entire or trilobed to 1–3 times pinnate, oval to obovate or trullate in outline, variously pubescent. Capitula discoid, terminal, subscapiform and solitary or usually in open corymbiform or paniculiform cymes, rarely reduced and congested in the centre of a rosette. Involucre cylindrical, campanulate or subhemispherical, phyllaries in 1–2 series. Receptacle flat to convex, epaleate. Florets bisexual, cells not sclerified, peripheral corollas sometimes with expanded lobes, sparsely to moderately pubescent with short to long stipitate glandular trichomes, lobes 5, sometimes densely papillose on adaxial surfaces; anther thecae white to white-pink, rarely yellow or purple-pink, anther appendages ovate to round, rarely oval, weakly to strongly carinate, partially to fully sclerified, with or without glandular trichomes on abaxial surfaces, median endothecial cells with one polar thickening, stigmatic surfaces marginal, rarely meeting at the distal end of the style arm, style arm apices obtuse to rounded, most commonly narrowly tapered. Cypselae cylindrical, terete to shallowly convex, usually with a shallow to prominent neck, walls carbonized, glabrous to densely pubescent but without glandular trichomes. Pappus of 5–10 ovate, narrowly oval to round, rarely bilobed, erose scales or rarely multiple, erose or setose, linear to obovate scales fused at the base, deciduous and dispersing as a unit.

Three genera and approximately 29 species of the western USA and north-western Mexico.

Tribe Chaenactideae was named by Baldwin et al. (2002) to accommodate most genera of classical Helenieae having a pappus of scales without thickened bases or midribs and striate cypselae, and revealed in molecular studies as a distinctive lineage of the Heliantheae alliance. Chaenactideae have traditionally been included in a broad concept of Helenieae. *Dimeresia* has been placed in Inuleae and Senecioneae (Karis and Ryding 1994b). Robinson (1981) placed *Chaenactis* and *Orochaenactis* in his Chaenactidinae whereas *Dimeresia* was viewed as an unusual element of obscure affinity and, therefore, placed in its own subtribe Dimeresiinae. Karis and Ryding (1994b) were also unable to clarify the affinities of *Dimeresia*. Recent molecular studies of the helenioid members of the Heliantheae alliance by Baldwin et al. (2002) resulted in the recognition of tribe Chaenactideae to include only three genera – *Chaenactis*, *Dimeresia* and *Orochaenactis*. These results have been confirmed by chloroplast DNA data (Panero and Funk 2002). The latter studies also show that the members of the tribe are sister to Bahieae (sensu Baldwin et al. 2002).

Key to the Genera

1. Capitula with one or two florets **1224. *Dimeresia***
– Capitula with more than two florets 2
2. Cypselae epappose or, if pappose, then with persistent and free pappus elements **1225. *Chaenactis***
– Cypselae with obovate to pandurate pappus elements fused at the base and collectively deciduous **1226. *Orochaenactis***

Genera of Chaenactideae

1224. *Dimeresia* A. Gray

Dimeresia A. Gray, Syn. Fl. N. Am., ed. 2, 1(2): 448 (1886).

Prostrate annuals with taproot with multiple, short, congested shoots, forming a tiny rosette-like structure subtending the congested inflorescence. First pair of leaves opposite to subopposite, subsequent leaves alternate on short internodes, sessile, blades oval to obovate, those subtending the heads narrowly spathulate, with a few floccose trichomes at the base, triplinerved. Capitula with only one or two florets, in terminal, congested cymes. Involucre cylindrical, phyllaries one or two enclosing each floret. Receptacle flat. Florets bisexual, corollas white, reddish purple on abaxial surface when old or dried, white on adaxial surface, glabrous to sparsely pubescent with widely scattered glandular trichomes; anthers whitish with thecal arc in connective purplish, appendages ovate to round; style arms with obtuse papillose apices, style bases without trichomes. Cypselae cylindrical, terete to shallowly biconvex, glabrous. Pappus of multiple, setose, linear scales fused at the base, deciduous and dispersing as a unit. $x = 7$. One species, *D. howellii* A. Gray, western USA.

1225. *Chaenactis* DC. Fig. 88

Chaenactis DC., Prodr. 5: 659 (1836); Stockwell, Contr. Dudley Herb. 3: 89–168 (1940), rev.

Annual or perennial herbs, rarely subshrubs. Leaves alternate, distalmost sometimes subopposite or opposite, sometimes basal producing a rosette, petiolate, entire, trilobed, pinnatifid or 2–3-pinnatifid, blades rarely linear or trilobed, most commonly oval or trullate in outline, sometimes densely pubescent. Capitula terminal, solitary and subscapose or in open corymbiform or paniculate cymes. Involucres campanulate to subhemispherical. Receptacle flat to convex. Florets bisexual, corollas white, creamy white, pink to purple or yellow, peripheral florets sometimes with expanded lobes; anthers whitish to pale pink or light yellow, appendages ovate to round or rarely narrowly oval; style arms with obtuse or narrowly tapered papillose apices, style bases with papillae and some multicellular trichomes. Cypselae terete, glabrous to densely pubescent, with a shallow to prominent cyathiform neck. Pappus absent or more commonly of 5–10 ovate, narrowly oval to round, rarely bilobed or obovate,

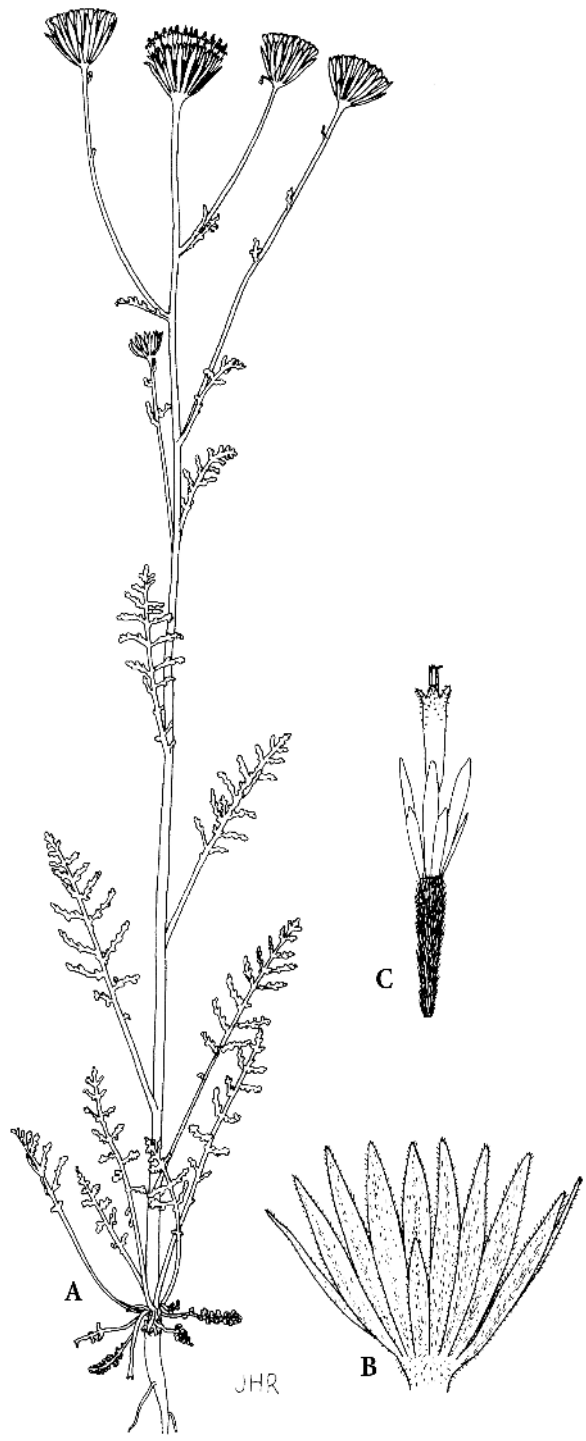

Fig. 88. Compositae-Chaenactideae. *Chaenactis douglasii* var. *achilleifolia*. **A** Habit. **B** Involucre. **C** Floret. (Reproduced from Vascular Plants of the Pacific Northwest, with permission of University of Washington Press; see Hitchcock et al. 1959; artist John H. Rumely)

erose scales, sometimes pappus of peripheral florets not uniform, with scales facing phyllaries much shorter. $x = 5, 6, 7, 8$. Twenty-seven species, western USA, north-western Mexico.

1226. *Orochaenactis* Coville

Orochaenactis Coville, Contr. U.S. Natl Herb. 4: 134 (1893).

Annual herbs. Leaves alternate, distalmost subopposite, blades linear, sparsely pubescent and glandular. Capitula in open paniculiform cymes. Involucres campanulate. Receptacle flat to convex. Corollas creamy white, without sclerified cells, sparsely pubescent with scattered glandular trichomes, lobes papillose on adaxial surface, veins of most lobes meeting at lobe apices; anthers whitish, appendages ovate; style arms with obtuse to tapered papillose apices, style bases with trichomes. Cypselae cylindrical, terete, sparsely pubescent with short and broad twin trichomes. Pappus of multiple, erose, obovate scales fused at the base, deciduous and dispersing as a unit. $x = 9$. One species, *O. thysanocarpha* Coville, western USA.

XXIV. Tribe Bahieae B.G. Baldwin (2002).

J.L. Panero

Annual, biennial or perennial herbs, rarely shrubs, some subalpine or dry grassland species forming caespitose woody caudices, herbage usually glandular. Leaves alternate or opposite, sessile to petiolate, blades linear to cordiform, entire to 1–4-pinnate. Capitula terminal, scapose to subscapose or in open paniculiform, rarely congested corymbiform cymes, radiate or discoid, rarely disciform. Involucres cylindric, turbinate to hemispheric, phyllaries in 1–4 series, subequal, sometimes gradate, mostly with abundant glandular trichomes on abaxial surfaces. Receptacles flat to convex, usually epaleate. Ray florets pistillate. Disc florets bisexual, pentamerous, rarely tetramerous, corollas mostly actinomorphic, in a few genera zygomorphic; anther appendages ovate, rarely cochleate, with or without abaxial glandular trichomes, endothecium of quadrate or fusiform cells with 1–4 polar thickenings, rarely radial (*Chamaechaenactis*); style bases sometimes papillose or pubescent, arms with parallel, narrow or broad and sometimes touching stigmatic surfaces, not confluent at apices, with or without appendages. Cypselae obpyramidal to subterete, obscurely to strongly 4–5-sided, rarely biconvex and obcompressed, usually striate, walls carbonized. Pappus persistent, of oblong to obovate, erose scales with or without prominent midribs, midribs usually protruding as an awn or bristle, sometimes absent or of multiple bristles.

The tribe contains 20 genera and approximately 83 species found mostly in the south-western USA to central Mexico, with a few species in temperate and Andean South America. The monotypic genus *Apostates* is endemic to Rapa Island, French Polynesia whereas *Hypericophyllum* is found in tropical Africa.

Tribe Bahieae was named by Baldwin (Baldwin et al. 2002) to accommodate most genera of classical Helenieae having a pappus of scales with thickened midribs and striate cypselae, and revealed in molecular studies as a distinctive lineage of the Heliantheae alliance. Molecular studies of Asteraceae (Panero and Funk 2002) show that Bahieae are a derived lineage sister to Chaenactideae, and collectively sister to Tageteae and Neurolaeneae. The tribe is characterized by its pappus morphology, epaleate receptacles, a tendency to have large glandular trichomes on the anther appendages and corollas, and cuneate or obpyramidal, striate cypselae. Only *Loxothysanus* and *Hymenoppapus* lack striate cypselae, and these occupy a basal position in the tribe, along with the genera *Thymopsis*, *Chamaechaenactis* and *Bartlettia* (Baldwin et al. 2002). These five genera are sister to three clades informally recognized by Baldwin et al. (2002) as the Bahia, Peucephyllum and Chaetymenia clades. The circumscription of Bahieae recognized in this treatment follows mostly results from molecular studies (Baldwin et al. 2002). The genera *Apostates* and *Welwitschiella* were the only genera of the classical Helenieae allied to Bahieae not sampled by Baldwin (Baldwin et al. 2002), and therefore we lack molecular information as to their relationships. *Apostates* shares most of the characteristics of Bahieae, and it is accepted here as a member of the tribe following Karis (1998). *Welwitschiella* differs from most members of Bahieae by having obovate cypselae with a pappus of scales fused at the base, the cypsela walls are apparently not carbonized, the cypselae lack striations, the main 4 ribs of the cypsela are strongly thickened and well developed even in immature cypselae, the endothecium is composed of uniformly thickened cells, the involucre is composed of 4–5 se-

ries of lanceolate phyllaries which are somewhat indurate at base with herbaceous apices, the disc florets appear to be functionally staminate, and the peripheral florets are zygomorphic. The geographical distribution and morphology of *Welwitschiella* provide support for its placement in Athroismeae.

Key to the Genera

1. Capitula discoid or disciform 2
– Capitula radiate 17
2. Style bases papillose; style arms with prominent appendages as long as or longer than stigmatic surfaces; endothecium with radial thickenings **1233. *Chamaechaenactis***
– Style bases smooth, without papillae or trichomes; style arms without appendages, if appendiculate, then appendages much shorter than length of stigmatic surface; endothecium with polar thickenings 3
3. Corollas tetramerous or tetramerous and pentamerous in the same capitulum 4
– Corollas pentamerous 6
4. Pappus of a few scales fused at base and forming a cup; capitula disciform **1246. *Thymopsis***
– Pappus of approximately 8–10 free scales; capitula discoid 5
5. Leaves ovate, entire; anthers dark brown to black **1236. *Holoschkuhria***
– Leaves filiform or linear, 1–3-pinnate; anthers hyaline to yellow **1245. *Schkuhria***
6. Leaves opposite 7
– Leaves alternate below inflorescence branches, opposite only on basal nodes 10
7. Leaves distinctly petiolate; capitula in corymbiform cymes 8
– Leaves sessile to shortly petiolate, capitula solitary or in open paniculiform cymes 9
8. Leaves ovate to trilobed, triplinerved, densely glandular, abaxial surfaces densely pubescent, sometimes appearing or drying white; plants from eastern, tropical Mexico **1240. *Loxothysanus***
– Leaves broadly ovate to elliptical, palmately veined, sparsely pubescent, not glandular, concolorous; plants endemic to Rapa Island, French Polynesia **1229. *Apostates***
9. Pappus of obovate scales with a prominent midrib, midrib sometimes protruding beyond scale as a thickened, straight awn, never uncinate; corollas with a very short throat, approximately 1/5 the length of the lobes; corolla tubes thickened and with expanded bases; plants of Mexico and Central America **1234. *Espejoa***
– Pappus of capillary bristles or scales with a prominent midrib extending as a bristle, rarely of bristles alternating with small scales, bristle apices mostly uncinate, corollas with throat as long or longer than lobes; corolla tubes not thickened, nor with expanded bases; plants of tropical Africa **1239. *Hypericophyllum***
10. Anther appendages glabrous 11
– Anther appendages with glandular trichomes on abaxial surfaces 14
11. Style arms acuminate, without appendages; papillae covering abaxial surfaces of style arms and reaching below bifurcation point **1241. *Palafoxia***
– Style arms with strongly acuminate to deltate apices and sometimes with minute to prominent, tapered appendages; papillae on abaxial surfaces of style arms confined mostly to distalmost end 12
12. Corollas of all florets or of only the peripheral florets zygomorphic 13
– Corollas actinomorphic **1245. *Schkuhria***
13. Corollas with two lobes longer than other three **1235. *Florestina***
– Corollas with one or all lobes of unequal length, sometimes with one sinus much longer (more deeply cut) than others **1237. *Hymenothrix***
14. Shrubs **1242. *Peucephyllum***
– Annual or perennial herbs 15
15. Corollas with strongly recurved lobes **1237. *Hymenopappus***
– Corollas without strongly recurved lobes 16
16. Plants with most leaves confined to the base and scapose inflorescences; pappus of multiple bristles; leaves ovate, entire **1244. *Psathyrotopsis***
– Plants with leaves evenly spaced along stems, inflorescences not scapose; pappus of approximately 8–10 obovate to fusiform scales, leaves filiform or dissected **1245. *Schkuhria***
17. Ray and disc corollas deep pink or purple **1241. *Palafoxia***
– Ray corollas white, yellow or yellow-orange, if pink, then disc corollas not pink 18
18. Anther appendages without glandular trichomes on abaxial surfaces 19
– Anther appendages with glandular trichomes on abaxial surfaces 25
19. Ray corollas white **1227. *Achyropappus***
– Ray corollas yellow 20
20. Leaves opposite, sessile **1232. *Chaetymenia***
– Leaves alternate, sometimes confined to base and inflorescences subscapose 21
21. Cypselae obcompressed, biconvex **1231. *Bartlettia***
– Cypselae obpyramidal to subterete, 4–5-sided 22
22. Leaves entire, narrowly elliptic to ovate or suborbicular **1243. *Platyschkuhria***
– Leaves filiform or linear, 1–4-pinnate 23
23. Capitula in congested, corymbiform cymes; pappus of multiple capillary bristles **1237. *Hymenothrix***
– Capitula solitary or in open paniculiform cymes; pappus of obovate or fusiform scales sometimes with midrib extending as a bristle 24
24. Capitula with more than 5 ray florets **1228. *Amauriopsis***
– Capitula with 1–3, rarely 5 ray florets **1245. *Schkuhria***
25. Lobes of disc corollas strongly recurved **1237. *Hymenopappus***
– Lobes of ray corollas spreading or straight, not strongly recurved 26
26. Capitula with more than 5 ray florets **1230. *Bahia***
– Capitula with 1–3, rarely 5 ray florets **1245. *Schkuhria***

Genera of Bahieae

1227. *Achyropappus* Kunth

Achyropappus Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp., folio ed. 4: 202 (1818).

Annual herbs. Leaves opposite, blades deltate to ovate in outline, once or twice pinnate, segments linear. Capitula in terminal, open paniculiform cymes, radiate. Involucres hemispheric, phyllaries in 1–2 series, subequal. Receptacles convex. Ray florets pistillate, corollas white. Disc florets bisexual, corollas yellow, throats abruptly narrowed into tube; anther appendages cochleate, without glandular trichomes; style arms acute to deltate with a minute aristate appendage, stigmatic surfaces narrow. Cypselae obpyramidal, 3–5-sided, black, moderately sericeous, ray cypselae triquetrous. Pappus of approximately 8 erose scales, acute or bilobed without thickened midribs. $x = 10$. Two species, Mexico.

1228. *Amauriopsis* Rydb.

Amauriopsis Rydb., N. Amer. Fl. 34: 37 (1914).

Annual herbs. Leaves alternate, blades deltate to broadly ovate in outline, 1–4-pinnate, segments filiform to linear. Capitula in terminal, open paniculiform cymes, radiate. Involucres broadly campanulate to hemispheric, phyllaries in 2 series, subequal. Receptacles flat to shallowly convex. Ray florets pistillate, corollas yellow-orange. Disc florets bisexual, rarely functionally pistillate and with staminodes, corollas yellow-orange, sometimes zygomorphic; anther appendages ovate, without glandular trichomes; style arms acute to deltate, with narrow stigmatic surfaces. Cypselae obpyramidal, obscurely angled, sparsely to moderately pubescent. Pappus of approximately 8–15 erose scales, midrib rarely protruding beyond scale, sometimes absent. $x = 12, 18$. Five species, south-western USA, northern Mexico

1229. *Apostates* N.S. Lander

Apostates N.S. Lander, Austral. Syst. Bot. 2: 129 (1989); Karis, Bot. Jahrb. Syst. 120: 131–135 (1998), syst.

Shrubs. Leaves opposite, blades ovate. Capitula in terminal, congested corymbiform cymes, discoid. Involucres campanulate, phyllaries in 2–3 series, subequal. Receptacles flat to shallowly convex. Florets bisexual, corollas white; anther appendages with glandular trichomes; style arms acute to deltate, with narrow stigmatic surfaces. Cypselae narrowly obpyramidal, quadrate, pale brown, sparsely sericeous. Pappus of multiple, erose awns. One species, *A. rapae* (F. Brown) N.S. Lander, Rapa Island, French Polynesia.

1230. *Bahia* Lag. Fig. 89

Bahia Lag., Gen. Sp. Pl.: 30 (1816); Ellison, Rhodora 66: 65–86, 177–215, 281–311 (1964), rev.

Annual, biennial or perennial herbs, sometimes rhizomatous. Leaves opposite, blades linear to ovate, entire to 1–3-pinnate, segments filiform to linear. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2–3 series, subequal, herbaceous. Receptacles flat to convex. Ray florets pistillate, corollas yellow or white. Disc

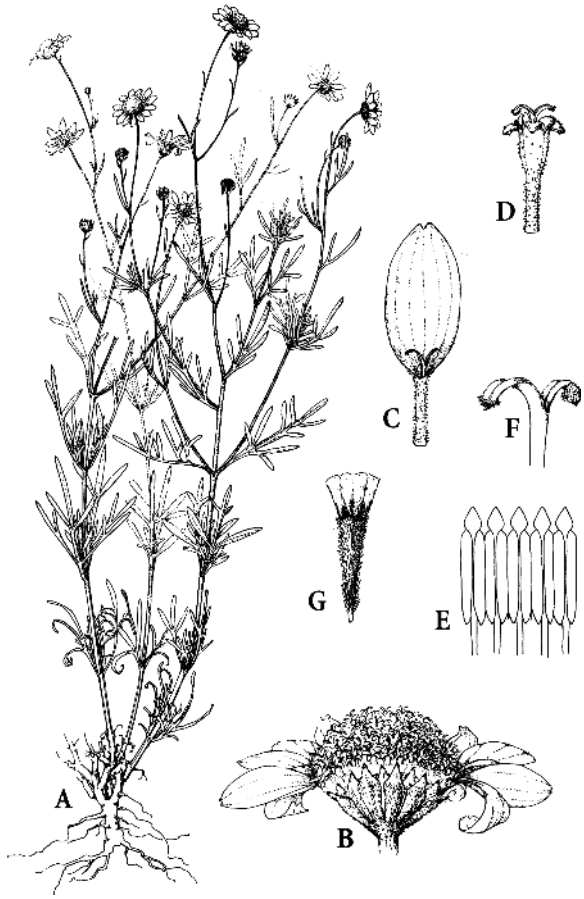

Fig. 89. Compositae-Bahieae. *Bahia absinthifolia*. **A** Habit. **B** Capitulum with rays partly removed. **C** Ray corolla. **D** Disc corolla. **E** Anthers. **F** Style arms. **G** Cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

florets bisexual, corollas yellow; anther appendages glandular; style arms acute to deltate, stigmatic surfaces narrow. Cypselae obpyramidal, 4-sided, black, sparsely to moderately pubescent. Pappus of approximately 6–10 obovate or lanceolate scales with thickened midribs sometimes excurrent as an awn or bristle. $x = 8, 11, 10, 12$. Approximately ten species, western USA, Mexico, Chile.

1231. *Bartlettia* A. Gray

Bartlettia A. Gray, Mem. Amer. Acad. Arts 5: 323 (1855); Powell, Southw. Naturalist 8: 117–120 (1963), rev.; Strother, N. Amer. Fl. ser. II, 10: 146 (1978), rev.

Annuals. Leaves alternate, blades narrowly trullate, deltate or trilobed, subentire to deeply mucronate, serrate. Capitula in terminal, open paniculiform cymes, radiate. Involucres hemispherical, phyllaries in 2 series, subequal. Receptacles flat to shallowly convex. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow; anther appendages ovate, without glandular trichomes; style arms acute to blunt with a tuft of papillae, stigmatic surfaces narrow. Cypselae obcompressed, narrowly biconvex with one weak rib on centre of each tangential face, shiny black, pubescence denser on edges and tangential ribs, moderately sericeous. Pappus of multiple capillary bristles. $x = 11$. One species, *B. scaposa* A. Gray, northern Mexico, south-western USA.

1232. *Chaetymenia* Hook. & Arn.

Chaetymenia Hook. & Arn., Bot. Beechey Voy. 298 (1838).

Perennial herbs or small, multi-stemmed shrubs of riparious areas. Leaves opposite, linear to narrowly lanceolate, semisucculent. Capitula terminal, solitary or in open paniculiform simple cymes, radiate, on long, distally fistulose peduncles. Involucres turbinate to campanulate, phyllaries gradate. Receptacles convex. Ray florets pistillate, corollas bright yellow, drying orange. Disc florets bisexual, corollas yellow; anther appendages without glands; style arms acute to deltate, with broad stigmatic surfaces, touching at the very tip. Cypselae narrowly obpyramidal, 4-angled, strigose, especially on angles. Pappus of multiple, awn-like, subplumose bristles. $x = 9$. One species, *C. pedunculatis* Hook. & Arn., Mexico.

1233. *Chamaechaenactis* Rydb.

Chamaechaenactis Rydb., Bull. Torrey Bot. Club 33: 155 (1906); Preece & Turner, Madroño 12: 99–103 (1953).

Small perennial herbs with a long taproot growing in exposed rocky areas, rosette apices densely lanate. Leaves alternate, on short internodes, forming a rosette, blades broadly ovate to subcordate on long petioles, semisucculent, glaucous. Capitula terminal, solitary, scapose on long, leafless peduncles, discoid. Involucres campanulate, phyllaries in 2 series, subequal. Receptacles flat to convex. Florets bisexual, corollas white, turning brown-mustard with age, sometimes drying purple, with conspicuous glandular trichomes; anther appendages broadly ovate, glandular; style arms with long, thickened appendages, stigmatic surfaces narrow, base of style with numerous trichomes and elongated cells. Cypselae obpyramidal, shallowly quadrate, densely sericeous. Pappus of 7–10, obovate, erose scales with thickened midribs, acute or sometimes bilobed. $x = 16$. One species, *C. scaposa* (Eastw.) Rydb., south-western USA.

1234. *Espejoa* DC.

Espejoa DC., Prodr. 5: 660 (1836).

Annual herbs. Leaves opposite, semisucculent. Capitula terminal, solitary or in open paniculiform cymes, discoid, peduncles shallowly fistulose. Involucres turbinate to campanulate, phyllaries in 3 series. Receptacles flat to convex. Florets bisexual, corolla tubes yellow-green, tube base conspicuously broad and as wide as open throat, throats yellow-purple, edges of lobes thickened; anther appendages narrowly oblong, without glands; style arms short, acute to acuminate, stigmatic surfaces thin, purple. Cypselae narrowly obpyramidal, 4–5-angled, densely sericeous. Pappus of multiple ovate, erose scales sometimes with the thickened midrib extending as an awn. $x = 9$. One species, *E. mexicana* DC., Mexico, Central America.

1235. *Florestina* Cass.

Florestina Cass., Bull. Sci. Soc. Philom. Paris 1817: 11 (1817); Turner, Brittonia 15: 27–46 (1963), rev.

Annual or perennial herbs. Leaves opposite proximally, alternate distally, blades linear to ovate-elliptic, cordiform, entire or crenate. Capitula in terminal, open paniculiform cymes, discoid. Involucres obconic to subhemispherical, phyllaries in 1–2 series, equal to subequal. Receptacles flat to shallowly convex. Florets bisexual, corollas white or purple, asymmetrical with two lobes appearing longer than others due to deeper sinuses; anther appendages ovate, without glan-

dular trichomes; style arms narrowly acuminate, tapered, stigmatic surfaces thin, purple. Cypselae obconic to obpyramidal-quadrate, black, sparsely to moderately pubescent. Pappus of 8 obovate or fusiform, erose scales, sometimes with thickened midribs protruding as a bristle or awn, sometimes with alternating obovate, awn-less scales. $x = 10$, 12. About eight species, southern USA, Mexico, Central America.

1236. *Holoschkuhria* H. Rob.

Holoschkuhria H. Rob., Comp. Newslett. 38: 48–50, f. 1 (2002).

Annual or perennial herbs, weak shrubs. Leaves opposite, blades simple, ovate to elliptic. Capitula in terminal, open paniculiform cymes, sometimes decussate, capitula discoid. Involucres hemispheric, phyllaries in 1–2 series, subequal. Receptacles flat. Florets bisexual, corollas white, tetramerous; anther appendages ovate, with glandular trichomes; style arms acute to deltate, with narrow stigmatic surfaces. Cypselae obpyramidal, 4-sided, black, moderately pubescent. Pappus of approximately 8 erose scales with a weak midrib. One species, *H. tetramera* H. Rob., southern Ecuador, northern Peru.

1237. *Hymenopappus* L'Hér.

Hymenopappus L'Hér., Hymenopappus 1 (1788); Turner, Rhodora 58: 163–186, 208–269, 295–308 (1956), rev.

Annual or perennial herbs, sometimes biennial, rosulate or most leaves basal. Leaves alternate, blades ovate in outline, 2-pinnate, segments filiform to linear. Capitula in terminal, subscapose, open paniculiform cymes, capitula discoid, rarely radiate. Involucres campanulate to hemispheric, phyllaries in 3 series, subequal to slightly gradate. Receptacles convex, rarely paleate. Ray florets pistillate, corollas white, rarely suffused with pink, shallowly trilobed. Disc florets bisexual, corollas white or yellow, abruptly narrowed into tube, glandular, lobes reflexed soon after anthesis, corollas spreading to slightly reflexed well above the involucre; anther appendages with glandular trichomes; style arms acute to acuminate, stigmatic surfaces narrow. Cypselae shallowly obcompressed, obpyramidal, shallowly quadrate, sometimes concave, not striate, glabrous to moderately pubescent, black. Pappus of approximately 8–10 erose, obovate scales with a thickened midrib. $x = 17$. Approximately 14 species, south-western USA, northern Mexico.

1238. *Hymenothrix* A. Gray

Hymenothrix A. Gray, Mem. Amer. Acad. Arts 4: 102 (1849); Turner, Brittonia 14: 101–120 (1962).

Annual or perennial herbs. Leaves alternate, deltate to ovate in outline, 1–4-pinnate, segments filiform to linear. Capitula in terminal, congested corymbiform or open paniculiform cymes, discoid or radiate. Involucres turbinate to broadly campanulate, phyllaries in 2 series, subequal. Receptacles flat. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow, white or lavender, deeply dissected, lobes reflexed, especially the peripheral ones, irregularly lobed; anther appendages without glandular trichomes; style arms acute to deltate with narrow stigmatic surfaces. Cypselae obpyramidal, 4-sided, sparsely to moderately pubescent. Pappus of multiple bristles or narrowly fusiform scales with strong midribs, midribs protruding as awns or bristles. $x = 12$. Four species, south-western USA, Mexico.

1239. *Hypericophyllum* Steetz

Hypericophyllum Steetz in Peters, Naturwissensch. Reise: 498 (1864).

Perennial herbs. Leaves opposite, blades ovate, oblong, trullate or obovate, entire to shallowly serrate. Capitula terminal, solitary or in open paniculiform cymes, discoid. Involucres broadly campanulate, phyllaries in 3–5 series, gradate. Receptacles convex. Florets bisexual, corollas mostly yellow-orange or red, rarely white or greenish white; anther appendages without glands; style arms acute to deltate, with broad stigmatic surfaces. Cypselae narrowly obconic to obovate, obscurely 4–5-sided, black or brown, glabrescent to moderately pubescent. Pappus of multiple aristate scales or bristles, sometimes bristles alternating with narrow scales, awns straight but most commonly uncinate, golden copper in colour. Seven species, tropical Africa.

1240. *Loxothysanus* B.L. Rob.

Loxothysanus B.L. Rob., Proc. Amer. Acad. Arts 4: 43 (1907); Turner, Wrightia 5: 45–50 (1974), rev.

Shrubs. Leaves opposite. Capitula in terminal, small corymbiform cymes, discoid. Involucres campanulate to hemispheric, phyllaries in 2 series, subequal. Receptacles convex. Florets bisexual, corollas abruptly narrowed into tube, white, glandular, especially those of peripheral florets

zygomorphic; anther appendages with a few glandular trichomes; style arms acute to deltate, with broad stigmatic surfaces. Cypselae narrowly obconic to shallowly quadrate, especially with age, shallowly striate, black, sparsely pubescent. Pappus of multiple, erose scales, asymmetrical, scales awn-like and longer on adaxial side of cypsela. $x = 15$. Two species, Mexico.

1241. *Palafoxia* Lag.

Palafoxia Lag., Gen. Sp. Pl.: 26 (1816); Shinners, Field Lab. 20: 92–102 (1952); Turner & Morris, Rhodora 78: 567–628 (1976), rev.

Annual or perennial herbs, rarely shrubs. Leaves opposite proximally, alternate distally, blades linear to ovate. Capitula in terminal, open paniculiform cymes, discoid or radiate. Involucres turbinate or campanulate, phyllaries in 2 series, subequal, herbaceous, linear. Receptacles flat. Ray florets pistillate, corollas pink or pink-purple, deeply trilobed. Disc florets bisexual, corollas white, pink, magenta, actinomorphic to slightly zygomorphic; anther appendages without glands; style arms acuminate, without appendages, papillae covering entire length of abaxial surface of style branches and extending slightly below point of bifurcation. Cypselae narrowly obpyramidal, 4-sided, black or brown, glabrous to moderately pubescent. Pappus of 4–10 obovate or more commonly fusiform or linear scales with prominent midribs, midribs sometimes protruding as awns, ray cypselae sometimes with very reduced scales. $x = 10, 11, 12$. Twelve species, south-western USA, northern Mexico.

1242. *Peucephyllum* A. Gray

Peucephyllum A. Gray, Rep. U.S. Mex. Bound., Bot. 74 (1859); Strother, N. Amer. Fl. ser. II, 10: 170–171 (1978), rev.

Shrubs. Leaves alternate, filiform to linear. Capitula terminal, solitary or in simple corymbiform cymes, discoid. Involucres campanulate, phyllaries in 1 series. Receptacles flat. Florets bisexual, corollas yellow-green, lobes purplish; anther appendages ovate with a few glandular trichomes; style arms acute to deltate, with broad stigmatic surfaces, papillae on abaxial surface reaching style bifurcation. Cypselae narrowly obconic, black, moderately pubescent. Pappus of multiple, narrowly linear scales with prominent midribs protruding as bristles, or of capillary bristles, hyaline to stramineous. $x = 10$. One species, *P. schottii* A. Gray, western USA, Mexico.

1243. *Platyschkuhria* Rydb.

Platyschkuhria Rydb., Bull. Torrey Bot. Club 33: 154 (1906); Ellison, Brittonia 23: 269–279 (1971), rev.

Perennial herbs with a woody caudex. Leaves alternate, blades narrowly ovate, succulent. Capitula few, subscapose, in terminal, open, corymbiform cymes, radiate. Involucres hemispheric, phyllaries in 2 series, subequal. Receptacles convex. Ray florets pistillate, sometimes with staminodes or additional lobes, corollas golden yellow. Disc florets bisexual, corollas yellow; anther appendages glabrous; style arms acute to deltate, with broad stigmatic surfaces. Cypselae obpyramidal, shallowly quadrate, with multiple striations, black, sparsely pubescent. Pappus of multiple obovate scales with prominent midribs, midribs sometimes protruding as awns, hyaline to slightly purplish. $x = 12$. One polymorphic species, *P. integrifolia* Rydb., south-western USA.

1244. *Psathyrotopsis* Rydb.

Psathyrotopsis Rydb., N. Amer. Fl. 34: 360 (1927); Strother & Pilz, Madroño 23: 24–40 (1975), rev.
Pseudobartlettia Rydb. (1927).

Annual or perennial herbs. Leaves tightly clustered at base of plant, opposite at first nodes, alternate above, blades ovate to trullate, sometimes broadly ovate to suborbicular, entire to serrate-crenulate. Capitula terminal, scapose, solitary or in open paniculiform cymes, discoid. Involucres campanulate to subhemispheric, phyllaries in 2 series, subequal. Receptacles convex. Florets bisexual, corollas yellow or white, sometimes tinged with pink; anther appendages glandular on abaxial surface; style arms long, acuminate, sometimes coiled, with broad stigmatic surfaces. Cypselae narrowly obconic, with multiple striations or shallow ribs, black or sometimes golden copper in colour because of dense pubescence. Pappus of multiple, unequal bristles, golden stramineous. $x = 19$. Three species, south-western USA, northern Mexico.

1245. *Schkuhria* Roth Fig. 90

Schkuhria Roth, Catal. Bot. 1: 116 (1797), nom. cons.; Heiser, Ann. Missouri Bot. Gard. 32: 265–278 (1945), rev.; Turner, Phytologia 79: 364–368 (1996), part. rev.
Cephalobembix Rydb. (1914).

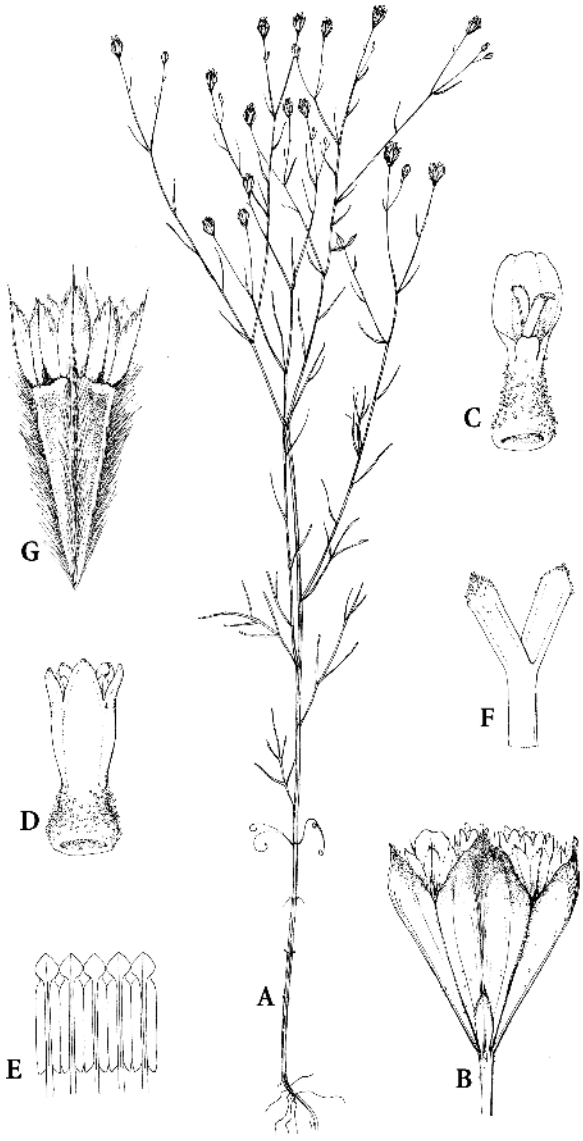

Fig. 90. Compositae-Bahieae. *Schkuhria pinnata*. **A** Habit. **B** Flowering capitulum. **C** Ray corolla. **D** Disc corolla. **E** Anthers. **F** Style arms. **G** Cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

Annual herbs. Leaves alternate, filiform or linear, ovate to trullate in outline, 1–3-pinnate, segments linear. Capitula terminal, solitary or in open paniculiform cymes, discoid or radiate. Involucres obovate to obtrullate in outline, phyllaries in 1–3 series, gradate or subequal. Receptacles flat. Ray florets 1–3, rarely 5, pistillate, corollas sometimes irregular with an additional, small limb opposite the main limb, apices trilobed or acute. Disc florets bisexual, corollas yellow, pentamerous, sometimes tetramerous and pentamerous in the same capitulum; anther appendages with or without glandular trichomes; style arms acute, with narrow stigmatic surfaces and a minute aristate appendage. Cypselae obpyramidal and strongly quadrate, sparsely pubescent sometimes only on angles. Pappus of 8–10 obovate or fusiform, sometimes aristate scales, stramineous, sometimes flecked with purple. $x = 8$, 10, 11. Six species, North and South America, introduced elsewhere.

1246. *Thymopsis* Benth.

Thymopsis Benth. in Benth. & Hook. f., Gen. Pl. 2: 201, 407 (1873).
Neothymopsis Britt. & Millsp. (1920).

Annual or perennial herbs. Leaves opposite, blades trullate or ovate. Capitula terminal or axillary, solitary or in simple cymes, sessile, disciform. Involucres narrowly campanulate, phyllaries in 1–2 series, subequal. Receptacles flat. Florets dimorphic; peripheral florets pistillate, lacking stamens, corollas cylindric, with 4 minute lobes, innermost florets bisexual with white, tetramerous corollas with prominent glandular trichomes; anther appendages without glands; style arms deltate, narrow stigmatic surfaces with a short, aristate appendage. Cypselae obcompressed to subterete, essentially glabrous to sparsely pubescent, black. Pappus of a few erose scales forming a cup, the scales fused at base and without a thickened midrib. Two species, West Indies.

XXV. Tribe Polymnieae (H. Rob.) Panero (2002).

Subtribe Polymniinae H. Rob. (1978).

J.L. Panero

Perennial herbs. Leaves opposite, petiolate, blades cordate to deltate in outline, entire or deeply pinnatifid. Capitula in terminal, paniculiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries in 2–3 series, subequal, herbaceous, densely glandular abaxially. Receptacles convex to shallowly conical, paleate. Ray florets pistillate, corollas white to creamy-white, limbs trilobed with central lobe longer and wider than flanking lobes, abaxially pubescent. Disc florets functionally staminate, corollas 5-lobed, yellow to white-yellow, with multicellular trichomes, without glandular

trichomes, throats broadly campanulate; ovaries very reduced; anthers yellow to brown, ecalcarate, ecaudate, appendages deltate, glandular on abaxial surface, endothecium of fusiform cells with 1–3 polar bridges; disc floret style arms fused except for deltate apices, style arms of ray florets tapered, without abaxial papillae, stigmatic surface a continuous line at edges of style arms. Cypselae obcompressed, without striations, walls carbonized, broadly obovate, biconvex, with 3(–5) sutures or ribs, sutures on angles and median adaxial surface of cypsela, rarely with two additional sutures on abaxial, stipitate, dark brown to greenish brown, glabrous or sometimes with a few twin trichomes on apices. Pappus a shallow crown or absent.

Polymnia was circumscribed by Robinson (1978a) to include only two (now three, Pittman and Bates 1989) closely related species endemic to temperate forests of the eastern USA. The other species of *Polymnia*, mostly large shrubs or small trees of tropical America, were placed by him (Robinson 1978b) in the genus *Smallanthus*. He considered *Polymnia* to be a distinctive taxon not closely related to members of Melampodiinae and, therefore, placed the genus in subtribe Polymniinae (Robinson 1978a). He considered Polymniinae to be closely related to subtribes Melampodiinae and Milleriinae in his circumscription (Robinson 1981). Molecular studies of the family using chloroplast DNA (Panero et al. 2001c; Panero and Funk 2002), and of members of subtribe Espeletiinae and related members using nrDNA (Rauscher 2002) confirm that Polymniinae are not related to Espeletiinae, Melampodiinae or Milleriinae sensu Robinson (1981). Polymniinae represent a distinctive helianthoid lineage splitting off just above Helenieae and Coreopsideae (Panero and Funk 2002). Molecular results support the recognition of Polymniinae as tribe Polymnieae.

Only one genus:

1247. *Polymnia* L.

Polymnia L., Sp. Pl. 2: 926 (1753); Wells, Brittonia 17: 144–159 (1965), reg. rev.
Polymniastrum Lam. (1798).

Characters of the tribe. $x = 15$. Three species, eastern USA.

XXVI. Tribe Heliantheae Cass. (1819).

J.L. Panero

Annual or perennial herbs, shrubs, scandent shrubs, lianas or trees. Leaves alternate or opposite, blades generally simple, rarely divided, mostly ovate, triplinerved, adaxial surfaces usually scabrous, abaxial surfaces not as scabrous. Capitula in terminal, rarely axillary, open paniculiform cymes, sometimes congested, or corymbiform cymes, sometimes solitary on long peduncles, rarely sessile, sometimes arranged in second-order capitula. Involucres cylindric to hemispheric, sometimes reflexed or patent. Phyllaries subequal to gradate, in 1–7 series, normally innermost smaller than outermost and resembling paleae. Receptacles flat to convex, conic or sometimes columnar, paleate (epaleate in *Tetranthus*, *Trichocoryne*, *Riencourtia*, and some functionally staminate capitula in Ambrosiinae), paleae conduplicate, rarely wrapping around and shed as a unit with cypselae (perigynia), usually persistent. Capitula radiate, discoid, rarely disciform. Ray florets 5–13(–21+), rarely 1 or 2, sometimes none, pistillate and fertile, styliferous and sterile or neuter, corollas sometimes without a tube, apices trilobed, sometimes bilobed. Disc florets bisexual or functionally staminate, rarely functionally pistillate, corollas actinomorphic, rarely zygomorphic, throats urceolate or campanulate, sometimes tubular, throats gradually or abruptly expanding above tube, lobes 5, rarely 3 or 4, erect or spreading, rarely coiled. Stamens 5, rarely 4 or 3, filaments glabrous, rarely papillose, anthers connate or free, rarely shallowly tailed, mostly sagittate or with acute to acuminate lobes, ecalcarate, rarely shallowly calcarate, appendages mostly ovate, endothecial cells fusiform or isodiametric, rarely quadrate to round, with 1–5 polar thickenings, sometimes with radial thickenings or encircled by uniform thickenings, filaments glabrous or rarely with papillae. Pollen echinate, caveate, exines with internal foramina ('Helianthoid' pattern). Styles with 2, rarely one, vascular strand, papillae increasing in density on median to distal portions of abaxial surface of style arms, stigmatic surfaces divided or fused, style arms normally with a tuft of papillae on distal ends or with non-vascularized, cylindric appendages. Cypselae normally compressed, rarely obcompressed, biconvex, rarely shallowly quadrate, narrowly to broadly obovate to suborbicular in

outline, rarely terete, walls carbonized, prismatic or ribbed, those of the ray triquetrous and obcompressed, walls smooth or striate, with uniseriate or biseriate trichomes, sometimes with juicy exocarp and resembling a drupe, winged or wingless; pappus of persistent awns and squamellae, disposed in a narrowly oval to linear pattern on cypsela neck, rarely in a radial pattern, pappus elements sometimes reduced to an erose crown, rarely caducous, or lacking. $x = 19$ (7–18, dysploid).

The tribe contains 113 genera and approximately 1,500 species. Its distribution is pantropical, with most species in Mexico and seasonally dry regions of tropical and temperate South America. The tribe contains an important proportion of the shrubs and trees of the family, most of these found in the open pine-oak forests of western and southern Mexico. The tribe is important economically, with *Helianthus annuus*, the commercial sunflower, being cultivated worldwide for oil production and cut flowers. Several species of *Echinacea*, *Rudbeckia* and *Zinnia* are important components of summer gardens across the world.

Tribe Heliantheae was named by Cassini (1819) to include sunflowers with mostly radiate capitula, paleaceous receptacles, opposite leaves and yellow corollas. In 1829, Cassini presented his final classification for Heliantheae which contained five major divisions and excluded Ambrosiinae and Tageteae. Bentham (1873b) adopted many of the findings and taxonomic conclusions of Cassini. He included in Helenieae most Heliantheae having epaleate receptacles. He believed Helenieae to be closely related to Heliantheae but probably not natural. This decision was to dominate the debate as to the phylogenetic relationships and limits of Heliantheae for decades to come. With minor revisions, Hoffmann (1894) adopted Bentham's concept for *Die natürlichen Pflanzenfamilien*. Stuessy (1977) outlined the characteristics of Heliantheae and provided a careful revision of the historic decisions leading to the circumscription of the Heliantheae-Helenieae alliance. His taxonomic decisions were based on morphological features but influenced greatly by chromosome number information. His tribe Heliantheae contained 15 subtribes and, like Cronquist (1955) but with some reservations, he believed Heliantheae to be the basalmost lineage of the family. Robinson (1981) dismissed this idea and instead placed Heliantheae at the base of Asteroideae as the next lineage to split from its ancestral stock, Eupatorieae. He believed Helenieae to be a derived group within the alliance, with subtribe Madiinae bridging the morphological gap between the two tribes. His treatment includes 35 subtribes, and is not a mere merger of traditional tribes Heliantheae and Helenieae and their corresponding subtribes but a meaningful comparison of salient morphological features which he used deftly to accommodate genera in his classification scheme. Karis (1993a) summarized the literature of the Heliantheae-Helenieae alliance, providing interesting and important insight on the phylogenetic relationships and morphology of the group. His studies were later formalized in a new classification for tribe Heliantheae (Karis and Ryding 1994a) and the recognition of a paraphyletic tribe Helenieae (Karis and Ryding 1994b), with Eupatorieae and the *Athroisma* group (Eriksson 1991) basal to a series of sequentially splitting Helenieae lineages ending in a monophyletic Heliantheae. These conclusions were partly supported by the studies of Kim and Jansen (1995) using sequence data of the chloroplast gene *ndh*F. The classification of the Heliantheae-Helenieae alliance was significantly improved recently with the publication by Baldwin et al. (2002) of a nuclear ribosomal ITS phylogeny

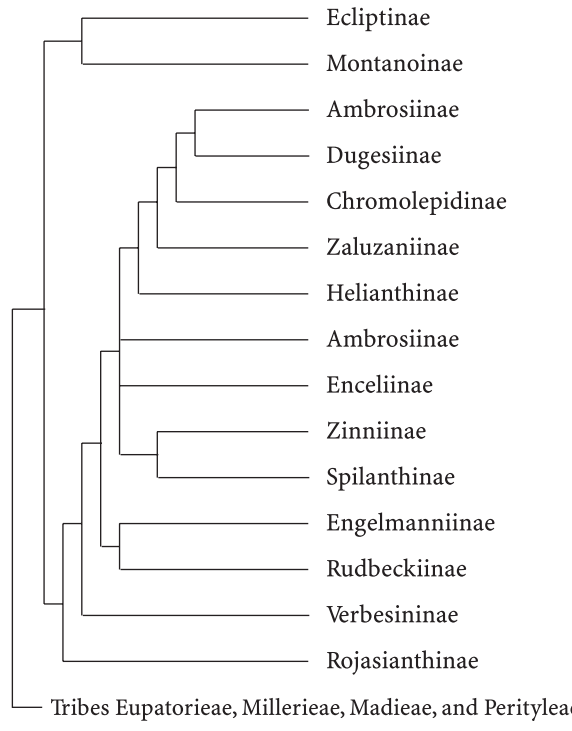

Fig. 91. Phylogenetic relationships of subtribes of Heliantheae based on chloroplast DNA sequences (after Panero et al. 2001c)

which includes representatives of nearly all genera of tribe Helenieae and outgroups. This study supported the basal position of tribe Helenieae in the strict sense (Gaillardiinae and Marshalliinae sensu Robinson 1981) and provided evidence for the recognition of several groups carved out of the classical Helenieae. The impetus to implement this classification was not the evidence about the strength of the support for the groups themselves but rather the finding that Eupatorieae were derived from a helenioid lineage. This finding inevitably leads to the dismemberment of Helenieae. The new classification system outlined by Baldwin (Baldwin et al. 2002) included six tribes carved out from classical Helenieae, namely Bahieae, Chaenactideae, Helenieae, Madieae, Perityleae and Tageteae. The concept of tribe Heliantheae adopted here is based primarily on results from comparative studies of chloroplast DNA data (Panero et al. 2001c, and unpubl. data). These studies support the conclusions of Baldwin et al. (2002), and a more exclusive concept of tribe Heliantheae. Taxa with mostly glandular herbage, functionally staminate disc florets, cypselae somewhat terete with radial pappi of bristles and formerly included in subtribes Galinsoginae, Melampodiinae and Milleriinae sensu Robinson (1981) are treated under tribe Millerieae and excluded from Heliantheae. As presently circumscribed, Heliantheae include 14 subtribes, namely Ambrosiinae, Chromolepidinae, Dugesiinae, Ecliptinae, Enceliinae, Engelmanniinae, Montanoinae, Helianthinae, Rojasianthinae, Rudbeckiinae, Spilanthinae, Verbesininae, Zaluzaniinae and Zinniinae (Fig. 91). Members of these subtribes for the most part share paleate receptacles, triplinerved blades, yellow corollas, radiate capitula, moderately to strongly conduplicate paleae, herbaceous, sometimes foliaceous phyllaries, strongly flattened cypselae and, therefore, pappi arranged in a narrowly oval to linear disposition on the neck of the cypselae, and scabrous herbage. Our understanding of the phylogenetic relationships of members of Heliantheae has improved considerably since the last treatment of the tribe by Karis and Ryding (1994a). This has allowed me to redefine the concept of certain subtribes and to propose the recognition of new ones which are for the first time used here. It can be argued that the taxonomy of the tribe has benefited enormously from the use of floral microcharacters, the main force behind the overhauling of the classification of the tribe by Robinson (1981). Most of the characters used by him to circumscribe the major subtribes of Heliantheae have apparently evolved several times when compared with phylogenies produced by DNA studies. For example, the fibres flanking or embedding the vascular strands of the throats of the disc corollas are present in several groups of Ecliptinae and all members of Engelmanniinae. These groups are not closely related to each other, nor do they grow under similar environmental conditions. The adaptive significance of this and other characters exhibited by the floral parts of the members of Heliantheae remains unclear. Therefore, I stress results based on comparative studies of DNA as the major component in the circumscription of the main lineages of the tribe. The subtribes and their associated genera are organized alphabetically. The circumscription of certain taxa continues to be problematic and no doubt will change as more data become available. This is the case for the limits and phylogenetic relationships within *Melanthera*, *Viguiera*, and *Wedelia* and relatives.

Key to the Subtribes

1. Paleae accrescent after anthesis 2
– Paleae never accrescent after anthesis 3
2. Stamen filaments papillose **9. *Rojasinthinae*** (p. 470)
– Stamen filaments without papillae **8. *Montanoinae*** (p. 469)
3. Phyllaries with black markings; ray corollas white with black veins on abaxial surfaces; plants aquatic, forming loose rosettes **2. *Chromolepidinae*** (p. 446)
– Phyllaries without black markings; ray corollas otherwise; plants terrestrial, if aquatic, then not forming rosettes 4
4. Disc florets bisexual, fertile; style arms of disc florets with continuous stigmatic surfaces 5
– Disc florets bisexual, fertile or functionally staminate; style arms of fertile disc florets with parallel stigmatic surfaces, sometimes these meeting at the apices 10
5. Disc corollas with prominent fibres embedding vascular strands **6. *Engelmanniinae*** (p. 461)
– Disc corollas without prominent fibres embedding vascular strands 6
6. Ray corollas fused to cypselae, if ray florets sterile, then disc floret corollas deeply lobed and lobes densely papillose on adaxial surface or ray ovary with 3 minute projections and receptacles columnar **14. *Zinniinae*** (p. 475)
– Ray corollas not fused to cypselae 7
7. Receptacles conspicuously conic or columnar; paleae with decurrent bases; rarely capitulum with 4 florets with phyllaries enclosing the cypselae (*Tetranthus*) **11. *Spilanthinae*** (p. 471)
– Receptacles flat to convex, rarely conic; paleae without decurrent bases; capitula otherwise 8
8. Ray florets fertile **13. *Zaluzaniinae*** (p. 474)
– Ray florets sterile 9

9. Paleae deciduous after anthesis; cypselae with long sericeous trichomes **5. *Enceliinae*** (p. 460)
– Paleae persistent, rarely deciduous, if deciduous, then tightly enclosing cypselae (perigynia) **7. *Helianthinae*** (p. 464)
10. Receptacles epaleate; disc florets fertile **14. *Zinniinae*** (*Trichocoryne*)
– Receptacles paleate, if epaleate, then disc florets sterile 11
11. Disc florets functionally staminate and styles with a single vascular strand, if with two vascular strands, then ray cypselae fused to adjacent 2–4 disc florets and their associated paleae or capitula with 2 series of ray florets 12
– Disc florets bisexual, fertile, if functionally staminate, then styles with two vascular strands and ray cypselae not fused to adjacent disc florets and associated paleae nor with capitula with 2 series of ray florets 14
12. Disc corollas with slender to prominent fibres embedding the vascular strands **6. *Engelmanniinae*** (p. 461)
– Disc corollas without fibres embedding the vascular strands 13
13. Ray corollas prominent, yellow with greenish veins on abaxial surfaces **3. *Dugesiinae*** (p. 446)
– Ray corollas absent, if present, then limbs wanting or, if conspicuous, then ray cypselae fused to adjacent 2 disc florets and associated paleae **1. *Ambrosiinae*** (p. 443)
14. Receptacles conic to columnar with age **10. *Rudbeckiinae*** (p. 470)
– Receptacles flat to convex, rarely conic, never columnar with age 15
15. Ray corollas white, disc corollas yellow; cypselae narrowly stipitate **12. *Verbesininae*** (*Podachaenium*)
– Ray corollas mostly yellow or yellow-orange, if white, then disc corollas also white (*Steiractinia*, *Verbesina* or *Wedelia*); cypselae rarely stipitate 16
16. Ray cypselae mostly compressed, rarely obpyramidal, stipitate with a pappus of several squamellae; shrubs or small trees of the highlands of Mexico and Guatemala **12. *Verbesininae*** (*Squamopappus*)
– Ray cypselae and corresponding pappus otherwise; annual or perennial herbs, shrubs or trees of America 17
17. Resin in the ducts of disc corollas red; cypselae obpyramidal, quadrate; pappus of 4 scales or sometimes of 4 awns at angles of cypselae alternating with 4 squamellae; plants of Mexico and Mesoamerica **12. *Verbesininae*** (*Tetrachyron*)
– Resin in the ducts of disc corollas yellow or orange, never red; cypselae and pappus otherwise; plants of America 18
18. Disc cypselae strongly compressed, obovate in outline with two, stramineous, equivalent (rarely asymmetrical) wings at angles of cypselae, wings fused to pappus; pappus of 2 awns each at angles of cypsela, rarely of 1 awn or missing; stigmatic surfaces of disc floret style arms narrow and not touching each other, florets never functionally staminate; disc corollas without fibres embedding the vascular strands **12. *Verbesininae*** (*Verbesina*)
– Disc cypselae compressed to quadrate in cross-section, pappus various, cypselae of various shapes, winged or wingless, if with two wings at angles of cypselae and a pappus of two awns, then either wings strongly asymmetrical and cypselae narrowly oblanceolate (*Otopappus*) or cypsela oblanceolate with narrow wings and disc corollas with fibres (*Calyptocarpus*, *Lasianthaea*, *Tuxtla*), without fibres (*Oblivia*) or wings forming a cup around neck, surrounding the disc corolla tubes (*Dimerostemma*), or paleae filiform (*Eclipta*) **4. *Ecliptinae*** (p. 446)

XXVI.1. Subtribe Ambrosiinae Less. (1830); Bolick, Adv. Clad. 2: 125–141 (1983); Karis, Syst. Bot. 20: 40–54 (1995); Miao et al., Amer. J. Bot. 82: 924–932 (1995).

Tribe Ambrosieae Cass. (1819).
Family Ambrosiaceae Link (1829).

Annual or perennial herbs, shrubs, rarely small trees. Leaves alternate or opposite, blades simple, unlobed to deeply dissected, venation mostly triplinerved. Capitula in terminal, paniculiform or spiciform cymes, sometimes unisexual with female capitula at base of spicate male inflorescence, discoid, disciform or radiate, mostly wind-pollinated, capitula mostly nodding. Involucres campanulate to hemispheric, phyllaries in 1–3 series, subequal or gradate, free or fused. Receptacles flat, convex to minutely conical, usually paleate. Ray florets absent or in bisexual capitula peripheral florets female, corollas tubular or sometimes reduced to a shallow ring, sometimes minutely radiate with bilobed limbs, yellow or white. Disc florets functionally staminate, mostly pentamerous, rarely tetramerous, corollas hyaline or light yellow, without fibres embedding vascular strands, sometimes ovaries absent; stamens 5, anthers yellow to hyaline rarely with dark connectives or light brown, filaments free or fused, anthers free or partially connate, endothecium cells quadrate with multiple polar and radial thickenings, styles with one or two vascular strands, style arms of fertile florets with divided stigmatic surfaces, style arms of sterile florets fused, terete with only one, rarely two, vascular strands. Cypselae of unisexual heads enclosed in a conceptacle in which phyllaries are fused to the fruits, cypselae of bisexual corollas obcompressed, sometimes winged or forming a unit associated with the subtending phyllary and the adjacent disc florets/paleae. Pappus absent, a minute crown of squamellae or trichomes, or 2–3 awns or scales. Eight genera, 70 species, America, introduced elsewhere.

Preliminary chloroplast DNA studies show that Ambrosiinae may be a paraphyletic assemblage (see Fig. 91).

Key to the Genera

1. Ray cypselae obcompressed and associated with 2 functionally staminate disc florets and their corresponding paleae 2
– Ray cypselae compressed or obcompressed or enclosed in a conceptacle but never associated with adjacent 2 disc florets and their corresponding paleae 3
2. Ray florets always 5; ray corollas with a small limb **1254. *Parthenium***
– Ray florets 6–8; ray corollas without a limb **1253. *Parthenice***
3. Capitula unisexual; plants monoecious 4
– Capitula bisexual; if unisexual, plants dioecious or population gynodioecious 5
4. Phyllaries of male capitula connate **1248. *Ambrosia***
– Phyllaries of male capitula free **1255. *Xanthium***
5. Staminal filaments connate up to anther collars; inner phyllaries accrescent after anthesis **1249. *Dicoria***
– Staminal filaments free; inner phyllaries not accrescent 6
6. Capitula or pair of capitula subtended by bracts as long as or longer than capitulum **1252. *Iva***
– Capitula not subtended by bracts or, if bracts present, then these minute and subtending inflorescence branch of 5 or more capitula 7
7. Corollas of peripheral florets tubular, sometimes reduced to a minute ring around style **1250. *Euphrosyne***
– Corollas absent and replaced by a few glandular or moniliform trichomes around style **1251. *Hedosyne***

Genera of Ambrosiinae

1248. *Ambrosia* L. Fig. 92

Ambrosia L., Sp. Pl. 2: 987 (1753); Payne, J. Arnold Arb. 45: 401–430 (1964), rev.; Strother & Baldwin, Madroño 49: 143–144 (2002), incl. *Hymenoclea*.
Franseria Cav. (1793) [1793–1794], nom. cons.
Hymenoclea Torr. & A. Gray (1848).

Annual or perennial herbs, shrubs. Leaves opposite or upper alternate, blades lobed or dissected, deltate, ovate to subrotundiform in outline, triplinerved. Capitula discoid, unisexual, sessile, pistillate capitula solitary or in clusters at base of spiciform cymose inflorescences of functionally staminate capitula; phyllaries of functionally staminate capitula connate. Involucres campanulate to hemispheric. Receptacles in staminate capitula paleate. Pistillate florets without corollas and stamens, commonly more than 1 floret aggregated into a conceptacle, staminate corollas 4- or 5-lobed, light yellow or hyaline; filaments free, rarely connate, anthers free; style arms of staminate florets fused, terete, with only one, rarely two, vascular strands. Disseminule a conceptacle in which phyllaries are fused to the fruits, smooth or variously with transverse scarious bracts in one plane or spirally arranged or more commonly with hooked or spine projections. Pappus absent. $x = 12, 17, 18$. Thirty species, America, introduced elsewhere.

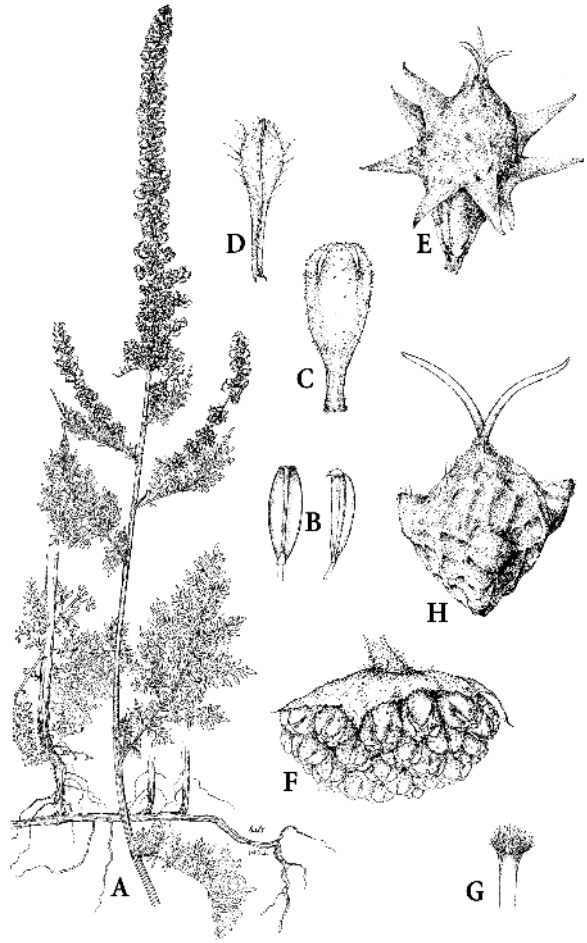

Fig. 92. Compositae-Heliantheae. *Ambrosia canescens*. **A** Habit. **B** Anther in abaxial and lateral views. **C** Staminate corolla. **D** Palea. **E** Involucre. **F** Staminate capitulum. **G** Apex of stylar remnant in staminate floret. *Ambrosia polystachya*. **H** Involucre. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

1249. *Dicoria* Torr. & A. Gray

Dicoria Torr. & A. Gray, Rep. U.S. Mex. Bound. 86 (1859).

Annual or perennial herbs, shrubs. Leaves alternate, petiolate, blades simple, narrowly lanceolate to ovate, suborbicular. Capitula in terminal, open, ebracteate paniculiform cymes, disciform, sometimes unisexual. Involucres campanulate, phyllaries in 2 series, accrescent. Receptacles convex. Peripheral florets pistillate, corollas a shallow ring or absent, other florets functionally staminate,

5-lobed, corollas yellow; filaments connate up to anther collars; styles with one vascular strand. Cypselae obcompressed, sometimes with prominent pectinate or smooth wings, glabrous. Pappus absent or of a few hyaline trichomes. $x = 18$. Four species, northern Mexico, south-western USA.

1250. *Euphrosyne* DC.

Euphrosyne DC., Prodr. 5: 530 (1836).
Cyclachaena Fres. (1836).
Oxytenia Nutt. (1848).
Chorisiva Rydb. (1922).
Leuciva Rydb. (1922).

Annual or perennial herbs, sometimes semi-aquatic. Leaves alternate or opposite, petiolate, blades oval to ovate in outline, unlobed to lobed or 2–3 times pinnate. Capitula in terminal, ebracteate, paniculiform cymes, disciform. Involucres hemispheric, phyllaries in 1–2 series, subequal, herbaceous. Receptacles usually paleate. Peripheral florets pistillate, corollas tubular or a shallow ring, yellow, other florets functionally staminate, 5-lobed, corollas yellow; filaments free, anthers free; styles with one vascular strand. Cypselae obcompressed, sometimes winged at maturity, glabrous or with glandular or setose trichomes. Pappus a minute crown. $x = 18$. Five species, Mexico, USA.

1251. *Hedosyne* (A. Gray) Strother

Hedosyne (A. Gray) Strother, Madroño 47: 204 (2000).

Annual herbs. Leaves alternate, blades ovate in outline, 1–2 times pinnate, segments lobed. Capitula in terminal, mostly ebracteate, paniculiform cymes, disciform. Involucres hemispheric, phyllaries in 2 series. Receptacles paleate. Peripheral florets fertile, corollas missing, other florets functionally staminate, corollas 5-lobed, yellow; filaments free. Cypselae obcompressed, oblong, black, glabrous. Pappus absent. One species, *H. ambrosiifolia* (A. Gray) Strother, northern Mexico, south-western USA.

1252. *Iva* L.

Iva L., Sp. Pl. 2: 988 (1753); Jackson, Univ. Kansas Sci. Bull. 41: 793–876 (1960), rev.; Bolick, Taxon 34: 81–84 (1985), phylog.

Annual or perennial herbs. Leaves alternate or opposite. Capitula in terminal, bracteate paniculiform cymes or congested spicate cymes, disciform. Involucres campanulate to hemispheric, phyllaries in 1–2 series. Receptacles convex. Peripheral florets pistillate, corollas tubular, yellow, other florets functionally staminate, 5-lobed, corollas yellow; filaments free, anthers free; styles with one vascular strand. Cypselae obcompressed to terete, glabrous to sometimes completely covered with glandular trichomes. Pappus absent. $x = 16, 17$. Ten species, North America, introduced elsewhere.

1253. *Parthenice* A. Gray

Parthenice A. Gray, Smithsonian Contr. Knowl. 5: 85 (1853).

Annual herbs. Leaves alternate, petiolate, blades ovate to deltate or subcordate, triplinerved. Capitula in terminal, paniculiform cymes, disciform. Involucres hemispheric, phyllaries in 2–3 series, dimorphic. Receptacles convex. Peripheral florets pistillate, 6–8, corollas tubular, white or green-white. Disc florets functionally staminate, corollas white or creamy white; filaments and anthers free. Cypselae obcompressed, deeply concave, wings involute, associated with subtending phyllary and adjacent two disc florets and paleae. Pappus absent. $x = 18$. One species, *P. mollis* A. Gray, Mexico, south-western USA.

1254. *Parthenium* L.

Parthenium L., Sp. Pl. 2: 988 (1753); Rollins, Contr. Gray Herb. II, 172: 1–72 (1950), rev.

Annual or perennial herbs, shrubs, rarely small trees. Leaves alternate, petiolate, blades unlobed or lobed sometimes 2 times pinnate, ovate to subsagittate. Capitula in terminal, simple, open or congested paniculiform cymes, radiate. Involucres hemispheric, phyllaries in 2 series, mostly 5 in each series, dimorphic. Receptacles flat to convex. Ray florets pistillate, 5, corollas with small bilobed limbs, white or green-white. Disc florets functionally staminate, 5- or 4-lobed, corollas white or creamy white, styles with one vascular strand; filaments and anthers free. Cypselae obcompressed, shallowly concave or flat, associated with subtending phyllary and paleae and florets of adjacent two disc florets, paleae enclosing the disc florets, forming a corky disseminule. Pappus of 2–3 awns or scales or absent. $x = 9$. Sixteen species, America.

1255. *Xanthium* L.

Xanthium L., Sp. Pl. 2: 987 (1753); Millspaugh & Sherff, Field Mus. Nat. Hist. Publ. Bot. ser. IV, 204: 9–49 (1919), reg. rev.

Annual herbs, sometimes spiny. Leaves alternate, petiolate, blades ovate to deltate, simple or lobed, triplinerved. Capitula discoid, unisexual, sessile, pistillate solitary or in clusters at base of terminal or axillary spiciform cymose inflorescences composed of functionally staminate heads; phyllaries of functionally staminate capitula free. Involucres campanulate to hemispheric. Receptacles in staminate heads paleate. Pistillate florets without corollas and stamens, commonly more than 1 floret aggregated into a conceptacle; staminate corollas light yellow or hyaline; anthers free, filaments connate; styles of staminate florets wanting. Disseminule a conceptacle in which phyllaries are fused to the fruits, with hooked or spine projections. Pappus absent. $x = 18$. Three species of disturbed habitats, warm and temperate regions of the world.

XXVI.2. Subtribe Chromolepidinae Panero (2005).

Rosulate perennial semi-aquatic herbs. Leaves alternate, petiolate, semi-succulent, ovate to narrowly lanceolate, entire or pinnatifid. Capitula axillary, solitary, long-pedunculate, radiate. Involucres campanulate, phyllaries dimorphic in 2–3 series, subequal, membranaceous with black markings. Receptacles convex, paleate. Ray florets pistillate, fertile, corollas white. Disc florets bisexual, fertile, corollas pentamerous, yellow, without fibres embedding vascular strands; stamens 5, anthers black, appendages ovate to deltate, without glandular trichomes; styles with two vascular strands, style arms with divided stigmatic surfaces, apices broadly acute to shallowly deltate. Ray cypselae obcompressed, triquetrous to weakly quadrate, glabrous. Disc cypselae obpyramidal, quadrate, sparsely pubescent, conspicuously smaller than ray cypselae. Pappus a crown of minute awns and squamellae, absent in ray cypselae.

Only one genus:

1256. *Chromolepis* Benth.

Chromolepis Benth., Pl. Hartw. 40 (1840).

Characters of the subtribe. One species, *C. heterophylla* Benth., Mexico.

XXVI.3. Subtribe Dugesiinae Panero (2005).

Prostrate, rhizomatous, stoloniferous perennial herbs. Leaves alternate, petiolate, blades obovate to oval in outline, runcinate to pinnatifid. Capitula axillary, solitary or in small paniculiform cymes, radiate. Involucres hemispheric, phyllaries in 2–3 series, subequal, outermost foliaceous. Receptacles flat to slightly convex. Ray florets pistillate, in two series, corollas lemon to golden yellow with greenish to black veins on abaxial sides, rays deeply 2- rarely 3-lobed. Disc florets functionally staminate, corollas pentamerous, yellow, without fibres embedding vascular strands; stamens 5, anthers black, endothecium of fusiform cells with 1–2 polar bridges or evenly thickened; styles with two vascular strands, style arms of disc florets narrowly tapered and papillose, style arms of ray florets spreading with broad, divided stigmatic surfaces. Ray cypselae obcompressed, biconvex, glabrous with a few trichomes on the neck, margins with shallowly lacerate wings. Pappus absent or a minute crown.

Only one genus:

1257. *Dugesia* A. Gray.

Dugesia A. Gray, Proc. Amer. Acad. Arts 17: 215 (1882).

Characters of the subtribe. $x = 18$. One species, *D. mexicana* A. Gray, central Mexico.

XXVI.4. Subtribe Ecliptinae Less. (1831); Villaseñor & Strother, Syst. Bot. 14: 529–540 (1989); Strother, Syst. Bot. Monogr. 33: 1–111 (1991), rev.; Panero et al., Amer. J. Bot. 86: 413–427 (1999), phylog.

Subtribe Clibadiinae H. Rob. (1978).

Annual or perennial herbs, shrubs, lianas or trees. Leaves usually opposite, blades lanceolate to ovate, mostly unlobed. Capitula terminal, rarely axillary, solitary or in open paniculiform or rarely congested corymbiform cymes, radiate, rarely discoid or disciform. Involucres campanulate to hemispheric, rarely cylindrical, phyllaries in 1–7 series, indurate at base with herbaceous, sometimes foliaceous apices, innermost sometimes larger, broader and chartaceous. Receptacles usually flat to convex. Ray florets pistillate or sometimes neuter. Disc florets bisexual, sometimes functionally staminate, corollas usually pentamerous, with or without fibres embedding the vascular strands; stamens 5, rarely 4; styles with two vascular strands, style arms with divided stigmatic surfaces, apices with or without papillae, sometimes with a papillose

appendage, in functionally staminate disc florets style arms fused. Ray cypselae obcompressed and triquetrous, disc cypselae compressed, biconvex, sometimes shallowly quadrate, usually black, mostly winged on angles, faces glabrous or moderately pubescent, sometimes tuberculate, with or without elaiosomes. Pappus of easily caducous or persistent awns, normally as many as angles of cypsela with or without intermediate squamellae, squamellae sometimes fused with awns and forming a crown, sometimes this elevated on a rostrum, rarely a minute crown or absent.

Key to the Genera

1. Capitula with 1 round phyllary; involucres planocompressed **1263. *Delilia***
– Capitula without round phyllaries; involucres campanulate to hemispheric 2
2. Capitula nodding; anthers free; plants with tuberculate cypselae **1267. *Eleutheranthera***
– Capitula erect; anthers connate, rarely free; plants with or without tuberculate cypselae 3
3. Disc florets functionally staminate 4
– Disc florets bisexual, fertile 10
4. Ray corollas yellow; corolla limbs expanded or patent and protruding above involucres 5
– Ray corollas white; corolla reduced to a tube or corolla limbs minute and not expanded above involucres 8
5. Anthers yellow to pale brown; Australia **1286. *Pentalepis***
– Anthers brown or black; neotropical 6
6. Cypselae without wings; pappus a crown of minute scales **1258. *Baltimora***
– Cypselae winged; wings fused to a pappus of two awns 7
7. Shrubs; style arms of disc florets fused except for distal end; cypsela wings stramineous; Central America **1291. *Rensonia***
– Annual herbs; style arms of disc florets not fused; cypsela wings black; Ecuador **1293. *Schizoptera***
8. Capitula with more than one pistillate, fertile floret **1261. *Clibadium***
– Capitula with one pistillate, fertile floret 9
9. Leaves alternate; capitula with only 2 functionally staminate florets; Cuba and Hispaniola **1257. *Lantanopsis***
– Leaves opposite; capitula with more than 2 functionally staminate florets; mostly eastern, tropical South America **1292. *Riencourtia***
10. Ray florets absent or, if present, then neuter or pistillate and sterile 11
– Ray florets present, pistillate and fertile 31
11. Capitula with 1–6 disc florets 12
– Capitula with more than 6 disc florets 14
12. Capitula with 4 disc florets; cypselae obcompressed, linear to narrowly rhombic in cross-section, with lacerate, stramineous wings; Argentina, Bolivia and Paraguay **1297. *Synedrellopsis***
– Capitula with 5 or 6 disc florets; cypselae obcompressed or terete, biconvex to circular in cross-section, without lacerate, stramineous wings; Philippines or western tropical Africa 13
13. Plants with two sterile ray florets; phyllaries 5 or more in 2 series; Philippines **1269. *Fenixia***
– Plants without ray florets; phyllaries 2 in 1 series; western tropical Africa **1270. *Hoffmanniella***
14. Plants dioecious, capitula discoid, receptacles globose; Chile **1290. *Podanthus***
– Plants not dioecious, capitula discoid or radiate, receptacles rarely globose, mostly flat to convex or conical; America, rarely of Chile or pantropical 15
15. Cypselae with a pappus of several, unequal, caducous awns on a circular or oval rostrum, rarely in combination with two awns at angles of cypselae or at base of rostrum 16
– Cypselae epappose or with a pappus of persistent awns or squamellae 18
16. Cypselae greyish black or black and always mottled, not tuberculate; phyllaries of innermost series broadly obovate or sometimes with orbicular apices, chartaceous, translucent and amber in colour; Colombia, Ecuador and Venezuela **1295. *Steiractinia***
– Cypselae black, rarely mottled, sometimes tuberculate; phyllaries of innermost series ovate to lanceolate, apices never orbicular nor broadly obovate, chartaceous, translucent or amber in colour 17
17. Cypselae with two slightly wider, longer, caducous awns; scandent shrubs of eastern Mexico, corollas yellow **1287. *Perymeniopsis***
– Cypselae awns equivalent in width, without two slightly wider, longer, caducous awns; pantropical herbs or weak shrubs with yellow or white corollas, those in Mexico with only white corollas **1280. *Melanthera***
18. Cypselae tuberculate 19
– Cypselae not tuberculate 22
19. Ray corollas deep orange or red; Venezuela **1300. *Tuberculocarpus***
– Ray corollas, when present, mostly yellow or yellow-orange; pantropical 20
20. Leaves linear; Galápagos Islands **1299. *Trigonopterum***
– Leaves mostly ovate, never linear 21
21. Pappus of a few lacerate squamellae or minute awns on a rostrum **1268. *Exomiocarpon***
– Pappus a lacerate crown, not constricted into a rostrum **1267. *Eleutheranthera***
22. Cypselae with a pappus on a rostrum or separated from the main body of the cypselae by a small constriction, the pappus of 0–3 awns fused to an erose cup of free or partially fused squamellae or small awns 23
– Cypselae epappose or with pappus various but never on a rostrum, continuous with the main body of the cypselae 26
23. Cypselae with a pappus on an eccentric, half sigmoid or geniculate rostrum; disc corollas white, ray corollas absent; central Yucatan, Mexico **1289. *Plagiolophus***
– Cypselae with a pappus separated from the cypsela by a small constriction or on a straight rostrum; disc corollas yellow, if white, then ray corollas present, white; pantropical 24
24. Cypselae with a pappus on a rostrum **1303. *Wedelia***
– Cypselae with a pappus not on a rostrum but separated from the body of the cypsela by a small constriction 25

25. Plants from southern Mexico and adjacent Belize **1306. *Zyzyxia***
– Plants from Panama and tropical South America **1284. *Oyedaea***
26. Cypselae winged, wings either lacerate or smooth and normally of a lighter colour than cypselae, rarely concolorous, sometimes wings reduced to a smooth, corky rim 27
– Cypselae never winged 29
27. Cypselae broadly rhombic in cross-section, drupaceous when fresh; wings concolorous with the body of the cypsela **1298. *Tilesia***
– Cypselae linear to biconvex, rarely narrowly rhombic in cross-section, not drupaceous when fresh; wings not concolorous with the body of the cypsela 28
28. Wings of cypselae asymmetrical, distal end of one of the wings smoothly to abruptly broader than the corresponding wing on the other side of the cypsela **1283. *Otopappus***
– Wings fused at neck of cypselae producing a crown around the tube of the corolla **1264. *Dimerostemma***
29. Throats of disc corollas with fibres embedding the vascular strands **1266. *Elaphandra***
– Throats of disc corollas without fibres embedding the vascular strands or these wanting 30
30. Capitula discoid, corolla abruptly expanding above tube into a campanulate or broadly urceolate throat, cypselae fusiform; Ecuador and Peru **1281. *Monactis***
– Capitula radiate, corolla gradually expanding into a narrowly campanulate throat, cypselae obcuneate to obovate; central Chile **1277. *Leptocarpha***
31. Paleae fused to adjacent paleae at base on lateral sides (removing the cypsela and its associated palea on a single pull brings off half of the paleae of the contiguous cypselae; removing the cypsela before it is very mature and the capitulum very dry normally brings with it its associated palea) **1279. *Lundellianthus***
– Paleae not fused laterally nor to the cypsela 32
32. Disc corollas tetramerous 33
– Disc corollas pentamerous 34
33. Paleae filiform, ray floret limbs linear or narrowly lanceolate **1265. *Eclipta***
– Paleae not filiform, ray floret limbs oval **1278. *Lipochaeta***
34. Pappus of 2 to several caducous awns 35
– Pappus various, awns, when present, persistent 36
35. Leaves mostly lobed or compound, sometimes simple; cypselae sometimes tuberculate; Hawaii **1278. *Lipochaeta***
– Leaves simple; cypselae minutely tuberculate and appearing as if having striped faces; neotropical **1288. *Perymenium***
36. Cypselae tuberculate 37
– Cypselae not tuberculate 40
37. Involucres with outermost phyllaries resembling small foliage leaves **1273. *Jefea***
– Involucres with outermost phyllaries not resembling foliage leaves 38
38. Cypselae with two divergent awns **1260. *Calyptocarpus***
– Cypselae without awns 39
39. Leaves linear, cypselae obpyriform with a pappus a small crown on a small rostrum; Galápagos Islands **1299. *Trigonopterum***
– Leaves lanceolate to trullate, never linear, cypselae broadly fusiform with a pappus an erose crown continuous with cypselae; pantropical **1294. *Sphagneticola***
40. Capitula axillary 41
– Capitula terminal 42
41. Ray cypselae with lacerate wings, pappus of two slender awns fused to wings **1296. *Synedrella***
– Ray cypselae without wings, sometimes margins irregular, pappus of two divergent awns **1260. *Calyptocarpus***
42. Wings of cypsela fused around the neck forming a cup-like structure surrounding the tube of the corolla **1264. *Dimerostemma***
– Wings of cypselae not fused around the neck 43
43. Leaves alternate 44
– Leaves opposite, those associated with the capitula sometimes subopposite or alternate 46
44. Cypselae with a pappus on a rostrum **1259. *Blainvillea***
– Cypselae without a rostrum 45
45. Capitula with only 1–3 ray florets **1281. *Monactis***
– Capitula with more than three ray florets **1274. *Kingianthus***
46. Cypsela epappose **1262. *Damnxanthodium***
– Cypselae pappose, pappus sometimes reduced to a minute crown 47
47. Limbs of ray corollas narrowly oblanceolate to filiform and involute 48
– Limbs of ray corollas oval or oblong, sometimes obovate, rarely oblanceolate, never involute 49
48. Disc corolla throats with prominent fibres embedding the vascular strands, leaf-blades elliptic, awns of cypsela slightly curved outwards; Mexico and Costa Rica **1301. *Tuxtla***
– Disc corolla throats without fibres embedding the vascular strands, leaf-blades lanceolate-elliptic, awns of cypsela not curved; Panama and northern South America **1282. *Oblivia***
49. Disc corolla throats with prominent fibres embedding the vascular strands 50
– Disc corolla throats without fibres 52
50. Cypselae prominently winged **1293. *Schizoptera***
– Cypselae not winged or with a narrow hyaline margin along cypsela edges 51
51. Disc cypselae compressed, pappus of two awns, rarely with squamellae in between **1276. *Lasianthaea***
– Disc cypselae weakly quadrate, pappus of two awns and a few squamellae in between **1272. *Iogeton***
52. Involucres with outermost phyllaries resembling small foliage leaves **1273. *Jefea***
– Involucres with outermost phyllaries not resembling foliage leaves 53
53. Cypselae with a rostrum 54
– Cypselae without a rostrum 56
54. Cypselae without elaiosomes 55
– Cypsela with elaiosomes **1303. *Wedelia***
55. Cypselae winged **1305. *Zexmenia***
– Cypselae not winged **1259. *Blainvillea***
56. Cypselae without wings, disc cypselae shallowly quadrate, rarely pentagonal 57
– Cypselae with asymmetrical wings **1283. *Otopappus***
57. Cypselae weakly stipitate and shallowly navicular; small trees of central Ecuador **1271. *Idiopappus***
– Cypselae not weakly stipitate nor shallowly navicular; annual or perennial herbs, shrubs of Mexico and

Central America or south-eastern South America and Chile 58
58. Cypselae with a pappus a minute crown; annual or perennial herbs of south-eastern South America and central Chile **1285. *Pascalia***
– Cypselae with a pappus of a few awns or squamellae free or fused at the base 59
59. Leaves triplinerved 60
– Leaves pinnately veined **1272. *Iogeton***
60. Cypselae obpyramidal; Mesoamerica **1302. *Wamalchitamia***
– Cypselae oblong or obovate; coastal sand dunes of Indo-Pacific region **1304. *Wollastonia***

Genera of Ecliptinae

1258. *Baltimora* L.

Baltimora L., Mant. Pl. 2: 158, 288 (1771), nom. cons.; Stuessy, Fieldiana Bot. 36: 31–50 (1973), rev.

Annual erect herbs. Leaves opposite, petiolate, blades ovate, triplinerved. Capitula in terminal, open paniculiform cymes, radiate. Involucres cylindrical to campanulate, phyllaries in 2 series, subequal to shallowly gradate. Receptacles flat to convex. Ray florets pistillate, corollas yellow to yellow-orange. Disc florets functionally staminate, corollas yellow, without fibres embedding vascular strands, lobes deeply papillose on adaxial surface; anthers black, appendages with glandular trichomes; styles arms of ray florets with divided stigmatic surfaces, spreading. Cypselae triquetrous, obpyramidal, the apices with three protruding horns, black, strongly to shallowly tuberculate, puberulent. Pappus a crown of minute scales. $x = 12, 13$. Two species, neotropics.

1259. *Blainvillea* Cass.

Blainvillea Cass., Dict. Sci. Nat., ed. 2, 29: 493–494 (1823).

Annual or perennial erect herbs, weak shrubs. Leaves opposite or alternate, petiolate, blades lanceolate to broadly ovate, triplinerved. Capitula in terminal, open paniculiform cymes, radiate. Involucres subcylindrical, campanulate to oblong, sometimes hemispheric, phyllaries in 2–4 series, chartaceous with green longitudinal striae. Receptacles flat to minutely convex. Ray florets pistillate, corollas yellow or white. Disc florets bisexual, corollas yellow or white, without fibres embedding vascular strands, tubes long and slender; anthers black, appendages with or without glandular trichomes; style arms narrowly acuminate. Ray cypselae obcompressed, obpyramidal, black, glabrous. Disc cypselae compressed, biconvex, sometimes shallowly triquetrous to quadrate, black. Pappus on a rostrum, of 2–3 awns and sometimes with a few scales fused at the base. $x = 17$. Ten species, pantropical.

1260. *Calyptocarpus* Less.

Calyptocarpus Less., Syn. Gen. Comp. 221 (1832); McVaugh & Smith, Brittonia 19: 268–272 (1967), rev.

Prostrate to weakly erect perennial herbs or weak shrubs. Leaves opposite, petiolate, blades ovate to lanceolate, triplinerved. Capitula terminal and axillary, solitary or in simple cymes, radiate. Involucres campanulate, phyllaries in 1–2 series, mostly 5, herbaceous. Receptacles convex. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow, with fibres embedding vascular strands; anthers black, appendages with glandular trichomes; style arms narrowly acuminate. Cypselae compressed, narrowly obovate or obcuneate, often tuberculate, sometimes striate. Pappus of 2 divergent or reflexed awns. $x = 12$. Two species, southern USA, Mexico, Central America, Cuba.

1261. *Clibadium* L.

Clibadium L., Mant. Pl. 2: 161, 294 (1771); Arriagada, Brittonia 55: 245–301 (2003), rev.
Trichapium Gilli (1983).

Shrubs or trees. Leaves opposite, sessile to petiolate, blades lanceolate to broadly cordiform, triplinerved. Capitula in terminal open or congested paniculiform to corymbiform, sometimes glomerule-like cymes, disciform, rarely epaleate. Involucres cylindric, campanulate, hemispherical, phyllaries in 2–6 series, subequal, membranous, scarious, the inner enclosing the marginal cypselae, greenish to purple, sometimes white. Receptacles flat to shallowly convex. Pistillate florets in 1–2 series, corollas inconspicuous, white, greenish white or white-yellow, 2–5-lobed, sometimes weakly zygomorphic. Disc florets functionally staminate, corollas white or greenish white, 4- or 5-lobed; anthers black, appendages with glandular trichomes; style arms acuminate. Cypselae obcompressed, obovoid to obpyriform, black to blackish purple, sometimes drupe-like with juicy exocarp, glabrous to variously pubescent especially at apices. Pappus absent. $x = 16$. About 24 species, neotropics.

1262. *Damnxanthodium* Strother

Damnxanthodium Strother, Syst. Bot. 12: 41 (1987).

Erect to slightly decumbent perennial herbs. Leaves opposite, blades ovate to elliptic, 3–5-plinerved. Capitula solitary on long peduncles or in simple dichasial cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2 series, subequal, herbaceous. Receptacles convex. Ray florets pistillate, corollas golden yellow to yellow-orange. Disc florets bisexual, corollas yellow, with fibres embedding vascular strands, lobes densely papillose on adaxial surfaces; anthers black, appendages without glandular trichomes; style arms tapered, apices papillose. Cypselae obliquely pyriform to oblanceolate in outline, black to brownish black, glabrous with a few trichomes around neck. Pappus absent. $x = 12$. One species, *D. calvum* (Greenm.) Strother, western Mexico.

1263. *Delilia* Spreng.

Delilia Spreng., Bull. Sci. Soc. Philom. Paris 10: 54 (1823); Delprete, Pl. Syst. Evol. 194: 111–122 (1995), rev.
Elvira Cass. (1824).

Erect or decumbent annual herbs. Leaves opposite, blades ovate to lanceolate, triplinerved. Capitula in terminal and axillary umbelliform cymes, radiate. Involucres flattened, disc-like, plano-compressed, phyllaries 2–4, herbaceous, one orbicular the others suborbicular, ovate to obovate. Ray florets 1(–3), pistillate, corollas yellow. Disc florets 1(–4), functionally staminate, corollas yellow, with fibres embedding vascular strands; anthers black, appendages with glandular trichomes; style arms of ray floret spreading with divided stigmatic surfaces. Cypselae triquetrous, obovate in outline, glabrous with a few trichomes around apices. Pappus absent. $x = 12$. Two species, one widespread in tropical America, the other endemic to the Galápagos Islands.

1264. *Dimerostemma* Cass.

Dimerostemma Cass., Bull. Sci. Soc. Philom. Paris 11 (1817); Robinson, Proc. Biol. Soc. Wash. 97: 961–969 (1984), circumscr.; Robinson, Proc. Biol. Soc. Wash. 97: 618–626 (1984), new spp.; Dias de Moraes, Ph.D. Thesis, Universidade Estadual Campinas (2004), rev.
Angelphytum Barroso (1980).

Erect annual or perennial herbs, shrubs. Leaves opposite or alternate, petiolate or subsessile, blades narrowly lanceolate to ovate, sometimes subcordate, triplinerved. Capitula solitary or in paniculiform cymes, discoid or radiate. Involucres broadly campanulate to hemispheric, phyllaries in 3–4 series. Receptacles convex. Ray florets neuter or pistillate, corollas golden to bright yellow. Disc florets bisexual, corollas yellow without fibres embedding vascular strands; anthers black or brown, appendages ovate with glandular trichomes; style arms tapered, apices papillose. Cypselae compressed, biconvex (ray cypselae when present triquetrous), obovate in outline, brown to black, tuberculate, shallowly to prominently winged, rarely without wings. Pappus of 2–3 awns fused with the wings and forming a shallow cup around the corolla tube. Approximately 26 species, Bolivia, Paraguay, Argentina, Brazil.

1265. *Eclipta* L. Fig. 93

Eclipta L., Mant. Pl. 2: 157, 286 (1771), nom. cons.

Erect or decumbent annual or perennial herbs. Leaves opposite, blades lanceolate, narrowly ovate

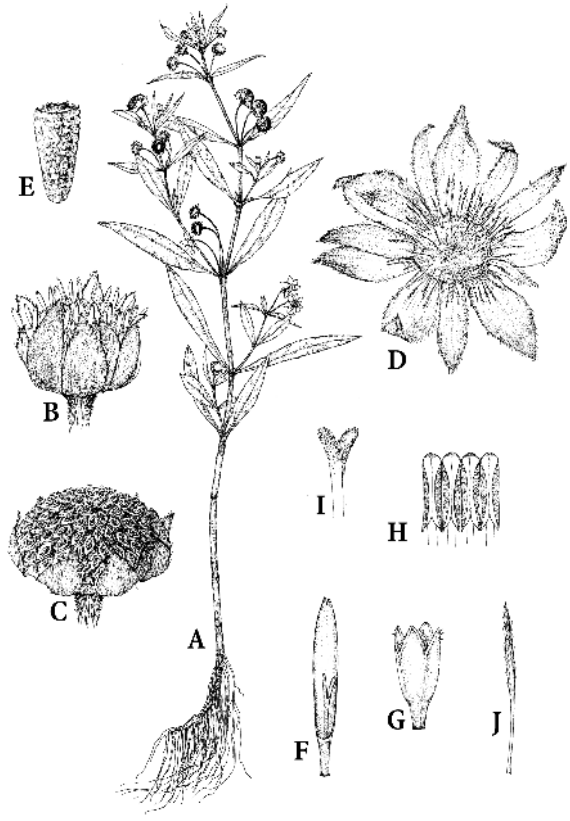

Fig. 93. Compositae-Heliantheae. *Eclipta prostrata*. **A** Habit. **B** Capitulum in flower. **C** Capitulum in fruit. **D** Capitulum past flower with persistent palea on receptacle. **E** Cypsela. **F** Ray corolla. **G** Disc corolla. **H** Anthers. **I** Style arms. **J** Palea. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

or oval, pinnately veined or triplinerved. Capitula axillary or terminal, solitary or in simple cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2–3 series, subequal. Receptacles shallowly convex, paleae filiform. Ray florets pistillate, corollas white to pale yellow, linear, apices bilobed or entire. Disc florets 4(–5)-lobed, bisexual, corollas white or yellow, without fibres embedding vascular strands; anthers yellow or black, appendages with or without glandular trichomes; style arms acuminate. Cypselae compressed (those of the ray sometimes triquetrous and obcompressed), shallowly 3–4-angled, tuberculate to rugose, dark brown, glabrous, sometimes broadly winged or with corky margins, with a few simple trichomes around neck. Pappus a minute corona sometimes with 2 teeth at angles of cypsela or of 2 awns fused to the wings. $x = 11$. Five species, America, Australia, introduced elsewhere.

1266. *Elaphandra* Strother

Elaphandra Strother, Syst. Bot. Monogr. 33: 17 (1991); Robinson, Phytologia 72: 144–151 (1992), new comb.; Pruski, Novon 6: 404–418 (1996), reg. rev.

Perennial herbs or shrubs. Leaves opposite, petiolate, blades lanceolate to ovate, triplinerved. Capitula in terminal, simple dichasial or open paniculiform cymes, radiate, rarely discoid. Involucres hemispherical, phyllaries in 2–3 series, subequal to gradate. Receptacles flat to convex. Ray florets neuter, corollas yellow to yellow-orange. Disc florets bisexual, corollas yellow or blackish green with yellow lobes, with fibres embedding vascular strands; anthers black, appendages rarely with glandular trichomes; style arms tapered, apices papillose. Cypselae compressed, shallowly quadrate, sometimes base narrowed or stipitate and then cypselae narrowly obpyriform, dark brown to black or reddish brown, glabrescent to moderately pubescent. Pappus absent or a bicornute, minute crown. $x = 13, 14$. Fourteen species, Panama, tropical Andes of South America.

1267. *Eleutheranthera* Poit. ex Bosc.

Eleutheranthera Poit. ex Bosc., Bull. Sci. Soc. Philom. Paris 3: 137 (1802); Lawalrée, Bull. Jard. Bot. Etat Bruxelles 17: 59 (1943), reg. rev.
Gymnolomia Kunth (1818).

Erect annual herbs. Leaves opposite, petiolate, blades ovate to trullate, triplinerved. Capitula axillary, simple, nodding, radiate or discoid. Involucres campanulate, phyllaries in 1 series, herbaceous. Receptacles flat. Ray florets neuter, corollas yellow to yellow-orange. Disc florets bisexual or functionally staminate (?), corollas yellow, without fibres embedding vascular strands, sometimes only 2 or 3 florets per head producing fertile cypselae; anthers black or golden brown, appendages with glandular trichomes; style arms tapered, apices papillose. Cypselae shallowly compressed, shallowly quadrate to terete, black, tuberculate. Pappus a small lacerate, tubular crown. $x = 10, 15$. Two species, neotropical, adventive in tropical regions of the Old World.

1268. *Exomiocarpon* Lawalrée

Exomiocarpon Lawalrée, Bull. Jard. Bot. Etat Bruxelles 17: 62 (1943).

Erect annuals. Leaves opposite, petiolate, triplinerved. Capitula axillary and terminal, solitary or in paniculiform cymes, discoid, rarely radiate. Involucres campanulate, phyllaries in 1–2 series, herbaceous. Receptacles flat to shallowly convex. Ray florets when present neuter, corollas yellow. Disc florets 5(–4)-lobed, bisexual, corollas yellow, with fibres embedding vascular strands at base of throat; anthers black, appendages ovate with glandular trichomes; style arms deltate with densely papillose apices. Cypselae obcompressed (outermost) or compressed (innermost), black or greyish black and mottled, obscurely winged, wings shallowly tuberculate, moderately pubescent. Pappus a small crown of minute, lacerate, filiform scales. One species, *E. madagascariense* (Humbert) Lawalrée, Madagascar.

1269. *Fenixia* Merr.

Fenixia Merr., Philipp. J. Sci., Bot. 12: 119 (1917).

Erect to prostrate annual herbs. Leaves opposite, petiolate, triplinerved. Capitula terminal, solitary or in simple dichasial cymes, radiate. Involucres campanulate, phyllaries in 2 series, herbaceous. Receptacles flat, epaleate. Ray florets 2, sterile, corollas yellow. Disc florets 5, bisexual, corollas tetramerous, yellow; anthers 4, black, appendages ovate; style arms tapered. Cypselae shallowly obcompressed to shallowly quadrate, winged, obovate, rugose, moderately pubescent. Pappus absent. One species, *F. pauciflora* Merr., Philippines.

1270. *Hoffmanniella* Schltr ex Lawalrée

Hoffmanniella Schltr ex Lawalrée, Westafr. Kautschuk-Exped. 325 (1900); Bull. Jard. Bot. Etat Bruxelles 17: 59 (1943).

Prostrate to erect annual herbs. Leaves opposite, petiolate, triplinerved. Capitula terminal, appearing axillary, solitary, sessile, discoid. Involucres cylindrical with only 2 opposite phyllaries. Receptacles flat. Florets 6, bisexual, corollas (3–)4-lobed, yellow, those subtended by phyllaries sometimes slightly zygomorphic, without fibres embedding vascular strands, sometimes a few fibrous cells flanking veins on distal area of throat; anthers black, free, appendages without glandular trichomes; style arms with round to subacute, smooth apices. Cypselae obcompressed, broadly obovate, depressed obovate in cross-section, brown to black, edges thickened, stramineous, glabrous except for densely pubescent apices. Pappus a minute, pubescent crown. One species, *H. sylvatica* Schltr ex Lawalrée, tropical west Africa.

1271. *Idiopappus* H. Rob. & Panero

Idiopappus H. Rob. & Panero, Syst. Bot. 19: 359–362 (1994).

Small trees. Leaves opposite, petiolate, broadly ovate to subcordate, triplinerved. Capitula in terminal, open paniculiform to thyrsoid cymes, radiate. Involucres hemispherical to shallowly patent with age, phyllaries in 3 series, subequal. Receptacles conical to subglobose with age. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow, without fibres embedding vascular strands, the throats expanding conspicuously above tube, subcampanulate, lobes coiled; anthers black, appendages without glandular trichomes; style arm apices deltate. Cypselae compressed, sometimes those of the ray trigonous, those of the disc shallowly quadrate, somewhat navicular, shallowly stipitate with curved bases, black, glabrous. Pappus of 1 or mostly 2, rarely 3 squamellae at main angles of cypsela. $x = 31–33$. One species, *I. quitensis* H. Rob. & Panero, Ecuador.

1272. *Iogeton* Strother

Iogeton Strother, Syst. Bot. Monogr. 33: 20 (1991).

Stoloniferous perennial herbs or weak shrubs. Leaves opposite, petiolate, blades narrowly lanceolate, pinnately nerved. Capitula terminal, solitary or in lax dichasial cymes, radiate. Involucres narrowly obconic, phyllaries subequal. Receptacles conical or hemispherical. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow; anthers brown, appendages ovate; style arms tapered. Immature ray cypselae and outermost disc cypselae triquetrous, brown to black. Innermost disc cypselae quadrate, brownish to black, hispidulous on the angles. Pappus of 2–4 slender, persistent, minutely barbellulate awns sometimes with 1–3 minute scales. One species, *I. nowickeanus* (D'Arcy) Strother, Panama.

1273. *Jefea* Strother

Jefea Strother, Syst. Bot. Monogr. 33: 22 (1991).

Basally woody perennials or shrubs. Leaves opposite or alternate, petiolate, blades deltate, ovate or lanceolate, triplinerved, sometimes densely tomentose beneath. Capitula terminal, solitary, radiate. Involucres broadly campanulate to hemispheric, phyllaries dimorphic, outermost leaf-like and spreading. Receptacles strongly convex to conic. Ray florets pistillate, corollas yellow to yellow-orange. Disc florets bisexual, corollas yellow to orangish, without fibres embedding the vascular strands; anthers yellow, brown or black, appendages lanceolate with glands; style arms tapered, apices papillose. Ray cypselae triquetrous, disc cypselae compressed, oblanceolate, wings continuous or shallowly lacerate, often corky. Pappus of 2–3 slender, unequal, caducous or persistent awns and 2–10 or more much shorter, free or basally connate squamellae, all inserted on apices of cypselae, not raised on a rostrum. $x = 14$. Five species, Mexico, Guatemala.

1274. *Kingianthus* H. Rob.

Kingianthus H. Rob., Phytologia 38: 415 (1978); Robinson, Phytologia 44: 70–78 (1979), new spp.

Shrubs. Leaves alternate, petiolate, blades ovate, triplinerved. Capitula in terminal, paniculiform cymes of congested corymbiform cymes, radiate. Involucres campanulate, phyllaries in 1–2 series, subequal. Receptacles convex. Ray florets pistillate, corollas light to golden yellow. Disc florets bisexual, corollas yellow to orange-yellow, without fibres embedding the vascular strands; anthers black, appendages with glands, sometimes glandular trichomes scattered lengthwise along the connective; style branch apices deltate. Cypselae quadrate, slightly navicular, shallowly stipitate with curved bases, black, glabrous. Pappus of 1

squamella or absent. x = 15, 16, 17. Two species, Ecuador, Peru.

1275. *Lantanopsis* C. Wright ex Griseb.

Lantanopsis C. Wright ex Griseb., Mem. Amer. Acad. Arts n.s. 8: 513 (1862).

Annual or perennial herbs, sometimes weak shrubs. Leaves opposite, petiolate, blades lanceolate to ovate, triplinerved. Capitula in terminal, congested corymbiform or pseudoscorpioid cymes, disciform. Involucres cylindrical to campanulate, phyllaries 4, in 2 series, subequal. Receptacles flat, epaleate. Florets 3, unisexual and dimorphic, the single pistillate floret tubular and the corolla with 2 or 3 lobes, the two functionally staminate florets with a tetramerous corolla, corollas white, without fibres embedding the vascular strands; anthers black, appendages with glandular trichomes; style arms tapered and at least 10 times as long as style. Cypselae obcompressed, obovoid to obpyriform, black or brown, densely covered with glandular and a few tapered trichomes especially on distal ends. Pappus absent. Three species, Cuba and Hispaniola.

1276. *Lasianthaea* DC.

Lasianthaea DC., Prodr. 5: 607 (1836); Becker, Mem. New York Bot. Gard. 31: 1–64 (1979), rev.

Perennial herbs or shrubs, rarely small trees. Leaves opposite, petiolate or subsessile, blades lanceolate to ovate or elliptic, triplinerved. Capitula terminal, solitary or in open to congested corymbiform or paniculiform cymes, radiate. Involucres cylindric to hemispheric, phyllaries in 3–5 series, subequal to imbricate, distal apices sometimes chartaceous, red, purple or yellow. Receptacles convex. Ray florets pistillate, corollas yellow, orange, vermillion, purple, sometimes lighter in colour abaxially. Disc florets bisexual, corollas yellow, orange, reddish-orange, purple, with fibres embedding the vascular strands; anthers brown or black, appendages without glandular trichomes; style arms tapered, apices papillose. Ray cypselae obcompressed, triquetrous, those of disc compressed, cuneate to slightly oblong in outline, black with hyaline or greenish edges, glabrous. Pappus of 2–3 awns continuous with cypsela edges, sometimes with a few free or connate squamellae. x = 8, 10, 11. Twelve species, south-western USA, Mexico, Central America, Venezuela.

1277. *Leptocarpha* DC.

Leptocarpha DC., Prodr. 5: 495 (1836).

Perennial herbs or weak shrubs. Leaves opposite or alternate, blades ovate, triplinerved. Capitula in terminal, simple dichasia or open paniculiform cymes, radiate. Involucres hemispherical to patent with age, phyllaries in 2 series. Receptacles convex with linear paleae. Ray florets neuter or pistillate but sterile, corollas yellow. Disc florets bisexual, corollas yellow, without fibres embedding the vascular strands; anthers brown, appendages with minute glandular trichomes; style arms small, apices deltate, not papillose. Cypselae compressed, biconvex to triquetrous, obovate, black, sparsely pubescent. Pappus of 2–4 small squamellae. One species, *L. rivularis* DC., Chile.

1278. *Lipochaeta* DC.

Lipochaeta DC., Prodr. 5: 610 (1836); Gardner, Rhodora 81: 291–343 (1979), reg. rev.; Wagner & Robinson, Brittonia 53: 539–561 (2002), delim.

Annual or perennial herbs, weak shrubs. Leaves opposite, petiolate or sessile, rarely ternate, blades ovate to elliptic, sometimes filiform, mostly triplinerved. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2 series, normally five in each. Receptacles convex, paleae sometimes deciduous. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas 4- or 5-lobed, yellow, without fibres embedding the vascular strands; anthers brown, appendages with glandular trichomes; style arms deltate, apices shallowly papillose. Ray cypselae obcompressed, triquetrous, black, tuberculate, with lacerate wings. Disc cypselae compressed, biconvex, oblong to obcuneate, otherwise as ray cypselae. Pappus of connate scales forming a corona, sometimes with caducous awns and intervening squamellae. x = 15, 26. Twenty species, Hawaii.

1279. *Lundellianthus* H. Rob.

Lundellianthus H. Rob., Wrightia 6: 41 (1978); Strother, Syst. Bot. 14: 544–548 (1989), delim.

Shrubs. Leaves opposite, petiolate to subsessile, blades ovate-elliptic to ovate, triplinerved. Capitula terminal, solitary or in simple dichasia, sometimes in open paniculiform cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2–3 series, outermost foliaceous. Receptacles convex,

tuberculate, paleae fused laterally. Ray florets pistillate, corollas yellow to orange-yellow. Disc florets bisexual, corollas yellow to yellow-orange, with or without fibres embedding the vascular strands; anthers black, appendages with or without glandular trichomes; style arms tapered, apices papillose. Ray cypselae triquetrous, oblanceolate in outline, black or stramineous, glabrous or sparsely pubescent, shallowly to prominently winged, wings corky, stramineous, in some species edges of wings fused and producing a tuberculate, stramineous cover on faces of cypsela. Disc cypselae compressed, primarily biconvex but with small ridges on faces rendering them shallowly quadrate and rhombic in outline. Pappus of 2 or 3 broad, lacerate awns at main angles of cypsela, with or without squamellae in between, awns sometimes fused with wings. $x = 16$. Eight species, Mexico, Central America.

1280. *Melanthera* Rohr

Melanthera Rohr, Skr. Naturhist.-Selsk. 2: 213 (1792); Wild, Kirkia 5: 1–17 (1965), reg. rev.; Parks, Rhodora 75: 169–210 (1973), reg. rev.; Wagner & Robinson, Brittonia 53: 539–561 (2002), delim.

Annual or perennial herbs, scandent or erect shrubs. Leaves opposite, blades narrowly obovate to linear-lanceolate, ovate, triplinerved, unlobed, trilobed or pinnately lobed. Capitula in terminal, open paniculiform cymes, rarely solitary, discoid or radiate. Involucres campanulate to hemispherical, phyllaries in 1–2 series, subequal. Receptacles convex. Ray florets pistillate but sterile or neuter, corollas yellow. Disc florets bisexual, corollas yellow or white, without fibres embedding the vascular strands, sometimes with a few sclerified cells along vascular strands; anthers black, appendages with glandular trichomes; style arms tapered to acute, apices shallowly papillose. Ray cypselae obcompressed, triquetrous to quadrate, obovate to obpyramidal, black, apices truncate, sometimes winged on angles of cypsela, glabrescent. Disc cypselae compressed, obconical, somewhat quadrangular, otherwise as ray cypselae. Pappus of several caducous awns. $x = 15, 16$. Twenty species, pantropical.

1281. *Monactis* Kunth

Monactis Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. folio ed. 4: 225 (1818); Robinson, Phytologia 34: 33–45 (1976), notes; Robinson, Phytologia 44: 70–78 (1979), new spp.

Shrubs or small trees. Leaves alternate, petiolate, blades lanceolate to broadly ovate or trullate, pinnately veined or triplinerved. Capitula in terminal, congested to open corymbiform cymes, radiate or discoid, only one or two ray florets per head, ray florets towards the outside of congested corymbiform cymes. Involucres cylindrical to campanulate, phyllaries in 1–2 series, gradate. Receptacles flat to shallowly convex. Ray florets pistillate, corollas yellow to orange-yellow. Disc florets bisexual, corollas white, greenish white, yellow or orange-yellow, without fibres embedding the vascular strands, the throats expanding conspicuously above tube, campanulate to subhemispheric, lobes coiled; anthers black, appendages with glandular trichomes, sometimes these scattered lengthwise along the connective; style arm apices deltate. Cypselae shallowly triquetrous or quadrate, fusiform, slightly asymmetrical, sometimes geniculate at apices, black, glabrous. Pappus of 1 rarely 2 squamellae or absent. $x = 27, 28, 30, 32$. About 10 species, Ecuador and Peru.

1282. *Oblivia* Strother

Oblivia Strother, Syst. Bot. 14: 541 (1989); Anderson et al., Syst. Bot. 4: 44–56 (1979), phylog.; Villaseñor & Strother, Syst. Bot. 14: 529–540 (1989), syst.; Robinson, Phytologia 76: 24–26 (1994), new spp.

Scandent shrubs. Leaves opposite, petiolate, blades lanceolate-elliptic to ovate, 3–5-plinerved. Capitula in terminal, congested corymbiform cymes, radiate. Involucres campanulate, phyllaries in 2–3 series, subequal. Receptacles convex. Ray florets pistillate, corollas dull yellow. Disc florets bisexual, corollas yellow, without fibres embedding the vascular strands; anthers black, appendages with glandular trichomes; style arms tapered. Cypselae obcompressed, triquetrous, narrowly oblanceolate in outline, shallowly winged. Disc cypselae compressed, otherwise as ray cypselae. Pappus of 2(–4) awns and a few squamellae in between. $x = 16$. About three species, Panama, tropical Andes.

1283. *Otopappus* Benth.

Otopappus Benth. in Benth. & Hook. f., Gen. Pl. 2: 196, 380 (1873); Hartman & Stuessy, Syst. Bot. 8: 185–210 (1983), rev.; Villaseñor & Strother, Syst. Bot. 14: 529–540 (1989), new spp.

Shrubs or small trees. Leaves opposite, petiolate, blades lanceolate to ovate, 2–7-plinerved. Capit-

ula terminal, solitary or in small paniculiform to corymbiform cymes, radiate or discoid. Involucres campanulate to hemispherical, phyllaries in 3–7 series, gradate. Receptacles convex to conic. Ray florets pistillate, rarely neuter, corollas yellow to yellow-orange. Disc florets bisexual, corollas yellow, rarely white, without fibres embedding the vascular strands; anthers black or deep purple, appendages with glandular trichomes; style arms tapered. Cypselae compressed, peripheral triquetrous, otherwise oblanceolate to obovate in outline, black or brown, glabrous to puberulent, especially at apices, with 1–3 wings of unequal width. Pappus of 1–3 awns with connate or free minute squamellae in between, awns fused to wings. x = 16. Fourteen species, Mexico, Central America.

1284. *Oyedaea* DC.

Oyedaea DC., Prodr. 5: 576 (1836); Blake, Contr. U.S. Natl Herb. 20: 411–422 (1921), rev.; Robinson, Wrightia 6: 43–48 (1979), reg. rev.; Pruski, Novon 6: 404–418 (1996), reg. rev.

Shrubs or small trees. Leaves opposite, petiolate, blades elliptic to ovate, pinnately veined or triplinerved. Capitula terminal, in simple or open paniculiform cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2–5 series. Receptacles shallowly convex to convex. Ray florets neuter, corollas yellow, rarely white. Disc florets bisexual, corollas yellow, rarely white, without fibres embedding the vascular strands; anthers black, appendages with or without glandular trichomes; style arms tapered, apices papillose with appendages. Cypselae oblong, compressed, winged at maturity. Pappus of 2 subequal awns on a rostrum, sometimes with intermediate squamellae. x = 14. Eighteen species, Central and South America.

1285. *Pascalia* Ortega

Pascalia Ortega, Novarum, aut Rariorum Plantarum Horti Reg. Bot. Matrit. 39 (1797); Strother, Syst. Bot. Monogr. 33: 1–111 (1991), rev.

Stoloniferous perennial herbs. Leaves opposite, sessile to shortly petiolate, blades lanceolate to broadly ovate or oval, triplinerved. Capitula terminal, solitary or in simple dichasia, radiate. Involucres hemispherical, phyllaries in 2–3 series. Receptacles convex to hemispherical. Ray florets pistillate, sometimes with staminodes, corollas yellow-orange. Disc florets bisexual, corollas yellow-orange, without fibres embedding the vascular strands; anthers yellow or brown, appendages without glandular trichomes; style arms acute, apices papillose. Cypselae compressed, broadly biconvex to quadrate, broadly obcuneate in outline, neck broad and flat, rhombic in outline, edge sinuate, brown, glabrous. Pappus a minute crown. x = 33. Two species, eastern South America, north-central Chile.

1286. *Pentalepis* F. Muell.

Pentalepis F. Muell., Trans. Bot. Soc. Edinburgh 7: 496 (1863); Karis et al., Austral. Syst. Bot. 6: 149–153 (1993), re-establ.

Erect annuals or shrubs. Leaves opposite, blades lanceolate to narrowly ovate, triplinerved. Capitula in terminal, congested corymbiform cymes or open paniculiform cymes, radiate. Involucres campanulate, phyllaries in 2 series. Receptacles shallowly convex. Ray florets pistillate, corollas yellow. Disc florets functionally staminate, corollas yellow, without fibres embedding the vascular strands; anthers yellow to brown, appendages without glandular trichomes; style arms of disc florets fused, style arms of ray florets with divided stigmatic surfaces, without appendages. Cypselae obcompressed, obovate, shallowly winged, with a few tuberculae on edge of wings, brown-black, glabrous with a few trichomes on neck. Pappus a minute crown. About three species, Australia.

1287. *Perymeniopsis* H. Rob.

Perymeniopsis H. Rob., Phytologia 40: 495 (1978).

Scandent shrubs. Leaves opposite, petiolate, blades oblong, triplinerved. Capitula in terminal, open paniculiform cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2–3 series. Receptacles convex. Ray florets neuter, corollas golden bright yellow. Disc florets bisexual, corollas yellow, without fibres embedding the vascular strands; anthers brown or black, appendages ovate with minute glandular trichomes; style arms tapered, apices papillose. Cypselae compressed, obovate, black or brown, shallowly winged, wings wider at distal apices, cypsela bases narrowed, essentially glabrous. Pappus of 2 easily caducous awns at angles of cypsela and a small rostrum bearing numerous minute and easily caducous awns. One species, *P. ovalifolia* (A. Gray) H. Rob., eastern Mexico.

1288. *Perymenium* Schrad.

Perymenium Schrad., Index Sem. (Göttingen) 1830: 4 (1830); Fay, Allertonia 1: 235–296 (1978), part. rev.

Perennial herbs, shrubs or small trees. Leaves opposite, blades lanceolate to ovate sometimes cordiform, triplinerved, rarely pinnately veined. Capitula in terminal, simple dichasia or open paniculiform cymes, radiate. Involucres hemispherical, phyllaries in 2–4 series. Receptacles convex. Ray florets pistillate, corollas golden yellow. Disc florets bisexual, corollas yellow, without fibres embedding the vascular strands, some sclerified cells scattered throughout throat; anthers brown or black, appendages with glandular trichomes; style arms deltate to tapered, apices shallowly papillose. Ray cypselae obcompressed, triquetrous, obovate to oblong, those of the disc compressed, biconvex, obovate, black, variously pubescent, shallowly to broadly winged, minutely tuberculate, tuberculae collectively appearing as shiny lines. Pappus of 0–3 awns at angles of cypselae and a rostrate crown of numerous unequal, easily caducous awns. $x = 15$. About 43 species, neotropics.

1289. *Plagiolophus* Greenm.

Plagiolophus Greenm., Publ. Field Columb. Mus., Bot. Ser. 3: 125 (1904).

Erect annuals. Leaves opposite, blades ovate, triplinerved. Capitula in terminal, open paniculiform cymes, discoid. Involucres hemispheric, phyllaries in 2 series, outermost 5, spreading, innermost appressed. Receptacles shallowly convex. Florets bisexual, corollas white, without fibres embedding the vascular strands; anthers black, appendages with glandular trichomes; style arms tapered, acuminate. Cypselae compressed, obovate, with geniculate, eccentric necks, winged at maturity. Pappus of 2 subequal awns and a few squamellae in between on a crown at apex of neck. One species, *P. millspaughii* Greenm., central Yucatan, Mexico.

1290. *Podanthus* Lag.

Podanthus Lag., Gen. Sp. Pl. 24 (1816), nom. cons.

Dioecious shrubs, sometimes with purplish stems. Leaves opposite, blades ovate to trullate. Capitula terminal, solitary, or in simple or leafy paniculiform cymes, discoid. Involucres patent or reflexed, phyllaries in 1–2 series, subequal. Receptacles convex to globose. Corollas yellow or green-yellow, without fibres embedding the vascular strands, dimorphic, those of functionally pistillate florets approximately half the size of those of functionally staminate florets and with much shorter tubes; anthers dark yellow or brown with black connectives and appendages, appendages without glandular trichomes; style arms small, apices deltate to acute, not papillose. Cypselae compressed to quadrate, obpyramidal, bases slender to narrowed. Pappus a minute crown of squamellae or absent. Two species, central Chile.

1291. *Rensonia* S.F. Blake

Rensonia S.F. Blake, J. Wash. Acad. Sci. 13: 144 (1923).

Shrubs. Leaves opposite, petiolate, blades ovate to oval, triplinerved. Capitula in terminal, paniculiform cymes, radiate. Involucres campanulate, phyllaries in 2 series, subequal. Receptacles flat to shallowly convex. Ray florets pistillate, corollas golden yellow. Disc florets functionally staminate, corollas golden yellow with fibres embedding the vascular strands; anthers black, sometimes shallowly calcarate, appendages without glandular trichomes; style arms of disc florets fused except for distal end. Cypselae obovate, glabrous, conspicuously winged. Pappus of 2 awns fused to wings. $x = 17$. One species, *R. salvadorica* S.F. Blake, Mexico, Central America.

1292. *Riencourtia* Cass.

Riencourtia Cass., Dict. Sci. Nat. 45: 466 (1827).

Annual or perennial herbs. Leaves opposite, petiolate or sessile, blades linear to elliptic or ovate, 1–5-veined. Capitula in terminal, open paniculiform cymes of tightly clustered glomerule-like cymes, disciform. Involucres cylindrical, phyllaries in 3–4 series, subequal. Receptacles flat, epaleate. Ray/tubular floret 1, pistillate, corolla white, tubular or with a very reduced limb. Disc florets functionally staminate and campanulate, the lobes with conspicuously long and stiff trichomes, without fibres embedding the vascular strands; anther appendages without glandular trichomes; style arms tapered. Cypselae broadly ellipsoid, biconvex, black or brown with a broad stramineous carpopodium on adaxial side, glabrous to sparsely pubescent especially on apices. Pappus absent. $x = 16$. About six species, neotropics, eastern South America.

1293. ***Schizoptera*** Turcz.

Schizoptera Turcz., Gen. Pl. 2: 191, 349 (1873).

Erect annual herbs. Leaves opposite, petiolate, blades ovate to oval, apices acuminate, triplinerved. Capitula in paniculiform cymes with subumbellate paracladia, on pedicels of various lengths, radiate. Involucres campanulate, phyllaries in 2 series, subequal. Receptacles flat to shallowly convex. Ray florets pistillate, in two rows, corollas golden yellow. Disc florets functionally staminate, rarely perfect, corollas golden yellow with fibres embedding the vascular strands; anthers black, appendages ovate; style arms of disc florets with no or very few stigmatic papillae, style arms of ray florets spreading. Ray cypselae broadly obovate, obcompressed, black, concave, glabrous, margins winged. Disc cypselae when present similar to ray cypselae. Pappus of two awns fused to wings. One species, *S. peduncularis* S.F. Blake, Ecuador.

1294. ***Sphagneticola*** O. Hoffm.

Sphagneticola O. Hoffm., Notizbl. Konigl. Bot. Gart. Berlin-Dahlem 3: 36 (1900); Strother, Syst. Bot. Monogr. 33: 1–111 (1991), rev.; Pruski, Novon 6: 404–418 (1996), reg. rev.
Thelechitonia Cuatrec. (1954).
Complaya Strother (1991).

Perennial herbs, prostrate, rooting at nodes. Leaves opposite, blades ovate to trullate, trilobed, triplinerved. Capitula terminal, appearing axillary, solitary, radiate. Involucres turbinate, phyllaries in 2 series, subequal, apices foliaceous, expanded. Receptacles convex to conical. Ray florets pistillate, corollas golden yellow to orange. Disc florets bisexual, corollas yellow to orange, with long multicellular trichomes on adaxial surface of lobes, without fibres embedding the vascular strands; anthers black, appendages with glandular trichomes; style arms tapered. Ray cypselae trigonal, clavate to obpyriform, winged, wings corky, stramineous, thicker at the base of cypselae, smooth to strongly tuberculate, glabrous. Disc cypselae compressed, biconvex to rounded-quadrate, otherwise as ray cypselae. Pappus an erose or lacerate corona on a stout rostrum, the rostrum and pappus sometimes covered by a corky collar continuous with the cypsela body. $x = 15$. Four species, pantropical.

1295. ***Steiractinia*** S.F. Blake

Steiractinia S.F. Blake, J. Bot. 53: 153 (1915); Díaz-Piedrahita & Vélez-Nauer, Asteraceae-Heliantheae 1. *Steiractinia*, Fl. Colomb. 13: 1–65 (1990), reg. rev.

Shrubs or small trees. Leaves opposite, blades lanceolate to ovate, pinnate or triplinerved. Capitula in terminal, simple or open paniculiform cymes, radiate. Involucres hemispherical, phyllaries in 2–4 series. Receptacles convex. Ray florets neuter, corollas golden yellow. Disc florets bisexual, corollas yellow with a few fibres embedding the vascular strands; anthers brown or black, appendages with or without glandular trichomes; style arms tapered, apices papillose with appendages. Cypselae compressed or obcompressed, shallowly biconvex to quadrate, oblong or obovoid, shallowly to broadly rhombic in outline, black to greyish black and mottled or striped, mostly with 2, rarely 3 or 4 wings. Pappus of numerous bristles disposed radially on neck of cypsela. $x = 14$. Twelve species, Colombia, Ecuador and Venezuela.

1296. ***Synedrella*** Gaertn.

Synedrella Gaertn., Fruct. Sem. Pl. 2: 456 (1791), nom. cons.; McVaugh & Smith, Brittonia 19: 268–272 (1967); Turner, Phytologia 76: 39–51 (1994), rev.

Erect to slightly decumbent annual or perennial herbs. Leaves opposite, shortly petiolate, blades ovate to elliptic, triplinerved. Capitula in axillary, simple cymes, radiate. Involucres cylindrical, phyllaries in 2 series. Receptacles flat. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow with fibres embedding the vascular strands; anthers black, appendages without glandular trichomes; style arms tapered, with papillose appendages. Ray cypselae obcompressed, biconvex, oblong, black, winged, wings deeply lacerate, stramineous, glabrous. Disc cypselae obcompressed, biconvex, obcuneate, black, slightly tuberculate, glabrous. Pappus of 2 awns, in ray cypselae fused to wings, in disc cypselae stout. $x = 18, 19, 20$. One species, *S. nodiflora* Gaertn., neotropics, adventive in other tropical regions.

1297. ***Synedrellopsis*** Hieron. & Kuntze

Synedrellopsis Hieron. & Kuntze, Rev. Gen. 3: 180 (1898); Cabrera, Fl. Prov. de Jujuy, Rep. Argent. 10 (1978), rev.

Prostrate to decumbent annual or perennial herbs rooting at the nodes. Leaves opposite, petiolate, blades ovate to trullate, triplinerved. Capitula axillary, solitary, discoid. Involucres cylindrical, phyllaries 2. Receptacles flat, epaleate. Florets 4, those subtended by the opposing phyllaries tubular, pistillate, corollas 3- or 4-lobed, the

internal bisexual, corollas 4-lobed, yellow and uniformly thickened with sclerified cells; anthers black, appendages without glandular trichomes; style arms tapered, without papillose appendages. Cypselae obcompressed, shallowly rhombic in cross-section, with a shallow ridge on each face, broadly oval to elliptic, black, wings corky, stramineous, deeply lacerate, sparsely pubescent, trichomes uniseriate. Pappus of 2 awns fused to wings. One species, *S. grisebachii* Hieron. & Kuntze, Argentina, Bolivia, Paraguay.

1298. *Tilesia* G. Mey.

Tilesia G. Mey., Prim. Fl. Esseq. 251 (1818); Pruski, Novon 6: 404–418 (1996), reg. rev.
Wulffia Neck. (1790), nom. non rite public.
Wulffia Neck. ex Cass. (1823), nom. cons. prop.

Perennial herbs, mostly scandent shrubs, stems striate. Leaves opposite, blades lanceolate, ovate or oval, pinnately veined or triplinerved. Capitula in terminal, simple or paniculiform cymes, discoid or radiate. Involucres hemispherical, phyllaries in 2–3 series. Receptacles shallowly convex. Ray florets neuter or pistillate but sterile, corollas yellow to orange. Disc florets bisexual, corollas yellow, rarely red, with a few fibres embedding the vascular strands; anthers black, appendages ovate with glandular trichomes; style arms tapered. Cypselae compressed, obpyriform to obovate, rhombic in cross-section, fleshy at maturity, exocarp drying brown, black beneath, glabrous to sparsely pubescent at the apices. Pappus absent or a minute crown. $x = 30$. Three species, tropical, humid forests of America.

1299. *Trigonopterum* Hook. f.

Trigonopterum Hook. f., Q. J. Sci. Lit. Arts ser. 2, 1: 104 (1828); Harling, Acta Horti Bergiani 20: 63–120 (1962), rev.; Eliasson, Bot. J. Linn. Soc. 88: 253–256 (1984), cytol.; Wagner & Robinson, Brittonia 53: 539–561 (2002), tax.

Shrubs. Leaves opposite, blades linear and slightly involute. Capitula terminal, solitary, radiate or discoid. Involucres campanulate to hemispherical, phyllaries in 2 series. Receptacles convex. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow without fibres embedding the vascular strands; anthers black, appendages without glandular trichomes; style arms tapered, apices papillose. Cypselae of ray floret triquetrous, otherwise biconvex, narrowly obpyriform, glabrescent, tuberculate, with 1 wing and 1 or 2 additional weakly developed wings or commissures. Pappus a small, rostrate crown. $x = 14$. One species, *T. laricifolium* (Hook. f.) W.L. Wagner & H. Rob., Galápagos Islands.

1300. *Tuberculocarpus* Pruski

Tuberculocarpus Pruski, Novon 6: 415 (1996); Pruski, Novon 6: 404–418 (1996), rev.

Perennial herbs or subshrubs. Leaves opposite, blades lanceolate, pinnately veined. Capitula terminal, solitary or in simple cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2–3 series. Receptacles flat to shallowly convex. Ray florets neuter, corollas red. Disc florets bisexual, corollas orange-red; anthers black, appendages with glandular trichomes, apices papillose; style arms tapered. Cypselae compressed to subterete, with small wings, black, tuberculate, glabrous with a few trichomes at apices. Pappus a minute crown. One species, *T. ruber* (Aristeg.) J.F. Pruski, southern Venezuela.

1301. *Tuxtla* Villaseñor & Strother

Tuxtla Villaseñor & Strother, Syst. Bot. 14: 537 (1989).

Lianas or scandent shrubs. Leaves opposite, blades elliptic, 3–5-plinerved. Capitula in terminal, corymbiform cymes, radiate. Involucres campanulate, phyllaries in 2–3 series. Receptacles convex. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow with fibres embedding the vascular strands; anthers brown or black, appendages with minute glandular trichomes extending to distal parts of connective; style arms tapered, apices shortly papillose. Ray cypselae triquetrous, brown or black with stramineous wings, glabrous. Disc cypselae compressed, biconvex, otherwise as ray cypselae. Pappus of 2–3 awns continuous with wings and body of cypsela. $x = 17$. One species, *T. pittieri* (Greenm.) Villaseñor & Strother, Mexico, Costa Rica.

1302. *Wamalchitamia* Strother

Wamalchitamia Strother, Syst. Bot. Monogr. 33: 30 (1991).

Shrubs. Leaves opposite, blades ovate to lanceolate, triplinerved. Capitula terminal, solitary or in open dichasial cymes, radiate. Involucres broadly cylindric to hemispheric, phyllaries in 2–4 series. Receptacles flat to convex. Ray florets pistillate, corollas yellow to red-orange. Disc florets bisexual, corollas yellow to orange without fibres embedding the vascular strands; anthers black, appendages

without glandular trichomes; style arms tapered, apices with a long papillose appendage. Cypselae prismatic, narrowly cuneate to linear in outline, those of the ray triquetrous, otherwise compressed, quadrate, rarely 5-angled, not winged, dark reddish brown to black, glabrous. Pappus of 1–5 unequal, fragile or persistent awns plus 0–6 minute, free or strongly connate squamellae, all inserted directly on apex of cypsela body and not raised on a rostrum. n = 89–96, 100–108, 110. Four species, Mexico and Central America.

1303. *Wedelia* Jacq.

Wedelia Jacq., Enum. Syst. Pl. 8: 28 (1760), nom. cons.; Strother, Syst. Bot. Monogr. 33: 1–111 (1991), rev.
Aspilia Thouars (1806).

Erect to prostrate annual or perennial herbs, shrubs. Leaves opposite, blades lanceolate to ovate, oval or elliptic, subcordate, usually triplinerved, sometimes trilobed, rarely deeply serrate. Capitula terminal, solitary or in open paniculiform cymes, radiate, rarely discoid. Involucres campanulate to hemispherical, phyllaries in 2–4 series. Receptacles convex. Ray florets pistillate, fertile or neuter, corollas yellow to yellow-orange, sometimes white, pink or burgundy. Disc florets bisexual, corollas yellow to orange, without fibres embedding the vascular strands; anthers light to dark brown or black, appendages with glandular trichomes; style arms tapered to deltoid, apices papillose. Cypselae of ray floret obcompressed, triquetrous, obovate or oblong, grey, brown or black, sometimes mottled, glabrous to moderately pubescent, winged at angles of cypselae or without wings, with an elaiosome. Disc cypselae like those of the ray, biconvex. Pappus on a rostrum, an erose cup or corona with 0–3 unequal, persistent awns. x = 11, 12, 13. Approximately 110 species, pantropical, most species in America.

1304. *Wollastonia* DC. ex Decne

Wollastonia DC. ex Decne, Nouv. Ann. Mus. Hist. Nat. 3: 414 (1834); Fosberg & Sachet, Smithsonian Contr. Bot. 45: 1–40 (1980), rev.; Wagner & Robinson, Brittonia 53: 539–561 (2002), rev.

Perennial herbs or weak shrubs. Leaves opposite, blades oval to ovate, triplinerved. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres hemispherical, phyllaries in 2 series. Receptacles convex. Ray florets pistillate, yellow. Disc florets bisexual, corollas yellow or greenish yellow, without fibres embedding the vascular strands; anthers brown to black. Ray cypselae cuneiform, triquetrous, with truncate, flat apices, hirtellous on distal end. Disc cypselae compressed and shallowly quadrate, shallowly rhombic in outline, otherwise as ray cypselae. Pappus absent or of a single awn. One species, *W. biflora* (L.) DC., Indo-Pacific coastal regions.

1305. *Zexmenia* La Llave & Lex.

Zexmenia La Llave & Lex., Nov. Veg. Descr. 1: 13 (1824); Strother, Syst. Bot. Monogr. 33: 1–111 (1991), rev.

Scandent to erect perennial herbs, shrubs or lianas. Leaves opposite, blades ovate-elliptic to lanceolate, pinnately nerved or triplinerved. Capitula in terminal, simple dichasia or umbelliform cymes, radiate. Involucres broadly campanulate to hemispheric, phyllaries in 2–3 series. Receptacles convex. Ray florets pistillate, corollas yellow to yellow-orange. Disc florets bisexual, corollas yellow to orange with or without a few fibres embedding the vascular strands; anthers black, appendages ovate with a few glandular trichomes; style arms tapered, apices papillose. Cypselae compressed, those of the ray triquetrous, oblanceolate to narrowly cuneate, winged, stramineous to dark brown or blackish, sparsely pubescent distally, the wings thin to corky. Pappus on a distinct rostrum, of 2–3 unequal awns plus 4–10 minute awns often connate to form a lacerate cup. Two species, Mexico and Central America.

1306. *Zyzyxia* Strother

Zyzyxia Strother, Syst. Bot. Monogr. 33: 91 (1991).

Shrubs or small trees. Leaves opposite, blades lanceolate to narrowly elliptic, pinnately nerved. Capitula terminal, solitary or in simple dichasia, radiate. Involucres broadly campanulate to hemispheric, phyllaries in 2–3 series, gradate. Receptacles convex. Ray florets neuter, corollas yellow. Disc florets bisexual, corollas yellow with fibres embedding the vascular strands; anthers brown, appendages without glandular trichomes; style arms tapered, apices papillose. Cypselae compressed, oblong, brownish, sparsely ciliate distally and on angles. Pappus of 2–3 persistent, unequal awns and 6–10 free or variously connate bristles between the awns, all borne on a rostrum. One species, *Z. lundellii* (H. Rob.) Strother, Mexico and Belize.

XXVI.5. Subtribe Enceliinae Panero (2005).

Annual or perennial herbs, shrubs, rarely trees. Leaves usually alternate, petiolate, sometimes with resinous exudates, blades linear to ovate or trullate, sometimes laciniate. Capitula terminal, solitary and scapose or in paniculiform or corymbiform cymes, radiate or discoid. Involucres turbinate, campanulate or hemispheric, phyllaries in 2–5 series, subequal, rarely gradate, herbaceous, rarely chartaceous, sometimes with resinous exudates. Receptacles flat to convex, paleae deciduous. Ray florets neuter or rarely pistillate but sterile, corollas sometimes with biseriate trichomes on tube, rarely on limb. Disc florets bisexual, corollas 5-lobed, mostly without fibres embedding the vascular strands, lobes sometimes with thickened cells or with glandular or multicelular trichomes on lobe abaxial surfaces; stamens 5, yellow, brown or black, appendages linear to ovate, sometimes with glandular trichomes, endothecium cells fusiform rarely quadrate with 1–3 polar bridges; styles with two vascular strands, style arms with fused stigmatic surfaces, some species with two stigmatic surfaces which fuse slightly above style bifurcation point, densely papillose below, apices acute to broadly acute. Cypselae compressed, rarely thickened or terete, obovate to oblong, densely sericeous, rarely glabrous, sometimes with conspicuous wings or bands/margins at cypselae edges and neck. Pappus of two slender awns with or without squamellae in between, rarely absent, rarely of awns fused into a crown surrounding the neck.

Key to the Genera

1. Plants with mostly solitary, large capitula on long, leafless peduncles **1308. *Enceliopsis***
– Plants otherwise 2
2. Shrubs or small trees 3
– Annual or perennial herbs 4
3. Cypselae strongly flattened with glabrous or sparsely pubescent faces and ciliate margins; leaves mostly canescent, never resinous or glutinous; disc corollas yellow or purple, rarely white **1307. *Encelia***
– Cypselae biconvex, not strongly flattened, with sparsely to densely pubescent faces and mostly without ciliate margins; leaves mostly green, resinous or glutinous or membranaceous; disc corollas yellow **1309. *Flourensia***
4. Phyllaries conspicuously ciliate; cypselae without a white or stramineous edge or this wanting; cypselae apices with a conspicuous crown surrounding neck of cypsela and fused to awns **1310. *Geraea***
– Phyllaries glabrescent to variously pubescent, rarely ciliate; cypselae mostly with a conspicuous white/yellow (when fresh) or stramineous (when dry) wing surrounding cypselae; cypselae apices without a crown surrounding neck 5
5. Cypselae with a pappus of two awns and intervening squamellae, rarely squamellae absent, cypselae mostly without conspicuously ciliate margins **1311. *Helianthella***
– Cypselae epappose or with a pappus of two awns and without intervening squamellae, cypselae mostly with conspicuously ciliate margins **1307. *Encelia***

Genera of Enceliinae

1307. *Encelia* Adans.

Encelia Adans., Fam. Pl. 2: 128 (1763); Blake, Proc. Amer. Acad. Arts 49: 346–396 (1913), rev.

Annual or perennial herbs, shrubs. Leaves alternate, blades linear to ovate sometimes laciniate, triplinerved or with a single vein. Capitula terminal, solitary or in open paniculiform cymes, rarely in a corymbiform cyme, radiate or discoid. Involucres campanulate to hemispherical, phyllaries in 2–4 series, subequal. Receptacles shallowly convex. Ray corollas yellow, rarely white, sometimes with biseriate trichomes on tube and along veins. Disc corollas yellow or deep purple; anthers yellow or black, appendages ovate with glandular trichomes; style arms with fused stigmatic surfaces, sometimes divided at very base, apices acute. Cypselae broadly obovate to oblong, margins deeply ciliate, sparsely to densely pubescent. Pappus of two awns, rarely of one or absent. $x = 17, 18$. Fifteen species, Mexico, western USA, Galápagos Islands, Peru, Chile.

1308. *Enceliopsis* (A. Gray) A. Nelson

Enceliopsis (A. Gray) A. Nelson, Bot. Gaz. 47: 432 (1909).

Perennial herbs or shrubs (caulirosula). Leaves alternate, petiolate, leaf internodes very short above taproot producing a rosette, blades ovate to oblong, sometimes glaucous, bluish when fresh, semisucculent, triplinerved. Capitula terminal, solitary (rarely with 2–3 capitula) on long leafless scapes, radiate or discoid. Involucres hemispheric, phyllaries in 2–4 series, subequal. Receptacles shallowly convex. Ray corollas yellow, sometimes with biseriate trichomes on tube. Disc corollas yellow; anthers yellow, appendages ovate with glandular trichomes; style arms with stigmatic surfaces continuous, sometimes divided at very base, apices acute. Cypselae broadly obovate to oblong with yellow-

ish and strongly ciliate or glabrous margins, sometimes with trichomes on centre of cypselae. Pappus of two awns or small shoulders with few squamellae in between. $x = 17, 18$. Four species, western USA.

1309. *Flourensia* DC.

Flourensia DC., Prodr. 5: 592 (1836); Dillon, Fieldiana Bot. n.s. 16: 1–66 (1984), rev.

Shrubs or small trees. Leaves alternate, blades lanceolate to ovate, pinnately nerved, usually with resinous exudates, entire to broadly dentate. Capitula terminal, solitary or in paniculiform or corymbiform cymes, radiate or discoid. Involucres turbinate, campanulate to hemispheric, phyllaries in 2–5 series, subequal to gradate. Receptacles flat to convex. Ray florets rarely pistillate and sterile, corollas golden yellow, sometimes with biseriate trichomes on tube. Disc corollas golden yellow; anthers yellow or black, appendages sometimes with glandular trichomes; style arms with continuous stigmatic surfaces, apices acute to broadly acute. Cypselae thickened, rarely terete, obovate to oblong, glabrous to densely sericeous with ciliate margins. Pappus absent or most commonly of 2 rarely 3 or 4 persistent or caducous awns. $x = 18$. About 33 species, Mexico, south-western USA, south-central Andes and interior of central Argentina.

1310. *Geraea* Torr. & A. Gray

Geraea Torr. & A. Gray, Proc. Amer. Acad. Arts 1: 48 (1846) [1847].

Erect annuals. Leaves alternate, blades ovate to trullate, triplinerved. Capitula in terminal, open paniculiform cymes, radiate or discoid. Involucres hemispheric, phyllaries in 2–3 series, subequal, conspicuously ciliate. Receptacles shallowly convex. Ray corollas golden yellow. Disc corollas golden yellow; anthers yellow, appendages with few glandular trichomes; style arms with continuous stigmatic surfaces, apices acute. Cypselae oblong to obovate, densely sericeous except for base, with yellowish wings and crown. Pappus of two awns fused to a crown projecting from the neck. $x = 18$. Two species, north-western Mexico, south-western USA.

1311. *Helianthella* Torr. & A. Gray

Helianthella Torr. & A. Gray, Fl. NW Coast 2: 333 (1842); Weber, Amer. Midl. Naturalist 48: 1–35 (1952), rev.

Perennial herbs. Leaves opposite, alternate distally, blades linear to ovate-lanceolate, triplinerved to pentanerved. Capitula terminal, solitary or in corymbiform cymes, radiate. Involucres hemispherical, phyllaries in 2–4 series, subequal, rarely gradate, the outermost sometimes enlarged and leaf-like. Receptacles flat or convex. Ray corollas yellow, sometimes with biseriate trichomes on tube. Disc corollas yellow, purple or brownish-purple; anthers brown or black, appendages sometimes with glandular and tapered trichomes; style arms with continuous stigmatic surfaces, sometimes at very base with two stigmatic areas parallel to each other, apices acute. Cypselae sometimes shallowly winged, cuneate to obcordate, blackish brown, glabrous to variously pubescent. Pappus absent or of two persistent awns, sometimes with a crown of short, lacerate squamellae. $x = 15$. Eight species, western Canada and USA, northern Mexico.

XXVI.6. Subtribe Engelmanniinae Stuessy (1977); Bolick, Adv. Clad. 2: 125–144 (1983), phylog.; Clevinger & Panero, Amer. J. Bot. 87: 565–572 (2000), phylog.; Moore & Bohs, Amer. J. Bot. 90: 1653–1660 (2003), phylog.

Annual or perennial herbs, rarely shrubs. Leaves alternate or opposite, blades ovate to oblong, trullate, rarely obovate or sagittate, sometimes perfoliate, entire or pinnatifid. Capitula terminal, solitary, sometimes on long scapes, or in open paniculiform cymes, radiate, rarely discoid. Involucres mostly hemispheric, sometimes campanulate, phyllaries in 2–4 series, usually subequal, sometimes gradate, ovate to suborbicular, mostly herbaceous, sometimes with indurate bases. Receptacles flat to convex. Ray florets pistillate, fertile, rarely in two series. Disc florets 5-lobed, bisexual or functionally staminate, corollas with slender to prominent fibres embedding vascular strands, glabrous to moderately pubescent; stamens 5, anthers rarely shallowly calcarate, rarely tailed, anther appendages with or without glandular trichomes; styles with two vascular strands, style arms either fused and filiform, or slender with parallel stigmatic surfaces fusing at distal end of style arms, sometimes with continuous stigmatic surfaces, sometimes with glandular trichomes. Ray cypselae obcompressed and in some species with functionally staminate disc florets associated with the 2(–4) adjacent disc florets and paleae, or shallowly quadrate or triquetrous.

Disc cypselae when present compressed, narrowly rhombic in cross-section. Pappus mostly of two awns at angles of cypselae sometimes associated with a few scales, sometimes of several minute scales, a cup of fused squamellae or absent.

Key to the Genera

1. Disc florets bisexual 2
– Disc florets functionally staminate 4
2. Fibre sheaths of disc corollas continuous along edges of lobes; paleae stiff, lignified, apices becoming acicular with age, stoloniferous shrubs of coastal marshes of North America, Caribbean and Peru **1313. *Borrichia***
– Fibre sheaths of disc corollas restricted to the throats; paleae flexible, not lignified, apices not acicular with age; perennial herbs or shrubs, rarely stoloniferous, of mountainous regions of North America 3
3. Shrubs of north-eastern Mexico; anthers with glandular trichomes on appendages and connectives **1318. *Vigethia***
– Perennial herbs of western North America; anthers with glandular trichomes on appendages, not on the connectives **1319. *Wyethia***
4. Capitula with 2 series of ray florets; ray cypselae not associated with adjacent 2–4 disc florets and associated paleae **1317. *Silphium***
– Capitula with 1 series of ray florets; ray cypselae associated with adjacent 2–4 disc florets and associated paleae 5
5. Leaves opposite **1314. *Chrysogonum***
– Leaves alternate 6
6. Leaves entire, ovate, rhombic or trullate, rarely trilobed 7
– Leaves pinnatisect or lyrate 8
7. Phyllaries suborbicular; styles with glandular trichomes **1312. *Berlandiera***
– Phyllaries ovate; styles without glandular trichomes **1316. *Lindheimera***
8. Disc corollas red; veins of ray corollas green or reddish; phyllaries of outermost series suborbicular; foliage dull green **1312. *Berlandiera***
– Disc corollas yellow; veins of ray corolla yellow; phyllaries of outermost series narrowly ovate; foliage bright green **1315. *Engelmannia***

Genera of Engelmanniinae

1312. *Berlandiera* DC. Fig. 94

Berlandiera DC., Prodr. 5: 517 (1836); Pinkava, Brittonia 19: 285–298 (1967), rev.

Perennial herbs, sometimes with strong, pungent odour. Leaves alternate, simple, ovate to obovate, sometimes pinnatifid, serrate to runcinate. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres hemispheric, phyllaries in 2–3 series, subequal, broadly ovate to suborbicular, bases indurate, herbaceous apices

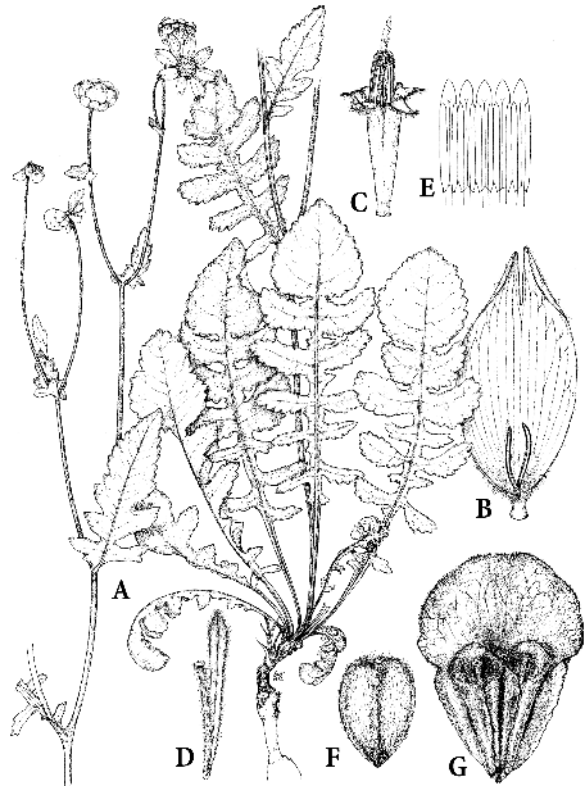

Fig. 94. Compositae-Heliantheae. *Berlandiera lyrata*. **A** Habit. **B** Ray corolla. **C** Disc corolla. **D** Ovary of sterile disc floret and attached palea. **E** Anthers. **F** Ray cypsela. **G** Inner face of phyllary and two attached paleae. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

spreading. Receptacles shallowly convex. Ray florets pistillate, corollas light to golden yellow. Disc florets functionally staminate, corollas yellow or deep red or burgundy; anthers black to reddish black, appendages densely covered with glandular trichomes on abaxial side; style arms of disc florets fused and filiform with glandular trichomes, of ray florets with divided stigmatic surfaces. Cypselae obcompressed, suborbicular, flat or with a median rib on each tangential side. Pappus of a few scales or absent. $x = 15$. Four species, Mexico, USA.

1313. *Borrichia* Adans.

Borrichia Adans., Fam. Pl. 2: 130, 527 (1763); Semple, Ann. Missouri Bot. Gard. 66: 681–693 (1978), rev.

Stoloniferous shrubs of muddy or sandy coastal marshes. Leaves opposite, blades obovate, succulent, perfoliate, entire to broadly serrate. Capitula terminal, solitary, radiate. Involucres hemispheric,

phyllaries in 2–4 series, subequal. Receptacles convex, paleae lignified, apices somewhat acicular, capitulum echinate. Ray florets pistillate, corollas yellow, sometimes persistent and shed with cypsela, tube lacking. Disc florets bisexual, fertile, corollas yellow, fibres meeting at each lobe apex; anthers black, with glandular trichomes on abaxial side of appendages and connectives; style arms with continuous stigmatic surfaces, tapered. Cypselae obcompressed, oblong, rhombic in outline, with a median rib on each tangential side. Pappus a cup with an erose, sinuate edge, sometimes with free squamellae. $x = 13, 14$. Two species, tropical and subtropical coasts of North America and Caribbean, Peru.

1314. *Chrysogonum* L.

Chrysogonum L., Sp. Pl. 2: 920 (1753); Stuessy, Rhodora 79: 190–202 (1977), rev.

Stoloniferous perennial herbs. Leaves opposite, petiolate, ovate to suborbicular, shallowly serrate. Capitula terminal, solitary or in simple dichasial cymes, radiate. Involucres hemispherical, phyllaries in 2 series, subequal, broadly ovate, dimorphic. Receptacles shallowly convex. Ray florets pistillate, corollas yellow. Disc florets functionally staminate, corollas yellow; anthers black, shallowly tailed, shallowly calcarate, appendages ovate; style arms of disc florets filiform, abaxial sides deeply papillose, style arms of ray florets 2–3, spreading, with a continuous stigmatic surface. Ray cypselae obcompressed, suborbicular, with a median rib on each tangential side. Pappus of two small awns or squamellae. $x = 16$. One species, *C. virginianum* L., south-eastern USA.

1315. *Engelmannia* Torr. & A. Gray

Engelmannia Torr. & A. Gray, Trans. Amer. Philos. Soc. n.s. 7: 343 (1840).

Perennial herbs. Leaves alternate, blades ovate to oval, pinnatifid, venation pectinate. Capitula in terminal, paniculiform cymes, radiate. Involucres hemispherical, phyllaries in 2–3 series, dimorphic. Receptacles shallowly convex. Ray florets pistillate, corollas yellow. Disc florets functionally staminate, corollas yellow; anthers black; style arms of disc florets filiform, those of ray florets spreading with fused stigmatic surfaces. Cypselae obcompressed, broadly ovate to oblong or suborbicular with a median rib on each tangential side. Pappus of 2–4 unequal awns, those at edge of cypselae longer. $x = 9$. One species, *E. peristenia* (Raf.) G.J. Goodman & C.A. Lawson, south-western USA, Mexico.

1316. *Lindheimera* A. Gray & Engelm.

Lindheimera A. Gray & Engelm., Proc. Amer. Acad. Arts 1: 47 (1846) [1847]; Hind, Kew Mag. 7: 128–131 (1990), rev.

Erect annuals. Leaves alternate or opposite, blades ovate to trullate, rarely sagittate, weakly triplinerved, sinuate to broadly dentate. Capitula in terminal, dichasial paniculiform cymes, rarely solitary, radiate. Involucres campanulate, phyllaries in 2 series, normally 5 in each series, strongly dimorphic. Receptacles shallowly convex. Ray florets pistillate, mostly 5, corollas golden yellow. Disc florets functionally staminate, corollas yellow; anthers black, appendages without glandular trichomes; styles of disc florets filiform, style arms fused, those of ray florets spreading with acute apices, stigmatic surfaces divided. Cypselae obcompressed, broadly ovate to oblong or suborbicular with a median rib on each tangential side, wings entire and fused to pappus. Pappus of two diverging awns. $x = 8$. One species, *L. texana* A. Gray, south-western USA, northern Mexico.

1317. *Silphium* L.

Silphium L., Sp. Pl. 2: 919 (1753); Clevinger & Panero, Amer. J. Bot. 87: 565–572 (2000), phylog.

Perennial herbs, sometimes forming a rosette. Leaves opposite or alternate, blades ovate to trullate, sometimes perfoliate, simple or deeply dissected, venation pectinate, rarely triplinerved. Capitula terminal, solitary or in paniculiform cymes, sometimes with very short internodes and pedicels and capitula congested on a short axis, radiate. Involucres hemispherical, rarely campanulate, phyllaries broadly ovate to suborbicular. Receptacles flat to shallowly convex. Ray florets pistillate, in 2 series, corollas golden yellow, stramineous or white. Disc florets functionally staminate, corollas pale to golden yellow or white; anthers black; style arms of disc florets fused, filiform, those of ray florets spreading with fused stigmatic surfaces. Cypselae obcompressed, broadly obovate to suborbicular or oblong, margins winged. Pappus of two small awns connate to the wings or absent. $x = 7$. About 25 species, USA, Canada.

1318. *Vigethia* W.A. Weber

Vigethia W.A. Weber, Madroño 7: 98 (1943).

Shrubs. Leaves alternate, ovate to subcordate, serrate. Capitula terminal, solitary or in simple dichasial cymes, radiate. Involucres hemispherical, phyllaries in 5–7 series, subequal, outermost reflexed. Receptacles convex. Ray florets pistillate, sometimes with staminodes, corollas light yellow. Disc florets bisexual, corollas yellow; anthers black, appendages with glandular trichomes on abaxial side and on connective; style arms of disc florets with stigmatic surfaces divided at the base, fused midway, tapered, papillose, style arms of ray florets spreading, with acute apices. Cypselae ovate to oblong, obcompressed to quadrate, ray cypselae triquetrous to shallowly quadrate. Pappus of several lacerate, minute scales. $x = 19$. One species, *V. mexicana* (S. Watson) W.A. Weber, north-eastern Mexico.

1319. *Wyethia* Nutt.

Wyethia Nutt., J. Acad. Nat. Sci. Philadelphia 7: 39 (1834); Sharp, Ann. Missouri Bot. Gard. 22: 51–153 (1935), rev.; Weber, Amer. Midl. Naturalist 35: 400–452 (1946), rev.; Moore & Bohs, Amer. J. Bot. 90: 1653–1660 (2003), phylog.

Balsamorhiza Nutt. (1840).

Scabrethia W.A. Weber (1999).

Agnorhiza W.A. Weber (1999).

Perennial herbs with thickened taproots, sometimes forming large stoloniferous colonies in shifting sand dunes, sometimes resinous. Leaves alternate or opposite, blades linear to deltate-ovate, spathulate, entire, deeply lobed to serrate. Capitula terminal, large, very showy, solitary or few in paniculiform cymes, on floral scapes with or without leaves, radiate or discoid. Involucres broadly campanulate to hemispheric, phyllaries in 2–6 series. Receptacles broadly convex. Ray florets pistillate, yellow to light yellow or white. Disc florets bisexual, corollas golden yellow, sometimes fibres wanting; anther appendages with glandular trichomes on abaxial side; style arms with parallel or continuous stigmatic surfaces, sometimes fused at mid to distal end. Cypselae ovate to oblong, compressed to shallowly quadrate, ray cypselae triquetrous to shallowly quadrate. Pappus absent or a crown of persistent scales, some species with slender awns at angles of cypselae. $x = 19$. About 28 species, western North America.

XXVI.7. Subtribe Helianthinae Dumort. (1827).

Subtribe Lagasceinae Benth. & Hook. f. (1873).

Annual or perennial herbs, shrubs, trees. Leaves alternate or opposite, blades unlobed to dissected, pinnately veined to mostly triplinerved, rarely pentanerved, entire to deeply serrate. Capitula terminal, rarely axillary, solitary or in simple to large monochasial or dichasial paniculiform or corymbiform cymes, sometimes with fistulose peduncles, capitula discoid or radiate, rarely disciform. Involucres cylindrical to hemispherical, phyllaries in 2–7 series, subequal to gradate, most commonly with an indurate base and herbaceous apices, innermost normally smaller than outermost, outermost often foliaceous. Receptacles flat to conic, paleae sometimes forming perigynia and shedding with cypselae as a unit. Ray florets neuter, sometimes with a vestigial style or fertile anther. Disc florets bisexual, rarely functionally pistillate, corollas pentamerous, without fibres embedding the vascular strands, sometimes apices of lobes with sclerified cells; stamens 5, filaments rarely papillose; styles with two vascular strands, style arms with fused stigmatic surfaces, deltate, sometimes with long and tapered apices, sometimes with a narrow, cylindric appendage. Cypselae compressed, biconvex in cross-section, rarely quadrate to terete, mostly black, striate, glabrous to densely pubescent. Pappus absent or more commonly of two awns with or without squamellae in between, sometimes a crown of awns.

Key to the Genera

1. Capitula with 1–6(–8) disc florets — 2
– Capitula with more than 10 disc florets — 4
2. Phyllaries fused except for distal herbaceous apices — **1328. *Lagascea***
– Phyllaries free — 3
3. Leaves opposite; cypselae terete, circular in cross-section; pappus of multiple awns — **1321. *Alvordia***
– Leaves alternate; cypselae biconvex to weakly quadrangular, rhombic in cross-section; pappus absent — **1323. *Calanticaria***
4. Capitula with paleae tightly wrapping cypselae (perigynia) and shed with cypsela as a unit — 5
– Capitula with paleae not tightly wrapping cypselae, if deciduous, then generally not shed with cypselae as a unit — 6
5. Disc florets with black papillose trichomes on adaxial surface of throat; anthers mostly yellow — **1333. *Sclerocarpus***
– Disc florets without black papillose trichomes on adaxial surface of throat; anthers black — **1320. *Aldama***

6. Plants forming weak rosettes with scapose capitula; cypselae shallowly quadrate, broadly rhombic in outline; corollas pink, purple or yellow, rarely white **1327. *Iostephane***
– Plants otherwise with capitula in paniculiform or corymbiform cymes, rarely scapose; cypselae biconvex; corollas yellow to golden yellow 7
7. Cypselae with a well-developed elaiosome; pappus of two broad awns and mostly 4 intervening squamellae; perennial herbs or shrubs of the western Andes in central Peru **1336. *Syncretocarpus***
– Cypselae without elaiosomes; pappus various; plants from America 8
8. Leaves alternate, capitula in monochasial cymes, rarely solitary 9
– Leaves opposite, capitula in dichasial cymes, rarely solitary 19
9. Shrubs or trees of the Galápagos Islands; corollas mostly white, rarely greenish **1332. *Scalesia***
– Annual or perennial herbs, shrubs or trees of continental America, Caribbean; corollas yellow, very rarely white (*Viguiera*) 8
10. Peduncles shallowly to strongly fistulose **1337. *Tithonia***
– Peduncles never fistulose 11
11. Pappus caducous, rarely absent 12
– Pappus persistent 17
12. Pappus absent 13
– Pappus of two awns and sometimes a few intervening squamellae, mostly easily caducous 14
13. Abaxial leaf surfaces with glandular trichomes; cypselae glabrous **1325. *Heliomeris***
– Abaxial leaf surfaces without glandular trichomes; cypselae pubescent **1326. *Hymenostephium***
14. Plants with tuberous roots 15
– Plants without tuberous roots 16
15. Cypselae shallowly quadrate, tubers long, cylindrical **1330. *Phoebanthus***
– Cypselae biconvex, never shallowly quadrate, tubers round or elliptic; North America **1324. *Helianthus***
16. Annual or perennial herbs, apices of paleae trilobed; anther thecae brown or deep purple **1324. *Helianthus***
– Annual or perennial herbs, shrubs; apices of paleae round to acute; if perennial herbs, then anther thecae yellow, otherwise brown or black; Colombia, Ecuador and Peru **1329. *Pappobolus***
17. Capitula in congested corymbiform cymes arranged in paniculiform cymes; phyllaries shortly aristate, narrow tips spreading and with long, white trichomes **1335. *Stuessya***
– Capitula in open corymbiform or paniculiform cymes; phyllaries acute to acuminate, never shortly aristate, trichomes otherwise 18
18. Phyllaries with ovate, indurate bases and linear, spreading, herbaceous apices; shrubs; Sonoran and Mojave deserts, Baja California; $x = 18$ **1322. *Bahiopsis***
– Phyllaries various, rarely with ovate, indurate bases and spreading, herbaceous apices; annual or perennial herbs, shrubs; America, rarely in Sonoran or Mojave deserts or in Baja California; $x = 17$ **1338. *Viguiera***
19. Cypselae with a narrow corky rim; accessory branches of the inflorescences mostly arising at nearly 90° from main axis; south-western Mexico **1331. *Rhysolepis***
– Cypselae without a narrow corky rim; accessory branches of the inflorescences mostly arising at 40–70° from main axis; America 20
20. Involucres cylindrical to narrowly campanulate, phyllaries strongly indurate with narrow herbaceous apices; cypselae epappose; Sonora, Mexico **1321. *Alvordia***
– Involucres various, if cylindrical to narrowly campanulate and phyllaries strongly indurate, then phyllaries with a herbaceous rim, cypselae pappose and plants from coastal ranges of Sonora (*Viguiera* in part) 21
21. Plants with solitary capitula, shrubs with bicoloured, small, ovate to trullate, rarely round leaves, abaxial side densely pubescent **1323. *Calanticaria***
– Plants with capitula in paniculiform cymes, rarely solitary, if solitary, then leaves not conspicuously bicoloured 22
22. Leaves mostly auriculate; cypselae strongly flattened, nearly linear in cross-section, mostly with embryo as an oval protuberance in the centre of cypselae, if cypsela plump throughout and biconvex in cross-section, then ray corollas pale lemon-yellow with conspicuous greenish or reddish corolla veins; apices of lobes of disc corollas mostly with sclerified cells **1334. *Simsia***
– Leaves not auriculate; cypselae not strongly flattened, biconvex in cross-section, corollas mostly yellow or golden yellow, rarely with pale lemon-yellow ray corollas and veins conspicuously contrasting against corolla background; apices of lobes of disc corollas without sclerified cells 23
23. Cypselae with a pappus of two awns and some intervening squamellae **1338. *Viguiera***
– Cypsela with a pappus of several squamellae or absent 24
24. Leaves mostly lanceolate with glandular trichomes on abaxial surface; temperate North America **1325. *Heliomeris***
– Leaves mostly ovate, rarely lanceolate, without glandular trichomes on abaxial surface; tropical America **1326. *Hymenostephium***

Genera of Helianthinae

1320. *Aldama* La Llave

Aldama La Llave, Nov. Veg. Descr. 1: 14 (1824); Feddema, Ph.D. Thesis, University of Michigan, Ann Arbor: 1–132 (1966); Feddema, Phytologia 21: 308–314 (1971), rev.

Erect annuals. Leaves opposite, alternate towards the inflorescences, blades lanceolate to narrowly ovate. Capitula in open corymbiform cymes, radiate or discoid. Involucres campanulate to subhemispheric, phyllaries in 2–3 series, subequal. Receptacles convex to hemispheric, paleae indurate and wrapping tightly around cypselae (perigynia), appearing tubular, deciduous with the cypsela. Ray floret corollas yellow to orange. Disc floret corollas yellow; anthers black. Cypselae biconvex to slightly trigonous, black, adaxial side straight to slightly

concave, glabrous. Pappus a minute corona of lacerate squamellae or absent. $x = 17$. Two species, Mexico, Central America, northern South America.

1321. *Alvordia* Brandegee

Alvordia Brandegee, Proc. Calif. Acad. Sci. ser. 2, 2: 174 (1889); Carter, Proc. Calif. Acad. Sci. 30: 157–174 (1964), rev.
Agiabampoa Rose ex Hoffm. (1894).

Shrubs. Leaves opposite, blades lanceolate to ovate. Capitula in congested corymbiform cymes or open paniculiform cymes of congested corymbiform cymes, discoid or radiate. Involucres cylindrical to narrowly campanulate, phyllaries in 2–5 series, gradate. Receptacles flat. Ray floret corollas yellow. Disc florets 1 to few per head, corollas bright yellow; anthers yellow. Cypselae obovoid, slightly flattened to quadrangular, black, glabrous. Pappus of multiple, lanceolate, lacerate squamellae or absent. $x = 17$. Four species, Mexico.

1322. *Bahiopsis* Kellogg

Bahiopsis Kellogg, Proc. Calif. Acad. 2: 35 (1863); Schilling, Madroño 37: 149–170 (1990), rev. as *Viguiera*; Schilling & Panero, Bot. J. Linn. Soc. 140: 65–76 (2002), phylog.
Viguiera Kunth sect. *Bahiopsis* (Kellogg) E.E. Schill. (1990).

Shrubs. Leaves opposite, blades ovate to deltate, unlobed or rarely laciniate. Capitula solitary and scapose or mostly in open paniculiform cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2–4 series, subequal, distally tapered and herbaceous. Receptacles convex. Ray floret corollas golden yellow. Disc floret corollas yellow; anthers black to reddish brown. Cypselae biconvex, obovate, black or brown, glabrous to moderately pubescent. Pappus of 2 awns and few lacerate squamellae. $x = 18$. Twelve species, north-western Mexico, south-western USA.

1323. *Calanticaria* (B.L. Rob. & Greenm.) E.E. Schill. & Panero

Calanticaria (B.L. Rob. & Greenm.) E.E. Schill. & Panero, Bot. J. Linn. Soc. 140: 73 (2002); González Elizondo et al., Acta Bot. Mexicana 53: 35–48 (2000), new spp., as member of *Viguiera*; Schilling & Panero, Bot. J. Linn. Soc. 140: 65–76 (2002), phylog.

Shrubs. Leaves opposite or alternate, blades ovate, trullate to round. Capitula solitary or few in tight corymbiform cymes, radiate, rarely discoid. Involucres campanulate to hemispheric, phyllaries in 2–3 series, subequal. Receptacles convex. Ray floret corollas yellow to golden yellow. Disc floret corollas yellow; anthers brown or yellow. Cypselae biconvex, obovate to cuneate, black or mottled black and brown, glabrous to moderately pubescent. Pappus of 2 awns and few, lacerate squamellae or absent. Five species, northern Mexico.

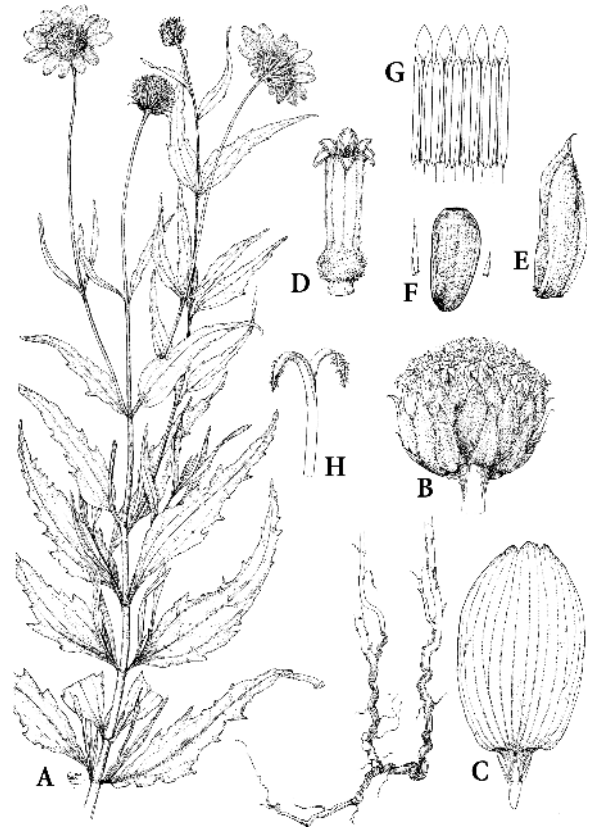

Fig. 95. Compositae-Heliantheae. *Helianthus laciniatus*. **A**. Habit, terminal and lower portions of plant. **B** Capitulum. **C** Ray corolla. **D** Disc corolla. **E** Palea. **F** Cypsela with caducous awns. **G** Anthers. **H** Style arms. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

1324. *Helianthus* L. Fig. 95

Helianthus L., Sp. Pl. 2: 904 (1753); Heiser, Mem. Torrey Bot. Club 22: 1–218 (1969), rev.; Heiser & Schilling, Taxon 30: 393–403 (1981), class.; Schilling et al., Syst. Bot. 23: 177–187 (1998), phylog.

Erect annual or perennial herbs, occasionally with tuberous roots. Leaves alternate, sometimes opposite, blades unlobed. Capitula solitary or in open paniculiform cymes, discoid or radiate. Involucres

campanulate to hemispherical, phyllaries in 2–5 series, subequal. Receptacles flat to shallowly convex, paleae with trilobed apices. Ray corollas yellow to golden yellow. Disc floret corollas yellow to greenish yellow, golden yellow, reddish or burgundy; anthers black or deep purple; style arms sometimes with cylindric appendages. Cypselae biconvex, obovate to oblong, black or greyish brown and mottled, glabrous or sparsely pubescent. Pappus of two awns sometimes with a few squamellae in between, caducous. $x = 17$. Approximately 50 species, North America.

1325. *Heliomeris* Nutt.

Heliomeris Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 19 (1848); Yates & Heiser, Proc. Indiana Acad. Sci. 88: 364–372 (1979), rev.; Schilling & Panero, Bot. J. Linn. Soc. 140: 65–76 (2002), phylog.

Erect annual or perennial herbs. Leaves opposite or alternate, blades linear to ovate, sometimes revolute. Capitula solitary or in open paniculiform cymes, radiate. Involucres hemispherical, phyllaries in 2 series, subequal. Receptacles convex to conical. Ray corollas yellow to orange. Disc floret corollas yellow to yellow-orange, tube narrow and opening into a broad cylindrical throat, densely pubescent at base of throat on abaxial surface; anthers black or reddish brown. Cypselae biconvex, obovate, black, glabrous. Pappus absent. $x = 8, 13, 14$. Five species, Mexico, USA.

1326. *Hymenostephium* Benth.

Hymenostephium Benth. in Benth. & Hook. f., Gen. Pl. 2: 382 (1873); Schilling & Panero, Bot. J. Linn. Soc. 140: 65–76 (2002), phylog.

Erect annual or perennial herbs, sometimes scandent shrubs. Leaves opposite, blades ovate to deltate, rarely narrowly lanceolate. Capitula solitary but mostly in open paniculiform cymes, radiate or discoid. Involucres cylindric to campanulate, rarely hemispherical, phyllaries in 2–3 series, subequal. Receptacles flat to shallowly convex. Ray floret corollas pale yellow to golden yellow or orange. Disc floret corollas yellow, orange or red, rarely greenish white; anthers black, brown or yellow. Cypselae biconvex, black or brown, glabrous to densely pubescent, sometimes with a prominent elaiosome. Pappus of several lacerate round to apiculate squamellae or absent. $x = 17?, 20$. Approximately 26 species, Mexico to Argentina, with a distinctive group of species in the Andes of Venezuela.

1327. *Iostephane* Benth.

Iostephane Benth. in Benth. & Hook. f., Gen. Pl. 2: 368 (1873); Sharp, Ann. Missouri Bot. Gard. 22: 51–153 (1935); Strother, Madroño 30: 34–38 (1983), rev.

Perennial herbs. Leaves alternate in a lax to congested rosette, leaves erect or flat, blades lanceolate to ovate, deltate, unlobed to deeply 3-lobed. Capitula solitary on scapes or in open paniculiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries in 2–3 series, subequal. Receptacles convex. Ray florets sometimes styliferous but neuter, corollas pale purple to pink, white, ochroleucous, yellow to orange. Disc floret corollas yellow to whitish yellow, greenish yellow sometimes with purplish tips; anthers black. Cypselae weakly compressed, mostly quadrate or round in cross-section, oblong in outline, brownish black, glabrous to sparsely puberulent. Pappus of 1–2 reduced awns and few smaller squamellae or most commonly absent. $x = 17$. About four species, Mexico.

1328. *Lagascea* Cav.

Lagascea Cav., Anales Ci. Nat. 6: 331 (1803), nom. cons.; Stuessy, Fieldiana Bot. 38: 75–133 (1978), rev.

Erect annual or perennial herbs, erect or scandent shrubs. Leaves opposite, blades lanceolate to ovate to oblanceolate or elliptic. Capitula of 1 or 2 (rarely 8) florets, aggregated into tight glomerule-like clusters and subtended by leafy bracts producing a compound capitulum, discoid. Involucres cylindrical, phyllaries in 1 series, fused, subequal. Receptacles epaleate. Corollas white, pink or purple-pink, yellow or orange-yellow; anthers black, pink or yellow. Cypselae biconvex, oblanceolate to obovate, black, glabrous to sparsely pubescent. Pappus absent or a small crown of fused, lacerate, minute squamellae, sometimes those at angles of cypsela longer. $x = 17$. Nine species, neotropical, most species in southern Mexico, introduced elsewhere.

1329. *Pappobolus* S.F. Blake

Pappobolus S.F. Blake, Hooker's Icon. Pl. pl. 3057 (1916); Panero, Syst. Bot. Monogr. 36: 1–195 (1992), rev.
Helianthopsis H. Rob. (1979).

Annual or perennial herbs, shrubs, small trees. Leaves opposite or alternate, blades linear to

broadly ovate. Capitula solitary or in simple dichasial or monochasial to paniculiform or corymbiform cymes, sometimes subaxillary, radiate. Involucres campanulate to hemispherical, phyllaries in 3–6 series, subequal to gradate, sometimes outermost spreading and leaf-like. Receptacles flat to convex. Ray floret corollas yellow to yellow-orange. Disc florets sometimes functionally pistillate, corollas yellow to golden yellow sometimes with blackish lobes; anthers yellow or black. Cypselae biconvex, cuneate to oblong, brown to black, glabrous to densely pubescent. Pappus of 2 or many caducous awns, sometimes with few minute lacerate squamellae between the two awns. $x = 17$. About 38 species, Colombia, Ecuador, Peru.

1330. *Phoebanthus* S.F. Blake

Phoebanthus S.F. Blake, Proc. Amer. Acad. Arts 51: 520 (1916).

Perennial herbs with tuberous roots. Leaves alternate, blades filiform to narrowly lanceolate. Capitula solitary or in open paniculiform cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2–4 series. Receptacles convex. Ray floret corollas yellow. Disc floret corollas yellow; anthers black. Cypselae slightly quadrate, black, glabrous. Pappus of 2 awns. $x = 17$. Two species, Florida, USA.

1331. *Rhysolepis* S.F. Blake

Rhysolepis S.F. Blake, Contr. Gray Herb. 52: 36 (1917); Blake, Contr. Gray Herb. 54: 1–205 (1918), rev.; Robinson & Moore, Proc. Biol. Soc. Wash. 117: 323–446 (2004), rev.

Perennial herbs or weak scandent shrubs. Leaves opposite or alternate, blades lanceolate, ovate to oval. Capitula in open paniculiform cymes, paracladia branching at nearly 90° from main axis, radiate. Involucres campanulate to hemispherical, phyllaries in 3–4 series. Receptacles convex. Ray floret corollas golden yellow to yellow-orange. Disc floret corollas yellow; anthers black. Cypselae biconvex, cuneate, black, glabrous. Pappus of 2 awns and several minute squamellae, or of a few squamellae, sometimes easily caducous. Three species, Mexico.

1332. *Scalesia* Arn.

Scalesia Arn., Nat. Syst. ed. 2: 443 (1836); Eliasson, Opera Bot. 36: 1–120 (1974), rev.
Zemisne Degener & Sherff (1935).

Shrubs, trees. Leaves alternate, blades lanceolate to ovate, rarely cordate, unlobed to deeply lobed or 2-pinnate. Capitula solitary or in corymbiform cymes, discoid, disciform or radiate. Involucres campanulate to hemispherical, phyllaries in 2–4 series, subequal to gradate, sometimes outermost spreading and leaf-like. Receptacles flat to shallowly convex, paleae sometimes with trilobed apices. Ray florets sometimes styliferous but neuter or staminiferous with some pollen, corollas white. Disc floret corollas white, sometimes greenish white to dull yellow with age, peripheral corollas sometimes bent outwards; anthers black. Cypselae biconvex, cuneate to oblong, brown to black, glabrous. Pappus of 1 or 2 awns or of a few lacerate squamellae or absent. $x = 34$. About eleven species, Galápagos Islands.

1333. *Sclerocarpus* Jacq.

Sclerocarpus Jacq., Icon. Pl. Rar. 1: 17, pl. 176 (1781); Feddema, Ph.D. Thesis, University of Michigan, Ann Arbor: 1–132 (1966); Schilling & Panero, Bot. J. Linn. Soc. 140: 65–76 (2002), phylog.

Erect annual or perennial herbs. Leaves alternate, blades lanceolate to ovate, unlobed to deeply lobed. Capitula solitary or in open paniculiform cymes, radiate. Involucres campanulate to hemispherical, phyllaries 0 to few in 1–2 series, subequal. Receptacles conical, paleae indurate and tightly wrapping cypselae (perigynia), appearing tubular, shed with the cypsela. Ray floret corollas bright yellow to orange. Disc floret corollas yellow to orange, mostly with black papillae on adaxial surface of throat; anthers black or yellow. Cypselae broadly biconvex, black or brown, adaxial side straight to slightly concave, glabrous. Pappus a crown of lacerate squamellae or absent. $x = 11, 12, 13, 18$. Eight species, southwestern USA, Mexico, Central America, Venezuela, Africa.

1334. *Simsia* Pers.

Simsia Pers., Syn. Pl. 2: 478 (1807); Robinson & Brettell, Phytologia 24: 361–377 (1972), reg. rev.; Spooner, Syst. Bot. Monogr. 30: 1–90 (1990), rev.

Erect annual or perennial herbs, shrubs. Leaves opposite, auriculate, blades lanceolate, ovate to subcordate, sometimes deltate, trilobate, unlobed to shallowly lobed. Capitula solitary or in open paniculiform cymes, radiate or discoid. Involucres broadly cylindrical, turbinate, rarely hemispherical, phyllaries in 2–4 series, gradate. Receptacles

convex. Ray floret corollas lemon to golden yellow, white or cherry red. Disc floret corollas yellow to golden yellow, white or cherry red, corollas mostly with sclerified cells on tips of lobes; anthers black, brown or yellow, sometimes bicoloured; style arms long and tapered, sometimes curled. Cypselae narrowly biconvex to biconvex, mostly with embryo confined to centre of cypselae with a flat rim around it, black, brown or mottled, glabrous. Pappus of 2 awns or absent. $x = 17$. About 22 species, America.

1335. *Stuessya* B.L. Turner

Stuessya B.L. Turner, Brittonia 32: 209 (1980).

Erect annuals. Leaves alternate, blades narrowly lanceolate to ovate. Capitula in corymbiform cymes arranged in open paniculiform cymes, radiate. Involucres broadly cylindrical to campanulate or ovoid, phyllaries in 3–4 series, gradate, shortly aristate. Receptacles shallowly convex. Ray floret corollas bright yellow. Disc floret corollas yellow; anthers black or yellow; style arms tapered. Cypselae biconvex, black, glabrous. Pappus of two awns and several minute, lacerate squamellae. $x = 17$. Three species, Mexico.

1336. *Syncretocarpus* S.F. Blake

Syncretocarpus S.F. Blake, Bot. Jahrb. Syst. 54: 49 (1916); Panero & Granda Paucar, Phytologia 87: 109–112 (2005), new sp., tax.

Erect annual or perennial herbs, shrubs. Leaves alternate, blades narrowly lanceolate to ovate. Capitula in open paniculiform cymes, radiate. Involucres campanulate to hemispherical, phyllaries in 2–3 series, subequal. Receptacles shallowly convex, paleae deciduous. Ray floret corollas golden yellow to lemon yellow. Disc floret corollas yellow; anthers black. Cypselae biconvex, with long sericeous trichomes (encelioid) and a distinctive corky margin, with or without a prominent elaiosome. Pappus of 2 awns and 4 lacerate squamellae. $x = 17$. Two or three species, south-central Peru.

1337. *Tithonia* Desf.

Tithonia Desf., Gen. Pl. 189 (1789); La Duke, Rhodora 84: 453–522 (1982), rev.

Erect annual or perennial herbs, shrubs, rarely trees. Leaves alternate, blades narrowly ovate to ovate, sometimes auriculate, bases attenuate. Capitula solitary or in open paniculiform cymes, in most species on fistulose peduncles, radiate. Involucres hemispherical, phyllaries in 2–5 series, subequal, sometimes outermost foliaceous. Receptacles shallowly convex. Ray floret corollas yellow to orange-red. Disc floret corollas yellow to orange; anthers black, brown or yellow. Cypselae biconvex to weakly quadrate, black or greyish brown or mottled, glabrous to moderately pubescent. Pappus a crown of fused squamellae or 2 awns with fused squamellae or absent. $x = 17$. About 11 species, south-western USA to northern South America, one or two species introduced in most other tropical regions of the world.

1338. *Viguiera* Kunth

Viguiera Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. folio ed. 4: 176 (1818); Blake, Contr. Gray Herb. 54: 1–205 (1918), rev.; Panero & Schilling, Syst. Bot. 13: 371–406 (1988), sect. rev.

Erect rarely decumbent annual or perennial herbs, shrubs, rarely trees. Leaves opposite or alternate, linear to ovate, sometimes cordate or deltate. Capitula solitary or in congested to open paniculiform cymes, radiate, rarely discoid. Involucres cylindrical to hemispherical, phyllaries in 2–7 series, subequal to prominently gradate. Receptacles flat to convex, rarely conical. Ray florets sometimes styliferous but neuter, corollas yellow to yellow-orange, rarely dull red or white. Disc floret corollas yellow to orange, rarely dull red; anthers yellow, brown or black, rarely reddish. Cypselae biconvex, obovate to oblong, cuneate, black, brown or greyish brown, sometimes mottled with age, glabrous to densely pubescent. Pappus of 2 persistent or somewhat easily caducous awns, with or rarely without squamellae, sometimes only squamellae present, or absent. $x = 17$. Approximately 140 species, America.

XXVI.8. Subtribe Montanoinae H. Rob. (1978).

Erect perennial herbs (?), shrubs, trees. Leaves opposite, blades mostly ovate, entire or pinnatifid, triplinerved, rarely 5–7-plinerved. Capitula terminal, mostly in paniculiform to corymbiform or thyrsoid cymes, radiate, rarely discoid. Involucres mostly hemispherical, phyllaries 3–7 in 1–2 series, subequal. Receptacles convex, paleae accrescent after anthesis and enfolding cypselae. Ray florets neuter, corollas creamy white to white. Disc florets bisexual, rarely functionally staminate, corollas

pentamerous, yellow, green-yellow, greyish white, creamy white, without fibres embedding vascular strands; stamens 5, anthers black or yellow, appendages ovate with glandular trichomes; styles with two vascular strands, style arms with divided stigmatic surfaces, apices deltoid with a linear appendage. Cypselae weakly compressed to obconical and shallowly quadrangular in cross-section, black to brownish black or reddish brown, striate, glabrous to sparsely pubescent. Pappus absent.

Only one genus:

1339. ***Montanoa*** Cerv. in La Llave & Lex.

Montanoa Cerv. in La Llave & Lex., Nov. Veg. Descr. 2: 11 (1825); Funk, Mem. New York Bot. Gard. 36: 1–133 (1982), rev.

Characters of the subtribe. $x = 19$. About 25 species, most species in Mexico, Central America, northern South America south to northern Peru.

XXVI.9. Subtribe Rojasianthinae Panero (2002).

Shrubs or small trees. Leaves opposite, blades palmate, suborbicular in outline, palmately lobed. Capitula in terminal, open paniculiform dichasial cymes, radiate. Involucres hemispherical, phyllaries in 2–3 series, subequal, herbaceous. Receptacles shallowly convex, paleae with acicular projections, accrescent after anthesis and enfolding cypselae. Ray florets neuter, corollas white, sometimes suffused with pink on abaxial surfaces. Disc florets bisexual, corollas pentamerous, white, distal half black, without fibres embedding the vascular strands; stamens 5, anthers black, filaments densely papillose, papillae black, appendages with glandular trichomes; styles with two vascular strands, style arms with divided stigmatic surfaces, apices acute to acuminate. Cypselae compressed, obovate, raspberry colour when immature, brown-black, striate, glabrous to sparsely pubescent. Pappus of several caducous, golden, barbellate awns.

Only one genus:

1340. ***Rojasianthe*** Standl. & Steyerm.

Rojasianthe Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 311 (1940).

Characters of the subtribe. $x = 19$. One species, *R. superba* Standl. & Steyerm., Mexico, Guatemala.

XXVI.10. Subtribe Rudbeckiinae H. Rob. (1978); Urbatsch et al., Syst. Bot. 25: 539–565 (2000), phylog.

Erect annual or perennial herbs. Leaves alternate, blades ovate, unlobed to pinnatifid. Capitula in terminal, paniculiform cymes, radiate, rarely discoid. Involucres flat to reflexed, rarely hemispherical or hemispherical at the beginning of anthesis, phyllaries in 2–3 series, sometimes dimorphic. Receptacles conical to columnar, paleae sometimes shed with cypsela. Ray florets neuter. Disc florets bisexual, corollas pentamerous, without fibres embedding the vascular strands; stamens 5, anthers black, sometimes shallowly calcarate, endothecium with mostly radial thickenings; styles with two vascular strands, style arms with divided stigmatic surfaces, these broad and touching each other, sometimes with long papillose appendages. Cypselae compressed, quadrate, striate, oblong to obpyramidal, glabrous to sparsely pubescent, sometimes minutely winged. Pappus a small crown of minute scales or few squamellae or absent.

Key to the Genera

1. Leaves pinnatifid, phyllaries in 2 dimorphic series, paleae deciduous with the cypselae, cypselae sometimes minutely winged and with multiseriate trichomes **1341.** ***Ratibida***
– Leaves mostly entire to trilobed, rarely plants with pinnatifid leaves associated with inflorescences, phyllaries in 2 or more series, subequal, paleae not deciduous with the cypselae, cypselae never winged, rarely with multiseriate trichomes **1342.** ***Rudbeckia***

1341. ***Ratibida*** Raf.

Ratibida Raf., Fl. Ludov. 73 (1817); Richards, Rhodora 70: 348–393 (1968), rev.; Correll & Johnston, Man. Vasc. Pl. Texas: 1523–1736 (1970), reg. rev.; Urbatsch & Cox, Syst. Bot. 15: 394–402 (1990), phylog.; Urbatsch & Jansen, Syst. Bot. 20: 28–39 (1995), phylog.; Urbatsch et al., Syst. Bot. 25: 539–565 (2000), phylog.

Leaf-blades ovate, unlobed or pinnatifid. Capitula radiate. Involucres flat to reflexed, phyllaries in 2 series, dimorphic. Receptacles columnar, paleae deeply keeled and densely pubescent distally, shed with cypsela. Ray floret corollas yellow, reddish brown or bicoloured. Disc floret corollas yellow,

purple or greenish. Cypselae oblong to oblanceolate, tangential angles weakly defined, glabrous to sparsely pubescent, sometimes with a minute wing. Pappus of 1–2 small awns or projections, rarely a minute crown or 1 awn or absent. $x = 16$. Seven species, North America.

1342. *Rudbeckia* L.

Rudbeckia L., Sp. Pl. 2: 906 (1753); Perdue, Rhodora 59: 293–299 (1957), subg. rev.; Correll & Johnston, Man. Vasc. Pl. Texas: 1523–1736 (1970), reg. rev.; Urbatsch & Cox, Syst. Bot. 15: 394–402 (1990), phylog.; Urbatsch & Jansen, Syst. Bot. 20: 28–39 (1995), phylog.; Urbatsch et al., Syst. Bot. 25: 539–565 (2000), phylog.
Dracopis Cass. (1825).

Leaf-blades ovate to broadly ovate, unlobed or pinnatifid, rarely sessile and cordate, sometimes glaucous. Capitula in terminal, paniculiform cymes, radiate, rarely discoid. Involucres flat to reflexed, rarely hemispheric or hemispherical at the beginning of anthesis. Receptacles conic to columnar. Ray floret corollas golden to lemon yellow, orange or reddish, or bicoloured. Disc floret corollas yellow to purplish, often bicoloured. Cypselae oblong to obpyramidal, glabrous or with some thick multicellular trichomes on radial angles. Pappus a small crown of minute scales or 2–4 small scales or absent. $x = 16, 18, 19$. Seventeen species, North America.

XXVI.11. Subtribe Spilanthinae Panero (2005).

Erect or decumbent annual or perennial herbs, sometimes rooting at the nodes, rarely scandent shrubs. Leaves opposite, blades linear to ovate, sometimes reniform, unlobed, triplinerved. Capitula axillary or terminal, solitary or in simple to congested cymes, on sometimes fistulose peduncles, discoid or radiate. Involucres campanulate to hemispherical, phyllaries in 1–5 series, subequal, rarely dimorphic, mostly herbaceous. Receptacles convex to conical especially with age, mostly paleate, paleae chartaceous, rarely coriaceous, bases slightly decurrent. Ray florets pistillate. Disc florets bisexual, corollas pentamerous, rarely tetramerous, without fibres embedding the vascular strands; stamens 5, rarely 4; styles with two vascular strands, style arms with fused stigmatic surfaces, apices acute and papillose, without appendages. Ray cypselae obcompressed, triquetrous, obovoid, sparsely to densely ciliate. Disc cypselae compressed, sometimes peripheral ones triquetrous, terete, sometimes quadrate and narrowly rhombic, rarely square in outline, black or brown, rarely striate, mostly shallowly or sometimes conspicuously winged, corky, ciliate, glabrous to sparsely pubescent. Pappus a minute crown, a single awn fused to a broad ring around the neck of the cypsela or more commonly of 2–3 slender awns as a continuation of the wings, sometimes with squamellae in between.

Key to the Genera

1. Capitula with 4 florets **1347. *Tetranthus***
– Capitula with more than 4 florets 2
2. Cypselae strongly striate or shallowly ribbed; pappus a whitish crown, sometimes with a single awn **1344. *Oxycarpha***
– Cypselae and pappus otherwise 3
3. Leaves subsessile, rarely petiolate; cypselae winged or with broad corky edges, sometimes lacerate and ending in a stout shoulder or awn **1346. *Spilanthes***
– Leaves petiolate; cypselae narrowly winged or with narrow corky edges 4
4. Plants herbaceous; leaves thin; capitula discoid or radiate; corollas yellow or white **1343. *Acmella***
– Plants shrubby, sometimes scandent; leaves coriaceous; capitula discoid; corollas white, rarely purplish-white **1345. *Salmea***

Genera of Spilanthinae

1343. *Acmella* Rich. ex Pers.

Acmella Rich. ex Pers., Syn. Pl. 2: 472 (1807); Jansen, Syst. Bot. Monogr. 8: 1–115 (1985), rev.

Erect or decumbent annual or perennial herbs, sometimes rooting at the nodes. Leaf-blades filiform to mostly ovate, triplinerved. Capitula terminal or axillary, solitary or in open paniculiform cymes, discoid or radiate. Involucres hemispherical, sometimes patent with age, phyllaries in 1–3 series, subequal. Receptacles conic, paleate. Ray florets pistillate, purplish to yellow-orange or white. Disc floret corollas pentamerous or sometimes tetramerous, creamy white to yellow-orange; anthers black, appendages with or without glands. Ray cypselae triquetrous, obovoid to ellipsoid, black, glabrous to densely pubescent, sometimes densely ciliate. Disc cypselae compressed, obovoid to ellipsoid, black, rarely brownish, sometimes with a light brown corky margin, pubescence as ray cypselae. Pappus absent or of few soft bristles, or more commonly of two persistent, slender awns at the angles of the cypsela. $x = 12, 13$. About

30 species, pantropical, most species in the New World.

1344. *Oxycarpha* S.F. Blake

Oxycarpha S.F. Blake, Contr. Gray Herb. ser. 2, 53: 52 (1918).

Stoloniferous, succulent, perennial herbs or weak low shrubs. Leaf-blades filiform, succulent. Capitula terminal, solitary, discoid. Involucres campanulate, phyllaries in 3–5 series, gradate, coriaceous. Receptacles conic, paleae coriaceous, apices aristate to acicular. Corollas white, yellow (?); anthers brown. Cypselae oblanceolate, weakly biconvex but mostly terete with conspicuous ribs, one side with a minute wing wider at base, black, glabrous. Pappus a crown sometimes with a single awn. One species, *O. suaedifolia* S.F. Blake, Venezuela.

1345. *Salmea* DC.

Salmea DC., Cat. Pl. Horti Monsp.: 140 (1813), nom. cons.; Blake, J. Bot. 53: 193–201 (1915), rev.; Bolick, Syst. Bot. 16: 462–477 (1991), rev.

Erect or scandent shrubs. Leaf-blades lanceolate to ovate, coriaceous, triplinerved. Capitula in open paniculiform cymes of variously congested corymbiform cymes, discoid. Involucres campanulate to hemispherical, sometimes patent with age, phyllaries in 2–5 series, subequal or gradate. Receptacles conical, paleate. Corollas white or creamy white, sometimes purplish; anthers brown or black, appendages with or without glandular trichomes. Cypselae obovoid to ellipsoid, compressed, black, rarely brownish sometimes with a light brown corky margin, sparsely pubescent. Pappus of 2(–3) slender awns, sometimes with a few squamellae in between, rarely a crown. $x = 18$. Ten species, neotropics.

1346. *Spilanthes* Jacq.

Spilanthes Jacq., Enum. Syst. Pl. 8, 28 (1760); Jansen, Syst. Bot. 6: 231–257 (1981), rev.

Perennial herbs, some prostrate and becoming woody at base. Leaf-blades linear to elliptic, weakly triplinerved. Capitula terminal, rarely axillary, solitary or in simple cymes, discoid. Involucres hemispherical, phyllaries in 2–3 series, subequal. Receptacles convex to conic, paleate. Corollas white or purplish white; anthers black, appendages without glands. Cypselae obovate, strongly compressed at maturity, shallowly quadrate, rhombic in outline, in most species with a conspicuous corky, ciliate margin. Pappus of 1–3 subequal awns. $x = 16$. Six species, pantropical.

1347. *Tetranthus* Sw.

Tetranthus Sw., Prodr. 7: 115 (1788).

Prostrate perennial herbs. Leaf-blades oval to reniform, triplinerved, unlobed. Capitula axillary, scapose, solitary, discoid. Involucres campanulate, phyllaries dimorphic, outer approximately 1/10 the length of inner, inner enclosing the cypselae (perigynia). Receptacles epaleate. Disc florets 4, corollas sometimes tetramerous, white; anthers black, appendages with minute glandular trichomes; Cypselae quadrate, obpyramidal, black, glabrous. Pappus a minute crown. Between two and four species, Caribbean.

XXVI.12. Subtribe Verbesininae Benth. (1873).

Erect, rarely decumbent annuals or perennial herbs, shrubs, rarely vines, sometimes trees. Leaves alternate or opposite, rarely in whorls, rarely forming rosettes, blades various, 3–5-nerved, rarely pectinate, rarely perfoliate, unlobed to deeply lobed, pinnately veined or triplinerved. Capitula terminal, simple, sometimes scapose, or in paniculiform or corymbiform cymes, rarely thyrses, discoid or radiate. Involucres cylindrical to hemispherical, phyllaries in 2–4 series, subequal or gradate. Receptacles flat to convex, rarely globose, paleate. Ray florets pistillate, sometimes pistillate but sterile or neuter, corollas rarely with biseriate trichomes on tube. Disc florets bisexual, corollas pentamerous, rarely tetramerous, without fibres embedding the vascular strands; stamens 5, rarely 4; styles with two vascular strands, style arms with divided stigmatic surfaces, appendages lacking. Cypselae compressed, rarely obpyramidal and quadrate, sometimes stipitate, ray cypselae sometimes triquetrous and obpyramidal, winged or wingless, black or brown, not striate, rarely striate, glabrous to densely pubescent. Pappus of awns or squamellae at angles of cypsela.

Key to the Genera

1. Cypsela quadrate, obpyramidal with a pappus of 4 awns or squamellae at angles of cypsela, sometimes these longer and alternating with 4 squamellae **1350. *Tetrachyron***
– Cypsela and pappus otherwise 2
2. Cypselae winged, not stipitate **1351. *Verbesina***

– Cypselae not winged, stipitate 3
3. Ray corollas white **1348. *Podachaenium***
– Ray corollas yellow **1349. *Squamopappus***

Genera of Verbesininae

1348. *Podachaenium* Benth.

Podachaenium Benth., Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1852 (5/7): 98–99 (1853); Jansen et al., Syst. Bot. 7: 476–483 (1982), circumscr.; Turner & Panero, Phytologia 73: 143–148 (1992), reg. rev.

Shrubs or trees. Leaves opposite, blades ovate to broadly ovate, palmate, shallowly serrate, venation palmate or triplinerved, rarely pectinate. Capitula in terminal, corymbiform cymes or in thyrses, radiate. Involucres hemispherical, sometimes becoming reflexed. Receptacles convex to globose. Ray florets pistillate, corollas white to creamy white. Disc corollas yellow to yellow-orange; anthers black or yellow, appendages with glandular trichomes; style arms with broadly acute to round apices. Cypselae compressed, obovate, those of the ray obpyramidal and triquetrous, sometimes conspicuously tapered at the base, sparsely pubescent. Pappus of several erose squamellae, those on the angles of the cypsela longer. $x = 18, 19$. Six species, Mexico, Central America, Colombia.

1349. *Squamopappus* R.K. Jansen, N.A. Harriman & Urbatsch

Squamopappus R.K. Jansen, N.A. Harriman & Urbatsch, Syst. Bot. 7: 480 (1982).

Shrubs or small trees. Leaves opposite below, then alternate, blades ovate, shallowly serrate, triplinerved. Capitula in terminal, compact corymbiform cymes, radiate. Involucres campanulate to subhemispherical. Receptacles convex. Ray florets pistillate, corollas golden yellow. Disc corollas yellow; anthers black, appendages without glandular trichomes; style arms with acute apices. Cypselae compressed, obovate, those of the ray obpyramidal and triquetrous, somewhat tapered at the base, sparsely pubescent. Pappus of several erose squamellae, those on the angles of the cypsela longer, awn-like. $x = 19$. One species, *S. skutchii* (S.F. Blake) R.K. Jansen, N.A. Harriman & Urbatsch, Mexico, Guatemala.

1350. *Tetrachyron* Schltr

Tetrachyron Schltr, Linnaea 19: 744 (1847); Wussow & Urbatsch, Syst. Bot. 4: 297–318 (1979), rev.; Jansen et al., Syst. Bot. 7: 476–483 (1982), circumscr.

Erect, open to densely branched shrubs. Leaves opposite, blades linear to lanceolate, ovate, trullate, or rarely suborbicular to round, entire to shallowly serrate, pinnately veined or triplinerved, sometimes densely pubescent on abaxial surfaces. Capitula in terminal, simple or paniculiform cymes or thyrses, radiate. Involucres turbinate to hemispherical. Receptacles shallowly convex to convex. Ray florets pistillate, corollas yellow to yellow-orange, sometimes with biseriate trichomes on tube. Disc corollas yellow or yellow-orange; anthers yellow, appendages with or without glandular trichomes; style arms with acute apices and conspicuous resin and crystal deposits. Cypselae obpyramidal, quadrate, conspicuously tapered at the base, sometimes striate, with a conspicuous carpopodium, sparsely pubescent. Pappus of four awns or squamellae, sometimes squamellae alternating with awns. $x = 15, 16, 17$. About eight species, Mexico, Guatemala.

1351. *Verbesina* L. Fig. 96

Verbesina L., Sp. Pl. 2: 901 (1753), nom. cons.; Robinson & Greenman, Proc. Amer. Acad. Arts 34: 534–566 (1899), rev.; Correll & Johnston, Man. Vasc. Pl. Texas: 1523–1736 (1970), reg. rev.; Olsen, Pl. Syst. Evol. 149: 47–63 (1985), sect. rev.; Turner, Pl. Syst. Evol. 150: 237–262 (1985), sect. rev.; Olsen, Brittonia 38: 362–368 (1986), sect. rev.; Olsen, Sida 13: 45–56 (1988), sect. rev.; Panero & Jansen, Amer. J. Bot. 84: 382–392 (1997), phylog.

Annual or perennial herbs, erect, rarely vine-like or straggly shrubs, or trees sometimes up to 25 m tall. Leaves alternate or opposite, sometimes with petiolar wings decurrent, sometimes forming dainty rosettes, blades linear, lanceolate, ovate, suborbicular, sagittate, deltate, unlobed or deeply dissected, rarely perfoliate, triplinerved, rarely pinnately veined. Capitula terminal, solitary, sometimes scapose, or in paniculiform or corymbiform cymes, discoid or radiate. Involucres cylindrical, turbinate, campanulate, hemispheric. Receptacles flat to convex, rarely globose, paleae tapered, sometimes with rounded flat tips. Ray florets pistillate, sometimes pistillate but sterile or neuter, corollas white, orange, red, yellow, greenish white, white-pink, purplish green. Disc corollas rarely tetramerous, yellow, orange, red, green, white, purple or a combination of these colours on throat and lobes; anthers brown or black, rarely red, pink or yellow, anther appendages with or without glandular trichomes; style arms long and tapered or with broadly acute or deltoid

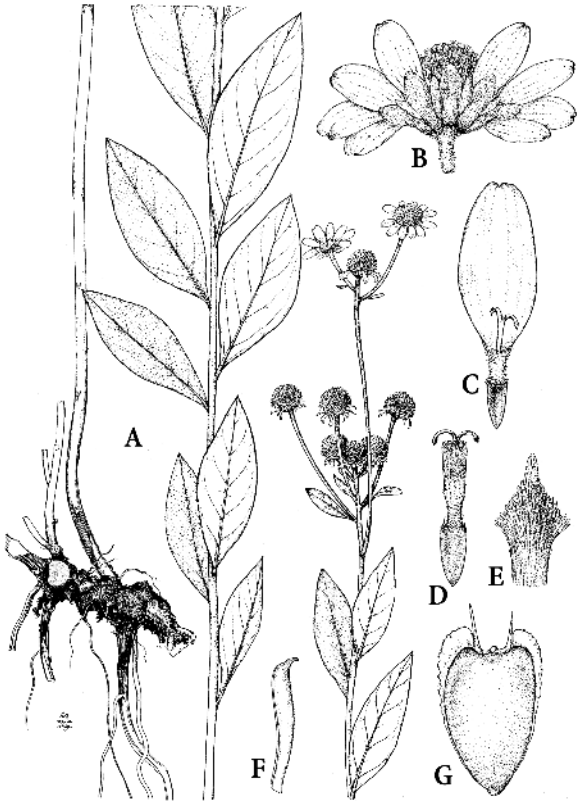

Fig. 96. Compositae-Heliantheae. *Verbesina pietatis*. **A** Portions of flowering plant. **B** Flowering capitulum with facing ray floret removed. **C** Ray floret. **D** Disc floret. **E** Abaxial view of style tip. **F** Palea. **G** Slightly immature disc cypsela (wings starting to develop). (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

apices. Cypselae strongly compressed, sometimes ray cypselae triquetrous, broadly obovate, oblanceolate to narrowly cuneate, symmetrically to asymmetrically winged, stramineous to dark brown or blackish, sparsely pubescent distally, the wings thin to corky. Pappus of two awns, erect, rarely uncinate, sometimes triquetrous ray cypselae with 3 awns, or rarely absent. $x = 16, 17, 18$. About 300 species, America, highest number of species in Mexico and tropical Andes.

XXVI.13. Subtribe Zaluzaniinae H. Rob. (1978).

Erect annual or perennial herbs, shrubs. Leaves alternate, petiolate, blades mostly ovate, unlobed, rarely trilobed or pinnatifid, triplinerved. Capitula in terminal, paniculiform or corymbiform cymes, discoid or radiate. Involucres campanulate to hemispherical, phyllaries in 2–3 series, subequal. Receptacles convex to conical, paleate. Ray florets pistillate. Disc florets bisexual, corollas pentamerous, without fibres embedding the vascular strands; stamens 5, anther appendages with glandular trichomes; styles with two vascular strands, style arms with fused stigmatic surfaces. Cypselae compressed and weakly quadrate, obovate, sometimes asymmetrical with adaxial side straight to concave and abaxial side convex, glabrous. Pappus absent or rarely of a few squamellae on ray cypselae.

Key to the Genera

1. Leaves deeply dissected, pinnatifid; paleae linear; anthers black **1352. *Hybridella***
– Leaves unlobed to trilobed, sometimes lobes dissected; paleae oval, never linear; anthers yellow **1353. *Zaluzania***

1352. *Hybridella* Cass.

Hybridella Cass., Bull. Sci. Soc. Philom. Paris 1817: 12 (1817); Olsen, Madroño 24: 29–36 (1977), re-establ.

Perennial herbs. Leaf-blades lanceolate in outline, twice pinnate. Capitula in terminal, paniculiform cymes, radiate. Involucres hemispheric, phyllaries reflexed. Receptacles conical, paleae linear. Ray floret corollas yellow. Disc floret corollas yellow; anthers black; style arms with somewhat canaliculate stigmatic surfaces, apices round to truncate. Cypselae compressed and weakly quadrate, obovate, asymmetrical, glabrous. Pappus absent. $x = 16$. One species, *H. globosa* Cass., Mexico.

1353. *Zaluzania* Pers.

Zaluzania Pers., Syn. Pl. 2: 473 (1807); Olsen, Rhodora 81: 449–500 (1979), rev.

Erect annual or perennial herbs, shrubs. Leaf-blades cordate to ovate, serrate to deeply laciniate. Capitula in terminal, paniculiform cymes, discoid or radiate. Involucres campanulate to hemispheric. Receptacles convex to shallowly conical. Ray floret corollas yellow, rarely white. Disc floret corollas yellow, rarely white; anthers yellow; style arms with acute to acuminate apices. Cypselae compressed and weakly quadrate, obovate, sometimes asymmetrical, glabrous. Pappus absent or rarely of a few squamellae on ray cypselae. $x = 17, 18$. Ten species, Mexico, south-western USA.

XXVI.14. Subtribe Zinniinae Benth. (1873).

Erect annual or perennial herbs, shrubs. Leaves alternate or opposite, petiolate or sessile, blades linear to ovate, unlobed, pinnately veined to triplinerved. Capitula terminal, rarely axillary, solitary and scapose or in open paniculiform cymes on sometimes fistulose peduncles, radiate, rarely discoid. Involucres turbinate to hemispherical, rarely globose and phyllaries reflexed, phyllaries in 2–5 series, subequal to strongly gradate. Receptacles convex to conic, globose, paleate, rarely epaleate. Ray florets pistillate, rarely neuter, corollas marcescent and fused to the cypselae, rarely deciduous, often without a tube. Disc florets bisexual, sometimes functionally staminate, corollas pentamerous, tubes and throat bases densely thickened with additional layers of cells, without fibres embedding the vascular strands; stamens 5, anther appendages with glandular trichomes; styles with two vascular strands, style arms with fused stigmatic surfaces, rarely divided, apices acute to deltate with small papillose appendages. Ray cypselae obpyramidal to terete or obcompressed, black to stramineous, sometimes with striations, sometimes with uncinate trichomes. Pappus absent or of mutiple awns or rarely a crown, ray cypselae with either 1 or 3 awns at the angles of the cypselae.

Key to the Genera

1. Disc florets functionally staminate **1360. *Zinnia***
– Disc florets bisexual 2
2. Paleae at anthesis 1.5–2 times as long as disc florets 3
– Paleae at anthesis as long as or shorter than disc florets 4
3. Ray florets sterile **1354. *Echinacea***
– Ray florets fertile **1358. *Tehuana***
4. Tubes of ray and disc corollas and abaxial surfaces of lobes of disc corollas densely covered with black, moniliform trichomes with an expanded terminal cell; plants aquatic; northern Mexico (western Durango state) **1359. *Trichocoryne***
– Tubes and lobes of ray and disc corollas glabrous or variously pubescent but never with black moniliform hairs; plants terrestrial, rarely aquatic; American 5
5. Pappus of ray cypselae with at least one broad awn as a continuation of adaxial angle of cypsela and opposite the ray corolla sinus 6
– Pappus of ray cypselae various or absent but always without a broad awn opposite the ray corolla sinus 7
6. Ray cypselae with 1 awn **1356. *Philactis***
– Ray cypselae with 3 awns **1357. *Sanvitalia***
7. Ray corollas often without a tube; cypselae either compressed or obcompressed, sometimes shallowly quadrate to terete; pappus of cypselae absent or of 1 or 2 awns **1360. *Zinnia***
– Ray corollas with a tube; cypselae terete to quadrate; pappus of cypselae of a few teeth or a crenulate, minute rim **1355. *Heliopsis***

Genera of Zinniinae

1354. *Echinacea* Moench

Echinacea Moench, Methodus 591 (1794); McGregor, Univ. Kansas Sci. Bull. 48: 113–142 (1968), rev.; Correll & Johnston, Man. Vasc. Pl. Texas: 1523–1736 (1970), reg. rev.; Urbatsch & Cox, Syst. Bot. 15: 394–402 (1990), phylog.; Urbatsch & Jansen, Syst. Bot. 20: 28–39 (1995), phylog.; Urbatsch et al., Syst. Bot. 25: 539–565 (2000), phylog.; Binns et al., Syst. Bot. 27: 610–632 (2002), rev.

Annual or perennial herbs. Leaves alternate, blades linear to ovate, pinnately veined or triplinerved, entire to shallowly serrate. Capitula terminal, solitary and scapose or in open paniculiform cymes, radiate. Involucres patent or reflexed, phyllaries in 2–4 series, reflexed. Receptacles convex to strongly conical or globose, paleate, paleae with pointed or rounded, stiff tips. Ray florets neuter, corollas pink or purple, rarely white or yellow. Disc florets bisexual, corollas green, pink, purple, rarely yellow; anthers mostly black; style arms with fused stigmatic surfaces, apices acute. Cypselae compressed to quadrate, cuneate, black, glabrous to sparsely pubescent. Pappus a small crown. $x = 11$. Between four and 11 species, Canada, USA.

1355. *Heliopsis* Pers.

Heliopsis Pers., Syn. Pl. 2: 473 (1807), nom. cons.; Fisher, Ohio J. Sci. 57: 171–191 (1957), rev.

Erect to decumbent annual or perennial herbs, weak shrubs. Leaves opposite, sometimes alternate distally, blades filiform to suborbicular, mostly ovate, pinnately veined or triplinerved, entire to deeply serrate or lobed. Capitula terminal, solitary, sometimes on long peduncles or in open paniculiform cymes on sometimes fistulose peduncles, radiate or discoid. Involucres turbinate to hemispherical, phyllaries subequal, herbaceous. Receptacles convex to conical to columnar with age, paleae with rounded flat tips. Ray florets pistillate, corollas yellow to orange, purple, sometimes greenish with age. Disc florets bisexual, corollas yellow to orange, purple; anthers mostly black, rarely yellow; style arms with fused stigmatic surfaces, apices acute. Cypselae ovoid to terete, weakly 3–4-angled, greenish brown to black, smooth to tuberculate, glabrous to sparsely

puberulent. Pappus a minute crenulate rim or of 2–3 small teeth. $x = 14$. Fifteen species, Central and northern South America.

1356. *Philactis* Schrad.

Philactis Schrad., Index Sem. (Göttingen) (1832); Torres, Brittonia 21: 322–332 (1969), rev.

Shrubs. Leaves opposite, petiolate, blades lanceolate to ovate, triplinerved, serrate. Capitula terminal, solitary or in simple cymes, radiate. Involucres hemispherical, phyllaries in 2–3 series, subequal. Receptacles convex, paleate, paleae with pointed, stiff tips. Ray florets pistillate, corollas yellow to yellow orange, sometimes dull greenish to blue-green with age, tube very short. Disc florets bisexual, corollas yellow-orange; anthers black, appendages ovate; style arms with fused stigmatic surfaces, apices acute. Ray cypselae obpyramidal, triquetrous, brown with lengthwise striations. Disc cypselae compressed, obpyramidal, biconvex to quadrate, brown, without phytomelanin (?) Pappus of mostly 2, rarely many awns and of 1 awn on adaxial side of ray cypsela facing corolla sinus. $x = 14$. One polymorphic or 3 or 4 species, Mexico, Guatemala.

1357. *Sanvitalia* Lam.

Sanvitalia Lam., J. Hist. Nat. 2: 176 (1792); Torres, Brittonia 16: 417–433 (1964), rev.

Erect or prostrate annual or perennial herbs, rarely shrubs. Leaves opposite, blades linear to ovate, mostly triplinerved, entire to shallowly serrate. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres hemispherical, phyllaries in 2–4 series, subequal. Receptacles convex, paleate, paleae with pointed, stiff tips. Ray florets pistillate, corollas yellow, greenish yellow or yellow-orange, without tube. Disc florets bisexual, corollas yellow, greenish yellow or deep purple; anthers black, brown or purplish; style arms with fused stigmatic surfaces, apices acute. Ray cypselae obpyramidal, triquetrous to terete, stramineous with uncinate trichomes. Disc cypselae compressed, obpyramidal, triquetrous to quadrate, winged, peripheral cypselae sometimes wingless. Pappus absent or of many awns or of three awns one each on adaxial and tangential sides of ray cypselae. $x = 8, 9, 11$. Seven species, Mexico, Central America, Bolivia, Argentina.

1358. *Tehuana* Panero & Villaseñor

Tehuana Panero & Villaseñor, Syst. Bot. 21: 555 (1996) [1997].

Erect annuals. Leaves opposite, blades ovate, triplinerved, shallowly serrate. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres patent or reflexed, phyllaries in 2–3 series, subequal. Receptacles conical to columnar with age, paleate, paleae with acicular tips. Ray florets pistillate, corollas orange-yellow, tube very short. Disc florets bisexual, corollas green, yellow-orange distally; anthers black, appendages with glandular trichomes; style arms with fused stigmatic surfaces, apices acute. Ray cypselae obpyramidal, triquetrous, brown-black, minutely strigose with lengthwise striations. Disc cypselae obpyramidal, rounded-quadrate in cross-section, the 4 ribs with minute twin trichomes, areas between ribs with minute uniseriate trichomes. Pappus absent or of one awn on adaxial side of ray cypselae. $x = 14$. One species, *T. calzadae* Panero & Villaseñor, Mexico.

1359. *Trichocoryne* S.F. Blake

Trichocoryne S.F. Blake, Contr. U.S. Natl Herb. 22: 648–649 (1924).

Aquatic annual or perennial (?) herbs. Leaves opposite, sessile, linear to narrowly ovate, uninerved, entire. Capitula axillary, solitary on short shoots, radiate. Involucres hemispherical, phyllaries in 2 series, subequal. Receptacles convex to conical, epaleate. Ray florets 5, pistillate, sterile, corollas white with two green-black veins on abaxial side, not marcescent. Disc florets bisexual, corollas white to creamy white with conspicuous black trichomes on tube and abaxial side of lobes; anthers black; style arms with divided stigmatic surfaces, apices acute to deltate. Cypselae compressed to quadrate, obovate to cuneate, black, glabrous. Pappus absent. One species, *T. connata* S.F. Blake, north-western Mexico.

1360. *Zinnia* L.

Zinnia L., Syst. Nat., ed. 10: 1189, 1221, 1377 (1759), nom. cons.; Torres, Brittonia 15: 1–25, 290–302 (1963), part. rev.
Crassina Scepin (1758), nom. rej.
Lepia Hill (1759), nom. rej.
Tragoceros Kunth (1818).

Erect annual or perennial herbs or shrubs. Leaves opposite, linear to ovate, entire, rarely serrate. Ca-

pitula terminal, solitary or in open paniculiform cymes on sometimes fistulose peduncles, radiate, rarely discoid. Involucres turbinate, campanulate or hemispherical, phyllaries in 2–5 series, subequal to highly gradate. Receptacles convex to conic, paleate, paleae with rounded, flat tips. Ray florets pistillate, corollas yellow, green, burgundy, red, orange, pink, marcescent, often without a tube. Disc florets bisexual, sometimes functionally staminate, sometimes zygomorphic, corollas pink, red, yellow, yellow-orange, burgundy, sometimes with conspicuous papillae on adaxial surface; anthers yellow, brown or black; style arms with fused stigmatic surfaces, sometimes with glandular trichomes on abaxial surfaces, apices acute. Ray cypselae mostly obcompressed, triquetrous, black to brown or greyish, smooth to tuberculate, glabrous to variously pubescent. Disc cypselae compressed, convex to shallowly quadrate, tuberculate or smooth, glabrous to variously pubescent, sometimes winged. Pappus absent or of one or two awns. $x = 10, 11, 12$. About 25 species, south-western USA, neotropical region.

XXVII. Tribe Millerieae Lindl. (1829).

J.L. Panero

Annual or perennial herbs, shrubs or trees, sometimes rosulate or caulirosulate; herbage sometimes conspicuously and densely glandular, sometimes viscous. Leaves usually opposite, petiolate or sessile, sometimes leaf bases ampliated or forming a cupule (invaginated) around the stem (Espeletiinae), blades linear to ovate, sometimes suborbicular, entire to variously serrate to lacerate or pectinate, triplinerved, sometimes pinnately veined or pentanerved. Capitula in terminal or axillary, open to congested paniculiform or corymbiform cymes, sometimes scapose, radiate or discoid, rarely disciform. Involucres turbinate to hemispheric, phyllaries in 1–5+ series, sometimes dimorphic or subequal to gradate, rarely outer series broadly deltate, valvate and enclosing the developing capitulum, commonly moderately to densely pubescent, sometimes second series fused to developing ray cypselae (Melampodiinae). Receptacles convex to conic, rarely flat, wholly or partially paleate, paleae flat to navicular, sometimes cucullate. Ray florets pistillate, rarely neuter, sometimes in multiple series or rows (especially in Espeletiinae), corolla rarely shallowly bilabiate, limbs sometimes extremely short or lacking, apices conspicuously trilobed, rarely shallowly trilobed. Disc florets bisexual or functionally staminate, actinomorphic or sometimes the peripheral zygomorphic with 3 longer abaxial lobes, pentamerous, rarely tetramerous, throats gradually tapered or abruptly expanded above the tube, normally pubescent with glandular trichomes; anthers sometimes free, appendages lanceolate to ovate, sometimes cochleate, with or without glandular trichomes, appendages weakly, rarely strongly sclerified, endothecium of quadrate to oblong or isodiametric cells with 1–5 polar thickenings, sometimes with radial thickenings, rarely thickenings surrounding the whole cell; style arms of disc florets wholly or partially fused or spreading with parallel, rarely fused stigmatic surfaces, appendages wanting to prominent. Ray cypselae essentially similar to disc cypselae, except that sometimes variously enclosed by inner phyllaries or paleae, obcompressed, broadly ovate to suborbicular, sometimes incurved, black, rarely with a basal caruncle or elaiosome (*Guardiola*), otherwise obconic to obpyramidal, sometimes quadrate, striate, glabrous or densely pubescent. Disc cypselae obconic to obpyramidal, sometimes incurved, quadrate to round, rarely oval in cross-section, subterete to shallowly angled, black, glabrous to densely pubescent. Pappus absent or variously of minute scales, acuminate scales, or barbellate or plumose bristles, bristles of equal or unequal length, sometimes caducous.

The tribe contains 34 genera and approximately 400 species found mostly in central Mexico and the northern Andes with a few species in tropical regions of the Old World, especially Africa. Some members of the Espeletiinae are the defining element of the paramos of northern South America.

Millerieae have recently been resurrected (Panero et al. 2001c; Panero and Funk 2002) to accommodate the genera variously placed by Robinson (1981) and other authors (Stuessy 1977; Karis and Ryding 1994a) in subtribes Desmanthodiinae, Espeletiinae, Galinsogiinae, Guardiolinae, Melampodiinae and Milleriinae. The present circumscription of the tribe is based primarily on results of chloroplast DNA sequence analyses (Panero et al. 2001c). The tribe does not have any single character which defines it but most of its species tend to have opposite leaves, glandular herbage, scarious paleae, subterete cypselae, a pappus, when present, of scales or bristles arranged radially on the neck of the cypsela,

and trilobed ray corollas. The tribe contains five main lineages, namely Dyscritothamninae, the three subtribes Galinsoginae, Jaegeriinae and Desmanthodiinae, Guardiolinae, Milleriinae (including Espeletiinae) and Melampodiinae. Millerieae are sister to Madieae, Perityleae and Eupatorieae, and these collectively are sister to Heliantheae (Panero and Funk 2002). Based on historical considerations, Guardiolinae are tentatively placed in Millerieae, as there is no strong support for their inclusion here or in any of the sister tribes. Subtribe Dyscritothamninae was recently described (Panero 2005), based on results from molecular studies of chloroplast DNA (Panero et al. 2001c), to include the genera *Dyscritothamnus*, *Tetragonotheca*, *Tridax*, *Cymophora* and *Bebbia*. All these genera, with the exception of *Tetragonotheca*, share variously pubescent, subterete cypselae with a pappus of plumose or barbellate scales or bristles; the pappus is rarely absent. *Tetragonotheca* is distinctive in the group by having quadrate cypselae with a pappus of minute scales. The inclusion of *Tetragonotheca* in Dyscritothamninae, although well-supported by the available data, is nevertheless perplexing, as its morphology is quite divergent from that of the other genera of the subtribe. Molecular data support the sister-group relationship of Dyscritothamninae and Melampodiinae.

Melampodiinae have always been recognized as a distinctive group within the Heliantheae alliance (Stuessy 1977; Robinson 1981; Karis and Ryding 1994a) because of their involucres with dimorphic phyllaries, the outer series being herbaceous and the inner fused to the ray cypselae. Furthermore, all Melampodiinae have functionally staminate disc florets. Molecular data support a narrow interpretation of Melampodiinae to include only the genera *Acanthospermum*, *Lecocarpus* and *Melampodium*. The cypselae of Melampodiinae, like those of Milleriinae, lack a pappus. Melampodiinae and Dyscritothamninae are sister to all the other subtribes of Millerieae, with the exception of Guardiolinae. Results from studies based on sequence data of chloroplast DNA (Panero et al. 2001c) and the ITS region of nuclear ribosomal DNA (Panero and Plovanich-Jones, unpubl. data) provide important insights into the evolution and phylogenetic relationships of subtribe Galinsoginae. These studies reveal that *Galinsoga*, as traditionally circumscribed (Canne 1977), is a paraphyletic assemblage and that the genera *Sabazia* and *Alloispermum* need to be included in its concept to maintain a monophyletic *Galinsoga*. I have opted to follow the traditional circumscription of *Alloispermum*, *Galinsoga* and *Sabazia*, until more comprehensive studies are available. The monotypic genus *Freya* from western Venezuela is considered here to be part of *Sabazia* because it shares with this genus opposite leaves, trilobed white ray corollas and scarious, striate phyllaries. *Aphanactis*, *Oteiza*, *Schistocarpha* and *Selloa* are sister to the *Galinsoga* lineage. *Aphanactis* was revised by Turner (1980) and subsequently emended by Robinson (1997) who transferred all species of *Aphanactis* from Mexico and Central America to *Selloa*, arguing that those species were extraneous in *Aphanactis* because their peduncles did not elongate after anthesis, a characteristic seen in all species of South American *Aphanactis*. Molecular studies show that the Mexican species of *Aphanactis* are sister to the Andean species, and not to *Selloa*. Based on these results, *Selloa* is here recognized to contain only one species, *S. plantaginea* of central Mexico. *Selloa plantaginea* differs from *Aphanactis* by having a pappus of bristles and fused stigmatic surfaces. The same data support, albeit weakly, the sister relationship of *Oteiza* and *Alepidocline* with the monotypic genus *Cuchumatanea* in a derived position within *Alepidocline*; *Cuchumatanea* is here placed in the synonymy of *Alepidocline*. Monographic studies of these genera may support the placement of *Alepidocline* in *Oteiza*; I have refrained from merging them here, as their chromosome numbers are different and, in the case of *Oteiza*, may reflect past hybridization (Strother and Panero 1994). The same studies show that *Desmanthodium* and *Jaegeria* are basal elements of Galinsoginae, and they are recognized here as distinctive subtribes. Galinsoginae, Jaegeriinae and Desmanthodiinae are sister to the Milleriinae/Espeletiinae clade. Molecular studies of members of the Heliantheae alliance (Panero et al. 2001c) show that Milleriinae contain two main lineages, one composed of *Smallanthus*, *Ichthyothere* and Espeletiinae, another containing the other members of the subtribe. These results have been corroborated independently by Rauscher (2002) who, by using a more extensive sampling, was able to provide some important insights into the relationships of the genera of the subtribe. His findings show that several genera of Milleriinae are not monophyletic, namely *Rumfordia*, *Sigesbeckia* and *Trigonospermum*. They also demonstrate that the traditional seven genera of the Espeletiinae,

as outlined by Cuatrecasas (1976), appear not to be monophyletic and that the characters used to define them, including mostly phyllotaxy and inflorescence morphology, have evolved in parallel several times. These data have persuaded me to recognize in Espeletiinae only the genera *Carramboa* and *Espeletia*. The genus *Tamananthus* is here placed in Espeletiinae, as suggested by Badillo (1992). Examination of a fragment of the type of *Tamananthus* (through the kindness of Dr. V.M. Badillo) allowed me to conclude that the disc florets are functionally staminate and not perfect, as stated in the original description (see Badillo 1992). Functionally staminate disc florets are a characteristic of nearly all Espeletiinae. The genus differs from all other arboreal or shrubby espeletias in having leaves without invaginated bases. For this reason, I have opted to recognize *Tamananthus* as distinctive from *Espeletia*.

Delimitation of monophyletic groups at the subtribal level in Millerieae is still tentative, and the classification provided here is based solely on results from molecular studies of chloroplast DNA. Similar assessments based on the nuclear ribosomal ITS region (Rauscher 2002; Panero and Plovanich-Jones, unpubl. data) are sometimes incongruent with plastid phylogenies, and are indicative of the possibility of past hybridization or lineage sorting in the evolution of the group.

Key to the Subtribes

1. Leaves alternate, with expanded leaf bases or more commonly forming a cupule (invaginated) around stem; ray florets fertile **3. *Espeletiinae*** (p. 482)
– Leaves opposite, if alternate, then leaves not forming a cupule nor leaf bases expanded around stems and ray florets neuter 2
2. Anther filaments pubescent **5. *Guardiolinae*** (p. 486) **20. *Guardiola***
– Anther filaments without trichomes 3
3. Second series of phyllaries fused to developing cypselae forming a variously spined, verrucose or awned conceptacle **7. *Melampodiinae*** (p. 487)
– Phyllaries never fused to cypselae, rarely tightly wrapped around cypselae forming a perigynium-like structure 4
4. Ray floret cypselae tightly wrapped or completely encased in a perigynium-like structure 5
– Ray floret cypselae never enclosed nor tightly wrapped by innermost phyllaries 6
5. Disc florets functionally staminate; ray (tubular floret) cypselae enclosed in a perigynium-like structure **1. *Desmanthodiinae*** (p. 479)
– Disc florets fertile; ray cypselae tightly wrapped by flaps or hyaline wings of innermost phyllaries **6. *Jaegeriinae*** (p. 487)
6. Capitula with dimorphic phyllaries normally in 2 series, the outer series broad, herbaceous, either reflexed or erect, 2–6, inner series cucullate, scarious, phyllaries of both series normally with conspicuous, glandular stipitate trichomes, rarely covered with long sericeous tapered trichomes; cypselae glabrous and epappose **8. *Milleriinae*** (p. 488)
– Capitula with subequal or gradate phyllaries, never dimorphic, the outermost never broad and loosely arranged around the capitulum, nor the inner ones cucullate, phyllaries without large stipitate glandular trichomes, if present, the glandular tip smaller than the trichome base; cypselae glabrous to densely pubescent, with or without a pappus 7
7. Pappus various but mostly of persistent capillary or plumose bristles of equivalent length, if of small scales, then cypselae quadrate in cross-section and capitula with 4, broadly deltate, valvate phyllaries, or disc and ray corollas white, or ray corollas shallowly bilabiate with 2, very small lobes opposite trilobed limb **2. *Dyscritothamninae*** (p. 480)
– Pappus various but mostly caducous, if persistent, then either of capillary bristles or scales, if of bristles, these of equivalent size and arising from a shallowly cyathiform cypselae neck and plants with large corymbiform cymes and broadly ovate leaves or the ray cypselae lacking a pappus, if of scales, then ray cypselae usually enclosed by phyllary/paleae structure consisting of the innermost phyllary subtending the ray floret and 2–3 adjacent paleae **4. *Galinsoginae*** (p. 483)

XXVII.1. Subtribe Desmanthodiinae Benth. (1873).

Perennial herbs, shrubs or treelets. Leaves opposite, sometimes perfoliate, blades ovate to lanceolate, triplinerved or pentanerved. Capitula disciform or discoid, in glomerules, glomerules normally with three smaller, capitulum-like glomerules each, each capitulum-like glomerule with 1–3 capitula in various stages of development, each glomerule subtended by green bracts rimmed with white or pink, arranged in terminal, congested, corymbiform or paniculiform cymes. Involucres cylindric to campanulate. Receptacles shallowly to strongly convex, epaleate? Tubular ('ray') florets normally 1 per glomerule, throat very short and reduced to a ring protruding through perigynium, corollas white. Disc florets functionally staminate, corollas white; anthers hyaline, appendages short, round; styles of disc florets penicillate, undivided, those of the tubular florets large, arms lanceolate. Cypselae fusiform to oval, black, glabrous, enclosed in perigynium. Pappus absent.

Only one genus:

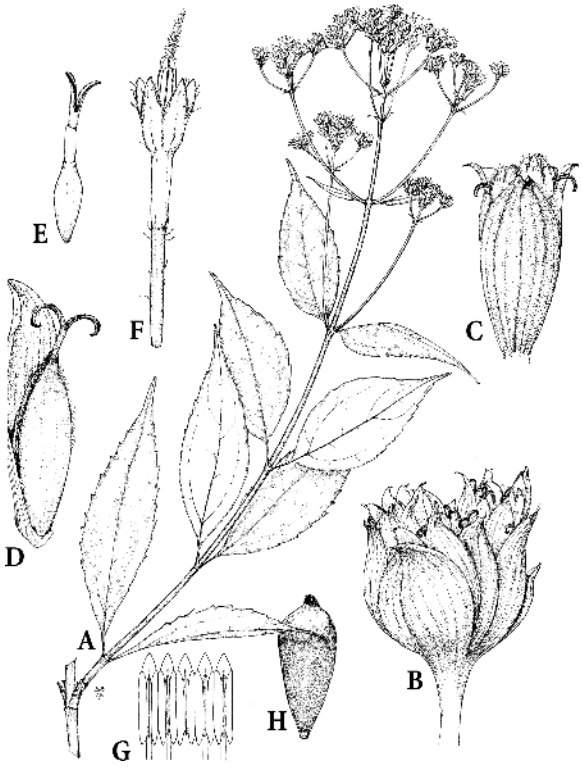

Fig. 97. Compositae-Millerieae. *Desmanthodium fruticosum*. **A** Flowering branch. **B** Cluster of flowering capitula. **C** Flowering capitulum. **D** Phyllary enclosing fertile floret, and subtending bract. **E** Immature phyllary and projecting style. **F** Staminate floret. **G** Anthers. **H** Cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

1361. *Desmanthodium* Benth. Fig. 97

Desmanthodium Benth., Hooker's Icon. Pl. 12: 14, pl. 1116 (1872).

Characters of the subtribe. $x = 17, 18$. Eight species, Mexico, Central America, northern South America.

XXVII.2. Subtribe Dyscritothamninae Panero (2005).

Annual or perennial herbs, sometimes shrubs. Leaves usually opposite, blades linear to ovate, rarely deltate/hastate or semisucculent, mostly triplinerved, sometimes with a single vein or pinnately veined. Capitula terminal, solitary or in open paniculiform or corymbiform cymes, discoid or radiate, sometimes disciform. Involucres turbinate, campanulate to hemispheric, phyllaries in 1–5 series, imbricate, rarely valvate, subequal or gradate. Receptacles convex to conic, paleate. Ray florets pistillate, rarely neuter, sometimes shallowly bilobed, corollas mostly yellow. Disc florets bisexual, outer in discoid capitula sometimes zygomorphic with three abaxial lobes enlarged, corollas yellow, pink, green or white; anther appendages lanceolate to ovate, sometimes broadly deltate, with or without glandular trichomes; style arms with broad, parallel stigmatic surfaces, rarely stigmatic surfaces fused, appendages short to prominent, subulate to cylindric, papillose. Cypselae obconic to obpyramidal, sometimes quadrate, sparsely to densely pubescent, sometimes with multiple ridges, black to silvery-sericeous. Pappus of multiple barbellate or plumose bristles, rarely of scales with or without plumose projections, rarely absent, in some species ray cypselae with smaller pappus or epappose. $x = 9, 10, 11, 20$.

Approximately 43 species.

Key to the Genera

1. Phyllaries dimorphic, outer series valvate, broadly deltate, 4 **1365. *Tetragonotheca***
– Phyllaries imbricate, subequal or gradate, never valvate, 5 to numerous 2
2. Ray and disc floret corollas white or creamy white **1363. *Cymophora***
– Ray and disc floret corollas of contrasting colours, if ray corollas white, then disc corollas yellow, yellow-green or pink 3
3. Wiry, multi-stem shrubs, mostly without leaves; capitula discoid, corollas yellow-orange **1362. *Bebbia***
– Annual or perennial herbs, if shrubs, these with a few branches and with many leaves; capitula radiate or discoid, if discoid, then plants with glaucous and linear leaves 4
4. Leaves alternate **1364. *Dyscritothamnus***
– Leaves opposite **1366. *Tridax***

Genera of Dyscritothamninae

1362. *Bebbia* Greene

Bebbia Greene, Bull. Calif. Acad. Sci. 1: 179 (1885); Whalen, Madroño 24: 112–123 (1977), rev.

Multi-stemmed shrubs forming dense, circular mounds. Leaves opposite or alternate, shortly petiolate, blades linear to sagittate, sometimes hastate, with a single vein or triplinerved. Capitula in terminal, open paniculiform cymes or sometimes broad, compact corymbiform cymes, discoid. Involucres campanulate to hemispheric, phyllaries in 2–3 series, subequal. Receptacles shallowly convex, paleae shallowly trilobed. Florets bisexual, corollas yellow-orange; anther appendages ovate, with glandular trichomes;

style arms long, subulate, with parallel stigmatic surfaces, not confluent at the apices, appendages short, tapered, papillose. Cypselae obconic, terete to obscurely angled, sometimes with 4–5 shallow angles, striate, brown, densely pubescent. Pappus of several plumose bristles of equal length. Two species, Mexico, south-western USA.

1363. *Cymophora* B.L. Rob.

Cymophora B.L. Rob., Proc. Amer. Acad. Arts 43: 39 (1907); Turner & Powell, Madroño 24: 1–6 (1977), rev.; Keil et al., Madroño 34: 354–358 (1987), part. rev.

Annual herbs. Leaves opposite, petiolate, blades broadly lanceolate to ovate, sometimes trullate, rarely deltate/hastate, acute to obtuse, triplinerved. Capitula in terminal, large, open paniculiform cymes, discoid to disciform or radiate. Involucres cylindric to turbinate, phyllaries in 2–3 series, subequal. Receptacles convex. Ray florets pistillate, corollas white or creamy white. Disc florets bisexual, those on the periphery sometimes zygomorphic with three longer abaxial lobes, corollas white or creamy white; anther appendages ovate, with or without glandular trichomes; style arms with broad, parallel stigmatic surfaces, rarely fused, appendages subulate to cylindric, papillose, sometimes wanting. Cypselae compressed or obcompressed, sometimes broadly convex, obovate, sparsely to densely pubescent, silvery to rusty silvery. Pappus absent, of multiple plumose bristles or sometimes of ciliate/fimbriate scales, cypselae of zygomorphic florets normally with shorter pappi or eppapose or absent (even if pappus present in actinomorphic disc florets). $x = 9$. Four to five species, Mexico, Venezuela.

1364. *Dyscritothamnus* B.L. Rob.

Dyscritothamnus B.L. Rob., Contr. Gray Herb. 65: 25, f. 1 (1922).

Shrubs. Leaves alternate, petiolate to subsessile, blades filiform to lanceolate, semisucculent, sometimes glaucous, pinnately veined. Capitula in terminal, corymbiform cymes, discoid or radiate. Involucres campanulate, phyllaries in 2–3 series, subequal to gradate, herbaceous to membranaceous. Receptacles shallowly to strongly convex. Ray florets neuter, corollas light yellow, apices bilobed or trilobed. Disc florets bisexual, corollas yellow; anther appendages ovate to lanceolate, hyaline to light yellow; style arm apices long, subulate, appendages minute, papillose. Disc cypselae obconic, densely pubescent with long shiny trichomes. Pappus of multiple barbellate to plumose bristles. $x = 11, 20$. Two species, central Mexico.

1365. *Tetragonotheca* L.

Tetragonotheca L., Sp. Pl. 2: 903 (1753); Turner & Dawson, Sida 8: 296–303 (1980), rev.

Annual or perennial herbs. Leaves opposite, petiolate or sessile, blades lanceolate to trullate, margins entire to dentate, lobed. Capitula terminal, solitary or in open corymbiform or paniculiform cymes, radiate. Involucres obconic, hemispheric after anthesis, phyllaries in two series, dimorphic, outer series of 4 phyllaries, valvate, herbaceous, enclosing the developing capitulum until anthesis, inner series smaller, scarious. Receptacles conic. Ray florets pistillate, corollas yellow or yellow-rust, apices shallowly to conspicuously trilobed. Disc florets bisexual, corollas yellow; anther appendages broadly ovate, with multiple glandular trichomes extending below appendages along connective; style arms with broad, parallel stigmatic surfaces, appendages prominent, conic with cylindric apices, papillose. Cypselae obconic to obpyramidal, commonly quadrate in outline, sometimes with multiple ridges or striae, sparsely to moderately pubescent, black. Pappus of a crown of minute squamellae, rarely wanting. $x = 17$. Four species, southern USA, northern Mexico.

1366. *Tridax* L. Fig. 98

Tridax L., Sp. Pl. 2: 900 (1753); Powell, Brittonia 17: 47–96 (1965), rev.
Ptilostephium Kunth (1829).
Mandonia Wedd. (1864).

Annual or perennial herbs, shrubs. Leaves opposite, blades linear to ovate, simple to deeply lobed, 1-veined or triplinerved. Capitula terminal, solitary or in open paniculiform cymes, discoid, disciform or radiate. Involucres campanulate to hemispheric, phyllaries in 2–5 series, subequal or gradate, herbaceous or somewhat scarious, sometimes apical halves translucent and yellow, pink or purple. Receptacles convex to conic, paleae trilobed with central lobe somewhat aristate. Ray florets fertile, corollas 3-lobed, sometimes shallowly bilabiate, with two very minute adaxial lobes, white, pink, pink-red, purple or yellow. Disc florets bisexual, corollas yellow, pink, green, pink-white, occasionally peripheral corollas in discoid capitula zy-

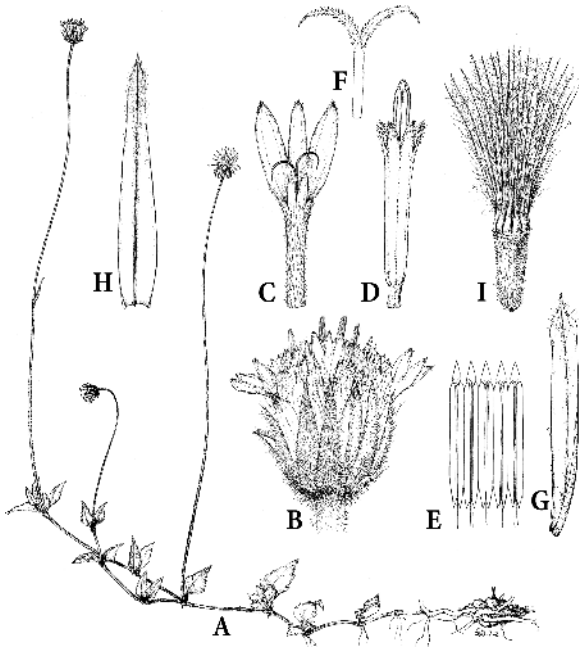

Fig. 98. Compositae-Millerieae. *Tridax mexicana*. **A** Habit. **B** Flowering capitulum. **C** Ray corolla. **D** Disc corolla. **E** Anthers. **F** Style arms. **G** Outer palea. **H** Inner palea. **I** Cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

gomorphic with three expanded lobes; anther appendages ovate to lanceolate, with or without a few, broadly cuneate glandular trichomes; style arms with broad, parallel stigmatic surfaces, subulate with tapered to cylindric appendages (acuminate). Cypselae obconic, sparsely to densely pubescent, sometimes glabrous, black to silvery. Pappus of multiple plumose bristles, these sometimes only as long as floral tube and appearing as squamellae, rarely wanting. $x = 9, 10$. Thirty species, neotropical, one species a pantropical weed.

XXVII.3. Subtribe Espeletiinae Cuatrec. (1976); Rauscher, Amer. J. Bot. 89: 1074–1084 (2002), phylog.

Acauli- and caulirosulate shrubs with marcescent leaves, sometimes few-branched or trees with most leaves concentrated on apices of branches, a few species monocarpic, some producing massive inflorescences of hundreds of capitula. Leaves alternate, with very short internodes and ampliated bases, sometimes forming a large rosette, mostly with leaf bases wrapping around stem forming a cupule, blades lanceolate to fusiform, invariably densely lanate on abaxial surface, pinnately veined. Capitula in terminal or axillary, dichasial or monochasial, corymbiform or paniculiform cymes, radiate or discoid. Involucres turbinate, campanulate to hemispheric; phyllaries in 2 to numerous series, thickened or herbaceous, glabrescent to densely lanate, flat to cucullate, sometimes glandular, sometimes with a few broad herbaceous phyllaries, these fused at the base. Receptacles convex to conic, paleate, sometimes with receptacular trichomes. Ray florets pistillate, sometimes in 2–5 rows, rarely bilabiate, corolla apices shallowly bilobed or trilobed, sometimes obtuse, mostly with a dense tuft of moniliform trichomes on tube. Disc florets functionally staminate, rarely bisexual; anther appendages ovate without glandular trichomes; style arms of disc florets fused forming a thickened, penicillate style, those of the ray thickened with broad, parallel, stigmatic surfaces, spreading. Cypselae obcompressed to narrowly obpyramidal, trigonous, slightly incurved, black, glabrous or sparsely pubescent. Pappus absent, very rarely of a few caducous setae or 3 awns. $x = 19$.

Approximately 90 species, Colombia, Ecuador and Venezuela.

Key to the Genera

1. Perennial herbs or shrubs, sometimes trees, never forming rosettes, if leaf bases forming a cupule around stem (invaginated), then leaves very large (25–50 cm long), shallowly bullate on adaxial surfaces, margins undulate, ray corollas yellow, and capitula nodding after anthesis 2
– Rosettes, if shrubs or trees and leaf bases wrapping around stem and forming a cupule (invaginated), then leaves without undulate margins, smooth on adaxial surface and ray corollas either white or greenish white or purplish-white, never yellow **1368. *Espeletia***
2. Perennial herbs or shrubs; leaves with ampliated bases, leaves never forming a cupule around stem **1369. *Tamananthus***
– Trees, leaves with undulate margins forming a cupule around stem **1376. *Carramboa***

Genera of Espeletiinae

1367. *Carramboa* Cuatrec.

Carramboa Cuatrec., Phytologia 35: 54 (1976).

Small trees with most leaves concentrated on apices of the branches. Leaves alternate, ovate to pandurate, petiolate, very large, bright green, margins undulate, adaxial surfaces shallowly bullate, peti-

oles and abaxial surface covered in a dense lanate, ferrugineous golden indumentum, leaf bases ampliated and forming a cupule around stem. Capitula in axillary, compact, large corymbiform cymes, radiate, nodding after anthesis. Involucres campanulate to hemispheric, phyllaries in 2–5 series, slightly gradate, thickened, cucullate, herbaceous to coriaceous, moderately pubsecent, sometimes densely glandular. Receptacles convex to conic, sometimes with trichomes between paleae. Ray florets pistillate, corollas bright yellow, shallowly bilobed or trilobed with a dense tuft of tapered trichomes on tube. Disc florets functionally staminate, corollas yellow; anther appendages ovate. Cypselae obcompressed to trigonous, obcuneate, slightly incurved, black, glabrous to very sparsely pubescent. Pappus absent or very rarely with a few caducous setae. Five species, Venezuela.

1368. *Espeletia* Mutis ex Humb. & Bonpl.

Espeletia Mutis ex Humb. & Bonpl., Pl. Aequinoct. 2: 10 (1808) [1809]; Smith & Koch, Brittonia 1: 471–530 (1935), rev.
Libanothamnus Ernst (1870).
Coespeletia Cuatrec. (1976).
Espeletiopsis Cuatrec. (1976).
Ruilopezia Cuatrec. (1976).
Tamania Cuatrec. (1976).
Paramiflos Cuatrec. (1995).

Acauli- or caulirosulate shrubs with marcescent leaves, sometimes tree-like with most leaves concentrated on apices of branches, a few species monocarpic. Leaves alternate, with very short internodes and ampliated bases, sometimes forming a large rosette, mostly with leaf bases wrapping around stem forming a cupule, blades lanceolate to fusiform, densely lanate on abaxial surfaces. Capitula in terminal or axillary, dichasial or monochasial, corymbiform or paniculiform cymes, radiate or discoid. Involucres hemispheric, phyllaries in 2 to numerous series, thickened or herbaceous, sometimes with a few broad herbaceous phyllaries fused at the base. Receptacles shallowly convex to conic, sometimes with trichomes between paleae. Ray florets pistillate, sometimes in 2 to 5 rows or series, rarely bilabiate, corollas yellow, white, greenish white, purplish, shallowly bilobed or trilobed, sometimes obtuse, mostly with a dense tuft of moniliform trichomes on tube. Disc florets functionally staminate, rarely bisexual, corollas yellow, white, green or purple; anther appendages ovate. Cypselae obcompressed, trigonous, slightly incurved, black, glabrous or sparsely pubescent. Pappus absent, rarely of 3 awns. $x = 19$. Approximately 85 species, Colombia, Ecuador and Venezuela.

1369. *Tamananthus* V.M. Badillo

Tamananthus V.M. Badillo, Ernstia 30: 25 (1985).

Perennial herbs or shrubs. Leaves alternate, sessile to shortly petiolate, bases expanded but not forming a cupule around stem, blades lanceolate to oval, sometimes narrowly obovate, with a single main vein. Capitula in terminal, open paniculiform cymes, radiate. Involucres turbinate, phyllaries in 3–5 series, herbaceous, densely pubescent. Receptacles convex, with trichomes between paleae. Ray florets pistillate, corollas yellow, sometimes bilabiate, apices trilobed, tubes densely pubescent. Disc florets functionally staminate or bisexual?, corollas yellow, tubes sparsely pubescent or glabrous, lobes with glandular trichomes, nectaries prominent and deeply lobed; anther appendages ovate; style arms of disc florets short, apices obtuse, those of the ray florets narrowly deltate to fusiform, with broad, parallel stigmatic surfaces. Cypselae narrowly obpyramidal to obcompressed, with a prominent carpopodium, black, essentially glabrous. Pappus absent. One species, *T. crinitus* V.M. Badillo, Venezuela.

XXVII.4. Subtribe Galinsoginae Benth. (1873).

Annual or perennial herbs, shrubs. Leaves opposite, petiolate or sessile, rarely forming rosettes, blades linear to ovate, rarely suborbicular, normally dentate, mostly triplinerved. Capitula terminal, solitary or in open to congested corymbiform or paniculiform cymes, radiate or discoid, rarely disciform. Involucres campanulate to hemispheric, phyllaries in 2–5 series, subequal to strongly gradate, herbaceous to membranaceous, striate. Receptacles commonly convex or conic, paleate, paleae oval to filiform, sometimes trilobed, sometimes caducous. Ray florets pistillate, corollas white, yellow or white suffused with pink, limbs sometimes inconspicuous. Disc florets bisexual or rarely functionally staminate, corollas yellow or yellow-green, sometimes purplish; anther appendages narrowly lanceolate to ovate, usually without glandular trichomes; style arms with broad parallel, rarely fused stigmatic surfaces, appendages wanting or short, rarely cylindric,

papillose. Cypselae obconic to obpyramidal, subterete to shallowly 4- to 5-angled, black, glabrous to moderately pubescent, sometimes cypselae held in pocket formed by phyllary and the fused, adjacent 2–3 paleae. Pappus absent or of a few tapered or truncate squamellae or bristles, of equal or different lengths, the bristles barbellate or sometimes plumose, persistent or caducous.

Key to the Genera

1. Perennial herbs with scapose inflorescences and leaves with very short internodes and forming a small rosette; plants endemic to high elevation meadows in central Mexico **1378. *Selloa***
– Annual or perennial herbs, sometimes shrubs, capitulescences various, rarely scapose (*Aphanactis*), if forming rosettes, then leaves either very densely pubescent as to appear silvery or leaves very light green (chartreuse) in colour, and plants from the paramos and jalcas of the northern and central Andes of South America 2
2. Pappus of disc floret cypselae of persistent capillary or flattened bristles 3
– Pappus of disc floret cypselae various or absent, if of bristles, these caducous 4
3. Ray floret cypselae without pappus **1371. *Alloispermum***
– Ray floret cypselae with pappus **1377. *Schistocarpha***
4. Ray florets tubular or with a very reduced limb **1373. *Faxonia***
– Ray florets when present not tubular 5
5. Pappus of several, caducous bristles of various lengths 6
– Pappus of several, persistent, truncate or tapered scales or absent 7
6. Annual herbs **1370. *Alepidocline***
– Erect or scandent shrubs **1375. *Oteiza***
7. Ray cypselae enclosed in a phyllary/palea structure, consisting of 2–3 paleae fused to adjacent phyllary **1374. *Galinsoga***
– Ray cypselae never enclosed by a phyllary/palea structure 8
8. Ray corollas, when present, yellow, if white, then central disc florets sterile, if discoid, then capitula on pedicels which grow after anthesis **1372. *Aphanactis***
– Ray corollas white or white suffused with pink, central disc florets fertile, pedicels never growing after anthesis **1376. *Sabazia***

Genera of Galinsoginae

1370. *Alepidocline* S.F. Blake

Alepidocline S.F. Blake, J. Wash. Acad. Sci. 24: 439 (1934); Turner, Phytologia 69: 387–392 (1990), syn.
Cuchumatanea Seid. & Beaman (1966).

Annual herbs. Leaves petiolate, blades lanceolate to broadly ovate, obscurely to strongly triplinerved. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres urceolate to hemispheric, phyllaries gradate in 3–5 series, herbaceous to scarious, striate, sometimes apices purple-tinged. Receptacles conic, paleae filiform to narrowly lanceolate, sometimes paleae caducous or a few absent. Ray floret corollas inconspicuous to showy, white to pink or light purple, apices conspicuously, rarely shallowly trilobed. Disc florets bisexual, corollas yellow or yellow-green; anther appendages ovate, rarely with glandular trichomes; style arms with parallel stigmatic surfaces, apices deltate to acute, appendages short, papillose. Cypselae obovate, sometimes shallowly asymmetrical and obcompressed, slightly incurved, otherwise terete, black, glabrous, carpopodium lateral. Pappus absent or of a few unequal caducous barbellate setae. $x = 8$. Five species, Mexico, Central America, Venezuela.

1371. *Alloispermum* Willd.

Alloispermum Willd., Gesell. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesamten Naturk. 1: 139 (1807); Robinson, Phytologia 38: 411–412 (1978), syn.

Perennial herbs or shrubs. Leaves subsessile to petiolate, blades linear-lanceolate to ovate, triplinerved. Capitula in terminal, simple, open to congested paniculiform or corymbiform cymes, radiate, rarely discoid. Involucres narrowly campanulate to hemispheric, phyllaries in 3–4 series, gradate, herbaceous to scarious. Receptacles flat to convex, paleae oval to filiform. Ray floret corollas white to creamy white, sometimes suffused with purple on abaxial surfaces, apices shallowly to moderately trilobed. Disc florets bisexual, corollas yellow; anther appendages ovate; style arms with broad, parallel stigmatic surfaces, appendages wanting. Cypselae obpyramidal to obovoid, blackish to brownish purple, ray cypselae glabrous, disc cypselae glabrous or pubescent. Pappus absent in ray cypselae, disc cypselae with a pappus of several, very narrowly lanceolate, tapered, barbellate scales, resembling bristles. $x = 8$. Approximately 15 species, Mexico, Central America and northern Andes.

1372. *Aphanactis* Wedd.

Aphanactis Wedd., Chlor. Andina 1: 142 (1856); Turner, Bol. Soc. Argent. Bot. 19: 33–44 (1980), rev.; Robinson, Brittonia 49: 71–78 (1997), tax.

Annual or perennial herbs, variously persisting as caespitose, matted, cushion-like shrubs, creeping

among forbs or small rosettes. Leaves sessile, shallowly perfoliate, blades oval to ovate or oblong, glabrous to densely silvery-pilose, sometimes forming rosettes. Capitula terminal, solitary or sometimes a few in tightly clustered corymbiform cymes, disciform or radiate. Involucres campanulate to hemispheric, phyllaries in 2–3 series, subequal, herbaceous to scarious. Receptacles convex to shallowly conic, paleae setiform or linear, sometimes caducous. Ray florets sometimes in 2–3 rows, corollas yellow to whitish-yellow, apices shallowly to conspicuously trilobed, sometimes limbs wanting and corolla appearing tubular. Disc florets bisexual or sometimes functionally staminate, corollas yellow to yellow-green, glabrous to moderately pubescent, sometimes glandular; anther appendages ovate; style arms with narrow to broad parallel stigmatic surfaces, apices acute to obtuse, essentially without appendages. Cypselae obovoid, obcompressed to subterete, sometimes shallowly 4–5-angled, black, essentially glabrous. Pappus absent. $x = 8$. Thirteen species, Mexico, Central America and neotropical Andes.

1373. *Faxonia* Brandegee

Faxonia Brandegee, Zoë 4: 403 (1894).

Annual herbs. Leaves petiolate, blades oval to ovate, pinnately veined. Capitula in terminal, open umbelliform cymes, radiate or disciform. Involucres campanulate, phyllaries in 2 series, subequal, herbaceous. Receptacles convex, paleae linear or trilobed. Ray floret limbs very reduced. Disc florets bisexual, corollas yellow; anthers free to partially free, appendages ovate. Cypselae subterete, slightly incurved, black, glabrous. Pappus absent. One species, *F. pusilla* Brandegee, Mexico.

1374. *Galinsoga* Ruiz & Pav.

Galinsoga Ruiz & Pav., Fl. Peruv. Prodr. 110, pl. 24 (1794); Canne, Rhodora 79: 319–389 (1977), rev.; Canne, Madroño, 25: 81–93 (1978), generic limits; Canne-Hilliker, Taxon 41: 661–666 (1992), part. rev.
Stenocarpha S.F. Blake (1915).

Annual or perennial herbs, rarely shrubs. Leaves petiolate or sessile, blades linear-lanceolate to ovate, triplinerved. Capitula terminal, solitary or in open simple to paniculiform cymes, radiate, rarely discoid. Involucres campanulate to hemispheric, phyllaries in 2–4 series, subequal to gradate, herbaceous to membranaceous or distally scarious. Receptacles convex to conic, paleae oval to filiform, sometimes weakly trilobed. Ray floret corollas mostly white, sometimes pink or purple. Disc florets bisexual, corollas yellow or greenish yellow, sometimes purplish; anther appendages ovate; style arms with broad, parallel stigmatic surfaces, rarely with continuous stigmatic surfaces, appendages wanting or tapered, cylindric, papillose. Cypselae obconic to shallowly obcompressed, blackish, glabrous to moderately pubescent, rarely ciliate, ray cypselae enclosed in structure formed by phyllary and the fused, adjacent 2–3 paleae. Pappus absent or of 8–20, cuneate to lanceolate, sometimes aristate squamellae. $x = 8$. Fifteen species, neotropical, 2 species adventive in the Old World.

1375. *Oteiza* La Llave

Oteiza La Llave, Reg. Trimestre 1: 41 (1832).

Erect or straggly shrubs, sometimes vine-like. Leaves petiolate or subsessile, blades narrowly to broadly ovate, triplinerved. Capitula in terminal, congested corymbiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries in 3–5 series, strongly gradate, membranaceous to scarious. Receptacles conic, paleae narrow. Ray floret corollas white or whitish green. Disc florets bisexual, corollas yellow; anther appendages ovate; style arms with broad, parallel stigmatic surfaces, apices acute to obtuse, appendages wanting, papillose. Cypselae obconic, black, glabrous. Pappus of multiple, unequal caducous bristles. $x = 17$. Four species, Mexico, Guatemala.

1376. *Sabazia* Cass.

Sabazia Cass., Dict. Sci. Nat. 46: 480 (1827); Longpre, Publ. Mus. Michigan State Univ., Biol. Ser. 4: 287–383 (1970), rev.; Urbatsch & Turner, Brittonia 27: 348–35 (1975), generic limits; Turner, Wrightia 5: 302–305 (1976), generic limits.
Tricarpha Longpre (1970).
Freya V.M. Badillo (1985).

Perennial herbs, rarely weak shrubs. Leaves petiolate or subsessile, blades lanceolate to ovate, sometimes margins deeply dentate, triplinerved. Capitula terminal, solitary or in open paniculiform cymes, radiate. Involucres hemispheric, phyllaries in 2–4 series, subequal to gradate, herbaceous to membranaceous. Receptacles convex to conic, paleae oblong to filiform, sometimes conspicuously trilobed. Ray floret corollas white or creamy white, sometimes with abaxial surfaces suffused

with pink or purple-pink, shallowly to strongly trilobed. Disc florets bisexual, corollas yellow; anther appendages without glandular trichomes; style arms with broad, parallel stigmatic surfaces, sometimes touching each other, appendages small or wanting, papillose. Cypselae obconic, subterete, black, glabrous to sparsely pubescent. Pappus absent or of multiple cuneate to spathulate, sometimes filiform scales or barbellate bristles. $x = 4$. Seventeen species, Mexico, Central America, northern South America.

1377. *Schistocarpha* Less.

Schistocarpha Less., Linnaea 6: 409 (1831); Robinson, Smithsonian Contr. Bot. 42: 1–20 (1979), rev.

Perennial herbs or subshrubs. Leaves petiolate, petioles variously winged, blades ovate to broadly ovate, triplinerved, margins sometimes deeply serrate. Capitula in terminal, congested paniculiform cymes, radiate or disciform. Involucres campanulate to hemispheric, phyllaries in 3–4 series, subequal to shallowly gradate, scarious. Receptacles shallowly convex to conic, paleae trilobed, not protruding beyond phyllaries. Ray floret corollas white, rarely yellow, apices acute to shallowly trilobed. Disc florets bisexual, corollas white, yellow or yellow-green; anther appendages narrowly lanceolate to ovate; style arms with continuous stigmatic surfaces, apices broadly acute to obtuse, appendages wanting. Cypselae narrowly obpyramidal, terete, with a constriction or narrowing below the neck, glabrous or sparsely pubescent, black. Pappus of multiple, barbellate, subequal bristles, more or less persistent, disposed in a radial pattern. $x = 8$. Sixteen species, neotropical, most species in Mexico and Central America.

1378. *Selloa* Kunth

Selloa Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. folio ed. 4: 208 (1818), nom. cons.; Longpre, Publ. Mus. Michigan State Univ., Biol. Ser. 4: 287–383 (1970), rev.; Robinson, Brittonia 49: 71–78 (1997), tax.

Perennial herbs with thickened caudices and roots. Leaves sessile or petiolate, internodes very short, leaves forming a rosette, blades lanceolate to ovate, sometimes suborbicular, bases sheathing, apices acute to broadly acute to obtuse, glaucous on abaxial surface, triplinerved. Capitula terminal, scapose, solitary or in simple cymes, radiate. Involucres campanulate, phyllaries in 3 series, gradate, outermost herbaceous to membranaceous, broadly ovate, inner progressively narrower, lanceolate and covered by exterior phyllaries, scarious. Receptacles convex to conic, paleae filiform. Ray floret corollas white suffused with pink, apices trilobed. Disc florets bisexual, corollas yellow; anther appendages broadly ovate without glandular trichomes; style arms with continuous stigmatic surfaces, apices acuminate, appendages short, papillose. Cypselae obconic to shallowly obpyramidal, subterete, sometimes slightly obcompressed, brown to black, essentially glabrous. Pappus of a few bristles, caducous. One species, *S. plantaginea* Kunth, Mexico.

XXVII.5. Subtribe Guardiolinae H. Rob. (1978).

Annual or perennial herbs, sometimes forming a xylopode, shrubs, sometimes rupicolous. Leaves opposite, blades narrowly lanceolate to deltate, sometimes shallowly hastate to suborbicular, dentate, acuminate to obtuse, abaxial surfaces sometimes glaucous, sometimes semisucculent, membranaceous. Capitula terminal, solitary on long peduncles or in corymbiform cymes, radiate. Involucres cylindric to campanulate, phyllaries dimorphic in two series, outer 3 broad, navicular, herbaceous, inner 2–3 scarious, smaller, similar to paleae. Receptacles flat to convex, paleate. Ray florets pistillate, corollas white, apices shallowly to moderately bilobed or trilobed. Disc florets functionally staminate, corollas white, with a long tube approximately 3–6 times as long as throat/lobe length, throat campanulate, lobes approximately twice as long as throat, spreading, corollas essentially glabrous; anther appendages ovate with one large, basal glandular trichome; style arms of disc florets long, very thin, subulate, those of the ray florets shorter and broader. Cypselae obcompressed, oval to oblong, slightly obovate, brown to black, rarely grey-black, essentially glabrous, sometimes conspicuously striate, with a large, truncate, flattened caruncle or elaiosome. Pappus absent, rarely of several, somewhat lignified scales. $x = 12$.

Only one genus:

1379. *Guardiola* Cerv. ex Hum. & Bonpl. Fig. 99

Guardiola Cerv. ex Hum. & Bonpl., Pl. Aequinoct. 1: 143, t. 41 (1807); Robinson, Bull. Torrey Bot. Club 26: 232–235 (1899),

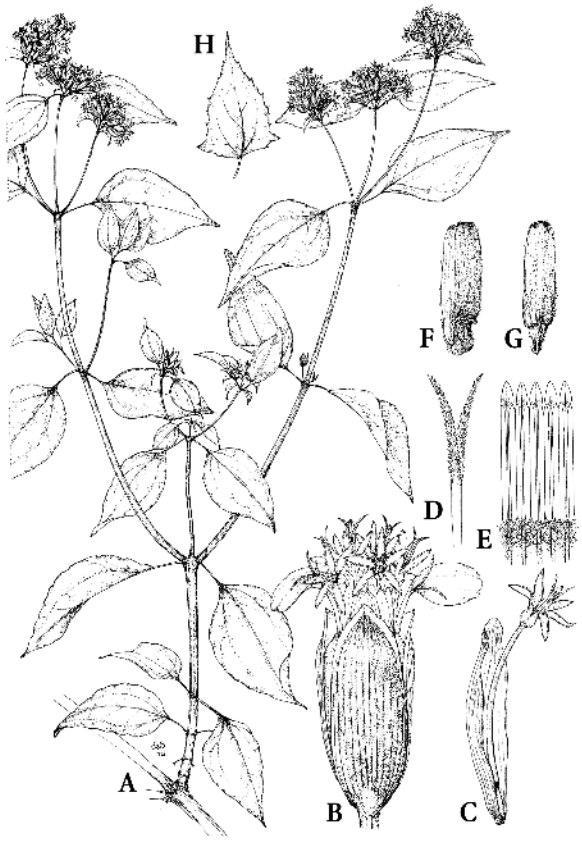

Fig. 99. Compositae-Millerieae. *Guardiola tulocarpus*. **A** Flowering branch. **B** Flowering capitulum. **C** Floret with palea. **D** Style arms. **E** Anthers. **F** Cypsela. *Guardiola mexicana* var. *mexicana*. **G** Cypsela. **H** Leaf. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

rev.; Van Faasen, Ph.D. Thesis, Michigan State University (1971), rev.

Characters of the subtribe. Ten species, Mexico, south-western USA.

XXVII.6. Subtribe Jaegeriinae Panero (2005).

Annual or perennial herbs, some aquatic, sometimes stems fistulose and rooting at nodes. Leaves opposite, sessile or petiolate, blades lanceolate to ovate, 3–5-nerved. Capitula terminal or axillary, solitary or in paniculiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries subequal, herbaceous, innermost trilobed with hyaline wings and enfolding ray cypselae or ovary. Receptacles convex to shallowly conic, paleate. Ray florets pistillate, fertile or sterile, corollas yellow or white suffused with pink. Disc florets bisexual, corollas yellow to greenish yellow, sometimes marked with purple, sometimes tetramerous; anther appendages ovate with or without glandular trichomes; style arms with parallel stigmatic surfaces, apices acute to obtuse, appendages wanting. Cypselae clavate, obovoid, black, glabrous. Pappus absent. $x = 9$.

Only one genus:

1380. *Jaegeria* Kunth

Jaegeria Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. folio ed. 4: 218 (1818); Torres, Brittonia 20: 52–73 (1968), rev.; Turner, Phytologia 55: 243–251 (1984), part. rev.

Characters of the subtribe. Nine species, neotropical, most species in Mexico.

XXVII.7. Subtribe Melampodiinae Less. (1830).

Annual or perennial herbs, shrubs. Leaves opposite, usually petiolate, entire to deeply pinnatifid or lacerate, blades linear to ovate, sometimes rhombic or trullate, uninerved or triplinerved, sometimes pinnately veined. Capitula terminal or axillary, solitary or in open paniculiform or corymbiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries dimorphic in 2 series, the outer 2–5 free to variously connate, inner fused to ray cypselae. Receptacles flat to convex, paleate, sometimes paleae and disc florets shed as a unit. Ray florets pistillate, corollas yellow, orange or white, rarely greenish yellow. Disc florets functionally staminate, corollas yellow to orange; anther appendages ovate, without glandular trichomes; style arms of disc florets fused, the style penicillate, those of the ray florets spreading. Cypselae enclosed in a conceptacle derived from the fused phyllary, conceptacle obconic to trigonal, sometimes incurved, smooth, verrucose or spinose, sometimes phyllary extended as an aristate and coiled appendage, rarely as disc- or saucer-shaped collar. Pappus absent. $x = 9, 10, 11, 12$.

Key to the Genera

1. Paleae and disc florets caducous as a unit after anthesis; ray corollas attached on abaxial side of the cypselae apices **1383. *Melampodium***
– Paleae and disc florets not caducous as a unit after anthesis, ray corollas not attached to the cypselae 2
2. Shrubs; cypselae with disc- or saucer-shaped collars, these sometimes with lacerate or spiny projections; endemic to the Galápagos Islands **1382. *Lecocarpus***

– Perennial herbs; cypselae without disc- or saucer-shaped collars; neotropical, one species in the Galápagos Islands **1381. *Acanthospermum***

Genera of Melampodiinae

1381. *Acanthospermum* Schrank

Acanthospermum Schrank, Pl. Rar. Hort. Monac. 53 (1820) ("1819"); Blake, Contr. U.S. Natl Herb. 20: 383–392 (1921), rev.

Annual herbs. Leaves petiolate to subsessile, blades elliptic, trullate or ovate, entire to lobed, triplinerved. Capitula terminal or axillary, solitary. Involucres hemispheric, phyllaries in 2 series, outer phyllaries 5–6, free to slightly connate at base, inner fused to ray cypselae. Receptacles flat. Ray florets pistillate, corollas yellow. Disc floret corollas yellow to yellow-green; anther appendages ovate. Conceptacle trigonal and strongly echinate to spinose. Pappus absent. $x = 10, 11$. Five to six species, neotropical, adventive in other tropical regions of the world.

1382. *Lecocarpus* Decne

Lecocarpus Decne, Voy. Monde Venus Bot. (1846); Eliasson, Svensk Bot. Tidskr. 65: 245–277 (1971), rev.; Adsersen, Bot. Tidsskr. 75: 63–76 (1980), rev.

Shrubs. Leaves petiolate, blades ovate to oblong in outline, deeply dissected to pectinate, semisucculent. Capitula terminal, solitary. Involucres hemispheric, outer phyllaries 4, herbaceous, connate at base, inner fused to developing ray cypselae. Receptacles flat to convex. Ray florets pistillate, corollas yellow, apices trilobed. Disc floret corollas yellow; anther appendages lanceolate, without glandular trichomes. Conceptacle shallowly trigonal, sometimes spinose, sometimes spines flattened, sometimes with a pappus-like structure resembling a bowl or saucer. Pappus absent. $x = 11$. Three species, Galápagos Islands.

1383. *Melampodium* L. Fig. 100

Melampodium L., Sp. Pl. 2: 921 (1753); Stuessy, Rhodora 74: 1–70, 161–219 (1972), rev.

Annual or perennial herbs some developing a woody caudex, erect or prostrate. Leaves usually petiolate, blades linear to ovate-rhombic to shallowly trullate, entire or lobed, uninerved or triplinerved, sometimes pinnately veined. Capitula terminal, solitary or in simple, paniculiform or corymbiform cymes. Involucres campanulate to hemispheric, phyllaries dimorphic, outer phyllaries 2–5, herbaceous, sometimes connate for 2/3 of their length, inner enclosing ray cypselae. Receptacles convex to conic, paleae and disc florets shed as a unit. Ray florets pistillate, corollas yellow, orange or white, rarely greenish yellow. Disc floret corollas yellow to orange; anther appendages ovate. Conceptacle obconic, blackish to pale brown, smooth or conspicuously tuberculate, sometimes with phyllaries extending as a coiled or stout appendage. Pappus absent. $x = 9, 10, 11, 12$. Forty species, neotropical.

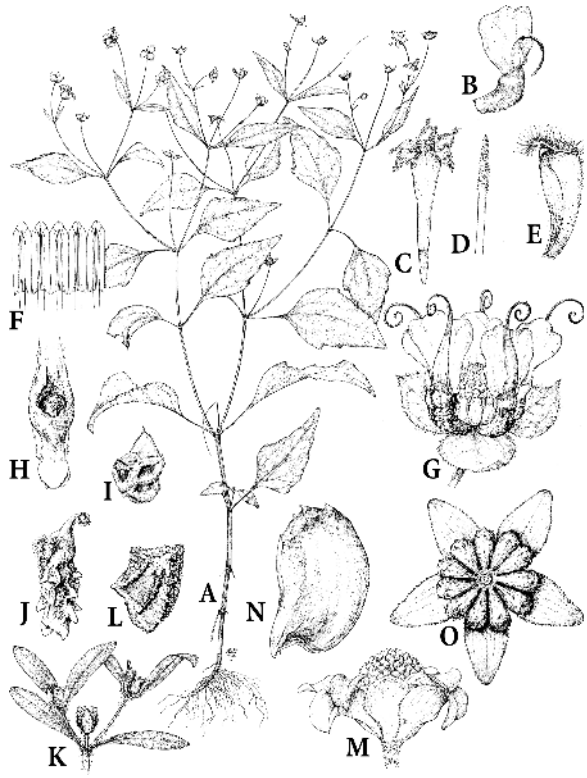

Fig. 100. Compositae-Millerieae. *Melampodium nutans*. **A** Habit. **B** Ray floret. **C** Disc floret. **D** Style apex. **E** Palea. **F** Anthers. **G** Flowering capitulum. **H** Fruit, adaxial view. *Melampodium dicoelocarpum*. **I** Fruit, lateral view. *Melampodium sericeum*. **J** Fruit, latero-adaxial view. **K** Flowering branchlet. *Melampodium divaricatum*. **L** Fruit, lateral view. **M** Flowering capitulum. *Melampodium perfoliatum*. **N** Fruit, lateral view. **O** Fruiting capitulum. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

XXVII.8. Subtribe Milleriinae Benth. (1873).

Annual or perennial herbs, shrubs, sometimes small trees. Leaves opposite, blades linear to broadly ovate, sometimes pinnatifid, mostly

triplinerved, sometimes pentanerved, rarely pinnately veined. Capitula in terminal, open to congested corymbiform or paniculifrom cymes, rarely solitary, radiate, rarely discoid. Involucres cylindric to hemispheric, phyllaries in 1–3 series, outermost series normally with approximately 5 phyllaries, broad, erect, cucullate or reflexed, sparsely to densely stipitate-glandular, inner erect, normally smaller than outer, membranaceous to scarious. Receptacles flat to conic, usually paleate, paleae cucullate, variously pubescent and glandular. Ray florets pistillate, sometimes corollas tubular and the limb wanting, corollas yellow, white or white suffused with purple, rarely red or purple, apices conspicuously trilobed. Disc florets bisexual, fertile or functionally staminate, corollas yellow or creamy white, sometimes purple, pentamerous, rarely tetramerous; endothecium of mostly polar thickenings, rarely radial; style arms of disc florets fused or spreading, with parallel stigmatic surfaces, those of the ray spreading, appendages wanting to well-developed, papillose. Cypselae compressed or obcompressed, black, glabrous. Pappus absent. $x = 10, 12, 15, 16, 17$.

Key to the Genera

1. Capitula with 1–3 ray florets 2
– Capitula with more than 3 ray or peripheral, tubular florets 4
2. Phyllaries becoming leathery with age and wrapping tightly around cypsela **1388. *Milleria***
– Phyllaries herbaceous or scarious, never becoming leathery nor wrapping tightly around cypselae 3
3. Capitula with one ray floret **1392. *Stachycephalum***
– Capitula with more than 1 ray floret **1394. *Unxia***
4. Ray florets tubular; receptacles stipitate; phyllaries white or white suffused with pink **1386. *Ichthyothere***
– Ray florets with a reduced to conspicuous limb, never tubular; receptacles never stipitate; phyllaries never white or pink 5
5. Disc corollas tetramerous, white **1387. *Micractis***
– Disc corollas pentamerous, white, purple or yellow 6
6. Disc florets bisexual 7
– Disc florets functionally staminate 10
7. Outermost phyllaries broad, cochleate or cucullate, rarely lanceolate, erect and enclosing inner phyllaries 8
– Outermost phyllaries linear to spathulate, spreading or reflexed, inner phyllaries not covered by outer phyllaries 9
8. Phyllaries and paleae with reddish striae; plants of tropical Africa **1385. *Guizotia***
– Phyllaries and paleae with dull green or no striae; plants of Mexico and Guatemala **1389. *Rumfordia***
9. Paleae 1.5 or 2 times as long as ovaries, not covered by adjacent disc corollas; leaves variously lobed and/or glaucous underneath **1384. *Axiniphyllum***
– Paleae as long as ovaries, covered by adjacent disc corollas; leaves never lobed, nor with glaucous abaxial surfaces **1390. *Sigesbeckia***
10. Outer series of phyllaries linear to spathulate, spreading or reflexed **1390. *Sigesbeckia***
– Outer series of phyllaries broadly ovate, sometimes cucullate, erect, enclosing inner phyllaries 11
11. Cypselae obpyramidal, triangular in cross-section **1393. *Trigonospermum***
– Cypselae obcompressed, broadly biconvex, oval in cross-section 12
12. Outer phyllaries with long, whitish, sericeous trichomes, paleae linear, vestigial **1394. *Unxia***
– Outer phyllaries without long, whitish, serieceous trichomes, paleae oval to ovate **1391. *Smallanthus***

Genera of Milleriinae

1384. *Axiniphyllum* Benth.

Axiniphyllum Benth., Hooker's Icon. Pl. 12: 16, t. 1118 (1872); Turner, Madroño 25: 46–52 (1978), rev.

Perennial herbs decumbent or erect, arising from a thickened root or caudex. Leaves petiolate, shallowly connate, petioles winged, blades mostly deltate to sagittate in outline, either unlobed or with three prominent lobes, abaxial surfaces sometimes whitish and contrasting with bright green adaxial surface. Capitula in terminal, open paniculiform cymes, radiate or discoid. Involucres hemispheric, sometimes dimorphic with herbaceous outermost phyllaries larger, otherwise subequal to gradate in 2–3 series, herbaceous, densely pubescent and glandular. Receptacles convex. Ray floret corollas yellow (?). Disc florets bisexual, corollas purple, yellow or white, throats abruptly expanded above tube; anther appendages ovate, without glandular trichomes; style arms with broad, parallel stigmatic surfaces not confluent at apices, with small papillose appendages. Cypselae obconic, shallowly to strongly quadrate in cross-section, slightly asymmetrical, concave, black, glabrous. Five species, Mexico.

1385. *Guizotia* Cass.

Guizotia Cass., Dict. Sci. Nat. 59: 237, 247, 248 (1829), nom. cons.; Baagøe, Bot. Tidsskr. 69: 1–39 (1974), rev.

Annual or perennial herbs, shrubs, sometimes repent. Leaves sometimes shallowly perfoliate, petioles variously winged, sometimes with auriculate bases, blades linear to lanceolate, ovate or deltate. Capitula terminal, solitary or in simple cymes or more commonly open corymbiform cymes, radiate. Involucres campanulate to hemi-

spheric, phyllaries dimorphic, the outer broad, herbaceous, normally 5 or 6, the inner much shorter, scarious to membranaceous. Receptacles convex, paleae flat to cucullate, with reddish striae. Ray floret corollas yellow, apices trilobed. Disc florets bisexual, corollas yellow with reddish resin canals; anther appendages ovate, normally with one large basal glandular trichome; style arms with parallel stigmatic surfaces, apices subulate, appendages papillose. Cypselae obcompressed to shallowly quadrate, black, glabrous. $x = 15$. Six species, mostly eastern Africa, one species in tropical western Africa and the Indian subcontinent. *Guizotia abyssinica* (L. f.) Cass. is commercially grown for oil (niger seed) and introduced in various parts of the world.

1386. *Ichthyothere* Mart.

Ichthyothere Mart., Repert. Pharm. 35: 195 (1830).

Perennial herbs or shrubs, aromatic. Leaves petiolate or sessile, blades lanceolate to ovate, glabrous or pubescent, membranaceous to semisucculent, triplinerved. Capitula in terminal, commonly congested simple, rarely open paniculiform cymes, disciform. Involucres campanulate to hemispheric, phyllaries in 1(–2) series, subcoriaceous, striate, white or pinkish white, wrapping around cypselae. Receptacles convex to conic, stipitate. Peripheral florets tubular, pistillate, corollas white or yellow-white, bent or incurved. Disc florets functionally staminate, corollas white or white-yellow, nectaries well-developed; anther appendages ovate to oval, cucullate with large glandular trichomes, trichomes extending down the connective; style arms of disc florets fused, penicillate, those of the ray florets spreading. Cypselae shallowly obcompressed, oblong, very broadly convex, black, essentially glabrous. $x = 16$. Twenty species, Panama, tropical South America.

1387. *Micractis* DC.

Micractis DC., Prodr. 5: 619 (1836); Schulz, Gleditschia 18: 211–218 (1990), rev.

Annual herbs. Leaves winged-petiolate or sessile, sometimes shallowly auriculate, blades lanceolate to ovate or deltate, triplinerved. Capitula in terminal, open paniculiform cymes, radiate. Involucres hemispheric, phyllaries in 2 series, herbaceous. Receptacles convex to shallowly conic. Ray florets pistillate, corollas yellow or yellow-white, mostly bilobed, sometimes trilobed. Disc florets bisexual, innermost sometimes functionally staminate, corollas yellow or yellow-white, tetramerous; anther appendages ovate without glandular trichomes; style arms with parallel stigmatic surfaces, apices deltate, appendages short, papillose. Cypselae compressed, obovate in outline, asymmetrical, incurved, brown to black, glabrous. Four species, eastern Africa, Madagascar.

1388. *Milleria* L. Fig. 101

Milleria L., Sp. Pl. 2: 919 (1753).

Annual herbs. Leaves perfoliate or auriculate, blades broadly lanceolate to suborbicular, sometimes trullate, triplinerved to pentanerved. Capitula in terminal, open paniculiform cymes with distinctive morphology, composed of several branching dichasia which end in multiple, diverging cincinni subtended by a small bract, radiate. Involucres campanulate, phyllaries in 2

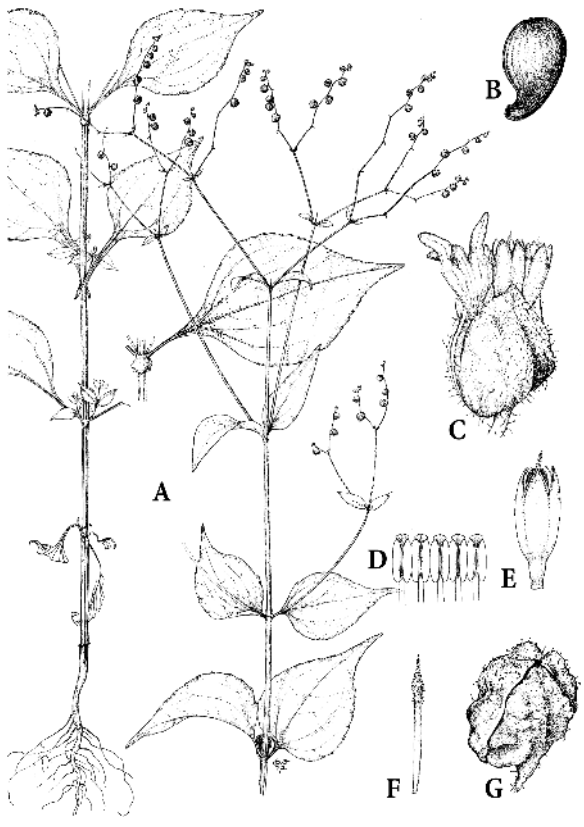

Fig. 101. Compositae-Millerieae. *Milleria quinqueflora*. **A** Habit. **B** Cypsela. **C** Flowering capitulum. **D** Anthers. **E** Disc corolla. **F** Undivided style of disc corolla. **G** Involucre at fruiting stage. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

series, outer 2, unequal, broad, flat to cupulate, inner around 5, scarious. Receptacles flat. Ray florets 1–2, pistillate, 3-lobed, corollas yellow. Disc florets 4–6, functionally staminate, corollas yellow; anther appendages broadly ovate, deep purple or black, with glandular trichomes; style arms of ray florets with parallel stigmatic surfaces, styles of disc florets undivided, penicillate, apices acute. Ray cypsela obpyriform, black, glabrous, covered tightly by the thickened phyllaries, resembling an anthocarp. $x = 15$. Two species, Mexico, Central America, northern South America, Peru.

1389. *Rumfordia* DC.

Rumfordia DC., Prodr. 5: 549 (1836); Sanders, Syst. Bot. 2: 302–316 (1977), rev.

Perennial herbs or mostly straggly or multi-stemmed shrubs. Leaf blades ovate to hastate, sometimes broadly trullate, bases attenuate into winged petiole, sometimes auriculate, triplinerved or pectinate, margins serrate. Capitula in terminal, open paniculiform cymes, radiate. Involucres hemispheric, outer phyllaries normally 5, foliose and variously pubescent, inner erect and much smaller, coriaceous to membranaceous, densely glandular-hairy. Receptacles convex. Ray florets in 1 or 2 rows, pistillate, corollas yellow, apices shallowly to conspicuously trilobed. Disc florets bisexual, corollas yellow; anther appendages lanceolate to ovate, glabrous or rarely with one glandular or tapered trichome; style arms with broad, parallel stigmatic surfaces not confluent at apices, without appendages. Cypselae compressed, rarely subterete, shallowly to strongly asymmetrical, sometimes with a prominent neck on abaxial side, black or black-brown, glabrous. $x = 12, 15$. Seven to eight species, Mexico, Guatemala.

1390. *Sigesbeckia* L.

Sigesbeckia L., Sp. Pl. 2: 900 (1753); McVaugh & Anderson, Contr. Univ. Michigan Herb. 9: 485–493 (1972), rev.; Schulz, Hausskechtia 4: 25–35 (1988), part. rev.; Schulz, Cat. Herb. Lipsiensis Pl. Neotrop. 2: 52–65 (1989), part. rev.
Schkuhria Moench (1794), nom. rej., non Roth (1797), nom. cons.

Annual or perennial herbs, sometimes forming a woody caudex with thickened roots and/or with fistulose stems. Leaves with winged petioles, sometimes perfoliate, blades ovate to trullate, rarely broadly ovate, triplinerved. Capitula in terminal, open paniculiform cymes, radiate. Involucres turbinate to campanulate, hemispheric, phyllaries dimorphic, outer lanceolate to shallowly oblanceolate, herbaceous, sometimes densely glandular, patent or strongly reflexed, inner erect, cucullate. Receptacles shallowly convex to conic. Ray florets pistillate, corollas yellow, white or white suffused with pink, apices trilobed. Disc florets bisexual, rarely functionally staminate, corollas yellow or creamy white; anther appendages ovate to lanceolate, without glandular trichomes, sometimes with large druses; style arms with broad, parallel stigmatic surfaces not confluent at apices, with small, sometimes cylindric, papillose appendages. Cypselae compressed, obpyramidal, asymmetrical, shallowly quadrate, rarely triquetrous, oblong in cross-section, black, glabrous. $x = 10, 15$. Eight species, pantropical, most species in Mexico.

1391. *Smallanthus* Mack.

Smallanthus Mack., Man. S.E. Fl. 1406 (1933); Wells, Brittonia 17: 144–159 (1965), rev.; Robinson, Phytologia 39: 47–53 (1978), generic limits.

Annual or perennial herbs, shrubs or small trees. Leaves petiolate, petioles variously winged, blades lanceolate to ovate, sometimes suborbicular or broadly deltate, entire to strongly dentate, triplinerved. Capitula in terminal, corymbiform or open paniculiform cymes, radiate, sometimes nodding after anthesis. Involucres hemispheric, outer phyllaries foliose, much longer than inner, sometimes reflexed, lanceolate or broadly ovate, inner resembling the pales, sometimes membranaceous, striate. Receptacles convex. Ray florets pistillate, corollas yellow or creamy white, rarely purple, apices shallowly trilobed. Disc florets functionally staminate, corollas yellow, white or purplish, glabrescent to moderately pubescent, sometimes with glandular trichomes; anther appendages broadly ovate to deltate, without glandular trichomes; style arms of ray florets with parallel stigmatic surfaces meeting at the apices, of disc florets variously fused, densely papillose. Ray cypselae shallowly compressed, obpyriform, isodiametric to oblong in cross-section, black to dark brown, glabrous. $x = 16, 17$. Twenty species, neotropical.

1392. *Stachycephalum* Sch. Bip. ex Benth.

Stachycephalum Sch. Bip. ex Benth., Hooker's Icon. Pl. t. 1102 (1872).

Perennial herbs or weak, straggly, short-lived shrubs. Leaves winged-petiolate, blades lanceolate

to broadly ovate, triplinerved. Capitula in terminal, congested corymbiform or scorpioid cymes, radiate, sometimes the female floret somewhat separated from the male disc florets on a stipitate, lateral receptacle (*Stachycephalum argentinum*); ray floret subtended by cochleate phyllary, disc florets subtended by one or two paleae/phyllaries and collectively subtended by a bract. Involucres cylindric, phyllaries in 1 series, 1 or 2, herbaceous. Receptacles flat, sometimes laterally stipitate, sometimes epaleate. Ray floret pistillate, corollas white or yellow (?). Disc florets functionally staminate, corollas white, yellow (?); anther appendages lanceolate to narrowly oval, without glands; style arms of ray florets with parallel stigmatic surfaces, these meeting at the apices, styles of disc florets, undivided, penicillate, apices acute. Ray cypselae obpyriform, black, glabrous, sometimes sterile (embryo fails to develop). Three species, Ecuador, Mexico, Argentina.

1393. *Trigonospermum* Less.

Trigonospermum Less., Syn. Gen. Comp. 214 (1832); McVaugh & Laskowski, Univ. Michigan Herb. 9: 495–506 (1972), rev.; Schulz, Cat. Herb. Lipsiensis Pl. Neotrop. 1: 52–59 (1988), syn.

Annual or perennial herbs. Leaves petiolate, blades ovate to broadly ovate, triplinerved. Capitula in terminal, open or congested paniculiform or corymbiform cymes, radiate. Involucres campanulate to hemispheric, phyllaries in 2 series, herbaceous. Receptacles convex. Ray florets pistillate, corollas yellow, apices deeply trilobed. Disc florets functionally staminate, corollas yellow, sometimes tetramerous; anther appendages ovate to round, without glandular trichomes; style arms of ray florets with parallel stigmatic surfaces meeting at the apices, styles of disc florets undivided, apices acute. Cypselae broadly obpyramidal, triquetrous, black, glabrous. $x = 15$. Four species, Mexico, Central America.

1394. *Unxia* L. f.

Unxia L. f., Suppl. Pl. 56, 368 (1781) [1782]; Stuessy, Brittonia 21: 314–321 (1969), rev.; Stuessy, Rhodora 73: 291–292 (1971), tax.

Annual or perennial herbs, shrubs. Leaves opposite, blades elliptic to lanceolate, triplinerved, entire to shallowly serrate. Capitula tightly clustered in terminal, simple cymes, radiate. Involucres hemispheric, phyllaries in 2–3 series, gradate, outermost 2–3 broadly ovate, herbaceous, strongly sericeous, inner scarious, striate. Receptacles convex. Ray florets pistillate, corollas yellow. Disc florets functionally staminate, corollas yellow-orange; anther appendages ovate, without glandular trichomes; style arms of disc florets fused, penicillate, those of the ray florets small, spreading. Cypselae obcompressed, ovoid, black, glabrous. $x = 16$. Three species, Panama, northern South America.

XXVIII. Tribe Madieae Jepson (1901).

B.G. Baldwin and J.L. Panero

Annual or perennial herbs, subshrubs, shrubs, trees or lianas. Leaves alternate, opposite or whorled, usually sessile, blades narrowly linear to ovate, oblanceolate to spathulate or elliptic, rarely deltate, entire or pinnately toothed to divided, sometimes glandular. Capitula terminal, usually corymbose, paniculate, racemose or solitary, sometimes glomerulate, ± umbellate or spicate, radiate, discoid or (rarely) disciform. Involucres cylindric to globose, phyllaries in 1–2 (rarely 3–4+) series, subequal or rarely gradate, flat to conduplicate (in Madiinae, each ± enveloping a ray ovary), herbaceous, distinct or connate, often sessile- or stipitate-glandular. Receptacles flat to conical, glabrous or setulose to villous, epaleate or wholly to partially paleate, the paleae usually in 1 series between ray and disc florets or, if capitula discoid, constituting a false involucre. Ray florets pistillate, corollas usually yellow or white, glabrous or pubescent. Disc florets bisexual or functionally staminate, corollas actinomorphic, rarely zygomorphic, (4–)5-merous, glabrous or hairy, sometimes glandular; anthers opaque, yellow to brown or reddish to dark purple; style arms each with two narrow to broad, parallel stigmatic surfaces, apices truncate or obtuse to deltate or subulate, rarely deltate-acuminate, appendages usually much shorter than stigmatic region or wanting. Cypselae fusiform or clavate to obovate or obpyramidal, terete, weakly or strongly angled, compressed, or obcompressed, ray and disc often dimorphic, black or brown, often striate, rarely glandular. Pappus usually of ovate to setiform, fimbriate to plumose scales, sometimes unlike and alternating, sometimes of ciliolate to plumose bristles, rarely absent. $x = 19$.

The tribe comprises 36 genera and more than 200 species, which occur mostly in the conterminous western USA (especially California),

south-western Canada and north-western Mexico (Baja California). Geographic outliers include three genera of Madiinae endemic to the Hawaiian islands, some species of *Arnica* in northern or eastern North America or Eurasia, and three species of Baeriinae and Madiinae that occur either disjunctly or solely in temperate South America. Tinctures from flowers or rhizomes of *Arnica* (especially *A. montana*) have been used widely in traditional cultures and folk or homeopathic medicine to promote healing of injuries. Historically, *Madia sativa* was cultivated widely for seed oil, and used by indigenous Americans for food and medicine.

Tribe Madieae was proposed by Jepson (1901) to apply to paleate, mostly dark-anthered composites with ray-ovary-clasping phyllaries known commonly as tarweeds, a mostly Californian group treated previously (and subsequently by most workers) as a subtribe, Madiinae or 'Madieae' (Bentham 1873a), and usually placed in tribe Heliantheae (e.g. Stuessy 1977; Robinson 1981), with other paleate, dark-anthered taxa. Carlquist's (1959) anatomical studies established the modern limits of subtribe Madiinae. Molecular phylogenetic studies affirmed Carlquist's (1959) circumscription of subtribe Madiinae, and led to reinstatement of tribe Madieae (in an expanded sense) for a mostly western North American lineage including tarweeds and a subset of epaleate taxa previously treated in Helenieae, Heliantheae or Senecioneae (Baldwin and Wessa 2000a; Baldwin et al. 2002; Panero and Funk 2002). Based on the molecular findings, expression of paleae and dark anthers in tribe Madieae is not strictly homologous with expression of those traits in Heliantheae and other closely related tribes. A well-supported sister-group relationship between Madiinae and *Arnica* (including *Mallotopus* and *Whitneya*), although not suggested prior to the cited molecular studies, is consistent with the close morphological, ecological, and chromosomal similarities between *Arnica* and the tarweed genus *Raillardella* – the sister group to all other tarweeds (Baldwin 2003a); the two genera were closely associated in classifications of Senecioneae from the time of Bentham (1873a), until Carlquist (1959) showed that *Raillardella* belonged in Madiinae [*Arnica* was disassociated from Senecioneae by Nordenstam (1977) and Robinson (1981)]. Genera of tribe Madieae that are closely related to *Arnica* (Arnicinae) and Madiinae include *Hulsea* and *Eatonella* (Hulseinae) and *Venegasia* (Venegasiinae), all of which share with *Arnica* a base chromosome number of $x = 19$, and also occur in montane or wet habitats somewhat similar to sites occupied by *Raillardella* but unlike habitats of most other members of Madiinae. Based on the molecular studies cited above, woolly sunflowers and relatives (e.g. *Eriophyllum*, *Lasthenia*) constitute a clade corresponding to subtribe Baeriinae, which parallels the tarweeds as examples of extensive diversification in the California Floristic Province within tribe Madieae. Relationships among members of tribe Madieae are subjects of continuing phylogenetic study.

Key to the Subtribes

1. Phyllaries each partially to wholly clasping a ray ovary or cypsela; receptacles wholly or partially paleate (paleae indistinguishable from phyllaries in discoid taxa); if heads discoid, plants annuals or rhizomatous perennials with pappus of plumose, subulate or lanceolate scales or plants of woody life-forms **4. Madiinae** (p. 497)
– Phyllaries not clasping ray ovaries or cypselae; receptacles epaleate; if heads discoid, plants annuals or rhizomatous perennials with pappus of bristles (sometimes plumose) or non-plumose scales 2
2. Leaves opposite (at least proximally); pappus of persistent bristles or, if absent, disc florets functionally staminate and ray corollas persistent **1. Arnicinae** (p. 493)
– Leaves opposite or alternate, sometimes in basal rosettes; pappus of awns, scales, or deciduous bristles, or, if absent, disc florets bisexual and ray corollas caducous 3
3. Subshrubs or shrubs; leaves distinctly petiolate, blades entire or coarsely toothed; phyllaries 3–4+-seriate, the outer 1(–2) series often reflexed; pappus absent **5. Venegasiinae** (p. 507)
– Herbs or, less commonly, subshrubs or shrubs; leaves usually sessile or winged-petiolate (distinctly petiolate in *Constancea* – with blades dissected), blades entire, toothed, lobed, or dissected; phyllaries 1–3-seriate, usually erect, sometimes the outermost series reflexed (in *Hulsea*); pappus present or absent 4
4. Phyllaries 1(–2)-seriate; anther endothecium of mostly quadrate cells with (1–)2–4 polar thickenings; style branches flat; cypselae usually not compressed nor ciliate **2. Baeriinae** (p. 494)
– Phyllaries 2–3-seriate; anther endothecium of fusiform cells with 1 polar thickening; style branches cucullate to canaliculate; cypselae compressed, densely ciliate along edges **3. Hulseinae** (p. 497)

XXVIII.1. Subtribe Arnicinae B.G. Baldwin (2002).

Perennial herbs, usually rhizomatous. Leaves all or mostly opposite, blades lanceolate to ovate or oblanceolate to obovate or orbiculate, entire or shallowly lobed, glabrous or tomentose, some-

times glandular. Capitula terminal, solitary or laxly corymbose, radiate or discoid. Involucres narrowly obconic to campanulate or hemispheric, phyllaries in (1–)2 series. Receptacles convex, epaleate, tomentose. Ray floret corollas yellow to yellowish-orange or rarely cream. Disc florets bisexual or rarely functionally staminate, corollas yellow to yellowish-orange, 5-lobed; anthers yellow or rarely purple (not blackened), endothecium of oblong cells with 1–2 polar thickenings; style arm apices much shorter than the stigmatic lines. Cypselae cylindrical or narrowly clavate to obovoid or obpyramidal, weakly to strongly angled, glabrous or hairy, the walls carbonized, striate. Pappus usually present and persistent, of white to tawny, barbellate to plumose bristles. $x = 19$ (polyploidy/apomixis extensive).

Only one genus:

1395. ***Arnica*** L. Fig. 102

Arnica L., Sp. Pl. 2: 884 (1753); Maguire, Brittonia 4: 386–510 (1943), rev.; Wolf & Denford, Rhodora 86: 239–309 (1984), part. rev.; Downie & Denford, Rhodora 90: 245–275 (1988), part. rev., Gruezo & Denford, Asia Life Sci. 3:89–212 (1994), part. rev., Baldwin, Novon 9: 460–461 (1999), tax.
Whitneya A. Gray (1865).
Mallotopus Franch. & Sav. (1878).

Characters of the subtribe. Circa 30 species, northern hemisphere (mostly montane or boreal).

Fig. 102. Compositae-Madieae. **A–C** *Arnica dealbata*. **A** Top view of a capitulum. **B** Side view of a capitulum. **C** Inflorescence. **D–H** *A. mollis*. **D** Top view of a capitulum. **E** Side view of a capitulum. **F** Ray floret. **G** Disc floret. **H** Habit. (From Baldwin 2003a; illustrations by Lesley Randall)

XXVIII.2. Subtribe Baeriinae Benth. & Hook. f. (1873).

Subtribe Eriophyllinae Rydb. (1915), as 'Eriophyllanae'

Annual herbs or shrubs, glabrous or moderately to densely lanate. Leaves usually alternate, usually sessile, blades linear to ovate, rarely succulent, entire or 1-, rarely 2-pinnate, faces sparsely to densely hairy, rarely glabrous. Capitula laxly to densely paniculate or corymbose or solitary, radiate, rarely discoid or disciform. Involucres cylindric to hemispheric, phyllaries in 1(–2) series, herbaceous, free or variously fused. Receptacles convex to conical, rarely globose, epaleate, variously foveolate, sometimes stipitate. Ray floret corollas usually yellow, sometimes tubular and limbs very reduced, apices entire or shallowly 2- to 3-lobed. Disc florets bisexual, corollas golden yellow, rarely tetramerous or zygomorphic, variously hairy with moniliform hairs, sessile or stipitate glands normally present, sometimes abundant; anthers opaque to yellow, appendages lanceolate to ovate with or without glands; style arm apices obtuse to deltate, rarely subulate, appendages wanting or reduced to a proliferation of papillae, rarely 0.5–1× length of stigmatic surfaces (*Syntrichopappus*). Cypselae obcuneate to obpyramidal, sometimes narrowly obovate, linear to fusiform, variously compressed or obcompressed, sometimes both conditions in the same capitulum, rarely ray and disc cypselae dimorphic, black, rarely brown, striate, glabrous or sparsely to densely hairy, sometimes with multiple, globose glands (*Baeriopsis*). Pappus absent or more commonly of scales (bristles in *Syntrichopappus*), sometimes with those at angles of cypsela longer and resembling awns, persistent or caducous. $x = 19$.

Key to the Genera

1. Leaves succulent; cypselae densely covered with globose glands; plants of Guadalupe Island, Mexico
1397. ***Baeriopsis***

– Leaves usually not succulent; cypselae without or with relatively few and widely scattered glands; plants of continental America or Californian Channel Islands 2
2. Shrubs; leaves petiolate (blades 1–2-pinnate, dissected); plants of San Clemente, Santa Barbara, and Santa Catalina islands **1398. *Constancea***
– Annual or perennial herbs; leaves sessile to subpetiolate; plants mostly of continental America 3
3. Leaves opposite **1400. *Lasthenia***
– Leaves alternate, at least distally 4
4. Phyllaries connate in proximal 1/2 (leaves lobed on at least part of plant); pappus absent or coroniform **1402. *Pseudobahia***
– Phyllaries free or, if connate, leaves entire; pappus of bristles or scales or absent 5
5. Disc corolla lobes narrowly lanceolate, subulate; anther appendages narrowly lanceolate; style-branch appendages subulate, length 0.5–1× stigmatic surfaces; pappus of bristles or absent **1403. *Syntrichopappus***
– Disc corolla lobes never narrowly lanceolate; anther appendages never narrowly lanceolate; style-branch appendages reduced to an obtuse to deltate proliferation of papillae, never subulate, length much less than 0.5× stigmatic surfaces; pappus of scales or absent 6
6. Anther appendages on an extended connective, half as long as thecae **1306. *Amblyopappus***
– Anther appendages never on an extended connective, 0.2–0.5× as long as thecae 7
7. Phyllaries broadly ovate, cucullate; ray corollas 'bilabiate' (with small adaxial lobe); ray cypselae triquetrous, obcompressed **1401. *Monolopia***
– Phyllaries oval to lanceolate; ray corollas not bilabiate; ray cypselae never triquetrous and obcompressed **1399. *Eriophyllum***

Genera of Baeriinae

1396. *Amblyopappus* Hook. & Arn.

Amblyopappus Hook. & Arn., J. Bot. (Hooker) 3: 321 (1841).

Annual herbs. Leaves mostly alternate, blades linear to ovate in outline, pinnatifid or the distal entire. Capitula congested-corymbose or congested-paniculate, radiate or disciform. Involucres cylindric to hemispheric, phyllaries broad, somewhat cucullate. Peripheral florets pistillate, corollas yellow, essentially tubular, limb reduced. Disc floret corollas yellow; anther appendages on extended connectives usually 1/2 length of thecae, ovate, without glands; style arms with narrow stigmatic surfaces, apices truncate to obtuse, papillose. Cypselae obcuneate, subterete to shallowly ridged, black, sparsely to moderately hairy and with scattered, large glands. Pappus of multiple, broadly spathulate to cuneate scales, central and basal areas shallowly thickened, edges papillose. $x = 8$. One species, *A. pusillus* Hook. & Arn., western USA, western Mexico, Peru, Chile.

1397. *Baeriopsis* J.T. Howell

Baeriopsis J.T. Howell, Leafl. W. Bot. 3: 152–154 (1942).

Caespitose shrublets. Leaves alternate, sessile, blades narrowly oblanceolate, succulent, entire, glabrous. Capitula solitary, radiate. Involucres hemispheric, phyllaries in 2 series, semi-succulent. Receptacles conical to globose. Ray floret corollas yellow, shallowly trilobed. Disc floret corollas golden yellow, lobes densely hairy with biseriate hairs; anther appendages ovate, with large glands; style arm apices deltate, appendages acuminate, papillose. Cypselae obpyramidal to shallowly biconvex (ray cypselae triquetrous), black-brown, sparsely hairy, with large glands. Pappus of multiple lanceolate to linear scales. $x = 8$. One species, *B. guadalupensis* J.T. Howell, north-western Mexico (Guadalupe Island, Baja California).

1398. *Constancea* B.G. Baldwin

Constancea B.G. Baldwin, Madroño 46: 159–160 (1999) [2000].

Shrubs, stems densely pubescent, white. Leaves alternate, petiolate, blades broadly ovate in outline, 1–2-pinnate, lobes linear to oblanceolate, densely white-tomentose to (adaxially) glabrate. Capitula congested-corymbose to congested-paniculate, radiate. Involucres cylindric to campanulate, phyllaries in 1–2 series, with a thickened central area or midrib. Receptacles convex. Ray floret corollas yellow. Disc floret corollas golden yellow; anther appendages ovate, with 1–2 glands; style arms with narrow stigmatic surfaces, apices obtuse to shallowly deltate, papillose. Cypselae narrowly obpyramidal to biconvex, oval to quadrate in cross-section, black, glabrous. Pappus mostly of 2 awn-like scales at angles of cypselae with intervening squamellae, sometimes with 3 or 4 awn-like scales. $x = 19$. One species, *C. nevinii* (A. Gray) B.G. Baldwin, western USA (San Clemente, Santa Barbara and Santa Catalina islands, California).

1399. *Eriophyllum* Lag.

Eriophyllum Lag., Gen. Sp. Pl. 28 (1816); Constance, Univ. Calif. Publ. Bot. 18: 69–136 (1937), rev.; Johnson, Novon 1: 119–124 (1991), tax.
Antheropeas Rydb. (1915).

Annual or perennial herbs, shrubs. Leaves mostly alternate, blades linear to ovate or trullate in outline, entire or toothed to pinnatifid or deeply lobed, lobes commonly linear to oblanceolate,

sparsely to densely lanate or glabrate. Capitula laxly or densely paniculate or corymbose, radiate or discoid. Involucres cylindric to hemispheric, phyllaries in 1(–2) series (usually 1 per ray floret), with a thickened central area or midrib, sometimes densely lanate. Receptacles convex to conical. Ray floret corollas yellow, rarely white, entire or shallowly trilobed. Disc floret corollas lemon or golden yellow; anther appendages ovate, with multiple glands, rarely eglandular; style arm apices obtuse, appendages reduced to a papillose rim. Cypselae cylindric to narrowly obovoid, terete or angled with 4 or 5 sides, sometimes biconvex, black, glabrous or sparsely hairy. Pappus absent or more commonly of several lacerate scales. x = 4, 5, 7, or 8 (16, 24, 32, polyploid; 15, dysploid). Thirteen species, western USA.

1400. *Lasthenia* Cass.

Lasthenia Cass., Opusc. Phytol. 3: 88 (1834); Ornduff, Univ. Calif. Publ. Bot. 40: 1–92 (1966), rev.; Chan et al., Intl J. Pl. Sci. 162: 1347–1360 (2001), phylog.
Baeria Fisch. & C.A. Mey. (Jan.? 1836).
Crockeria Greene ex A. Gray (1884).

Annual or perennial herbs, sometimes semi-aquatic. Leaves opposite, blades linear to lanceolate, entire or toothed to pinnatifid, sometimes ciliate, glabrous to sparsely hairy. Capitula laxly paniculate or solitary, radiate. Involucres cylindric to hemispheric, phyllaries in 1(–2) series, free or connate. Receptacles convex to conical. Ray floret corollas yellow, yellow-white, sometimes greenish yellow, entire or shallowly trilobed. Disc floret corollas yellow, sometimes tetramerous; anther appendages ovate, without glands; style arms with narrow stigmatic surfaces, apices deltate, appendages acuminate to cylindric, papillose. Cypselae subterete to biconvex, linear to fusiform, black, sparsely hairy, sometimes sparsely glandular. Pappus absent or of 2 fragile awns, or of awns and scales. x = 8 (4–7, dysploid; 12, 16, 24, polyploid). Eighteen species, western USA, south-western Canada, north-western Mexico (Baja California), Chile.

1401. *Monolopia* DC.

Monolopia DC., Prodr. 6: 74 (1837) [1838]; Crum, Madroño 5: 250–270 (1940), rev.; Baldwin, Novon 9: 460–461 (1999), tax.
Lembertia Greene (1897).

Annual herbs. Leaves mostly alternate, blades oval to lanceolate or oblanceolate, pinnately veined, sinuate to shallowly lobed or entire, sparsely to moderately lanate. Capitula laxly paniculate or solitary, radiate. Involucres hemispheric, phyllaries in 1 series, broadly ovate, free or connate, lanate, usually with black hairs towards apices. Receptacles convex to conical. Ray floret corollas yellow, rarely cream, 'bilabiate' (with small adaxial lobe), limbs sometimes inconspicuous (*M. congdonii*), trilobed. Disc floret corollas yellow; anther appendages ovate, usually with glands; style arms with broad stigmatic surfaces, apices obtuse, appendages mostly lacking or reduced to papillae. Ray cypselae obcompressed, obpyramidal, incurved, triquetrous, sometimes densely pubescent, disc cypselae flattened-biconvex, edges densely ciliate, faces glabrous or sparsely pubescent, sometimes with a longitudinal line of trichomes coinciding with linear interstice between adjacent cypselae. Pappus absent or (in *M. congdonii*) of mostly 2 lacerate scales, with or without 2 fragile, diverging awns. x = 10, 11, 12, or 13. Five species, western USA (California).

1402. *Pseudobahia* (A. Gray) Rydb.

Pseudobahia (A. Gray) Rydb., N. Amer. Fl. 34: 83 (1915).

Annual herbs. Leaves alternate, blades linear to ovate in outline, commonly pinnatifid, lobes linear, moderately lanate. Capitula laxly paniculate or solitary, radiate. Involucres campanulate to hemispheric, phyllaries in 1 series, bases to proximal half connate. Receptacles conical. Ray floret corollas yellow, entire to shallowly bilobed or trilobed, tubes densely pubescent distally. Disc floret corollas yellow, lobes thickened, tubes densely pubescent distally; anther appendages ovate, with glands; style arm apices obtuse to subtruncate, papillose, appendages wanting. Cypselae obcompressed or obpyramidal, biconvex to mostly triquetrous, sometimes with 4(–5) ridges, narrowly triangular in cross-section, black, sparsely pubescent. Pappus absent or a crown of scales. x = 8 (3, 4, dysploid). Three species, western USA (California).

1403. *Syntrichopappus* A. Gray

Syntrichopappus A. Gray, Pac. Railr. Rep. 4, 5(4): 106 (1857).

Annual herbs. Leaves alternate to subopposite, blades narrowly to broadly linear, entire or distally trilobed, moderately to densely lanate. Capitula laxly paniculate or corymbose, radiate. Involucres cylindric to campanulate, phyllaries in 1 series,

oval with a conspicuous midrib, margins scarious. Receptacles convex, shallowly stipitate. Ray floret corollas yellow, white or pink, shallowly bilobed or trilobed. Disc floret corollas lemon or golden yellow, with broad vascular strands, sometimes lobes ciliate; anther appendages narrowly lanceolate, without glands; style arms with narrow stigmatic surfaces, apices subulate to deltate, appendages well developed, 0.5–1× as long as stigmatic surfaces, densely papillose. Cypselae narrowly clavate, 3–5-angled, sparsely to densely hairy. Pappus absent or of multiple slender, flattened, caducous, barbellate bristles. $x = 6$ or 7. Two species, western USA.

XXVIII.3. Subtribe Hulseinae B.G. Baldwin (2002).

Biennial or perennial herbs, rarely annuals. Leaves cauline and/or in basal rosettes, alternate, sessile or winged-petiolate, entire or dentate or rarely lobed, glandular and/or woolly. Capitula terminal, laxly corymbose, racemose or paniculate or often solitary, radiate. Involucres usually hemispheric, phyllaries in 1–3 series, erect or the outermost series reflexed, narrow. Receptacles flat, epaleate, glabrous. Ray floret corollas yellow, orange, red or purplish. Disc florets bisexual, corollas yellow or orange, 5-lobed; style arms cucullate to canaliculate, appendages much shorter than the paired stigmatic lines or wanting. Cypselae ± cylindrical to clavate, ± compressed, 2-edged, ± thick-margined, carbonized, edges densely ciliate, faces shiny-glabrous or sparsely to densely hairy. Pappus persistent, of 1–2 opposite pairs of free, acuminate to truncate, noncostate, ± uniformly thick, apically erose scales. $x = 19$.

Key to the Genera

1. Phyllaries in (1–)2 series; ray corollas barely surpassing phyllaries; disc florets 4–12 **1404. *Eatonella***
– Phyllaries in 2–3 series; ray corollas showy; disc florets 20 or more **1405. *Hulsea***

1404. *Eatonella* A. Gray

Eatonella A. Gray, Proc. Amer. Acad. Arts 19: 19 (1883).

Annual herbs, sometimes densely branched, tufted. Leaves sessile or subpetiolate, blades linear to spathulate, entire, densely lanate. Capitula congested-paniculate or solitary, peduncles elongating after anthesis. Involucres cylindric to campanulate, phyllaries in (1–)2 series, narrowly lanceolate, densely lanate abaxially. Receptacles convex. Ray floret corollas white-yellow or white-pink, shallowly trilobed. Disc floret corollas white or yellow-white; anther appendages ovate, without glands; style arms with narrow stigmatic surfaces, canaliculate adaxially, apices somewhat expanded, obtuse, appendages lacking. Cypselae narrow, oblong to fusiform or linear, compressed or obcompressed, biconvex, margins densely ciliate, faces glabrous, black, shiny. Pappus of 2 plicate squamellae, each with a protruding awn (at edges of cypsela). One species, *E. nivea* A. Gray, western USA.

1405. *Hulsea* Torr. & A. Gray

Hulsea Torr. & A. Gray, Pac. Railr. Rep. 6: 77 (1858); Wilken, Brittonia 27: 228–244 (1975), rev.

Annual, biennial or perennial herbs. Leaves sessile or subpetiolate, blades broadly linear to lanceolate, rarely obovate, faces sometimes densely white-lanate. Capitula laxly paniculate or solitary, radiate. Involucres campanulate to hemispherical, phyllaries in 2–3 series. Receptacles flat to slightly convex. Ray floret corollas bright to golden yellow, sometimes orange or rusty red, entire to shallowly trilobed. Disc floret corollas yellow or orange; anther appendages ovate, without glands; style arms with broad stigmatic surfaces, branches canaliculate to cucullate, apices obtuse to round, papillose, appendages wanting. Cypselae narrowly obpyramidal to biconvex, compressed, sometimes quadrate, black, striate, moderately to densely silvery- or rusty-hairy. Pappus mostly of 4 scales, those at the angles of each cypsela longer, resembling awns, sometimes 4 awns. Seven species, western USA, north-western Mexico (Baja California).

XXVIII.4. Subtribe Madiinae Benth. & Hook. f. (1873) (as Madieae); Carlquist et al. (eds) Tarweeds & silverswords: evolution of the Madiinae (Asteraceae), Missouri Bot. Gard., St. Louis (2003), rev.

Subtribe Raillardellinae Rydb., N. Amer. Fl. 34, 4: 318 (1927), as 'Raillardellanae'

Annual or perennial herbs, lianas, rosette shrubs, subshrubs, shrubs or trees. Leaves alternate, opposite or whorled, usually sessile or subpetiolate,

blades usually oblanceolate to spathulate or linear to linear-elliptic, entire or serrulate to toothed, sometimes pinnately lobed or pinnatifid, usually ± parallel-nerved, usually sparsely to densely ± hirsute and stipitate-glandular, sometimes villous or sericeous or rarely glabrous. Capitula usually corymbose, paniculate, racemose, spicate, glomerulate or ± umbellate, sometimes solitary, radiate or discoid. Involucres cylindric to globose, phyllaries in 1(–2) series or 0 ('involucre' then interpreted as constituting 1 series of receptacular paleae), usually conduplicate (each partly or wholly investing a subtended floret, apices often attenuate), usually glandular. Receptacles flat or convex to conic, paleate (paleae usually in 1 series interior to phyllaries or, if capitula discoid, in 1 outer series and constituting an 'involucre', then sometimes connate and persistent, sometimes 1 subtending each disc floret, then usually distinct and often soon falling, rarely in 2–3+ series), hispidulous or glabrous. Ray floret corollas usually yellow or whitish, apices (2–)3-lobed. Disc florets bisexual or functionally staminate, corollas usually yellow, 5-lobed; anthers usually reddish to dark purple, sometimes yellow to brownish, appendages usually lanceolate-oblong to ovate-deltate, without glands, endothecium of mostly quadrate to cylindrical cells, with mostly 1–2(–4) polar thickenings; style arm apices usually lanceolate to subulate, rarely deltate or deltate-acuminate, appendages much shorter than stigmatic lines or wanting. Cypselae often obpyramidal, clavate or fusiform, compressed, obcompressed or terete, usually ray and disc dimorphic, black or brown, often striate or ribbed, glabrous or sparsely to densely hairy. Pappus absent or of awns, bristles or scales (sometimes in combination) in 1–2 series, the elements scabrid to plumose. $x = 17$ or 18.

Key to the Genera

1. Ray cypselae obcompressed (each mostly or completely enveloped by lateral margins of a phyllary); if rays 0, then plants pappose annuals 2
– Ray cypselae compressed, ± terete, or ± triangular in cross-section (if ± obcompressed, then each ± half enveloped by lateral margins of a phyllary); if rays 0, then plants perennials or epappose annuals 6
2. Plants annuals (1–20 cm); disc florets 1(–2) **1418. *Hemizonella***
– Plants annual or perennial herbs (2–150 cm); disc florets 3–120+ 3
3. Plants rhizomatous perennials; disc corollas white **1421. *Holozonia***
– Plants annuals; disc corollas yellow (sometimes reddish with age) 4
4. Pappus of 10, broad, apically obtuse scales **1406. *Achyrachaena***
– Pappus absent or of bristles or apically acute scales 5
5. Heads usually calyculate (involucre proper subtended by 2–5 bractlets); ray florets 5; disc florets 6, functionally staminate; disc pappus 0 **1424. *Lagophylla***
– Heads not calyculate; ray florets 0 or 3–27; disc florets 4–120+, bisexual; disc pappus of 2–32 bristles or scales, rarely 0 **1425. *Layia***
6. Annuals; styles of disc florets hairy proximal to minute arms; [receptacles paleate throughout, ray corollas white with abaxial purple lines, pappus of subulate, fimbriate to plumose scales] **1410. *Blepharipappus***
– Annuals or perennials; styles of disc florets glabrous proximal to arms 7
7. Perennial herbs, ± scapiform; disc pappus of subulate, ciliate-plumose scales **1428. *Raillardella***
– Annuals, leafy-stemmed perennial herbs, perennial rosette plants, or plants woody; disc pappus 0 or of scales (seldom both subulate and ciliate-plumose in herbaceous taxa) 8
8. Peduncular bracts sometimes each with an apical pit-gland, tack-gland(s), or spine (or apiculus); heads radiate; ray cypselae terete to subterete or slightly obcompressed (cross-section nearly circular except adaxial side ± flattened to slightly bulging, or ± 3-angled with abaxial side usually ± broadly 2-faced, angle between those faces usually 90+° and adaxial side ± flattened to slightly bulging), each ± half enveloped by a phyllary; if distal leaves spine-tipped or apiculate, then each ray cypsela ± enveloped by a phyllary and sometimes compressed 9
– Peduncular bracts each without an apical pit-gland, tack-gland, or spine (or apiculus); heads radiate or discoid; ray cypselae usually compressed, rarely ± terete (then cross-section usually ± 3-angled with abaxial side relatively broad, ± rounded, adaxial side ± 2-faced, angle between those faces 15–70°), each usually completely or mostly enveloped by a phyllary 15
9. Annuals; leaves filiform to linear, margins often strongly revolute; peduncular bracts usually with tack-glands; ray corolla lobes (lateral) often spreading (lengths often 1/2–5/6 of total laminae) 10
– Annuals, perennial herbs, subshrubs, or shrubs; leaves linear or broader, margins seldom strongly revolute; peduncular bracts usually without tack-glands; ray corolla lobes ± parallel (lengths usually 1/10–1/2 of total laminae) 11
10. Ray cypselae beaked; tack-glands absent **1427. *Osmadenia***
– Ray cypselae not beaked; tack-glands present **1412. *Calycadenia***
11. Ray corollas usually white, sometimes yellow, laminae often with abaxial purple lines; ray cypselae not beaked or each with an inconspicuous, straight beak (beak lengths less than diameters) 12
– Ray corollas yellow, laminae without abaxial purple lines; ray cypselae each with an adaxial, ascending beak (beak lengths longer than diameters) 13
12. Receptacles with paleae restricted to bases of outermost disc florets; disc florets bisexual; cypselae hairy **1411. *Blepharizonia***

– Receptacles with paleae throughout; disc florets functionally staminate; cypselae glabrous **1419. *Hemizonia***
13. Peduncular bracts apiculate or each with an apical spine **1414. *Centromadia***
– Peduncular bracts not apiculate, without apical spines 14
14. Plants annuals; peduncular bracts each with an apical pit-gland; receptacles paleate throughout **1420. *Holocarpha***
– Plants annuals or perennials; peduncular bracts without pit-glands; receptacles with paleae usually restricted to bases of outermost disc florets (if in 2–3+ series, then perennials) **1415. *Deinandra***
15. Plants woody or semi-woody, evergreen; Hawaiian islands 16
– Plants herbaceous or woody with seasonal foliage; North American or South American 18
16. Heads radiate on at least part of plant; (thick-leaved) rosette shrubs **1409. *Argyroxiphium***
– Heads discoid; lianas, (fibrous-leaved) rosette shrubs, subshrubs, shrubs, trees 17
17. Leaves 1–4 per node, free or weakly united; lianas, subshrubs, shrubs, trees **1416. *Dubautia***
– Leaves 7–15 per node, strongly connate at base; rosette shrubs **1429. *Wilkesia***
18. Disc pappus absent **1426. *Madia***
– Disc pappus of 5–21 scales (scales sometimes subulate to setiform, bristle-like) 19
19. Heads all discoid **1413. *Carlquistia***
– Heads radiate on at least part of plant 20
20. Plants shrubby; Mexico **1407. *Adenothamnus***
– Plants herbaceous; Californian (to north-western USA and south-western Canada) 21
21. Plants perennials 22
– Plants annuals 23
22. Involucres campanulate to hemispheric; anthers dark purple; ray cypselae beakless **1423. *Kyhosia***
– Involucres campanulate to ellipsoid or globose; anthers yellow to brownish; ray cypselae beaked **1408. *Anisocarpus***
23. Anthers yellow to brownish **1417. *Harmonia***
– Anthers ± dark purple **1422. *Jensia***

Genera of Madiinae

1406. *Achyrachaena* Schauer

Achyrachaena Schauer, Del. Sem. Hort. Vratislav. 3 (1837).

Annuals. Leaves proximally opposite, distally alternate, blades linear, entire or toothed, hirsute or villous and (distal leaves) sparsely glandular-pubescent. Capitula laxly ± corymbose or borne singly, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ± campanulate to cylindric or ellipsoid, phyllaries 3–8 in 1 series, each fully investing a ray ovary, ± lanceolate-linear, abaxially hirsute or villous and sparsely glandular-pubescent or eglandular. Receptacles flat to convex, setulose, paleae not persistent, in 1 series (between rays and disc), free. Ray florets 3–8, corollas yellow, turning reddish. Disc florets 4–35, bisexual, corollas yellow to reddish, abaxially pubescent; anthers ± dark purple, appendages ovate; styles glabrous proximal to arms, arms free, apices lanceolate-linear, hairy and papillose. Ray cypselae black, obcompressed, clavate, 10-ribbed, straight, glabrous or ± scabrous, not beaked. Disc cypselae similar, brown to black, ± scabrous. Ray pappus absent. Disc pappus of 10 white, oblong, apically obtuse scales. $x = 8$. One species, *A. mollis* Schauer, western USA, western Mexico (northern Baja California).

1407. *Adenothamnus* D.D. Keck

Adenothamnus D.D. Keck, Madroño 3: 6 (1935).

Shrubs, aromatic. Leaves proximally opposite, mostly alternate; blades linear, entire, ± evenly stipitate-glandular. Capitula ± corymbose or borne singly, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres campanulate, phyllaries 8–13 in 1 series, linear-attenuate, each fully investing a ray ovary, ciliolate, adaxially stipitate-glandular. Receptacles flat or convex, setulose, paleae not persistent, in 1 series between ray and disc florets, connate 1/2+ length. Ray florets 8–13, corollas yellow. Disc florets 12–50+, bisexual, corollas yellow, abaxially glabrous; anthers reddish to dark purple, appendages oblong-lanceolate; styles glabrous proximal to arms, arms free, apices lanceolate, hairy and papillose. Ray cypselae black, compressed, clavate, ± arcuate, glabrous, not beaked. Disc cypselae black, ± terete, clavate, ± straight, faces sparsely hispidulous. Ray pappus 0. Disc pappus of 15–20 setiform, ciliate-plumose scales. $x = 14$. One species, *A. validus* (Brandegee) D.D. Keck, western Mexico (northern Baja California).

1408. *Anisocarpus* Nutt.

Anisocarpus Nutt., Trans. Amer. Philos. Soc. n.s. 7: 388 (1841); Baldwin, Novon 9: 462–471 (1999), tax.
Raillardiopsis Rydb. (1927).

Perennial herbs. Leaves proximally rosulate or opposite, distally alternate, blades oblong to linear, lanceolate-linear or oblanceolate, entire or toothed, hirsute to strigose or pubescent and (distal leaves) stipitate-glandular. Capitula ± corymbose or racemose or borne singly, radiate or discoid. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ± globose or broadly ellipsoid to campanulate, phyllaries same number as ray flo-

rets, in 1 series, lanceolate to lanceolate-attenuate or oblanceolate, each 1/2 or fully investing a ray ovary, ciliolate, abaxially stipitate-glandular, sometimes also hirtellous. Receptacles flat to convex, glabrous or setulose, paleae not persistent, in 1 series between ray and disc florets, usually connate. Ray florets 0, 1–3 or 7–15, corollas yellow. Disc florets 5–30, bisexual or functionally staminate, corollas yellow, tubes and throats often abaxially glabrous, lobes sparsely hispidulous and minutely glandular abaxially; anthers yellow, appendages ovate; styles glabrous proximal to arms, arms free, apices subulate, densely hairy. Ray cypselae black or greyish, compressed or ± obcompressed, clavate, ± arcuate, glabrous or hairy, beaked. Disc cypselae (if present) black or greyish, ± terete, clavate, ± straight, hairy. Ray pappus 0 or coroniform. Disc pappus of 5–8 or 11–21 linear, lanceolate, quadrate or subulate, fimbrillate, erose or ciliate-plumose scales. $x = 7$. Two species, western USA, western Canada (Vancouver Island).

1409. *Argyroxiphium* DC. Fig. 103

Argyroxiphium DC., Prodr. 5: 668 (1836); Carr, Allertonia 3: 1–123 (1985), rev.; Baldwin & Robichaux in Wagner & Funk (eds) Hawaiian biogeography: evolution on a hot spot archipelago: 259–287 (1995), phylog.

Rosette shrubs (monocarpic or polycarpic). Leaves in rosettes, sessile, blades narrowly linear to lanceolate-linear or narrowly elliptic, entire, hispid, sericeous, silvery-floccose or glabrate. Capitula elongate-racemose or -paniculate, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres campanulate to broadly or depressed-hemispheric, phyllaries same number as ray florets, in 1 series, linear to lanceolate, oblanceolate or elliptic-oblong, each partially or wholly investing a ray ovary, glandular-hairy and sometimes floccose-lanate. Receptacles convex to conic, glabrous to hirsutulous, paleae not persistent, mostly in 1 series between ray and disc florets, connate. Ray florets (0–)1–45; corollas reddish, purplish, white or yellow. Disc florets 30–600, bisexual, corollas reddish, purplish, whitish, or yellow; anthers yellowish to brownish or reddish to dark purple, appendages ovate; styles glabrous proximal to arms, arms free, apices broadly deltate-acuminate to rounded-truncate, hairy and papillose. Cypselae ± terete or angular (usually ribbed), narrowly clavate, arcuate or (some disc cypselae) straight, glabrous, not beaked. Ray pappus coroniform. Disc pappus of 2–10, lanceolate-linear to oblong, fimbriate scales (most or all abaxial on each cypsela). $x = 14$. Five species, Hawaiian islands.

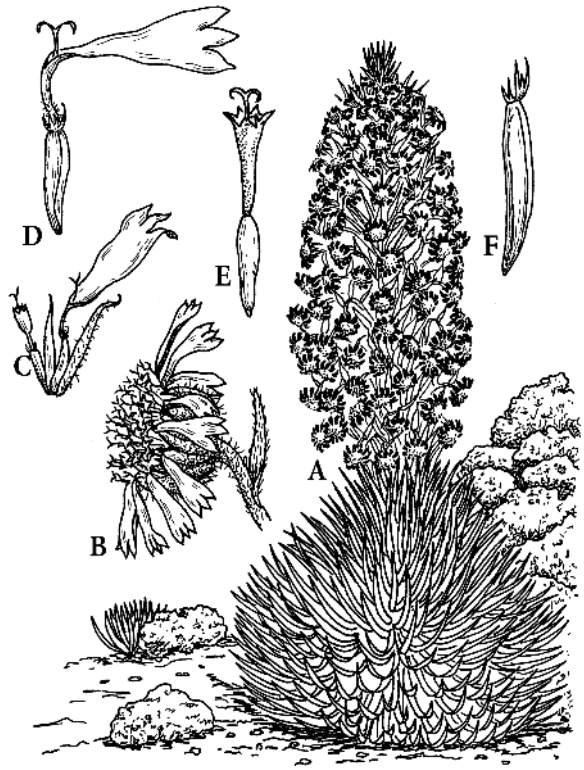

Fig. 103. Compositae-Madieae. *Argyroxiphium sandwicense* subsp. *macrocephalum*. **A** Habit. **B** Capitulum. **C** Phyllary, ray floret, palea, and disc floret (*right to left*). **D** Ray floret. **E** Disc floret with pappus removed. **F** Disc cypsela with pappus intact. (From Baldwin 2003b; illustrations by Lesley Randall)

1410. *Blepharipappus* Hook.

Blepharipappus Hook., Fl. Boreal.-Am. 1: 316. 1833 (sero) ('1840').

Annuals. Leaves proximally opposite, mostly alternate, blades narrowly spathulate to linear, entire, scabrous, hirsute, strigose, sericeous or villous (distal leaves usually also stipitate-glandular). Capitula laxly corymbose or borne singly, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres turbinate to campanulate or hemispheric, phyllaries (2–)3–5(–8) in 1 series, ± lanceolate or oblanceolate, each ± 1/2 investing a ray ovary, abaxially ± hirsute and/or stipitate-glandular. Receptacles convex, glabrous, paleae not persistent, subtending all or most disc florets. Ray florets (2–)3–5(–8); corollas whitish

(purple-veined abaxially). Disc florets 6–25(–60+), bisexual, corollas whitish, glabrous abaxially except for hispidulous lobes; anthers ± dark purple, appendages hemi-orbiculate or conical; styles hairy proximal to minute arms, arms free, apices truncate, papillose. Cypselae ± terete, ± obconic, ± villous, not beaked. Pappus 0 or of 12–18(–26) subulate, fimbriate to ciliate or plumose scales. $x = 8$. One species, *B. scaber* Hook., western USA.

1411. *Blepharizonia* (A. Gray) Greene

Blepharizonia (A. Gray) Greene, Bull. Calif. Acad. Sci. 1: 279 (1885); Baldwin et al., Syst. Bot. 26: 184–194 (2001), phylog., tax.
Hemizonia DC. subg. *Blepharizonia* A. Gray (1874).

Annuals, aromatic. Leaves proximally opposite (forming winter–spring rosettes, often not persistent), mostly alternate; blades narrowly spathulate to linear or the distal lanceolate, entire or serrate, hirsute to strigose, sericeous, pilose or villous (distal leaves also ± stipitate-glandular and/or bearing tack-glands). Capitula ± corymbose, spicate, paniculate or borne singly, radiate. Peduncular bract tips and margins usually bearing tack-glands. Involucres campanulate or obconic to ± globose, phyllaries 5–13 in 1 series, lanceolate or oblanceolate, each ± 1/2 investing a ray ovary, abaxially canescent to hirsute or hispid to glabrate, usually also bearing tack-glands. Receptacles flat, hirtellous, paleae not persistent, in 1 series between ray and disc florets, free. Ray florets 5–13, corollas whitish (often red- to purple-veined abaxially), lobes ± parallel. Disc florets 5–35(–60+), bisexual, corollas whitish to purplish, glabrous abaxially except for sparsely hispidulous lobes; anthers ± dark purple, appendages ovate to ovate-deltate; styles glabrous proximal to arms, arms free, apices subulate, densely hairy. Cypselae ± terete or ± obcompressed, clavate, 10-ribbed, ± sericeous, not beaked. Ray pappus 0 or coroniform. Disc pappus 0 or of 12–20+, reddish-brown, ciliate to plumose, ± subulate scales. $x = 14$. Two species, western USA (California).

1412. *Calycadenia* DC.

Calycadenia DC., Prodr. 5: 695 (1836); Carr, Amer. J. Bot. 64: 694–703 (1977), rev.; Baldwin & Markos, Mol. Phylog. Evol. 10: 449–463 (1998), phylog.

Annuals, often aromatic. Leaves proximally in rosettes or opposite, usually mostly alternate, blades linear, usually entire, sometimes toothed (revolute), the proximal often bristly-ciliate, often scabrous. Capitula ± corymbose, glomerulate, racemose, paniculate or spicate, or borne singly, radiate. Peduncular bract tips each usually bearing a tack-gland, lateral surfaces or margins sometimes with additional tack-glands. Involucres cylindric, obconic, ovoid or campanulate, phyllaries 1–6 in 1 series, each c. 1/2 investing a ray ovary, often with tack-glands and/or simple, sessile or stipitate glands. Receptacles ± flat, setulose, paleae sometimes persistent, in 1 series between ray and disc florets, connate. Ray florets 1–6, corollas white to reddish or yellow, sometimes bicoloured, lobes often spreading. Disc florets 1–25, bisexual, corollas white to reddish or yellow, lobes abaxially hispidulous, minutely glandular or not; anthers usually ± dark purple, appendages lanceolate-ovate to deltate; styles glabrous proximal to arms, arms free, apices subulate, hairy. Ray cypselae slightly obcompressed (± 3-angled, abaxial side ± 2-faced, angle between those faces 90+°, adaxial side ± flat), rugose or smooth, glabrous or hairy, not beaked. Disc cypselae ± terete or angular, clavate, glabrous or hairy. Ray pappus 0. Disc pappus of (0)6–13 subulate to lanceolate-aristate (or shorter, wider and often alternating) scales. $x = 7$ (4–6, dysploid). Ten species, western USA (mostly California).

1413. *Carlquistia* B.G. Baldwin

Carlquistia B.G. Baldwin, Novon 9: 463 (1999); Baldwin & Kyhos, Madroño 37: 43–54 (1990), rev.

Perennial herbs, rhizomatous, often matted. Leaves proximally opposite, distally alternate, blades lanceolate to linear, entire, hirsute to villous and glandular-pubescent. Capitula laxly corymbose or borne singly, discoid. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ± campanulate, phyllaries (modified paleae) (5–)7–16 in 1 series, lanceolate to lanceolate-linear, abaxially hirsute and glandular-pubescent. Receptacles flat, setulose, epaleate (except for bracts constituting 'involucre'). Florets 7–29, bisexual, corollas yellow, proximal throat and lobes abaxially hirtellous; anthers yellow to brownish, appendages broadly ovate-deltate; styles glabrous proximal to arms, arms free, apices subulate, densely hairy. Cypselae ± terete, scabrellous, not beaked. Pappus of 9–17 white to mauve or tawny, subulate, ± plumose scales (flattened bristles). $x = 8$. One species, *C. muirii* (A. Gray) B.G. Baldwin, western USA (California).

1414. *Centromadia* Greene

Centromadia Greene, Fl. Franciscana 424 (1897); Baldwin, Novon 9: 462–471 (1999), tax.

Annual or perennial, rhizomatous herbs. Leaves proximally in rosettes or opposite (not persistent), mostly alternate; blades oblanceolate to linear or lanceolate-linear, proximal 1–2-pinnatifid to toothed, distal entire, apices of the distal usually spine-tipped, glabrous, scabrous-hirtellous, ± hirsute or villous, often also glandular. Capitula glomerulate, ± spicate-paniculate or ± umbellate, radiate. Peduncular bracts each without a pit-gland or tack-gland, usually spine-tipped, sometimes apiculate. Involucres ± obconic or urceolate, phyllaries 5–75+ (as many as ray florets), lanceolate to lanceolate-attenuate or oblanceolate, each usually 1/2 investing a ray ovary, abaxially scabrous-hirtellous, hirsute, or villous and/or glandular, apices often spine-tipped. Receptacles flat to convex, setulose, paleae persistent, subtending all or most disc florets, free. Ray florets 5–75+; corollas yellow. Disc florets 6–200+, usually functionally staminate, rarely bisexual; corollas yellow, tubes/throats abaxially glabrous, lobes often abaxially hispidulous; anthers ± reddish to dark purple or yellow to brownish, appendages ovate; styles glabrous proximal to arms, arms free, apices ovate to subulate, densely hairy. Ray cypselae ± compressed, abaxially gibbous, glabrous, beaked or elevated adaxially. Ray pappus 0. Disc pappus 0 or of 3–12 linear, subulate or oblanceolate scales. $x = 13$ (9–12, dysploid). Four species, western USA, western Mexico (northern Baja California).

1415. *Deinandra* Greene

Deinandra Greene, Fl. Franciscana 424 (1897); Baldwin, Novon 9: 462–471 (1999), tax.

Annual and perennial herbs, subshrubs or shrubs, often aromatic. Leaves proximally in rosettes or opposite (usually not persistent), mostly alternate; blades oblanceolate to linear or lanceolate-linear, pinnatifid to toothed, serrate or entire, variously hairy (often also sessile- or stipitate-glandular) or glabrous with scabrous or hispid margins. Capitula often corymbose, ± paniculate, sometimes racemose or glomerulate, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ± obconic, campanulate, hemispheric or urceolate, phyllaries 3–35 in 1 series, ± lanceolate to lanceolate-attenuate or oblanceolate, each usually 1/2 investing a ray ovary, abaxially ± hirsute and sessile- or stipitate-glandular. Receptacles flat to convex, glabrous or setulose, paleae deciduous, usually in 1 series (between rays and disc), sometimes in 2–3+ series, connate or free. Ray florets 3–35, corollas deep or pale yellow. Disc florets 3–70, usually functionally staminate, seldom bisexual, corollas yellow, tubes/throats abaxially glabrous or minutely glandular-hairy, lobes sometimes abaxially hispidulous or glandular; anthers usually reddish to dark purple or yellow to brownish, rarely maroon, appendages lanceolate-ovate to deltate; styles glabrous proximal to arms, arms free, apices subulate, densely hairy. Ray cypselae slightly obcompressed (adaxially), clavate, abaxially gibbous, often ± arcuate, glabrous, ± beaked, beaks offset adaxially, ascending. Ray pappus 0. Disc pappus usually of 1–15 lanceolate to subulate, entire or ± fringed to erose scales, sometimes absent or a crown of linear to fimbriate scales. $x = 12$ or 13 (9–11, dysploid). Twenty-one species, western USA (mostly California), Mexico (Baja California).

1416. *Dubautia* Gaudich.

Dubautia Gaudich., Voy. *Uranie* 469 (1830); Carr, Allertonia 3: 1–123 (1985), rev., tax.; Carr, Pac. Sci. 53: 144–158 (1999), rev.; Baldwin & Robichaux in Wagner & Funk (eds) Hawaiian biogeography: evolution on a hot spot archipelago: 259–287 (1995), phylog.; Baldwin in Givnish & Sytsma (eds) Molecular evolution and adaptive radiation: 103–128 (1997), phylog.

Railliardia Gaudich. (1830); *Raillardia* auct., sphalm.; *Railliarda* DC., sphalm.

Subshrubs, shrubs, trees or lianas. Leaves alternate, opposite or whorled (3–4 per node), blades linear to lanceolate-ovate, elliptic or obovate, entire, serrulate or toothed, glabrous or variously hairy, sometimes also glandular-glutinous. Capitula ± corymbose, racemose or paniculate or borne singly, discoid. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres cylindrical, campanulate, obconic, ellipsoid or ovoid, phyllaries (modified paleae) in 1–2 series, linear-oblong to obovate, abaxially glabrous or puberulent to villous, also often glandular. Receptacles flat to conic, hairy, paleae deciduous, in 1–2 'involucral' series or subtending most or all florets, often connate. Florets 2–45, corollas white or yellow, sometimes tinged or aging purplish, abaxially glabrous or with scattered hairs or proximally glandular; anthers yellowish to brownish or dark purple, appendages lanceolate-

oblong to ovate-oblong; styles glabrous proximal to arms, arms free, apices deltate to subulate, moderately hairy and papillose to densely hairy. Cypselae ± terete, ± clavate, straight, glabrous or hairy. Pappus of 8–28 lanceolate-ovate to setiform, laciniate-fimbriate, ciliate or plumose scales. $x = 14$ (13, dysploid). Twenty-four species, Hawaiian islands.

1417. *Harmonia* B.G. Baldwin

Harmonia B.G. Baldwin, Novon 9: 463 (1999); Baldwin, Madroño 48: 293–297 (2001), phylog., tax.

Annuals. Leaves proximally opposite, distally alternate, sessile, blades linear, entire or toothed. Capitula laxly ± umbellate to corymbose or borne singly, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres obovoid to obconic, phyllaries 3–8 (same number as rays) in 1 series, strongly conduplicate, lanceolate to oblanceolate, each wholly investing a ray ovary. Receptacles flat to convex, glabrous or setulose, paleae not persistent, in 1 series (between rays and disc), free or weakly connate. Ray florets usually 3–8, corollas bright yellow (laminae flabelliform to obovate). Disc florets 7–30, bisexual or functionally staminate (sometimes in same head), corollas bright yellow, tubes/throats abaxially glabrous or proximally hirtellous-hispidulous, lobes abaxially hispidulous; anthers yellow to brownish, appendages ovate-dentate to hemi-orbiculate; styles glabrous proximal to arms, arms free, apices subulate, densely hairy. Ray cypselae black, terete to ± compressed, weakly arcuate, gibbous or not, beaked or beakless, glabrous. Disc cypselae black, ± terete, ± clavate, glabrous or hairy. Ray pappus 0 or of 3–12, lanceolate to subulate, fimbrillate to plumose scales. Disc pappus of 7–11, lanceolate-attenuate to subulate, linear, oblong or quadrate, fimbriate, fimbrillate or plumose scales. $x = 9$. Five species, western USA (California).

1418. *Hemizonella* (A. Gray) A. Gray

Hemizonella (A. Gray) A. Gray, Proc. Amer. Acad. Arts 9: 189 (1874); Baldwin, Novon 9: 462–471 (1999), tax.
Hemizonia DC. § [unranked] *Hemizonella* A. Gray, Proc. Amer. Acad. Arts 6: 548 (1865).

Annuals. Leaves proximally opposite, distally alternate (often clustered proximal to branches), blades linear, entire or toothed, hirsute and (distal leaves) glandular-puberulent. Capitula corymbose or glomerulate or borne singly, radiate (peduncles filiform). Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ± obovoid, phyllaries 3–5 in 1 series, each mostly or wholly investing a ray ovary, ± oblanceolate, abaxially hirsute and glandular-hirtellous. Receptacles flat to convex, glabrous or sparsely setulose, paleae not persistent, in 1 series (between rays and disc), connate. Ray florets 3–5; corollas pale yellow. Disc florets 1–2, bisexual, corollas pale yellow, abaxially pubescent; anthers yellow to brownish, appendages hemi-orbiculate (reduced, not exceeding thecae); styles glabrous proximal to arms, arms free, apices subulate, densely hairy. Ray cypselae black, obcompressed, arcuate, sparsely hispidulous or glabrate, apices minutely beaked. Disc cypselae black, ± terete, clavate, ± hispidulous, apices minutely beaked. Pappus absent. $x = 21–22$. One species, *H. minima* (A. Gray) A. Gray, western USA, western Canada (British Columbia).

1419. *Hemizonia* DC.

Hemizonia DC., Prodr. 5: 692 (1836); Baldwin, Novon 9: 462–471 (1999), tax.

Annuals, often aromatic. Leaves proximally in rosettes or opposite (persistent or not), mostly alternate, blades narrowly elliptic to linear or lanceolate-linear, serrulate or entire, variously hairy, distal leaves also sometimes stipitate-glandular as well. Capitula ± glomerulate, paniculate, racemose or spicate or borne singly, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres hemispheric to ± urceolate or globose, phyllaries 5–14 in 1 series, linear to lanceolate or oblanceolate, each usually 1/2 investing a ray ovary, abaxially pubescent to hirsute or villous, and stipitate-glandular. Receptacles flat to conic, glabrous, paleae connate, forming cells around all or most disc florets (± deliquescent). Ray florets 5–14, corollas white or yellow, often purple-veined abaxially. Disc florets 5–60+, functionally staminate, corollas white or yellow, abaxially glabrous; anthers ± dark purple, appendages broadly ovate to ovate-deltate; styles glabrous proximal to arms, arms free or proximally united, apices lanceolate-subulate, densely hairy. Cypselae ± obcompressed (adaxially), abaxially gibbous, glabrous, beak absent or inconspicuous, straight. Pappus absent. $x = 14$. One species, *H. congesta* DC., western USA (California, southern Oregon).

1420. *Holocarpha* Greene

Holocarpha Greene, Fl. Franciscana, 426 (1897); Baldwin, Ann. Missouri Bot. Gard. 93:64–93 (2006), evol., phylog.

Annuals, aromatic. Leaves proximally in rosettes or opposite (usually not persistent), mostly alternate, blades linear to oblanceolate, serrate to serrulate or entire, hirsute to strigose, sericeous or villous (distal leaves sometimes also stipitate-glandular and/or resin-gland-dotted), apices of distal leaves usually with a pit-gland. Capitula ± corymbose, glomerulate, paniculate, racemose or spicate or borne singly; radiate. Peduncular bract tips each with a pit-gland. Involucres ± obconic or campanulate to ± globose, phyllaries 3–16 in 1 series, elliptic, oblanceolate or obovate, each usually 1/2 investing a ray ovary, abaxially with pit-gland-tipped processes, otherwise glabrous or puberulent to hispid, and/or sessile- or stipitate-glandular. Receptacles flat to convex, glabrous, paleae not persistent, subtending all or most disc florets. Ray florets 3–16; corollas yellow, lobes ± parallel. Disc florets 9–90, some bisexual, most functionally staminate; corollas yellow, proximally and distally glandular abaxially; anthers yellow to brownish or pinkish to dark purple, appendages ovate to ovate-deltate; styles glabrous proximal to arms, arms free, apices subulate to aristate, densely hairy. Ray cypselae ± obcompressed (adaxially), abaxially gibbous, glabrous, beaks adaxial, ascending. Disc cypselae ± clavate, glabrous, not beaked. Pappus absent. $x = 4$ or 6. Four species, western USA (California).

1421. *Holozonia* Greene

Holozonia Greene, Bull. Torrey Bot. Club 9: 122 (1882).

Perennials, rhizomatous. Leaves proximally opposite (basally connate), distally alternate; blades lanceolate to linear, entire, hirsute and (distal leaves) glandular-hirtellous (glands cup-shaped). Capitula laxly corymbose or borne singly, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ± obconic or turbinate, phyllaries 4–10 in 1 series, each mostly or wholly investing a ray ovary, ± lanceolate-linear, abaxially hirsute, sometimes glandular-hirtellous (glands cup-shaped). Receptacles flat to convex, glabrous or setulose, paleae not persistent, in 1 series (between rays and disc), connate. Ray florets 4–10, corollas whitish (abaxially purplish-veined). Disc florets 9–28, functionally staminate, corollas white, tubes/throats abaxially glabrous or with scattered hairs, lobes abaxially hispidulous; anthers ± dark purple, appendages ovate; styles glabrous proximal to arms; arms free or proximally united, apices subulate, hairy. Cypselae black, obcompressed, ± clavate, glabrous, not beaked (areolae broadly cupulate). Ray pappus 0 or coroniform, 0.1–0.3 mm. Disc pappus 0 or of 1–5 caducous, subulate scales. $x = 14$. One species, *H. filipes* (Hook. & Arn.) Greene, western USA (California).

1422. *Jensia* B.G. Baldwin

Jensia B.G. Baldwin, Novon 9: 464 (1999).

Annuals. Leaves proximally opposite (often crowded), distally alternate, blades spathulate to linear, entire or toothed, hirsute to strigose, distal leaves sometimes also stipitate-glandular. Capitula ± umbellate, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ± obconic or urceolate to globose, phyllaries 2–12 in 1 series, lanceolate to lanceolate-attenuate, each usually wholly investing a ray ovary, abaxially hirsute (hair tips ± uncinate). Receptacles flat to convex, glabrous or setulose, paleae not persistent, in 1 series (between rays and disc), connate. Ray florets 2–12, corollas yellow, sometimes purple-veined abaxially. Disc florets 1–65, functionally staminate, corollas yellow, abaxially glabrous except for hispidulous lobes; anthers ± dark purple, appendages ovate-deltate; styles glabrous proximal to arms, arms free, apices narrowly lanceolate-subulate, densely hairy. Cypselae compressed, clavate, arcuate, glabrous, beaked. Ray pappus a crown of scales, 0.1–1 mm. Disc pappus of 5–7 (white or purple-tipped) subulate, crisped, ciliolate scales, 2.5–3 mm. $x = 8$. Two species, western USA (California).

1423. *Kyhosia* B.G. Baldwin

Kyhosia B.G. Baldwin, Novon 9: 465 (1999).

Perennials, rhizomatous. Leaves proximally in rosettes or opposite, distally alternate, blades lanceolate-linear to linear, entire, hirsute and (distal leaves) glandular-hirtellous. Capitula laxly ± corymbose or borne singly, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ± campanulate to hemispheric, phyllaries 8–12 in 1 series, each mostly or wholly investing a ray ovary, lanceolate to lanceolate-linear, abaxially hirsute and glandular-hirtellous. Receptacles flat to convex, glabrous, paleae not persistent,

in 1 series (between rays and disc), weakly connate or free. Ray florets 8–12, corollas bright yellow. Disc florets 28–65, bisexual, corollas bright yellow, proximally pubescent, lobes abaxially hispidulous and minutely stipitate-glandular; anthers ± dark purple, appendages lanceolate-ovate to ovate; styles glabrous proximal to arms; arms free, apices subulate, densely hairy. Ray cypselae black, compressed, clavate, arcuate, glabrous or hispidulous, beakless. Disc cypselae brown to black, ± terete, straight or arcuate, hispidulous, otherwise similar to rays. Ray pappus 0 or a crown. Disc pappus of 5–10 stramineous to purplish, lanceolate to subulate, ciliate to plumose scales. $x = 6$. One species, *K. bolanderi* (A. Gray) B.G. Baldwin, western USA (California, southern Oregon).

1424. *Lagophylla* Nutt.

Lagophylla Nutt., Trans. Amer. Philos. Soc. n.s. 7: 390 (1841); Thompson, A biosystematic study of *Lagophylla* (Compositae: Heliantheae) and related taxa. Ph.D. Diss., Univ. Calif., Davis (1983), rev.

Annuals. Leaves proximally opposite (not persistent), mostly alternate, blades narrowly elliptic to linear or (proximal) sometimes oblanceolate to spathulate, entire or (proximal) sometimes toothed, hirsute to strigose, sericeous or villous (all or the distal sometimes also stipitate-glandular). Capitula ± paniculate to glomerulate, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ± hemispheric or obovoid to obconic, phyllaries 5 in 1 series, linear to oblanceolate, each wholly investing a ray ovary, abaxially piloso-hirsute to hirtellous or scabrellous. Receptacles flat to convex, densely hirtellous, paleae not persistent, in 1 series (between rays and disc), free or proximally connate. Ray florets 5, corollas yellow (often nerved with red to purple abaxially). Disc florets 6, functionally staminate, corollas yellow, glabrous or hairs scattered; anthers ± dark purple, appendages ± hemi-orbiculate to ovate-dentate; styles glabrous proximal to arms, arms united, apices subulate, densely to sparsely hairy. Cypselae obcompressed, glabrous, not beaked. Pappus absent. $x = 7$. Four species, western USA.

1425. *Layia* Hook. & Arn. ex DC.

Layia Hook. & Arn. ex DC., Prodr. 7(1): 294 (1838), nom. cons.; Baldwin, Ann. Missouri Bot. Gard. 93:64–93 (2006), evol., phylog.

Annuals. Leaves proximally in rosettes or opposite, mostly alternate, blades ovate, lanceolate or oblanceolate to linear, bipinnatifid to toothed or entire, glabrous or hirsute to strigose (distal leaves sometimes also stipitate-glandular). Capitula ± corymbose or borne singly, usually radiate, rarely discoid. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres cylindrical to ± hemispheric or urceolate, phyllaries as many as ray florets, in 1(–2) series, lanceolate to lanceolate-attenuate or oblanceolate, each wholly investing a ray ovary, abaxially hirsute to strigose or scabrous, often also glandular. Receptacles flat to convex, setulose, paleae not persistent, in 1 series (between rays and disc) or subtending ± all disc florets, free. Ray florets 0 or 3–27, corollas yellow, cream, white or bicoloured. Disc florets 5–120+, bisexual, corollas yellow, hirtellous or hispidulous and/or minutely stipitate-glandular; anthers ± dark purple or yellow to brownish, appendages narrowly triangular, lanceolate-oblong or lanceolate-ovate to ovate; styles glabrous proximal to arms, arms free (lengths unequal), apices subulate, hairy and papillose. Ray cypselae obcompressed, clavate, ± arcuate to falcate, glabrous to sparsely hairy, not beaked. Disc cypselae ± clavate, usually ± strigose to sericeous, sometimes glabrous. Ray pappus 0. Disc pappus of (0–)2–35, ovate, elliptic, lanceolate-attenuate, subulate or setiform, glabrous, scabrous or plumose scales or bristles, often basally villous and/or adaxially woolly. $x = 7$ or 8 (16, polyploid). Fourteen species, western USA, western Mexico (Baja California).

1426. *Madia* Molina

Madia Molina, Sag. Stor. Nat. Chili 136: 354 (1782); Baldwin in Hind & Beentje (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994, vol. 1: 377–391 (1996), phylog.; Baldwin, Novon 9: 462–471 (1999), tax.

Annuals, often aromatic. Leaves proximally in rosettes or opposite (often crowded), distally alternate, blades lanceolate or oblong-linear to linear, usually entire, hirsute to strigose, often also glandular-pubescent. Capitula corymbose, paniculate, racemose or spicate, usually radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ellipsoid to urceolate or ± globose, phyllaries as many as ray florets, in 1 series, usually ± lanceolate-linear to lanceolate-attenuate or oblanceolate, each mostly

or wholly investing a ray ovary, abaxially hispid or hirsute to ± villous, and also glandular-pubescent. Receptacles flat to convex, glabrous or setulose, paleae persistent or falling readily, in 1 series (between rays and disc), ± connate or free. Ray florets (0)1–22, corollas usually yellowish. Disc florets 1–80+, bisexual or functionally staminate, corollas usually yellow, glabrous to usually hirtellous or hispidulous and/or stipitate-glandular; anthers ± dark purple or yellow to brownish, appendages oblong to orbiculate-apiculate; styles glabrous proximal to arms, arms free, hairy throughout, apices narrowly triangular, densely hairy to sparsely papillose and hairy. Ray cypselae compressed, ± triquetrous (abaxial side rounded, adaxial side 2-faced) or rarely terete, clavate, often arcuate, glabrous, beaked or beakless. Disc cypselae similar, sometimes obovoid (often ± straight, basal attachments central, apices not beaked). Pappus absent. $x = 8$ (16, 24, polyploid; 14, dysploid). Ten species, (mostly western) USA, Canada (one species in Argentina, Chile and Hawaiian islands).

1427. *Osmadenia* Nutt.

Osmadenia Nutt., Trans. Amer. Philos. Soc. n.s. 7: 391 (1841); Carr, Amer. J. Bot. 64: 694–703 (1977), rev.; Baldwin & Markos, Mol. Phylog. Evol. 10: 449–463 (1998), phylog.

Annuals, aromatic. Leaves proximally in rosettes or opposite, mostly alternate, blades linear, entire (revolute), scabrous and ± hirsute. Capitula laxly paniculate or borne singly, radiate. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres ovoid, phyllaries 3–5 in 1 series, each c. 1/2 investing a ray ovary. Receptacles flat or convex, glabrous, paleae not persistent, in 1 series between ray and disc florets, connate. Ray florets 3–5, corollas white, fading reddish, laminae sometimes with central red spot, lobes spreading, lengths ± equal to total laminae. Disc florets 3–10, bisexual, corollas white, fading reddish, lobes sometimes with reddish blotch, tubes/throats glabrous, lobes hispidulous and minutely glandular; anthers ± dark purple, appendages lanceolate-oblong; styles glabrous proximal to arms, arms free, apices subulate, densely hairy. Ray cypselae slightly obcompressed (adaxially), ± triquetrous (abaxial side usually 2-faced, adaxial side almost flat), rugose, glabrous, beaked. Disc cypselae angular, ± clavate, hairy. Ray pappus 0. Disc pappus c. 8 alternating, lanceolate-attenuate and shorter, acute to truncate, fimbriate scales. $x = 9$. One species, *O. tenella* Nutt., western USA (southern California), western Mexico (northern Baja California).

1428. *Raillardella* (A. Gray) Benth. in Benth. & Hook. f.

Raillardella (A. Gray) Benth. in Benth. & Hook. f., Gen. Pl. 2: 442 (1873).
Railliardia Gaudich. § [unranked] *Raillardella* A. Gray (1865).

Perennials, rhizomatous. Leaves opposite, mostly crowded in basal rosettes, blades lanceolate or oblanceolate to linear, usually entire, glabrous or sericeous or sparsely hirtellous and/or stipitate-glandular. Capitula usually solitary on scapiform peduncles, rarely laxly ± corymbose, radiate or discoid. Peduncular bracts usually absent, if present, tips each without a pit-gland, tack-gland or spine. Involucres hemispheric or campanulate to cylindric, phyllaries 1–13 (as many as ray florets) or absent (the 'involucre' then consisting of 1 series of receptacular paleae), lanceolate or oblanceolate to linear, herbaceous, each usually 1/2+ investing the subtended ray floret proximally, abaxially hirsute and ± stipitate-glandular. Receptacles flat or convex, glabrous or setulose, paleae ± persistent, in ring at periphery of receptacle (constituting an 'involucre' in discoid heads), connate or free (sometimes overlapping). Ray florets 0 or 1–13, corollas yellow to yellow-orange or orange to red-orange. Disc florets 7–80+, bisexual, corollas concolourous with rays, glabrous or sparsely minute-hairy; anthers yellowish, appendages lanceolate-ovate to ovate-oblong; styles glabrous proximal to arms, arms free, apices subulate, densely hairy. Cypselae ± terete, ± clavate, strigose, not beaked. Ray pappus 0 or 8–30 ± subulate, ciliate to plumose scales. Disc pappus 8–30 ± subulate, ciliate to plumose scales. $x = 17$ or 18 (34, 35, polyploid). Three species, western USA.

1429. *Wilkesia* A. Gray

Wilkesia A. Gray, Proc. Amer. Acad. Arts 2: 160 (1852); Carr, Allertonia 3: 1–123 (1985), rev.; Baldwin & Robichaux in Wagner & Funk (eds) Hawaiian biogeography: evolution on a hot spot archipelago: 259–287 (1995), phylog.

Rosette shrubs, monocarpic or polycarpic. Leaves in rosettes, whorled (7–15 per node), sessile (basally connate, sheathing stem), blades linear,

entire, glabrous or ± sericeous and/or glandular. Capitula in elongate, verticilliform arrays, discoid. Peduncular bract tips each without a pit-gland, tack-gland or spine. Involucres broadly campanulate, phyllaries (modified paleae) in 1 series, oblong-oblanceolate to oblanceolate, glandular. Receptacles convex, glabrous, paleae deciduous, in 1 'involucral' series, connate. Florets 30–225, corollas cream, lobes setulose; anthers yellow; styles glabrous proximal to arms, arms free, hairy in distal half, apices cuneate-deltate, acuminate, acumen papillose. Cypselae ± terete, ± clavate, mostly straight, sericeous. Pappus of 6–13 lanceolate, fimbriate scales. $x = 14$. Two species, Hawaiian islands (Kauai).

XXVIII.5. Subtribe Venegasiinae B.G. Baldwin (2002).

Perennial herbs, subshrubs or weak shrubs. Leaves mostly alternate, proximally opposite, petiolate, blades rounded-deltate to ovate or cordate, subentire or toothed, abaxially minutely resin-dotted, adaxially glabrous. Capitula laxly corymbose or borne singly, radiate. Involucres hemispheric to globose. Phyllaries in 3–4+ series, outer 1(–2) series often reflexed, broadly ovate to deltate, inner 2(–3) series erect, membranous or scarious and progressively smaller. Receptacles flat or convex to shallowly conical, epaleate, sparsely tomentose. Ray floret corollas yellow, tubes densely pubescent and glandular, apices entire to obscurely bilobed or trilobed. Disc florets bisexual, corollas yellow, tubes densely glandular-pubescent; anthers yellow, appendages ovate, with numerous glands, endothecium of quadrate to oblong cells with 2–3 polar thickenings; style arms with broad stigmatic surfaces, apices deltate to obtuse, papillose, appendages wanting. Cypselae often curved, oblong with shallow ridges, black, striate, glabrous. Pappus absent. $x = 19$.

Only one genus:

1430. *Venegasia*

Venegasia DC., Prodr. 6: 43 (1837) [1838]; Turner & Zippin, Sida 15: 223–229 (1992), rev.

Characters of the subtribe. One species, *V. carpesioides* DC., western USA (southern California), western Mexico (northern Baja California).

XXIX. Tribe Perityleae B.G. Baldwin (2002).

J.L. Panero

Annual or perennial herbs but mostly rupicolous shrubs; herbage viscid with stipitate or sessile glandular trichomes. Leaves usually opposite, usually petiolate, sometimes succulent, sparsely to mostly densely glandular, blades linear to ovate, cordate, rarely hastate or deltate, triplinerved, sometimes 5-nerved or with a single vein and pectinate. Capitula discoid or radiate, solitary or in open, usually terminal and dichasial, paniculiform or corymbiform cymes. Involucres cylindrical, campanulate or hemispheric, rarely ovoid, phyllaries in 1 or 2 series. Receptacles flat to shallowly convex, usually epaleate. Ray florets pistillate, fertile. Disc florets 4- or 5-lobed, bisexual, fertile or functionally staminate, corollas covered with sessile and stipitate glandular trichomes, lobes shallowly papillose adaxially; anthers ecalcarate and ecaudate, usually white to yellow, appendages mostly ovate and eglandular, endothecium with 1–3 polar bridges; style arms with paired stigmatic surfaces rarely fusing at apices, apices tapered to acute or round, appendages present or absent. Cypselae variously cylindrical, biconvex or obpyramidal with 2 to 4 angles, compressed, rarely obcompressed, mostly black, walls carbonized, without striations, sometimes with corky, ciliate margins, rarely dimorphic (*Galeana*). Pappus of 2 (rarely 1) bristles and a short crown, rarely of multiple bristles or vestigial squamellae or absent, sometimes of a shallow crown of fimbriate scales, or of 4 squamellae and 4 bristles.

The tribe contains seven genera and 84 species distributed predominantly in northern Mexico and the south-western USA. *Lycapsus* is endemic to the Desventuradas Islands off the coast of northern Chile. *Perityle* has one or two species in the Andes of southern Peru and northern Chile. Most species of the tribe grow on rocky cliffs or very well-drained sandy washes in the deserts of North America.

Perityleae have traditionally been recognized as a distinctive group (subtribe) within the classical Helenieae because of their epaleate receptacles, tetramerous corollas, 2- or 4-angled, compressed cypselae, the densely glandular herbage, and involucres with one or two series of subequal, herbaceous phyllaries (Powell and Turner 1974). The phylogenetic position of *Perityle* and related genera has been clarified recently by molecular phyloge-

netic studies (Baldwin et al. 2002). The data of Baldwin et al. (2002) support the inclusion of *Correllia* in the synonymy of *Perityle*, the division of *Perityle* as advanced by Powell (1969, 1972, 1973, 1974), the position of *Eutetras* as sister to *Amauria*, *Pericome* and *Perityle* and, more importantly, the recognition of subtribe Peritylinae, as circumscribed by Robinson (1981), at the tribal level. The decision by Baldwin et al. (2002) to recognize Perityleae is also supported by molecular studies using chloroplast DNA sequences (Panero and Funk 2002). The same studies for the first time provide strong support for the placement of Eupatorieae as sister to Perityleae. The concept of tribe Perityleae, as circumscribed by Baldwin et al. (2002), is amended here to include *Galeana* and *Villanova*. The inclusion of these genera is based on evidence from molecular phylogenetic studies of chloroplast DNA (Panero et al. 2001c). The tribe is now composed of three subtribes, namely Galeaninae, Lycapsinae and Peritylinae. The description of *Lycapsus* is based on the literature and especially on the excellent account of this monotypic genus by Skottsberg (1937).

Key to the Subtribes

1. Disc corollas pentamerous	**1. Galeaninae** (p. 508)
– Disc corollas tetramerous	2
2. Receptacles paleate	**2. Lycapsinae** (p. 509)
– Receptacles epaleate	**3. Peritylinae** (p. 509)

XXIX.1. Subtribe Galeaninae Panero and B.G. Baldwin, subtribus nov. type: *Galeana* La Llave & Lex.

Subtribui Peritylinae similis, a qua differt corollis 5-lobis et cypselis triquetris.

Annuals with glandular herbage. Leaves alternate or opposite. Capitula in open paniculiform cymes, radiate. Involucres hemispherical or ovoid, phyllaries herbaceous, subequal, navicular. Receptacles epaleate. Ray florets pistillate, disc florets pentamerous, bisexual or functionally staminate. Cypselae triquetrous, pappus absent.

Key to the Genera

1. Ray cypselae with corky wings	**1431. *Galeana***
– Ray cypselae without wings	**1432. *Villanova***

1431. *Galeana* La Llave & Lex. Fig. 104

Galeana La Llave & Lex., Nov. Veg. Descr. 1: 12 (1824).
Chlamysperma Less. (1832).

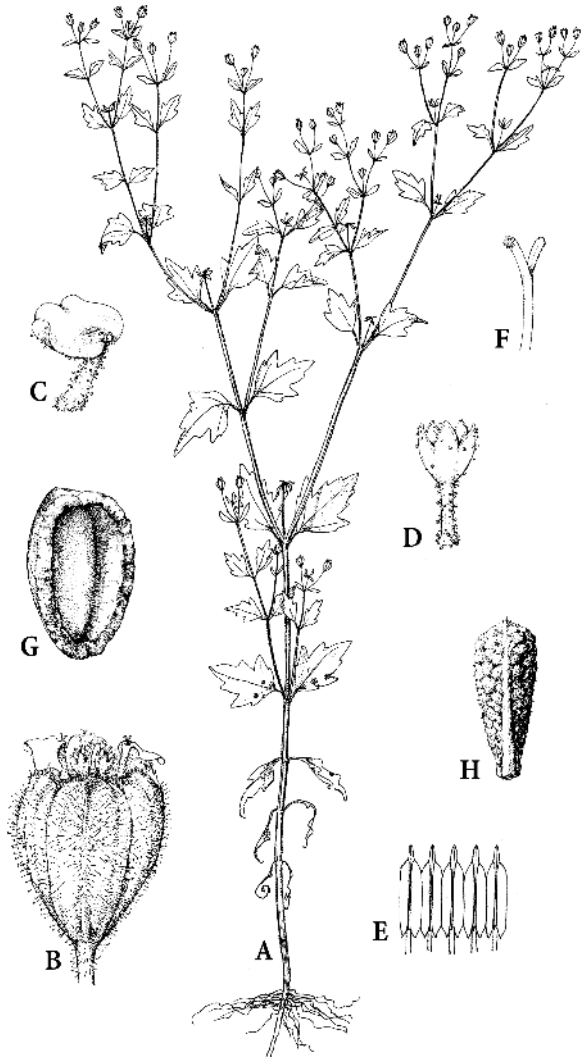

Fig. 104. Compositae-Perityleae. *Galeana pratensis*. **A** Habit. **B** Flowering capitulum. **C** Ray corolla. **D** Disc corolla. **E** Anthers. **F** Style arms. **G** Ray cypsela. **H** Disc cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

Leaves opposite, viscid, petiolate, blades deltate to ovate, triplinerved. Capitula in terminal, open corymbiform cymes. Involucres ovoid to cylindric, phyllaries 5, biseriate. Receptacles flat to shallowly convex. Ray florets 3, fertile, corollas creamy white. Disc florets 3–5, 5-lobed, fertile or functionally staminate, corollas creamy white, sparsely glandular-pubescent; anthers whitish to yellow, appendages acute to linear; style arms with round to deltate papillose apices. Ray cypselae obcompressed, with corky, concave wings, black, glabrescent. Disc cypselae obpyramidal, wingless, black, glabrescent, tuberculate with age. $x = 9$.

One species, *G. pratensis* Rydb., Mexico, Central America.

1432. *Villanova* Lag.

Villanova Lag., Gen. Pl. 31 (1816), nom. cons.
Vasquezia Phil. (1860).

Leaves opposite or alternate, viscid, petiolate, blades dissected, once pinnate, ovate in outline. Capitula in terminal, open, simple or corymbiform cymes. Involucres campanulate to hemispheric, phyllaries few, broad. Receptacles flat to shallowly convex. Ray florets fertile, corollas white to yellow. Disc florets fertile, sometimes innermost functionally staminate, sparsely glandular-pubescent; anthers yellow, appendages ovate and deeply carinate; style arms with round to deltate papillose apices. Cypselae triangular-obpyramidal, with abaxial side wider than other two, essentially glabrous. Ten species, Mexico, Central and South America.

XXIX.2. Subtribe Lycapsinae H. Rob. (1980).

Perennial herbs or weak shrubs. Leaves alternate, semisucculent, 1–2-pinnate, lobes linear. Capitula terminal in open paniculiform cymes, radiate. Involucres campanulate. Receptacles paleate, paleae lanceolate, involute. Ray florets pistillate, fertile, corollas white, disc florets tetramerous, bisexual, corollas white; anther thecae pale, appendages ovate; style arms with acute papillose apices. Cypselae fusiform, 4-angled, straight to slightly incurved. Pappus absent.

Only one genus:

1433. *Lycapsus* Phil.

Lycapsus Phil., Bot. Zeitung (Berlin) 28: 499 (1870); Robinson, Proc. Amer. Acad. Arts 49: 438–491 (1913), rev.; Johnston, J. Arnold Arb. 16: 440–447 (1935), rev.; Skottsberg, Göteb. Kungl. Vetensk. Vitterh. Samh. Hand. ser. 5, B, 5: 1–88 (1937), rev.

Characters of the subtribe. One species, *L. tenuifolius* Phil., San Felix and San Ambrosio Islands off the coast of northern Chile.

XXIX.3. Subtribe Perityllinae Rydb. (1914).

Subtribe Amauriinae Rydb. (1914).

Annual or perennial herbs or rupicolous shrubs. Leaves opposite or alternate. Capitula solitary or in open or congested corymbiform or paniculiform cymes, discoid or radiate. Receptacles epaleate. Ray florets pistillate, fertile, disc florets tetramerous, bisexual. Cypselae cylindric, 4-angled or most commonly biconvex, compressed, rarely obcompressed. Pappus of squamellae or bristles, most commonly of 1 or 2 bristles, rarely absent.

Key to the Genera

1. Cypselae 4-angled 2
– Cypselae narrowly biconvex 3
2. Pappus absent or a very reduced crown **1434. *Amauria***
– Pappus of 4 squamellae alternating with 4 bristles **1435. *Eutetras***
3. Leaves hastate or triangular, pappus of fimbriate scales **1436. *Pericome***
– Leaves various, never triangular nor hastate, pappus of 1 or 2 or multiple bristles, never of fimbriate scales **1437. *Perityle***

Genera of Perityllinae

1434. Amauria Benth.

Amauria Benth., Bot. Voy. Sulphur: 31 (1844); Powell, Madroño 21: 516–525 (1972), rev.

Annuals with glandular herbage. Leaves opposite or alternate, sometimes succulent, petiolate, blades ovate to cordate in outline, margins shallowly to deeply lobed and serrate. Capitula radiate, in open paniculiform cymes. Involucres campanulate or hemispheric. Receptacles shallowly convex. Ray corollas white, sometimes tinged with pink. Disc corollas yellow, sparsely glandular-pubescent; anthers white to yellow, appendages ovate; style arms with tapered to round apices. Cypselae cylindric, 4-angled, black, glabrous to sparsely pubescent with variously shaped trichomes, sometimes uncinate. Pappus absent or a shallow crown. $x = 17, 18$. Three species, Baja California, Mexico.

1435. *Eutetras* A. Gray

Eutetras A. Gray, Proc. Amer. Acad. Arts 15: 39 (1879); Turner, Southw. Naturalist 11: 118–122 (1966), rev.

Rupicolous shrubs with brittle branches. Leaves opposite, densely glandular, viscid, somewhat succulent, petiolate, blades deltate to ovate, margins serrate. Capitula solitary or in small corymbiform cymes, radiate, rarely discoid. Involucres campanulate to subhemispheric. Receptacles shallowly convex. Ray corollas white. Disc corollas white

or whitish-yellow, sparsely glandular-pubescent; anthers white to yellow, appendages oval; style arms with tapered apices. Cypselae cylindric, 4-angled, black, glabrous to sparsely pubescent. Pappus of 4 scales alternating with 4 bristles arising from the cypsela angles. $x = 18$. Two species, central Mexico.

1436. *Pericome* A. Gray

Pericome A. Gray, Smithsonian Contr. Knowl. 5: 81 (1853); Powell, Southw. Naturalist 18: 335–339 (1973), rev.

Perennial herbs or weak shrubs. Leaves opposite, petiolate, triangular, hastate. Capitula in congested corymbiform cymes, discoid. Involucres campanulate to urceolate. Receptacles flat. Corollas deep yellow or yellow-orange, sparsely glandular-pubescent; anthers yellow, appendages ovate; style arms with tapered to acute apices, essentially without appendages. Cypselae narrowly biconvex, compressed, with a corky margin. Pappus of a small crown of fimbriate scales sometimes with 1 or 2 caducous awns. $x = 18$. Two species, south-western USA, northern Mexico.

1437. *Perityle* Benth. Fig. 105

Perityle Benth., Bot. Voy. Sulphur 23, pl. 15 (1844); Niles, Mem. New York Bot. Gard. 21: 1–81 (1970), rev.; Powell, Rhodora 71: 58–93 (1969), sect. rev.; Sida 5: 61–128 (1973), sect. rev.; Rhodora 76: 229–306 (1974), sect. rev.
Pappothrix (A. Gray) Rydb. (1914).
Corellia A.M. Powell (1973).

Annual or perennial herbs but mostly rupicolous shrubs, some with brittle branches. Leaves opposite or alternate, petiolate, sometimes densely glandular and viscid, blades deltate to ovate, cordate or rarely linear to spathulate, entire to deeply dissected. Capitula solitary or in open corymbiform cymes, discoid or radiate. Involucres cylindric, campanulate to hemispheric. Receptacles flat to shallowly convex. Ray corollas white or yellow. Disc florets 4(–5)-lobed, corollas yellow, creamy white or white, sometimes reddish; anthers translucent whitish to yellow, appendages ovate; style arms with tapered apices, appendages tapered, papillose, vascularized. Cypselae narrowly biconvex, compressed, rarely obcompressed, sometimes with wings or most commonly with a well-developed corky, ciliate margin. Pappus of 2 (rarely 1) bristles and a short crown, rarely of multiple bristles or vestigial squamellae or absent, bristles retrorsely barbed. $x = 17, 19$. Sixty-five species, western USA, Mexico, Central America, Peru and Chile.

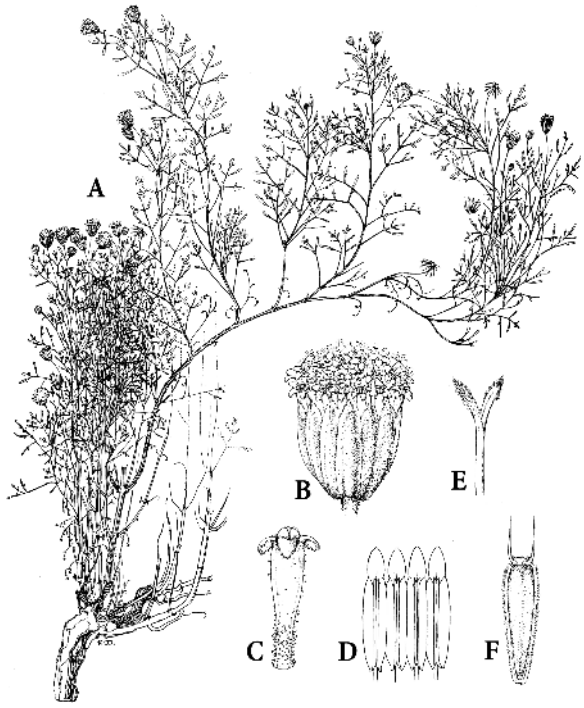

Fig. 105. Compositae-Perityleae. *Perityle feddemae*. **A** Habit. **B** Flowering capitulum. **C** Disc corolla. **D** Anthers. **E** Style arms. **F** Cypsela. (Reproduced from Flora Novo-Galiciana, vol. 12, with permission of the University of Michigan Herbarium; see McVaugh 1984)

XXX. Tribe Eupatorieae Cass. (1819).

D.J.N. Hind and H. Robinson

Herbs (rarely aquatic or semi-aquatic), subshrubs, shrubs, climbers, small trees, sometimes epiphytic. Leaves usually opposite, rarely strictly alternate, sometimes rosulate or verticillate, sessile or petiolate, lamina usually simple. Inflorescence usually a corymbose panicle, sometimes spicate. Capitula sessile or distinctly pedicellate, homogamous, discoid, rarely with some zygomorphic outer florets; involucre cylindrical, campanulate or hemispherical, rarely subtended by a subinvolucral bract; phyllaries in 1 to several series, few or numerous, imbricate, subimbricate or distant, equal, subequal or markedly gradate, persistent or variously deciduous, lanceolate or ovate; receptacle flat to convex, sometimes highly conical, usually naked, glabrous or sometimes pubescent. Florets

few, very rarely 1, often 4 or 5 to many, commonly fragrant; corollas funnelform to tubular, never truly yellow, lobes relatively short, commonly 5, very rarely 4; anther cylinders usually included within corolla tube; apical anther appendages obtuse or acute, rarely emarginate or lobed, as long as broad or shorter, sometimes absent, basal appendages short or almost absent, obtuse or rounded; anther collars indistinct, cylindrical or variously pronounced; nectary rarely visible; style base glabrous or pubescent, sometimes with a swollen node; styles usually very conspicuous and much exserted, glabrous or rarely pubescent; style arms linear to clavate, obtuse, stigmatic surfaces variously papillate. Achenes obovoid or oblong with phytomelanin in achene walls, usually 3–5-ribbed, sometimes 10-ribbed, body rarely flattened with 2 ribs or 5 winged ribs, sometimes glandular, glabrous or variously setuliferous; carpopodium often paler than achene body, rarely indistinct or absent, of several layers of variously enlarged, sometimes ornamented cells, usually symmetrical, rarely eccentric, annular, cylindrical, or stopper-shaped; pappus sometimes absent and reduced to an apical callus, rarely a laciniate crown, or vestigial, occasionally coroniform, usually of setae, commonly uniseriate, rarely biseriate or very rarely multiseriate, usually persistent, sometimes fragile, usually numerous, sometimes few, usually equal or subequal, rarely very short, or occasionally of flattened scales or awn-like scales, rarely of two distinct elements, very rarely of broad laciniate setae, or of few clavate apical appendages; setae commonly barbellate or laciniate, rarely plumose, apices acute or obtuse, usually gradually tapering, sometimes dilated, very rarely conspicuously narrowing. The chromosome base number of the tribe has been suggested to be either $x = 10$ (King et al. 1976; King and Robinson 1987) or $x = 17$ (Yahara et al. 1989; Watanabe et al. 1995; Ito et al. 2000a).

A tribe of 17 subtribes containing c. 2200 species in 182 genera. The tribe is mostly restricted to the western hemisphere, suggesting a Neotropical origin. There are many pantropical and pansubtropical weeds in the tribe. Uses of members of the tribe have been briefly summarized by King and Robinson (1987). More recent references on the topic include Garg and Sastry (1996; *Ageratum conyzoides*, *Mikania micrantha*), Huang and Ling (1996; *Ageratum houstonianum*, *Adenostemma*, Heinrich (1996; 31 Mexican species) and Vallès et al. (1996; *Eupatorium cannabinum*).

Several recent molecular systematic studies (Jansen and Kim 1996; Panero et al. 2001a, b, c; Baldwin et al. 2002) clearly position Eupatorieae nested within Heliantheae s.l. Panero et al. (2001a, b, c) suggested positioning Eupatorieae within a clade with Peritylinae and *Galeana-Villanova* clades. Recently, Jeffrey (2002) has, whilst discussing the current state of the systematics of the family, proposed the creation of the new rank, the supersubtribe, for Eupatorieae, thereby creating the Eupatoriodinae (Cass.) C. Jeffrey; this is not followed here. The submergence of Eupatorieae within Heliantheae would appear to be wholly impracticable. Baldwin et al. (2002) have suggested a modified scheme placing Eupatorieae alongside Bahiinae (raised to tribal rank as Bahieae) and Madieae. With the concept of 'taxon monophyly within our rank-based system of botanical nomenclature' (Baldwin et al. 2002), this has apparently left the continuing recognition of the broad concept of Heliantheae untenable if Eupatorieae are to be maintained – a partitioning of Heliantheae into 'tribes coordinate with Eupatorieae' was proposed; the result was the recognition of three new tribes. Opinions vary widely as to the usefulness of the classification system provided by King and Robinson (1987). In many recent flora accounts and checklists for South and Central America, a large and unwieldy *Eupatorium* sensu lato/amplo has been maintained (e.g. Santa Catarina/Brasil: Cabrera and Klein 1991; Paraguay: Cabrera 1996; Argentina: Cabrera and Freire 1999; New Mexico: McVaugh 1984; Mexico: Turner 1997). Other checklists and flora accounts with input from Robinson naturally used the scheme proposed by King and Robinson (e.g. Ecuador: Robinson 1999c; Guyana: Funk and Robinson 1996; Peru: Dillon and Hensold 1993). Bremer et al. (1994) briefly summarized the situation at the subtribal level, with comments on how some authors had treated some of the segregates proposed by King and Robinson (1987), and provided a tribal order in part based on the results of a series of cladograms. Inferences may be made from a small series of molecular systematic studies (Schilling et al. 1999; Schmidt and Schilling 2000; Ito et al. 2000a), together with the results presented by Funk et al. (2005). Apart from the latter dataset, however, none of the analyses are based on a particularly large sample of genera, or species within those genera, or even comparable taxa. Even the cladograms presented provide conflicting results, although some trends can indeed be detected. Bearing these

uncertainties in mind, we have chosen to base this account largely on the tribal concepts proposed by King and Robinson (1987), with modifications based on published cladistic, molecular systematic and cytological studies – evidently, this is certainly not the final picture.

Classification of the Eupatorieae

1. Subtribe Hofmeisteriinae R.M. King & H. Rob. (1980) Genera 1438–1439.
2. Subtribe Oxylobinae R.M. King & H. Rob. (1980). Genera 1440–1448.
3. Subtribe Mikaniinae R.M. King & H. Rob. (1980). Genus 1449.
4. Subtribe Trichocoroninae R.M. King & H. Rob. (1980). Genera 1450–1452.
5. Subtribe Adenostemmatinae B. L. Rob. (1913). Genera 1453–1455.
6. Subtribe Fleischmanniinae R.M. King & H. Rob. (1980). Genera 1456–1457.
7. Subtribe Ageratinae Less. (1832). Genera 1458–1483.
8. Subtribe Eupatoriinae Dumort. (1827). Genera 1484–1487.
9. Subtribe Liatrinae R.M. King & H. Rob. (1980). Genera 1488–1493.
10. Subtribe Praxelinae R.M. King & H. Rob. (1980). Genera 1494–1500.
11. Subtribe Gyptidinae R.M. King & H. Rob. (1980). Genera 1501–1529.
12. Subtribe Disynaphiinae R.M. King & H. Rob. (1978). Genera 1530–1535.
13. Subtribe Ayapaninae R.M. King & H. Rob. (1980). Genera 1536–1548.
14. Subtribe Alomiinae Less. (1832). Genera 1549–1571.
15. Subtribe Critoniinae R.M. King & H. Rob. (1980). Genera 1572–1611.
16. Subtribe Hebecliinae R.M. King & H. Rob. (1980). Genera 1612–1618.
17. Subtribe Neomirandeinae R.M. King & H. Rob. (1980). Genus 1619.

Key to the Subtribes

1. Phyllaries distant and bases not articulated; receptacles epaleaceous unsclerified, and changing shape with maturity **5. Adenostemmatinae** (p. 518)
– Phyllaries distant to imbricate and bases sclerified or articulated; receptacle sclerified between areolae or paleaceous 2
2. Paleae present, bearing floret in axil when removed; capitula solitary on erect peduncles **1. Hofmeisteriinae** (p. 513)
– Paleae absent or superficial on receptacle; capitula often in complex inflorescences 3
3. Capitula solitary on erect peduncles arising from a congested group of leaves **1. Hofmeisteriinae** (p. 513)
– Capitula often in complex inflorescences and peduncles not arising from pseudowhorls of leaves 4
4. Capitula with 4 subequal phyllaries and 4 florets, usually with a fifth unequal subinvolucral bract (subtending the involucre or pedicel); style arms never with clavate apices; pappus always present **3. Mikaniinae** (p. 516)
– Capitula not with 4 subequal phyllaries and 4 florets or with clavate style arm apices or with a defective pappus 5
5. Phyllaries all deciduous leaving a naked receptacle, remaining appressed until lost, not spreading with age **10. Praxelinae** (p. 532)
– At least some basal phyllaries persistent, phyllaries usually spreading with age 6
6. Aquatic or sub-aquatic plants with sessile or whorled leaves; Mexico and USA **4. Trichocoroniinae** (p. 517)
– Plants terrestrial or epiphytic and not aquatic or subaquatic, usually with petiolate leaves 7
7. Leaves alternate and plants usually rosulate; eastern USA **9. Liatrinae** (p. 530)
– Leaves opposite or plants from other than USA 8
8. Capitula becoming elongate on a highly elongated and paleaceous receptacle **13. Ayapaninae** (*Isocarpha*)
– Capitula not becoming elongated on a highly conical receptacle, receptacle paleaceous or epaleaceous 9
9. Plants epiphytes or growing in humus; leaves fleshy or coriaceous, often blackening on drying; pappus of numerous capillary setae **17. Neomirandeinae** (p. 574)
– Plants not epiphytic nor growing in humus, or pappus defective 10
10. Corolla lobes (usually) smooth on inner surface 11
– Corolla lobes papillose on inner surface 14
11. Pappus of awns, scales, crowns, or absent, never of wingless setae; pappus awns bristle-like in some 5-flowered species; plants rarely with densely spirally inserted leaves **7. Ageratinae** (p. 520)
– Pappus of capillary setae, sometimes short, rarely absent in some plants with densely spirally inserted leaves; capitula rarely with fewer than 6 florets 12
12. Style base usually with a distinct glabrous node; phyllaries usually distant and subequal **2. Oxylobinae** (p. 513)
– Style base lacking basal node; phyllaries distant or subimbricate, usually gradate 13
13. Receptacles convex to conical; style arms linear or with broadened apices; anther collars usually conspicuous and expanded; cells of inner surface of corolla lobes short and essentially isodiametric **11. Gyptidinae** (p. 535)
– Receptacles usually flat; style arms filiform; anther collars scarcely discernible and cylindrical; cells of inner surface of corolla lobes elongate with upper ends projecting as papillae **6. Fleischmaniinae** (p. 520)
14. Style arms long-clavate, thickened in both width and thickness, with few exceptions with 10-ribbed achenes, plumose pappus or with peg-like setulae on achenes; upper corolla limb often constricted beneath corolla lobes **14. Alomiinae** (p. 552)
– Style arms not thickened or thickened only at tips, if long-clavate, then flattened; achenes never 10-ribbed, never with plumose pappus setae and never with peg-

like eglandular achene setulae; corolla limb cylindrical or funnelform beneath corolla lobes 15
15. Style base glabrous and basal node absent; inner phyllaries usually deciduous 16
– Style base with basal node or pubescent or both 18
16. Capitula always with 5 florets; style arm apices papillose; pappus setae sometimes with bulbous-tipped apical cells; plants of eastern South America **12. Disynaphiinae** (p. 546)
– Capitula with 1–300 florets, rarely consistently 5-flowered; style arms usually smooth at least at apices; pappus setae never with bulbous-tipped apical cells; plants throughout tropical and subtropical America 17
17. Receptacles glabrous; anther collar usually less than 5 times as long as wide **15. Critoniinae** (p. 559)
– Receptacles usually pubescent; anther collar usually more than 5 times as long as wide **16. Hebecliniinae** (p. 572)
18. Style base lacking basal node, pubescent; capitula with fewer than 20 florets; receptacles epaleaceous; apical cells of pappus setae usually rounded **8. Eupatoriinae** (p. 528)
– Style base inflated above nectary, glabrous or pubescent; capitula usually with more than 20 florets, sometimes receptacle paleaceous; apical cells of pappus setae acute **13. Ayapaninae** (p. 548)

XXX.1. Subtribe Hofmeisteriinae R.M. King & H. Rob. (1980).

Subtribe Oaxacaniinae R.M. King & H. Rob. (1980).

Key to the Genera

1. Receptacles epaleaceous; pappus of barbellate tapering setae; leaves pseudowhorled below peduncle **1438. *Hofmeisteria***
– Receptacles paleaceous; pappus absent or a short laciniate crown, sometimes with one long seta; stems leafy throughout, leaves alternate **1439. *Oaxacania***

1438. *Hofmeisteria* Walp.

Hofmeisteria Walp., Repert. Bot. Syst. 6: 106 (1846); King, Rhodora 69, 779: 35–47 (1967), rev.

Perennial herbs or woody subshrubs. Leaves usually congested at flowering nodes, lamina broadly ovate to filiform, entire to lobed or greatly dissected. Capitula solitary on long erect bracteolate peduncles, broadly campanulate. Phyllaries c. 50–100, acute to pungent or obtuse; receptacle glabrous, areolate. Florets 100–175(–250), fragrant; corollas white, pink, or lavender, nearly tubular, usually glabrous on inner and outer surfaces, rarely short stipitate-glandular outside; lobes with papillae at tip, or papillose inside only; style arms slightly enlarged and flattened distally. Pappus setae 3–15, barbellate, tapering, with 6–10 intervening lacerate squamellae in species with few setae. $n = 18$, 19. Ten species, Mexico.

1439. *Oaxacania* B.L. Rob. & Greenm.

Oaxacania B.L. Rob. & Greenm., Amer. J. Sci., ser. 3, 50: 151 (1895); King, Rhodora 69, 777: 3–47 (1967), rev. *Carterothamnus* R.M. King (1967).

Sprawling subshrubs or shrubs. Leaf lamina herbaceous, orbicular to reniform, 3–7-cleft to 2/3 or more towards base. Capitula terminal on leafy branches, laxly cymose or solitary, broadly campanulate. Phyllaries c. 30–40, inner somewhat deciduous, apices narrowly acuminate or obtuse, densely fringed; receptacle paleaceous, paleae deciduous, linear-lanceolate, with single floret partially enclosed by base of each palea. Florets 50–100; corollas white, with basal tube long and slender with enlarged base and apex, outer surface of tube with numerous stipitate glands, a few smaller stipitate glands distally on limb or corollas glabrous; lobes c. 1.5 times as long as wide, papillose on inner surface, smooth and somewhat thickened on outer surface; style base conical, truncate below against nectary, arms narrow linear, densely long-papillose or scarcely mamillose. Pappus absent or a short laciniate crown or setae c. 10–12, narrow, short, with one barbed setae with bent or contorted apex. $n = 18$. Two species, Baja California, Mexico.

Turner (1987a, 1997) proposed that both *Oaxacania* and *Carterothamnus* be incorporated into a broadened concept of *Hofmeisteria*, simply noting that the only real difference was the presence of paleae in the *Oaxacaniinae*. Here, we 'sink' *Carterothamnus* into a slightly broadened concept of *Oaxacania* but maintain *Oaxacania* separate from *Hofmeisteria*.

XXX.2. Subtribe Oxylobinae R.M. King & H. Rob. (1978).

Perennial herbs or shrubs to small trees, usually erect. Leaves usually opposite, lamina deltoid to narrowly elliptical. Capitula clustered on short to moderately long pedicels in terminal, pyramidically to corymbosely paniculate inflorescences, phyllaries distant to weakly subimbricate, usually subequal; receptacle flat to slightly convex, paleaceous or epaleaceous. Florets 7–75; corollas narrowly funnelform or with slender basal tube

and campanulate limb, glabrous to rarely short-pubescent or glanduliferous on outer surface; lobes often distinctly longer than wide, usually densely papillose on inner surface, sometimes smooth or roughened; anther collar often more than 5 times as long as wide; apical anther appendages as long as wide; style base often with distinct enlarged node, glabrous; style narrowly linear, without enlarged tips, usually densely papillose. Achenes prismatic to fusiform, 5-ribbed; carpopodium usually distinct; pappus of numerous deciduous or persistent capillary setae, rarely squamellae, apical cells acute.

Key to the Genera

1. Leaves trifoliate **1446. *Standleyanthus***
– Leaves simple 2
2. Stems with fleshy cortex; leaves absent at anthesis **1444. *Pachythamnus***
– Stems not unusually thickened; plants not seasonally defoliated 3
3. Receptacles paleaceous **1443. *Jaliscoa***
– Receptacles epaleaceous 4
4. Pappus of persistent laciniate squamellae **1441. *Oxylobus***
– Pappus setae capillary and persistent or deciduous 5
5. Pappus setae easily deciduous 6
– Pappus setae persistent 7
6. Carpopodium indistinct and undifferentiated **1442. *Piptothrix***
– Carpopodium well defined and sometimes cylindrical **1440. *Ageratina***
7. Stems and leaves with a yellowish granular appearance (resulting from concertina'd multicellular uniseriate hairs); Colombia **1448. *Jaramilloa***
– Stems and leaves lacking yellowish granular appearance (when present, hairs sometimes crisped but not concertina'd) 8
8. Inflorescence lax-corymbose; Cuba **1445. *Spaniopappus***
– Inflorescence densely corymbose on branchlets; Argentina, Bolivia, Brazil, Ecuador, Peru **1447. *Kaunia***

Genera of Oxylobinae

1440. *Ageratina* Spach

Ageratina Spach, Hist. Nat. Veg. Phan. 10: 286 (1841); King & Robinson, Phytologia 24: 79–104. (1972), reg. rev.; King & Robinson, Phytologia 69: 61–86 (1990), reg. rev.; Turner, Phytologia Mem. 11: i–iv, 1–272 (1997), reg. rev.

Perennial, usually erect herbs or shrubs. Leaves usually opposite, lamina narrowly elliptical to deltoid, mostly toothed, lobed, serrate or crenate. Capitula laxly to densely corymbose. Phyllaries c. 30, 2- or 3-seriate, distant to weakly subimbricate, mostly subequal; receptacle usually slightly convex, glabrous or with minute scattered hairs. Florets 10–60, often sweetly scented; corollas white or lavender, usually with slender basal tube and campanulate limb in subgenera *Ageratina* and *Klattiella*, others narrowly funnelform; lobes distinctly longer than wide, inner surface densely papillose, outer surface smooth, glabrous or glanduliferous, usually with hairs in subgenus *Ageratina*; anther collar cylindrical, usually elongate; anther appendage large, ovate-oblong, longer than wide; style base usually enlarged except in subgenus *Apoda*; arms rarely slightly broadened distally, densely papillose with projecting cells on lateral and outer surface. Achenes prismatic or fusiform, usually 5-ribbed, setuliferous or glanduliferous or both; carpopodium distinct, cylindrical in subgenus *Ageratina*, in others rounded or shortly stopper-shaped; pappus setae uniseriate, 5–40, barbellate, often easily deciduous, capillary, often enlarged distally, often with outer series of shorter setulae. n = c. 10, c. 16, 17, 18, 20, c. 25, c. 40, c. 42. Circa 265 species, tropics and subtropics of the New World.

King and Robinson (1970) first provided an infrageneric division recognizing four subgenera, later raising subgenus *Pachythamnus* to generic status. Subsequently (King and Robinson 1978), they recognized a further two subgenera. A complete list of species in the five subgenera was provided by King and Robinson (1987).

1441. *Oxylobus* (Moçino ex DC.) A. Gray

Oxylobus (Moçino ex DC.) A. Gray, Proc. Amer. Acad. Arts 15: 25 (1879); Turner & Kerr, Pl. Syst. Evol. 151: 73–87 (1985), rev.

Decumbent herbs to low shrubs. Leaves opposite, lamina small, ovate to oblong, crenate to subentire. Capitula laxly to densely corymbose to subcymose. Phyllaries c. 10–15, distant, 2–3-seriate, mostly subequal; receptacle slightly convex, epaleaceous, glabrous. Florets 20–75, slightly scented; corollas white or pink, with a long narrow basal tube and a narrowly campanulate limb; lobes longer than wide, inner surface densely papillose, outer surface smooth with stalked glands or glabrous; anther collar cylindrical, elongate; apical anther appendages large, ovate, longer than wide; style base enlarged; arms densely long-papillose on lateral and outer surfaces. Achenes fusiform, 5-ribbed, bearing short setulae; carpopodium distinct, often stipitate, shortly rounded; pappus of a few,

short, laciniate persistent squamellae. $n = 16$. Five species, Colombia, Guatemala, Mexico, Venezuela.

1442. *Piptothrix* A. Gray

Piptothrix A. Gray, Proc. Amer. Acad. Arts 21: 383 (1886).

Erect herbs or weak shrubs. Leaves usually opposite, lamina ovate to narrowly ovate, serrulate to serrate, apex narrowly acute to acuminate. Capitula in a thyrsoid panicle with rather densely corymbose branches. Phyllaries c. 7–15, distant, biseriate, equal to subequal; receptacle slightly convex, epaleaceous, glabrous to spinose. Florets 7–18, fragrant; corollas white, with narrow basal tube and funnelform to slightly campanulate limb, outer surface glabrous; lobes c. 1.5–2 times as long as wide, inner surface mamillose to nearly smooth, outer surface smooth; anther collar cylindrical, narrow; apical anther appendages large, ovate or oblong, longer than wide; style base enlarged; arms scarcely broadened distally, densely papillose. Achenes prismatic, 5-ribbed, setuliferous; carpopodium indistinct; pappus setae c. 15–75, barbellate, often deciduous, sometimes only half as long as corolla, with outer series of very short, small setulae. $n =$ c. 17. Four species, Guatemala, Mexico.

1443. *Jaliscoa* S. Watson

Jaliscoa S. Watson, Proc. Amer. Acad. Arts 25: 153 (1890); McVaugh, Fl. Novo-Galic.: 1157 (1984), rev.; Turner, Phytologia Mem. 11: i–iv, 1–272 (1997), reg. rev.

Erect perennial herbs or shrubs. Leaves usually opposite, lamina ovate to deltoid, crenulate-serrulate to sharply serrate, apex shortly and often narrowly acuminate. Capitula in a lax pyramidal panicle, with rather densely corymbose lateral branches. Phyllaries c. 15–20, distant, biseriate, subequal to equal; receptacle slightly convex, paleaceous. Florets 11–25; corollas white, with narrow basal tube and funnelform to slightly campanulate limb; lobes c. 1.5 times as long as wide, mamillose to short-papillose on inner surface, smooth on outer surface; anther collar elongate, cylindrical; apical anther appendages large, ovate or triangular, slightly longer than wide; style base sometimes enlarged; arms densely papillose. Achenes prismatic, 4–5-ribbed, glabrous or bearing a few setulae near top; carpopodium usually distinct, symmetrical; pappus an obscure callus border, a laciniate crown or of rather short deciduous setae. Three species, Mexico.

1444. *Pachythamnus* (R.M. King & H. Rob.) R.M. King & H. Rob.

Pachythamnus (R.M. King & H. Rob.) R.M. King & H. Rob., Phytologia 23, 1: 153 (1972).

Shrubs or small trees. Stems swollen or somewhat succulent, wrinkled when dry. Leaves opposite, lacking at anthesis, lamina broadly ovate to deltoid, margins with a few blunt teeth, apiculate at tip. Capitula terminal in rather abrupt, dense corymb. Phyllaries c. 15, distant to scarcely subimbricate, 2–3-seriate, mostly subequal; receptacle slightly convex, with minute scattered hairs. Florets c. 15; corollas white or lavender, narrowly funnelform, with narrowly cylindrical basal tubes, puberulous on upper tube and lower throat, glabrous inside; lobes longer than wide, densely papillose on inner surface, outer surface and margins smooth below; anther collar cylindrical; apical anther appendage large, ovate, slightly longer than wide; style base not enlarged; arms not broadened distally, densely papillose. Achenes prismatic, usually 5-ribbed, setuliferous on ribs and sides; carpopodium distinct; pappus setae uniseriate, c. 25, barbellate, slender, rather easily deciduous, not broadened distally. One species, *P. crassirameus* (B.L. Rob.) R.M. King & H. Rob., El Salvador, Guatemala, Mexico, Nicaragua.

1445. *Spaniopappus* B.L. Rob.

Spaniopappus B.L. Rob., Contr. Gray Herb. n.s. 77: 45 (1926).

Erect perennial herbs or shrubs. Leaves opposite, lamina oblong-ovate to elliptical, entire to remotely serrate or lobate-crenate, apex acute to slightly acuminate, with immediate tip often rather blunt. Capitula in rather broad and lax corymbs. Phyllaries c. 15, weakly subimbricate, unequally 2–3-seriate; receptacle slightly convex, epaleaceous, glabrous. Florets 25–60; corollas purple, distally narrowly funnelform with basal tube narrowly cylindrical or constricted above nectary, inner and outer surfaces glabrous; lobes longer than wide, inner surface densely papillose with broad papillae, margins and outer surface papillose with strongly projecting cells; anther collar cylindrical, elongate; apical anther appendage large, ovate, slightly longer than wide; style base not or scarcely enlarged; arms scarcely broadened above base, mamillose to slightly papillose. Achenes prismatic, usually 5-ribbed, glabrous to sparsely setuliferous; carpopodium

indistinct or distinct; pappus of c. 40 uniseriate setae, barbellate, persistent, or of a few short bristles and a fringe of minute squamellae. Five species, Cuba.

1446. *Standleyanthus* R.M. King & H. Rob.

Standleyanthus R.M. King & H. Rob., Phytologia 22: 41 (1971).

Large flaccid shrub. Stems rather fleshy, leaves opposite, lamina divided into 3 leaflets, leaflets oblong-ovate, petiolulate, remotely crenate-undulate, narrowly acuminate, venation pinnate. Capitula in pyramidal panicles, terminal on branches. Phyllaries c. 12, distant, c. 2-seriate, subequal; receptacle slightly convex, epaleaceous, glabrous. Florets c. 17; corollas whitish (?), narrowly funnelform with long cylindrical basal tube, outer and inner surfaces glabrous; lobes triangular, slightly longer than wide, with dense prominent mamillae on inner surface, outer surface smooth below and somewhat mamillose above; anther collar cylindrical; apical anther appendages large, oblong-ovate, slightly longer than wide; style base scarcely thickened, arms scarcely broadened distally, slightly mamillose. Achenes prismatic, 4–5-ribbed, ribs prominent and usually pale, setuliferous, greatly expanded at base; carpopodium indistinct; pappus setae uniseriate, c. 20, barbellate, mostly persistent, contiguous, slender, not broadened distally. One species, *S. triptychus* (B.L. Rob.) R.M. King & H. Rob.

1447. *Kaunia* R.M. King & H. Rob.

Kaunia R.M. King & H. Rob., Phytologia 47: 258 (1980).

Erect shrubs or small trees. Leaves opposite, lamina usually ovate, entire to serrate, broadly to narrowly acute. Inflorescences terminal on branches, thyrsoid to corymbose with densely corymbose branches. Phyllaries c. 12–23, weakly subimbricate, c. 2–3-seriate, subequal to unequal; receptacle slightly convex, epaleaceous, glabrous. Florets (10–)16–50; corollas usually white or violet, narrowly funnelform, glabrous inside and on lower outer surface; lobes slightly longer than wide, inner surface nearly smooth, outer surface smooth and somewhat padded, with occasional glands; anther collar cylindrical, elongate; apical anther appendages large, ovate, slightly longer than wide, style base not enlarged; arms smooth to slightly mamillose. Achenes prismatic, 5-ribbed, base and apex usually densely setuliferous or glanduliferous; carpopodium distinct, symmetrical; pappus setae uniseriate, c. 25–30, barbellate, persistent, contiguous, slender, not broadened distally. n = c. 20, c. 26. Fourteen species, Argentina, Bolivia, Brazil, Ecuador, Peru.

1448. *Jaramilloa* R.M. King & H. Rob.

Jaramilloa R.M. King & H. Rob., Phytologia 47: 117 (1980); King & Robinson, Phytologia 47: 117–120 (1980), key.

Erect shrubs or small trees, to 3 m tall. Leaves opposite, lamina often large, broadly oblong, serrulate to scarcely undulate, apex short-acute. Inflorescences terminal on branches, broadly corymbose, capitula short-pedicellate or sessile in glomerules. Phyllaries c. 12–23, weakly subimbricate, unequally c. 3-seriate; receptacle slightly convex, epaleaceous, glabrous. Florets 14–20; corollas whitish, with narrow cylindrical basal tube and narrowly campanulate limb, glabrous on inner and lower outside surfaces; lobes scarcely to markedly longer than wide, slightly mamillose on inner surface; anther collar cylindrical, elongate; apical anther appendages large, subquadrate to shortly oblong-ovate; style base without node, style shaft slightly thickened; arms markedly papillose. Achenes prismatic, 5-ribbed, setuliferous or glanduliferous; carpopodium short-cylindrical, symmetrical; pappus setae 1–2-seriate, c. 25–50, barbellate, rather easily deciduous, slender, contiguous, sometimes borne on outer surface of callus, not broadened distally. Two species, Colombia.

XXX.3. Subtribe Mikaniinae R.M. King & H. Rob. (1980).

Usually woody vines, sometimes erect perennial herbs or shrubs, moderately branched, never rosulate. Leaves opposite or whorled, sessile to long-petiolate, lamina linear to broadly ovate, base narrow to cordate, membranous to coriaceous. Inflorescence terminal on stems or lateral branches, cymose to corymbose or thyrsoid, capitula clustered, sessile to pedicellate, with subinvolucral bract; phyllaries distant, 4, subequal, persistent, receptacle flat, epaleaceous. Florets 4; corollas white or pink, funnelform or with variously campanulate limb, with or without distinct basal tube, glabrous to pilosulous or glanduliferous on outer surface, with or without papillae on inside of throat or lobes; lobes broadly

triangular to narrowly oblong; anther collar broad; anther cylinder exserted from corolla throat; apical anther appendages as long as or longer than wide; style base thick, without distinct basal node, glabrous or sometimes papillose; arms narrowly linear, not broadened at apex, scarcely to strongly papillose. Achenes prismatic, 4–10-ribbed; carpopodium short-cylindrical; pappus setae numerous, persistent, capillary, apical cells obtuse to acute.

Only one genus:

1449. *Mikania* Willd. Fig. 106

Mikania Willd., Sp. Pl. 3, 3: 1742 (1803), nom. cons.; Aristeguieta, Fl. Venez. 10: 91–243 (1964), reg. rev.; Barroso, Arch. Jard. Bot. Rio de Janeiro 16: 239–333, pl. 1–31, foto 1–57 (1958), reg. rev. Brazil; Holmes, Sida 9: 147–158 (1981), reg. rev. USA; Holmes, Bot. Jahrb. Syst. 103: 211–246 (1982), reg. rev. Old World; Holmes, Sida, Bot. Misc. no. 9: 69 pp. (1993), reg. rev. Greater Antilles; Holmes & McDaniel, Fieldiana, Bot. n.s. 9: 1–57 (1982), reg. rev. Peru; Holmes & McDaniel, Candollea 44: 32–35 (1989), reg. rev. Paraguay; King & Robinson, Ann. Missouri Bot. Gard. 62: 965–981 (1975), reg. rev. Panama; Smith, Fl. Trop. E. Afr. Compositae, part 3 (2005), reg. rev.
Kanimia Gardner (1847).

Characters of the subtribe. n = 16, 17, 18, 19, 20, 21, 36, 54. Circa 400 species, pantropical, although principally neotropical with a few apparent natives in the Old World tropics.

The report of dioecy in the genus (Holmes 1991) is apparently restricted only to species from the Greater Antilles.

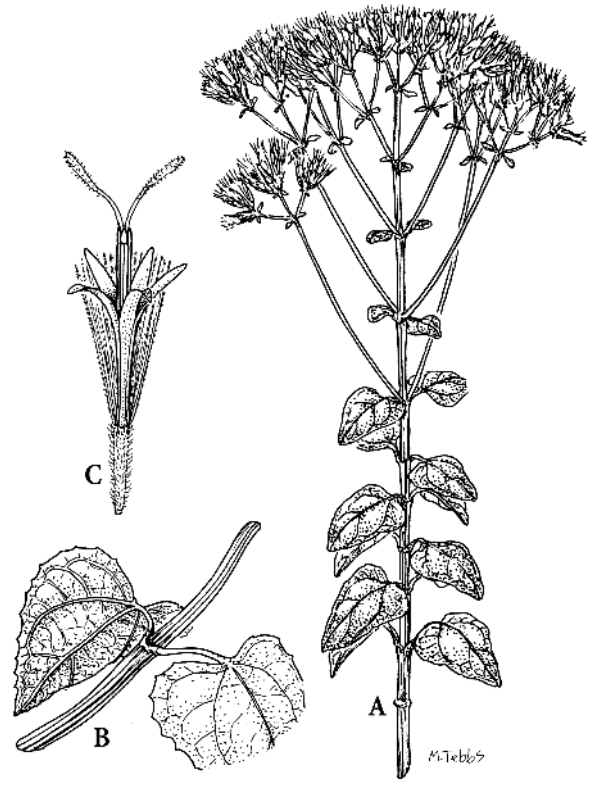

Fig. 106. Compositae-Eupatorieae. *Mikania grazielae* (Mikaniinae). **A** Flowering shoot. **B** Node. **C** Floret. (Drawings by Margaret Tebbs)

XXX.4. Subtribe Trichocoroninae R.M. King & H. Rob. (1980).

Erect to ascending, aquatic or sub-aquatic, perennial herbs, not or sparingly branched above base; leaves opposite, sometimes verticillate, sessile. Capitula often solitary on long peduncles, not or laxly clustered; phyllaries distant, persistent; receptacle convex to conical, epaleaceous, warty, glabrous. Florets 50–125; corolla lobes papillose inside and at tip and margins outside; apical anther appendages about as long as wide; style base not enlarged, glabrous; arms narrowly linear to broadly filiform or slightly clavate, flattened at least at tip, densely long-papillose. Achenes prismatic with 5 ribs; carpopodium distinct, sometimes with upper rim; pappus setae short, a crown, or absent.

Key to the Genera

1. Pappus absent; corolla tube narrow with abruptly campanulate throat **1451. *Shinnersia***
– Pappus of short setulae or of 5 broad scales; corolla tube relatively short with a long, tubular or funnelform throat 2
2. Pappus of 5 broad scales; leaves verticillate, linear and entire; inflorescences of solitary capitula; achenes glandular-punctate only **1452. *Sclerolepis***
– Pappus of short setulae; leaves opposite, sometimes becoming alternate above, lamina usually oblong, margins serrate; inflorescences of solitary capitula or laxly branched and few-headed; achenes setuliferous, setulae with acute apices **1450. *Trichocoronis***

Genera of Trichocoroninae

1450. *Trichocoronis* A. Gray

Trichocoronis A. Gray, Mem. Amer. Acad. Arts n.s. 4: 65 (1849); King & Robinson, Phytologia 19: 497–500 (1970), rev.

Erect, sub-aquatic, annual or perennial herbs. Leaves opposite, sometimes becoming alternate above, lamina membranous, oblong, serrate, acute. Inflorescences monocephalic to laxly branched. Phyllaries c. 30, 2–3-seriate, subequal, broadly lanceolate. Florets 75–125; corollas with a constricted, rather elongate basal tube, limb narrowly campanulate; lobes about as long as wide; anther collar cylindrical; apical anther appendages subquadrate, slightly longer than wide; style arms broadly filiform, densely long-papillose. Achenes prismatic to somewhat fusiform, 4–5-ribbed, ribs acutely setuliferous with sharp-pointed setulae; carpopodium stopper-shaped with distinct upper rim; pappus setae 2–6, short, barbellate, persistent. $n = 15$. Two species, USA, Mexico.

1451. *Shinnersia* R.M. King & H. Rob.

Shinnersia R.M. King & H. Rob., Phytologia 19: 297 (1970).

Ascending aquatic herbs. Leaves opposite, lamina obovate-spathulate, sinuate-incised, grossly dentate to partly dissected. Inflorescence usually monocephalic. Phyllaries c. 25–30, 2–3-seriate, essentially equal, oblong; receptacle convex to conical, warty, glabrous. Florets 90–100; corollas white, with narrow basal tube as long as limb, throat broadly and rather abruptly rounded-campanulate, with glands on tube, with numerous hairs on upper throat and outer surface of lobes; lobes broader than long; anther collar short-cylindrical; apical anther appendages ovate to subquadrate, about as long as wide; style arms broadly linear, flat, densely long-papillose. Achenes prismatic, 4–5-ribbed, with a few glands, ribs obtusely setuliferous; carpopodium short-cylindrical; pappus absent. n = c. 30. One species, *S. rivularis* (A. Gray) R.M. King & H. Rob., USA, Mexico.

1452. *Sclerolepis* Cass.

Sclerolepis Cass., Bull. Soc. Philom. Paris 1816: 198 (1816).

Erect, sub-aquatic to aquatic perennial herbs. Leaves verticillate, 4–6 per node, lamina linear, entire. Inflorescences terminal, usually monocephalic, produced only on 'stranded' stems, never on aquatic and emergent stems; capitula pedicellate; phyllaries 22–25, biseriate, subequal, broadly lanceolate. Florets c. 50; corollas pink, narrowly funnelform from slightly narrowed base, with glands on tube and base of throat; lobes short-triangular, with short thick hairs on outer surface; anther collar narrowly cylindrical; apical anther appendages scarcely wider than long; style arms narrowly linear to slightly clavate, rather flattened distally, densely long-papillose. Achenes prismatic, 5-ribbed, serrulate to slightly crested on ribs, with few glands near upper end; carpopodium subcylindrical; pappus of usually 5, thick, broadly oblong, blunt, indurate scales, margins densely crenulate-denticulate. $n = 15$, c. 30. One species, *S. uniflora* (Walter) Britton, Sterns & Poggenb., endemic to USA.

XXX.5. Subtribe Adenostemmatinae B.L. Rob. (1913).

Annual or perennial herbs, often creeping or with decumbent bases. Leaves opposite. Inflorescences terminal, unbranched or cymose. Capitula pedicellate; phyllaries distant, herbaceous without articulated or sclerified bases, receptacle glabrous, without sclerified tissue between achene scars, shallowly convex, becoming more convex with age, epaleaceous. Florets 10–200; corolla lobes smooth on inner surface; style base lacking basal node, glabrous; arms weakly mamillose to smooth. Achenes 3–5-angled; carpopodium distinct or scarcely distinguishable from body; pappus usually with 3 or 5 viscid-tipped knobs, or absent.

Key to the Genera

1. Pappus absent **1455. *Gymnocoronis***
– Pappus of 3 or 5 elongate knobs 2
2. Tips of knobs spherical and not decurrent on to surface of knob; anther appendages as long as wide; pappus always of 5 knobs; style shaft always glabrous; carpopodium scarcely distinguishable from body and slightly asymmetrical **1454. *Sciadocephala***
– Tips of knobs elliptical and decurrent on to surface of knob; anther appendages about 1/2 as long as wide; pappus usually of 3, rarely 5 knobs; style shaft glabrous or with long hairs; carpopodium distinct and asymmetrical **1453. *Adenostemma***

Genera of Adenostemmatinae

1453. *Adenostemma* J.R. Forst. & J.G. Forst.

Fig. 107

Adenostemma J.R. Forst. & J.G. Forst., Char. Gen. Pl.: 89 (1776); Grierson, Ceylon J. Sci. (Biol. Sci.) 10: 42–80 (1972), reg. rev. Sri Lanka; Koyama, Mem. Natl Sci. Mus. (Tokyo) 37: 159–168 (2001), reg. rev. E. Asia; Koyama, Bull. Natl Sci. Mus., B (Tokyo) 28: 49–60 (2002), reg. rev. Thailand;

Fig. 107. Compositae-Eupatorieae. *Adenostemma viscosum* (Adenostemmatinae). **A** Basal leaf. **B** Inflorescence. **C** Floret. (Drawings by Margaret Tebbs)

Panigrahi, Kew Bull. 30: 647–655 (1975), reg. rev. Indian reg.; King & Robinson, Phytologia 29: 1–20 (1974), reg. rev.

Perennial herbs. Leaf lamina narrowly elliptical to broadly ovate or hastate, crenate to strongly serrate, acute to slightly acuminate. Inflorescence very laxly cymose. Phyllaries 10–30, biseriate, ± overlapping, somewhat fused at base, equal to subequal; receptacle covered with discrete oval deeply concave scars. Florets 10–60; corollas usually white, narrowly funnelform or with narrow basal tube and broadly campanulate limb, usually with hairs or glands on outer surface, hairs often moniliform; lobes c. 1.5 times longer than wide, non-papillose, anther collar usually strongly expanded below; apical anther appendages distinctly shorter than wide; style shaft with or without long hairs; arms slightly to strongly clavate, often forming most showy part of head, fleshy, rounded apically, scarcely mamillose below. Achenes slightly curved, usually 3-angled without distinct ribs or 5-angled, often tuberculate; carpopodium forming a prominent asymmetrical knob; pappus of usually 3 or 5 terete clavate knobs, knobs with tips and upper outside surface covered with an elongated mass of viscid glands. n = 10. Circa 26 species, pantropical.

1454. *Sciadocephala* Mattf.

Sciadocephala Mattf., Notizbl. Bot. Gart. Berlin-Dahlem 14: 41 (1938); King & Robinson, Phytologia 29: 1–20 (1974), reg. rev.

Perennial herbs. Leaf lamina narrowly ovate to elliptical or slightly obovate, entire to serrate. Capitula solitary or laxly subcymose. Phyllaries c. 6–14, persistent, 1–2-seriate, subequal to equal, separate to base; receptacle with discrete oval scars separated by soft tissue. Florets c. 9–15; corollas white, narrowly funnelform, with sparse hairs on outer surface; lobes slightly to distinctly longer than wide; anther collar stout, not or slightly broadened below; apical anther appendages ovate, as long as wide or slightly longer; nectary usually glabrous, rarely pubescent; style arms long and narrow, rounded apically, scarcely mamillose below. Achenes narrowly prismatic, nearly terete, without distinct ribs; carpopodium only slightly asymmetrical, not enlarged; pappus of 5 terete clavate knobs, knobs with a short globular mass of glutiniferous glands apically. n = 10. Five species, Colombia, Ecuador, Guyana, Panama.

1455. *Gymnocoronis* DC.

Gymnocoronis DC., Prodr. 5: 106 (1836); King & Robinson, Phytologia 29: 1–20 (1974), reg. rev.

Annual to perennial erect herbs. Leaf lamina lanceolate to ovate or deltoid. Inflorescence strongly cymose. Phyllaries c. 20–50, biseriate, equal to subequal; receptacle with discrete oval scars and with soft tissue between. Florets 50–200; corollas white, narrowly funnelform, with short-stalked glands on outer surface; lobes as wide as long to wider than long; anther collar slightly enlarged; apical anther appendages small, wider than long; style arms very broadly oar-shaped, surface mamillose below, smooth above. Achenes slightly curved, prismatic (4–)5-ribbed, glanduliferous between ribs, ribs sometimes corky; carpopodium

short-cylindrical; pappus absent. Five species, Argentina, Bolivia, Brazil, Guatemala, Mexico, Paraguay, Peru, Uruguay. Recently naturalized in Japan (Suyama 2001).

XXX.6. Subtribe Fleischmanniinae R.M. King & H. Rob. (1980).

Erect annual or mostly perennial herbs, lacking rosulate basal leaves. Leaves opposite, rarely alternate. Inflorescence terminal on stems or branches, with corymbose or cymose branches, capitula clustered, usually pedicellate. Phyllaries usually distinctly subimbricate, gradate, persistent; receptacle flat to slightly conical, epaleaceous. Florets (10–)20–50; corollas with short basal tube, throat narrowly campanulate, with veins thickened below; lobes short-triangular; anther collar slender; apical anther appendages about as long as wide; style base usually not enlarged, glabrous below, or with scattered glands or hairs on shaft, arms filiform, not or scarcely broadened distally, densely papillose. Achenes prismatic, 5-ribbed or terete; carpopodium distinct with slight projecting upper rim or indistinct; pappus setae uniseriate, 5 to many, barbellate, capillary, with pointed apical cells.

Key to the Genera

1. Achenes 5-ribbed; style shaft glabrous **1456. *Fleischmannia***
– Achenes terete; style shaft pubescent and glandular **1457. *Sartorina***

1456. *Fleischmannia* Sch. Bip.

Fleischmannia Sch. Bip., Flora 33: 417 (1850); King & Robinson, Ann. Missouri Bot. Gard. 62: 835–1322 (1975), reg. rev. Panama; Robinson, Proc. Biol. Soc. Wash. 114: 529–556 (2001), new spp.; Wooten & Clewell, Rhodora 73: 566–574 (1971), reg. rev. eastern North America.
Eupatorium L. sect. *Microstemon* Cabrera (1991).

Erect annual or perennial herbs or subshrubs. Leaves usually opposite, lamina elliptical to rhomboidal or broadly cordate-ovate, upper part serrate or crenulate, or lamina dissected into long narrow segments. Inflorescence with laxly cymose to densely corymbose branches. Phyllaries 20–30, subimbricate, rarely distant, 2–4-seriate, usually unequal; receptacle glabrous or with minute scattered hairs. Florets (10–)20–50; corollas white, lavender, bluish or purple, with rather short basal tube, limb narrowly funnelform with ± campanulate base, with outer surface above or on the lobes often with short hairs or glands, veins greatly thickened in tube or throat; lobes short; apical anther appendages broadly ovate or oblong; style base glabrous; arms densely long-papillose. Achenes prismatic, 5-ribbed, usually with setulae on ribs of upper parts; carpopodium distinct with prominent upper rim; pappus setae 5–40, slender, sometimes slightly fragile. n = 4 (rarely), 10, 20 or 30 (rarely). Ninety-five species, neotropical.

1457. *Sartorina* R.M. King & H. Rob.

Sartorina R.M. King & H. Rob., Phytologia 28: 98 (1974).

Erect to partially decumbent perennial herbs. Leaf lamina broadly ovate to deltoid, crenulate to obtusely serrulate. Inflorescence subthyrsoid with subcorymbose branches. Phyllaries c. 20, subimbricate, c. 3-seriate, unequal, outer phyllaries ovate, inner oblong; receptacle flat, glabrous. Florets c. 15–22; corollas white or lavender (?), with short, narrowly cylindrical basal tube, limb narrowly funnelform with ± campanulate base, glabrous outside below lobes, veins greatly thickened in tube and throat; lobes broadly triangular, with glands on outer surface; apical anther appendages shortly oblong; style base slightly enlarged, glabrous; shaft sparsely short-pubescent and stipitate-glanduliferous; arms densely long-papillose. Achenes terete, narrowed below to a point, glabrous, with 5 narrow veins, without black deposits in walls; carpopodium undifferentiated; pappus setae c. 15, slender, somewhat non-contiguous, persistent. One species, *S. schultzii* R.M. King & H. Rob., Mexico (?).

XXX.7. Subtribe Ageratinae Less. (1832).

Subtribe Piqueriinae Benth. & Hook. f. (1873).

Erect to procumbent annual or perennial herbs, shrubs or trees. Leaves opposite, sometimes alternate above, rarely throughout. Inflorescence terminal, sometimes diffuse; capitula clustered, sessile to long-pedicellate. Phyllaries distant to subimbricate, persistent; receptacle scarcely convex to distinctly conical, paleaceous or epaleaceous. Florets 3–125; corolla lobes usually papillose; apical anther appendages short or absent to longer than wide, sometimes apically cleft or crenulate; style base not or rarely enlarged, usually glabrous, arms usually linear, sometimes long-clavate, not abruptly short-clavate at tips, usually densely papillose or

mamillose. Achenes usually prismatic, 5-ribbed, base sometimes contorted but not long-stipitate; carpopodium usually distinct, sometimes with upper margin procurrent on base of achene; pappus reduced, sometimes totally lacking, coroniform, or of awns or scales, rarely of more than 5 primary elements. Bremer's limited analysis (1994) suggests that the subtribe is monophyletic 'in some but not all the cladograms'.

Key to the Genera

1. Marginal florets conspicuously zygomorphic and with 3 ray-like, expanded outer lobes **1482. *Microspermum***
– Marginal florets actinomorphic (rarely with slightly zygomorphic marginal florets in *Ferreyrella*, *Metastevia* and *Revealia* but never conspicuously ray-like) 2
2. Phyllaries with conspicuous broadened, often coloured apical appendages **1464. *Scherya***
– Phyllaries acute, obtuse or rounded but without broadened and coloured apical appendages 3
3. Receptacles paleaceous 4
– Receptacles epaleaceous 9
4. Receptacle conical 5
– Receptacle flat or slightly convex 6
5. Apical anther appendages conspicuous and large, somewhat longer than wide; florets > 20 **1460. *Ageratum***
– Apical anther appendages abortive or much reduced; florets ≤ 14 **1472. *Nesomia***
6. Herbaceous; paleae with densely fimbriate apices 7
– Plants shrubby or tree-like with monopodial or sympodial branching 8
7. Corollas cylindrical, sparsely glandular-punctate; apical callus and abscission layer between achene and corolla absent; carpopodium absent or obscure; Brazil **1467. *Teixeiranthus***
– Corollas with constricted basal tube, tube stipitate-glandular; apical callus and abscission layer between achene and corolla present; carpopodium distinct, symmetrical and appearing short-cylindrical; Peru **1471. *Ferreyrella***
8. Leaves glabrous and glandular-punctate or variously eglandular-pubescent; pappus a short crown or a few awns; inflorescences on pseudowhorled side branches and plants usually with terminal vegetative lead shoot; Brazil **1458. *Acritopappus***
– Leaves glandular-punctate and short stipitate-glandular; pappus absent; inflorescences terminal or axillary, but not whorled, and plants without terminal lead vegetative shoot; Guatemala, Honduras **1463. *Blakeanthus***
9. Receptacle conical **1460. *Ageratum***
– Receptacle flat or slightly convex 10
10. Achenes compressed, 2-ribbed **1484. *Macvaughiella***
– Achenes prismatic usually 5-ribbed or sometimes 8–10-ribbed 11
11. Corollas 4-lobed; 4 stamens per floret; plants minute, < 10 cm tall 12
– Corollas 5-lobed; 5 stamens per floret; plants usually much more than 10 cm tall 13
12. Florets 3–7 per capitulum; phyllaries (4–)5–6; Mexico **1474. *Piqueriopsis***
– Florets c. 30 per capitulum; phyllaries 8–10; Costa Rica and Panama **1483. *Iltisia***
13. Plants repent with side shoots as small rosettes; inflorescence of clustered scapose capitula; pedicels shorter than leaves; Peru **1465. *Ascidiogyne***
– Plants erect or ascending, or if procumbent shoots leafy throughout; inflorescences usually exceeding leaves 14
14. Pappus absent 15
– Pappus present 21
15. Achenes setuliferous; corolla tube constricted and long stipitate-glandular, corolla limb markedly expanded and only sparsely long stipitate-glandular at base **1462. *Phalacraea***
– Achenes glabrous; corolla tube short or indistinguishable from funnelform limb, glabrous, short- or long-pubescent, rarely stipitate-glandular and then glandular hairs throughout lower half of corolla 16
16. Corolla throat densely pubescent inside; Mexico **1477. *Metastevia***
– Corolla throat glabrous inside 17
17. Corolla glabrous outside; Brazil (Céara) **1473. *Piqueriella***
– Corolla short- or long-pubescent outside 18
18. Corollas with constricted corolla tube, hairs eglandular 19
– Corollas funnelform and stipitate-glandular in lower half; florets 12–15; phyllaries biseriate, 10–12; Brazil (Goías) **1468. *Gardnerina***
19. Anther filaments papillose or short-pubescent at base; florets 3–5; phyllaries uniseriate, 3–5; Mexico, West Indies **1475. *Piqueria***
– Anther filaments glabrous; florets 6–40 20
20. Apical anther appendages as long as wide; corollas with conspicuously campanulate limb above constricted tube; florets 6–30; phyllaries 8–10; Brazil (Pará) **1466. *Cavalcantia***
– Apical anther appendages vestigial; corollas with funnelform limb above narrowed base; florets 15–40; phyllaries 10–20; Ecuador and Peru **1470. *Guevaria***
21. Capitula always with 5 florets and 5 phyllaries; phyllaries uniseriate; corolla throat pubescent inside **1476. *Stevia***
– Capitula usually with numbers of phyllaries and florets not equal (usually with > 10 florets and > 8 phyllaries, sometimes florets 4–6 and then phyllaries 6); phyllaries 2–4-seriate; corolla throat glabrous inside 22
22. Florets 35–70; phyllaries 4-seriate; Brazil and Uruguay **1459. *Radlkoferotoma***
– Florets 4–25; phyllaries 1–2-seriate 23
23. Leaves narrowly linear; style arms linear and terete with stigmatic lines close together on inner surface and reaching nearly to tip; Mexico and USA **1478. *Carphochaete***
– Leaves broadly linear to oblong, ovate or ovate-elliptical; style arms filiform or with expanded tips, and stigmatic lines on edges of inner surface and ending well before style arm appendage 24
24. Leaves sessile or very short-petiolate 25
– Leaves distinctly petiolate 26

25. Pappus setae of distinct long awns or squamellae; achenes 8–10-ribbed; stems erect, sparingly branched **1479. *Cronquistia***
– Pappus short, coroniform, of many short squamellae; achenes 5–6-ribbed; stems spreading and often procumbent, densely branched **1480. *Revealia***
26. Pappus of 5 squamellae; achenes usually glabrous; leaf lamina distinctly glandular-punctate beneath; florets 12–25; Cuba and West Indies **1461. *Phania***
– Pappus of c. 20 short squamellae; achenes moderately setuliferous; leaf lamina lacking distinct glandular punctae beneath; florets 10–12; Peru **1469. *Ellenbergia***

Genera of Ageratinae

1458. *Acritopappus* R.M. King & H. Rob. Fig. 108

Acritopappus R.M. King & H. Rob., Phytologia 24: 401 (1972); King & Robinson, Phytologia 45: 142–157 (1980), key.

Shrubs or trees. Leaves opposite, lamina ovate, ovate-elliptical, lanceolate or linear, glabrous or pubescent, often viscid, serrate to subserrulate or nearly entire, obtuse, short-acute to long-acuminate. Inflorescence on leafy side branches, branches densely subcymose to appearing subverticillate. Phyllaries 2–3-seriate, 5–25, distant; receptacle flat to convex, paleaceous, paleae linear, carinate. Florets 5–100; corollas usually pale lavender or pink, narrowly funnelform, glandular-punctate or glandular-stipitate on outer surfaces; lobes slightly longer than wide, inner surface with short cells usually with short papillae; style base not enlarged, glabrous, arms linear, densely short-papillose. Achenes 5-ribbed, glabrous; carpopodium distinct, short; pappus vestigial, a short crown, or of few awns. $n = 9$. Circa 16 species, Brazil.

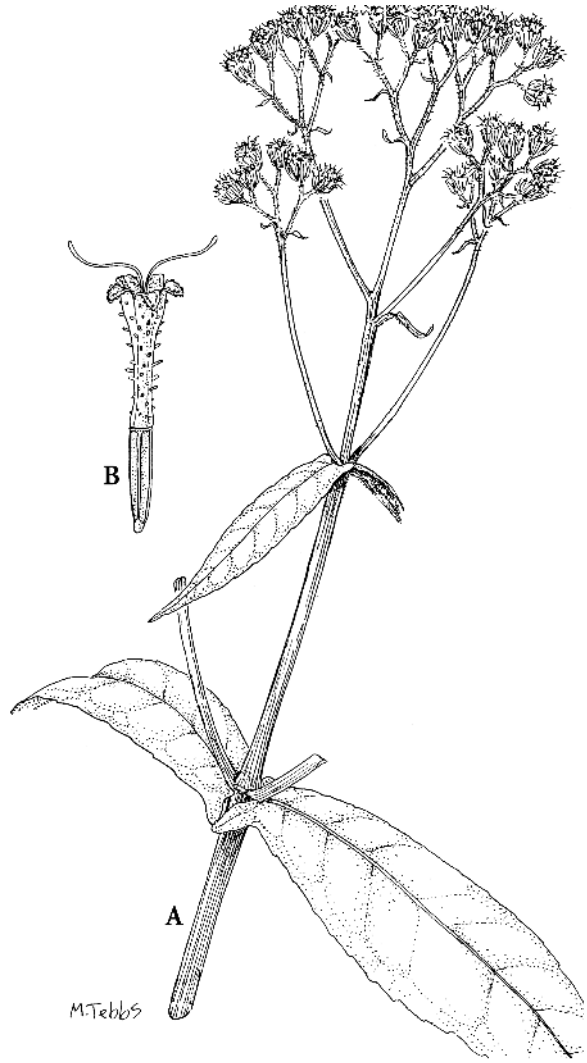

Fig. 108. Compositae-Eupatorieae. *Acritopappus connatifolius* (Ageratinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

1459. *Radlkoferotoma* Kuntze

Radlkoferotoma Kuntze, Revis. Gen. Pl. 1: 358 (1891); Cabrera, Bol. Soc. Argent. Bot. 6: 239–242 (1957), key, sub *Carelia* Less.

Shrubs or small trees. Leaves opposite, lamina ovate to lanceolate, serrate. Inflorescence corymbose. Phyllaries c. 35, markedly subimbricate, c. 4–5-seriate, gradate, inner somewhat deciduous; receptacle flat, glabrous. Florets c. 35–70; corollas white or rosaceous, funnelform, with only minute glands on outer surface; lobes about twice as long as wide, smooth on both surfaces; anther collar broadly cylindrical; style base not enlarged, glabrous, arms linear, scarcely or not broadened distally, densely papillose. Achenes prismatic, 4–5-ribbed, sparsely setuliferous; carpopodium cylindrical, procurrent on to base of achene ribs; pappus of 5 short broad scales. Three species, Brazil, Uruguay.

1460. *Ageratum* L.

Ageratum L., Sp. Pl. 2: 839 (1753); Johnson, Ann. Missouri Bot. Gard. 58: 6–88 (1971), rev.; Robinson, Phytologia 69: 93–104 (1990), reg. rev.

Annual to perennial herbs or subshrubs. Leaves opposite or sometimes alternate, lamina elliptical or lanceolate to deltoid or ovate, entire to dentate. In-

florescence cymose to subcymose, sometimes subumbellate. Phyllaries 30–40, distant, 2–3-seriate, equal or subequal, lanceolate, markedly indurate, often with scarious margins; receptacle conical, glabrous or paleaceous. Florets 20–125; corollas white, blue or lavender, funnelform or with distinct basal tube; lobes about as long as wide, papillose on inner surface, partially papillose and sometimes hispidulous on outer; anther collar cylindrical; style base not enlarged, glabrous, arms linear, usually strongly and densely papillose. Achenes prismatic, 4–5-ribbed, glabrous or ribs setuliferous; carpopodium distinct; pappus lacking, or coroniform, or of 5 or 6 free, flattened, sometimes awn-like scales. n = 10, 20. Circa 40 species, Central and South America.

One species (*A. houstonianum* Mill.) widely cultivated, and another (*A. conyzoides* L.), although sometimes cultivated, is a widespread weed throughout the tropics in both the Old and New Worlds.

1461. *Phania* DC.

Phania DC., Prodr. 5: 114 (1836).

Annual or perennial herbs or small shrubs. Leaves opposite, lamina ovate or deltoid to palmate, crenate-dentate to shallowly lobed. Inflorescence of small cymes or solitary capitula terminal on leafy branches. Phyllaries c. 10–20, distant, biseriate, equal or subequal, broadly lanceolate to narrowly oblanceolate; receptacle conical, epaleaceous, glabrous. Florets c. 12–25; corollas pale lavender to white, with short constricted basal tube abruptly expanding into short-campanulate limb, with scattered glandular punctae on outer surface; lobes about as long as wide or slightly wider, with large strongly mamillose cells on inner surface; anther collar rather long; style base not enlarged, glabrous, arms somewhat strongly clavate distally, short-papillose or mamillose. Achenes prismatic, 4–5-ribbed, glabrous or with few glands or setulae; carpopodia distinct, cylindrical, somewhat procurrent on to lower ribs of achene; pappus squamellae 5. Five species, Cuba, West Indies.

1462. *Phalacraea* DC.

Phalacraea DC., Prodr. 5: 105 (1836); King & Robinson, Phytologia 29: 251–256 (1974), rev.

Perennial herbs, procumbent or erect from decumbent bases. Leaves opposite, lamina ovate to broadly triangular, crenate to serrate. Inflorescence rather laxly cymose, with denser ultimate branching. Phyllaries 10–18, distant, 2–3-seriate, subequal, broad with short-acute non-scarious tips; receptacle flat to slightly convex, glabrous. Florets 10–18; corollas white, with constricted basal tube and abruptly expanding campanulate limb, many scattered minutely gland-tipped hairs on tube, more sparse on limb; lobes slightly longer than wide, papillose on inner surface; anther collar often rather stout; style base not enlarged, glabrous, arms broad, becoming slightly broader towards the broadly rounded tips, densely papillose. Achenes prismatic, 4–5-ribbed, moderately to densely setuliferous; carpopodium small; pappus absent. n = 20. Four species, Colombia, Ecuador, Peru.

1463. *Blakeanthus* R.M. King & H. Rob.

Blakeanthus R.M. King & H. Rob., Phytologia 24: 118 (1972).

Erect shrubs. Leaves opposite, lamina ovate, crenate to serrulate. Inflorescence a compact corymbose panicle, branches with ± glomerulous capitula. Phyllaries c. 20, distant, 2–3-seriate, subequal, lanceolate; receptacle flat to slightly convex, paleaceous. Florets c. 25; corollas white, narrowly funnelform; lobes slightly longer than wide, glandular-punctate on outer surface, smooth on inner; anther collar slender; style base not enlarged, glabrous, arms linear, not or scarcely broader at tips, mamillose to subpapillose. Achenes prismatic, 5-ribbed, mostly glabrous, with few minute spicules on ribs and some glands on upper callus; carpopodium symmetrical, short; pappus absent. One species, *B. cordatus* (S.F. Blake) R.M. King & H. Rob., Guatemala, Honduras.

1464. *Scherya* R.M. King & H. Rob.

Scherya R.M. King & H. Rob., Phytologia 38: 101 (1977).

Erect perennial herbs. Leaves opposite, lamina linear, entire. Inflorescence terminal, subscapose, cymose to subcymose. Phyllaries c. 20, distant, ± biseriate, subequal, with broad, rounded, chartaceous, coloured tips; receptacle flat to slightly convex, paleaceous. Florets c. 25; corolla pale, funnelform, with glands on outer surface; lobes slightly longer than wide, nearly smooth and glanduliferous on outer surface, densely papillose on inner; anther collar rather short; style base not enlarged, glabrous, arms filiform, densely papillose. Achenes prismatic, 5-ribbed, glabrous, bands of carbonization very narrow; carpopodium symmetrical, procurrent along ribs of achene;

pappus a laciniate crown with 5 long primary teeth, rather indurate. One species, *S. bahiensis* R.M. King & H. Rob., Brazil.

1465. ***Ascidiogyne*** Cuatrec.

Ascidiogyne Cuatrec., Ann. Missouri Bot. Gard. 52: 310 (1965).

Prostrate, somewhat fleshy, stoloniferous herbs with erect rosulate branches. Leaves of prostrate stems opposite, congested on erect stems, lamina ovate or obovate to narrowly elliptical, entire. Inflorescence of clustered short 1-headed scapes. Phyllaries 4–7, distant, biseriate, equal, broadly oblong to ovate; receptacle flat, glabrous, foveolate. Florets 5–7; corollas white, tube strongly constricted and pilose in upper part, limb broadly campanulate and glabrous; lobes up to twice as long as wide, smooth on most of inner surface; anther collar rather short, enlarged; style base not enlarged, glabrous, arms short, clavate, with short papillae denser towards tip. Achenes prismatic, 5-ribbed, glabrous; carpopodium slightly asymmetrical; pappus lacking or of a rim of callus forming a high 5-lobed crown. $n = 10$. Two species, Peru.

The peculiar fluid-filled sac, formed from the outer wall of the achene, is present only in the type, and evident only in fresh material.

1466. ***Cavalcantia*** R.M. King & H. Rob.

Cavalcantia R.M. King & H. Rob., Phytologia 47: 113 (1980).

Erect annual or short-lived perennial herbs. Lower leaves opposite, alternate above, lamina ovate to deltoid, distinctly shallowly lobed. Capitula strongly divaricately cymose or aggregated in glomerules. Phyllaries 8–10, distant, biseriate, subequal to equal, persistent, narrowly obovate to ovate; receptacle flat or conical, glabrous. Florets c. 6–30; corollas white; basal tube short, broad below and constricted above, densely pubescent; limb funnelform; lobes as long as wide, papillose on inner surface; anther collar slightly enlarged below; style base not enlarged, glabrous, arms filiform, densely papillose. Achenes prismatic, 5-ribbed, glabrous; carpopodium small; pappus absent. Two species, Brazil.

1467. ***Teixeiranthus*** R.M. King & H. Rob.

Teixeiranthus R.M. King & H. Rob., Phytologia 47: 108 (1980); King & Robinson, Phytologia 50: 379–384 (1982), rev.

Erect or decumbent, annual or short-lived perennial herbs. Leaves opposite, lamina elliptical to linear. Inflorescence a corymbose cyme. Phyllaries c. 10, distant, ± biseriate, equal, persistent, elliptical to narrowly obovate, with expanded apices; receptacle conical, paleaceous; paleae oblanceolate with expanded apices. Florets c. 30; corollas pale reddish, cylindrical with extreme base campanulate, base fused directly to top of achene, sometimes with poorly developed abscission zone; lobes slightly longer than wide, densely papillose on inner surface, smooth on outer; anther collar scarcely discernible; style base not enlarged, glabrous, arms filiform, slightly wider distally, densely and strongly papillose. Achenes prismatic to subfusiform, usually 5-ribbed; carpopodium apparently absent; pappus absent. Two species, Brazil.

1468. ***Gardnerina*** R.M. King & H. Rob.

Gardnerina R.M. King & H. Rob., Phytologia 49: 2 (1981).

Annual or short-lived perennial herbs, erect from decumbent bases. Leaves opposite below, alternate above, lamina ovate to rhomboid, repand-dentate to pinnatifid. Inflorescence a few-headed cyme. Phyllaries c. 10–12, distant, biseriate, equal to subequal, persistent, lanceolate, bicostate; receptacle flat, glabrous. Florets 12–15; corollas white, funnelform, with stipitate glands outside in lower part, throat with short non-glandular hairs inside on and near bases of filaments; lobes c. 1.25–1.5 times as long as wide, inner surface densely papillose, outer smooth; anther collar cylindrical; style base not or scarcely enlarged, glabrous, arms broadly clavate or strap-shaped, flattened, rather fleshy, densely short-papillose, mamillose distally. Achenes subprismatic, 5-ribbed, glabrous; carpopodium distinct, ± inflated; pappus absent. One species, *G. angustata* (Gardner) R.M. King & H. Rob., Brazil.

1469. ***Ellenbergia*** Cuatrec.

Ellenbergia Cuatrec., Proc. Biol. Soc. Wash. 77: 142 (1964).

Erect annual herb. Leaves opposite, a few alternate above, lamina ovate to ovate-elliptical, crenate-dentate, acute. Inflorescence a lax panicle with subcymose branches. Phyllaries 8, distant, biseriate, subequal, persistent, oblong-elliptical to obovate-elliptical; receptacle flat, foveolate, glabrous. Florets 10–12; corollas white (?), with distinct constricted basal tube, glandular-punctate

outside; throat broadly campanulate, papillate on inner surface; lobes about as long as wide, densely papillose on inner surface and margins; lower part of filament short, densely pubescent; anther collar slender; style base not enlarged, hirtellous, arms shortly clavate, densely papillose. Achenes prismatic, 5-ribbed, ribs setuliferous, narrowed and densely setuliferous above carpopodium, carpopodium distinct, shortly cylindrical; pappus of c. 20 short, lanceolate squamellae, densely scabrid on margins, nearly smooth on outer surface. One species, *E. glandulata* Cuatrec., Peru.

1470. *Guevaria* R.M. King & H. Rob.

Guevaria R.M. King & H. Rob., Phytologia 29: 259 (1974).

Small perennial herbs, decumbent or erect with decumbent bases. Leaves opposite or alternate, lamina ovate, crenulate to serrulate. Inflorescence laxly paniculate with cymose branches. Phyllaries 10–20, distant, 2–3-seriate, subequal, persistent, oblong; receptacle conical, glabrous. Florets 15–40; corollas white, with distinct constricted basal tube bearing many hairs; throat shortly and broadly campanulate; lobes 1–2 times as long as wide, densely papillose on inner surface and margins, with short hairs and glands on outer surface; anther collar only slightly expanded; style base not enlarged, glabrous, arms broadly linear, densely long-papillose. Achenes prismatic, obovate, 5-ribbed, glabrous; carpopodium cylindrical; pappus absent. $n = 10$. Five species, Ecuador, Peru.

1471. *Ferreyrella* S.F. Blake

Ferreyrella S.F. Blake, J. Wash. Acad. Sci. 47: 407 (1958).

Small, erect, annual herbs. Leaves opposite below, alternate above, lamina ovate to broadly elliptical, coarsely to finely serrate. Inflorescence a diffuse corymbose cyme. Phyllaries c. 15–25, distant, biseriate, subequal to equal, persistent, ovate to broadly oblanceolate, with rounded apices, pubescent; receptacle conical, paleaceous. Florets c. 30; corollas white, with short constricted basal tube bearing glandular or eglandular hairs; throat short and broad-campanulate; lobes as long as wide or outer lobes of peripheral florets longer, densely short-papillose on inner surface and margins; lower part of filament glabrous; anther collars rather short; style base not enlarged, glabrous; arms rather short-clavate, densely short-papillose; papillae larger and less dense below clavate tip. Achenes prismatic, 5-ribbed, glabrous; carpopodium distinct, short-cylindrical; pappus absent. Two species, Peru.

1472. *Nesomia* B.L. Turner

Nesomia B.L. Turner, Phytologia 71: 208 (1991).

Perennial herb. Leaves opposite, lamina ovate to deltoid, coarsely serrate, acuminate. Inflorescences congested paniculate corymbs. Involucres campanulate; phyllaries distant, oblanceolate, subequal, 1–2(–3)-ribbed, glabrous, margins ciliate; receptacles conical, paleaceous. Florets 12–14; corollas light purple or lavender, tube pubescent with glandular and eglandular hairs, throat campanulate, lobes broadly triangular, glabrous; anther collars linear; style arms linear, short-papillose. Achenes 4–5-ribbed, glabrous; carpopodium conspicuous; pappus absent. One species, *N. chiapensis* B.L. Turner, Mexico.

1473. *Piqueriella* R.M. King & H. Rob.

Piqueriella R.M. King & H. Rob., Phytologia 29: 264 (1974).

Small, annual or short-lived perennial herbs. Leaves usually opposite, lamina ovate, with many large teeth, shortly and narrowly acuminate. Inflorescence a lax cyme. Phyllaries c. 6, distant, biseriate, equal, persistent, broadly oblong, subtruncate, 3–5-denticulate; receptacle slightly convex, glabrous. Florets c. 8; corollas whitish, with distinct constricted basal tube, glabrous on outer surface; throat broadly and shortly campanulate; lobes longer than wide, densely papillose on inner surface and margins; anther collars rather short, stout; style base not enlarged, glabrous, arms short and subclavate, with dense long papillae. Achenes prismatic, 5-ribbed, glabrous; carpopodium strongly asymmetric; pappus absent. One species, *P. brasiliensis* R.M. King & H. Rob., Brazil.

1474. *Piqueriopsis* R.M. King

Piqueriopsis R.M. King, Brittonia 17: 352 (1965).

Minute, ephemeral, erect herbs. Leaves opposite, lamina ovate to elliptic-rhomboid, crenulate to undulate. Inflorescence a small panicle with few-headed cymose branches. Phyllaries (4–)5–6, distant, ± biseriate, equal to subequal, persistent, obovate to oblanceolate; receptacle convex, glabrous. Florets 3–7; corollas white, with distinct constricted short basal tube, bearing numerous stout non-glandular hairs near base; throat short and widely funnelform from a subcampanu-

late base; corolla lobes 4, c. 1.5 times as long as wide, strongly mamillose on inner surface, glabrous on outer; anther collar stout; style base slightly enlarged, glabrous, arms short, not or slightly clavate, mamillose. Achenes prismatic, 8–10-ribbed, glabrous; carpopodium forming a somewhat flaring annulus; pappus absent. One species, *P. michoacana* R.M. King, Mexico.

Turner (1987b, 1997) suggested that *Piqueriopsis* should be included within an expanded *Microspermum*, along with *Iltisia*.

1475. *Piqueria* Cav.

Piqueria Cav., Icon. 3: 18 (1794); Turner, Phytologia Mem. 11: i–iv, 1–272 (1997), key.

Erect, annual to perennial herbs or subshrubs. Leaves mostly opposite, lamina ovate to lanceolate, serrulate to serrate. Inflorescence laxly paniculate with laxly to densely subcymose branches. Phyllaries uniseriate, 3–5, distant, equal, persistent, obtuse to apiculate; receptacle flat, glabrous. Florets 3–5; corollas white to slightly lavender, with short, narrow, densely pubescent basal tube; throat short-campanulate; lobes 1.5–3 times as long as wide, densely papillose on inner surface, slightly papillose on margins and tip outside; anther collar broad; style base not enlarged, glabrous, arms with slightly to strongly clavate appendages, densely long-papillose on narrower parts, becoming nearly smooth on tips. Achenes prismatic, 5-ribbed, glabrous; carpopodium usually asymmetrical and large; pappus absent. n = 11, c. 22, c. 24. Six species, Central America, Mexico, West Indies.

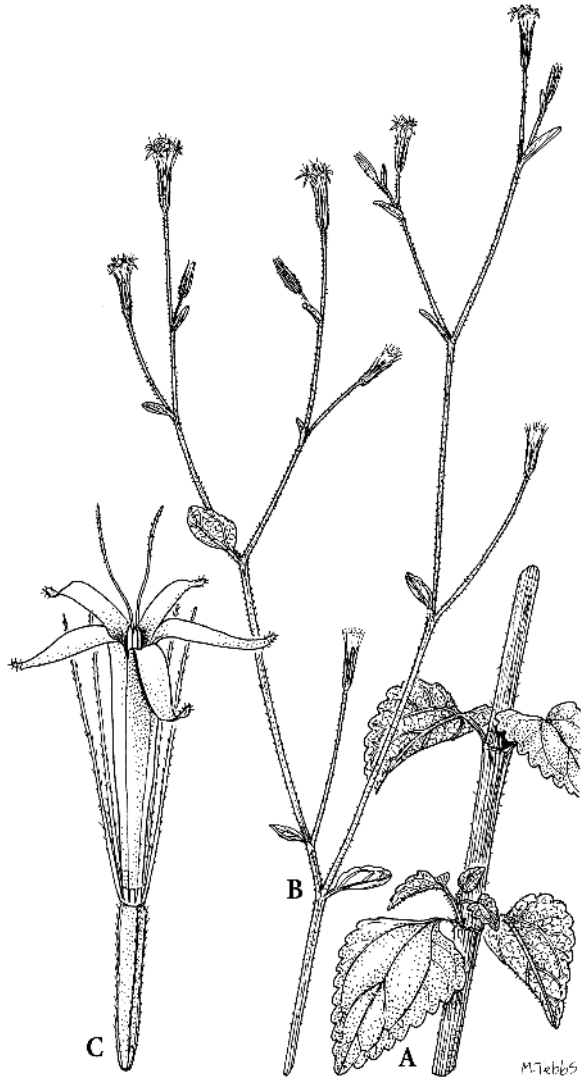

Fig. 109. Compositae-Eupatorieae. *Stevia morii* (Ageratinae). **A** Leafy basal portion of stem. **B** Part of inflorescence. **C** Floret. (Drawings by Margaret Tebbs)

1476. *Stevia* Cav. Fig. 109

Stevia Cav., Icon. 4: 32 (1797).

Mostly erect, annual or perennial herbs or shrubs. Leaves opposite or in some species alternate, lamina linear to orbicular, entire to serrate or dentate, rarely deeply lobed. Inflorescence diffuse or dense corymbose clusters on tips of branches. Involucres cylindrical, rarely funnelform, narrow at base; phyllaries uniseriate, 5, distant, equal to subequal, linear to elliptical; receptacle flat to slightly convex, glabrous. Florets 5; corollas white or lavender to purple, basal and distal parts sometimes of different colour, narrowly funnelform below lobes or with somewhat expanded throat, usually with hairs or glands on outer surface, with erect hairs on inner surface of throat; corolla lobes triangular or oblong-ovate, densely papillose on inner surface, smooth on outer surface, usually less than 2 mm long, unequal and zygomorphic in series *Podocephalae*, equal in others, longest lobes shorter than throat and tube; anther collar cylindrical or broadened below; style base often slightly enlarged, glabrous or in a few species papillose, arms filiform, densely long-papillose. Achenes narrowly fusiform to narrowly prismatic, strongly 5-ribbed, with few to many glands or setulae; carpopodium distinct, short; pappus at least a crown of free or united scales, often with 1–30 bristle-like awns, 1 or 2 achenes in each head often with more reduced pappus. n = 11, 12, 17. Circa 175–230 species, from USA

and Mexico south to Central (excluding the West Indies) and South America.

A difficult genus with an inadequate infrageneric division. Robinson's original treatments (Robinson 1930a, b, c, d, 1931a, b, c, 1932a, b) cover much of the distribution of the genus, with the exception of the Brazilian species. A number of more recent regional treatments (Argentina: Ariza Espinar and Cerana 1986; Cabrera and Freire 1997; Mexico: McVaugh 1984; Turner 1997; North America: Grashoff 1974) have been supplemented by the addition of many new species. A modern revision is certainly needed to adequately document the problems of hybridization and apomixis in the genus.

1477. *Metastevia* Grashoff

Metastevia Grashoff, Brittonia 27: 69 (1975).

Erect perennial herbs. Leaves opposite, basal pairs very small, lamina ovate, crenate to serrate, acute to obtuse. Inflorescence a lax panicle. Involucre narrowly campanulate, broad at base; phyllaries ± biseriate, 4–6, distant, equal to subequal, ovate-oblong; receptacle slightly convex, alveolate. Florets 4–6; corollas white, with narrow basal tube, expanding into narrowly campanulate throat, sparsely pubescent on inner surface of throat; corolla lobes more than 2.5 times longer than wide, 2–2.5 mm long, longest equal to throat and tube, sometimes zygomorphic with outer lobes longer, inner surface densely papillose, outer mostly glabrous, with a few papillae at tips; anther collar rather short; style base enlarged, glabrous, arms filiform, densely long-papillose. Achenes obconical, 5-ribbed, glabrous; carpopodium distinct, short; pappus absent. One species, *M. hintonii* Grashoff, Mexico.

1478. *Carphochaete* A. Gray

Carphochaete A. Gray, Mem. Amer. Acad. n.s. 4: 65 (1849).

Erect perennial herbs or small shrubs. Leaves opposite, lamina linear to elliptical-spathulate. Inflorescence single-headed or a loose corymbose cyme. Phyllaries c. 6, 2–4-seriate, distant to subimbricate, unequal to subequal, persistent, elliptical to oblong-lanceolate; receptacle flat to slightly convex, glabrous. Florets 4–6; corollas white, pink or purple, tubular below with narrowly funnelform throat, glabrous; lobes c. 2–3 times as long as wide, densely papillose on inner surface, smooth or nearly smooth on outer surface; anther collar expanded below; style base bulbous, glabrous, arms filiform, densely papillose, terete to slightly compressed. Achenes narrowly prismatic, 5–10-ribbed, ribs setuliferous; carpopodium distinct; pappus of 5–10 awns, longer than corolla, sometimes with a few shorter squamellae. $n = 11$. Circa 7 or 8 species, Mexico, USA.

Turner (1987b) treated *Carphochaete* in a broad sense and included the monotypic *Cronquistia* and *Revealia*.

1479. *Cronquistia* R.M. King

Cronquistia R.M. King, Brittonia 20: 11 (1968).

Erect perennial herbs. Leaves mostly opposite, often alternate above, lamina linear to oblong, entire. Inflorescence laxly corymbose. Phyllaries 10–15, distant, 1–2-seriate, equal or subequal, persistent, elliptical; receptacles flat to slightly convex, glabrous. Florets (5–)7–8(–12); corollas purplish, narrowly funnelform, with few glandular punctae outside, inner surface glabrous; lobes c. 3 times as long as wide, inner surface densely papillose, outer rather smooth; anther collar short; style base not enlarged, glabrous, arms distinctly flattened and somewhat long-clavate, densely short-papillose. Achene prismatic, 8–l0-ribbed, ribs setuliferous; carpopodium a narrow basal rim; pappus of a few winged awns or squamellae, or absent. $n = 12$. One species, *C. pringlei* (S. Watson) R.M. King, Mexico.

1480. *Revealia* R.M. King & H. Rob.

Revealia R.M. King & H. Rob., Phytologia 33: 277 (1976).

Spreading and often procumbent shrubs. Leaves opposite, lamina narrowly oblong, entire to obscurely crenulate-serrate, rather fleshy. Inflorescence usually of single capitula on short leafy branches. Phyllaries c. 10, distant, biseriate, equal to subequal, persistent; receptacle flat to slightly convex, glabrous. Florets c. 10; corollas purple, narrowly funnelform, with numerous small short-stalked glands on outer surface, upper throat short-pilose with numerous often septate hairs; lobes oblong, outer three lobes longer, densely papillose on inner surface, nearly smooth on outer surface; anther collar very short; style base with distinct enlargement, glabrous, arms filiform, terete, densely papillose. Achenes prismatic, 5-ribbed, ribs with minute setulae; carpopodium distinct, forming a narrow basal rim; pappus short, coroniform with many short squamellae. One species, *R. macrocephala* (Paray) R.M. King & H. Rob., Mexico.

1481. *Macvaughiella* R.M. King & H. Rob.

Macvaughiella R.M. King & H. Rob., Sida 3: 282 (1968).

Erect perennial herbs or small shrubs. Leaves opposite, lamina deltoid to rhomboid, serrate to dentate, short-acute to narrowly acuminate. Inflorescence densely corymbose. Phyllaries c. 10, distant, ± biseriate, equal to subequal, persistent; receptacle convex, glabrous. Florets 16–25; corollas white, with a narrow basal tube expanding into a narrowly campanulate throat, with several reddish glandular punctae on outer surface; lobes slightly longer than wide, inner surface densely papillose, outer only slightly roughened, with many uniseriate nonglandular hairs; anther collar elongate; style base not enlarged, glabrous, arms filiform, densely papillose, bearing numerous reddish glandular punctations. Achenes compressed, 2-angled, setuliferous; carpopodium distinct, slightly asymmetrical; pappus setae 2, rarely 1 or 3–4, coarsely barbellate, apical cells acute. n = c. 13. Two species, Mexico, Guatemala, El Salvador, Honduras.

1482. *Microspermum* Lag.

Microspermum Lag., Gen. Sp. Pl.: 25 (1816); Rzedowski, Bol. Soc. Bot. Mex. 32: 77–86 (1972), key.

Annual or perennial herbs. Leaves opposite, lamina lanceolate to rhomboid-ovate, serrate, obtuse to rounded. Capitula solitary or in lax cymose to corymbose panicles. Phyllaries 6–18, distant, ± biseriate, subequal, persistent, receptacle convex to low-conical, glabrous. Florets 8–25; corollas white, with narrow basal tube expanding rather abruptly into campanulate throat, glandular-punctate on outer surface; lobes 5, triangular, in peripheral zygomorphic corollas outer 3 lobes greatly expanded and oblong, partly fused at base, rather ray-like, densely papillose on inner surface, nearly smooth on outer surface; anther collar cylindrical; style base not enlarged, glabrous, arms rather short, linear, densely papillose. Achenes prismatic (4–)5(–7)-ribbed, setuliferous and glanduliferous; carpopodium distinct; pappus setae 0–4, coarsely barbellate, apical cells acute. n = 12. Seven species, Mexico.

1483. *Iltisia* S.F. Blake

Iltisia S.F. Blake, J. Wash. Acad. Sci. 47: 409 (1958).

Decumbent, annual or short-lived perennial herbs, striate, short-pilose, rooting at lower nodes. Leaves opposite, lamina orbicular to broadly ovate, crenate-serrate with 1 or 2 coarse teeth on each side, obtuse to rounded. Inflorescence cymose, with 3–7 capitula. Phyllaries 5–10, distant, biseriate, equal, persistent; receptacle slightly convex, glabrous. Florets c. 30; corollas white, with narrow basal tube, expanding into broadly campanulate throat, with a few glands externally; lobes (3–)4(–5), slightly wider than long, sometimes with 2 outer lobes of marginal florets enlarged, densely papillose on inner surface, scarcely mamillose on outer surface near apices; anther collar cylindrical; style base not enlarged, glabrous, arms short, appendages lanceolate, densely short-papillose, acute. Achenes prismatic, usually 4-ribbed, glabrous; carpopodium distinct, forming a narrow projecting rim; pappus absent. Two species, Costa Rica, Panama.

XXX.8. Subtribe Eupatoriinae Dumort. (1827).

Annual or perennial herbs and subshrubs, usually erect; leaves mostly opposite or whorled, alternate above. Inflorescence terminal, usually corymbose or pyramidal. Capitula short-pedicellate or sessile; phyllaries subimbricate, often broadly scarious or sclerified; receptacle scarcely convex, glabrous. Florets 3–23; corolla lobes smooth on inner surface; style base with hairs, usually without a basal node; arms usually without apical enlargement (enlarged in some *Stomatanthes*), densely short-papillose except on enlargements. Achenes 5-angled, glabrous; carpopodium obsolete to enlarged; pappus setae numerous, capillary.

Key to the Genera

1. Achene body setuliferous 2
– Achene body only with glands 3
2. Inflorescence pyramidal or thyrsoid (if corymbose, plants African) **1486. *Stomatanthes***
– Inflorescence corymbose **1487. *Hatschbachiella***
3. Carpopodium indistinct or absent. Widespread, but not present in South America **1484. *Eupatorium***
– Carpopodium large and distinct; South America **1485. *Austroeupatorium***

Genera of Eupatoriinae

1484. *Eupatorium* L.

Eupatorium L., Sp. Pl.: 836 (1753); Lamont, Mem. New York Bot. Gard. 72: 1–68 (1995), part. rev.
Eupatoriadelphus R.M. King & H. Rob. (1970).

Annual to perennial herbs. Leaves opposite or verticillate, upper subopposite to alternate, lamina linear to ovate, deltoid or trilobed, serrate to subentire. Capitula in a corymbose or pyramidal panicle. Phyllaries 10–22, weakly to strongly subimbricate, 2–5-seriate, sometimes inner deciduous; receptacle flat or weakly convex. Florets 3–23; corollas white to purple, lavender or pink, narrowly funnelform or with constricted basal tube and narrowly to broadly campanulate limb, outer surface with glands often concentrated at base of throat and on outer surfaces of lobes, rarely with a few hairs; lobes usually slightly longer than wide; anther collar cylindrical; apical anther appendages large, ovate-triangular, c. 1.5 times as long as wide; style base puberulous or rarely glabrous, with or without enlargement; arms filiform to slightly broadened or flattened distally, papillose. Achenes prismatic, 5-ribbed; carpopodium not or slightly differentiated; pappus setae 25–40, barbellate, persistent, apical cells with rounded to short-acute tips. n = 10, 15, 20. Forty-five species, Eurasia, North America.

The results of the studies by Schmidt and Schilling (2000) and those of Ito et al. (2000b) are in conflict as to the re-recognition of *Eupatoriadelphus*. Schmidt and Schilling (2000) favour a distinct *Eupatoriadelphus* (= the '*Eutrochium* group') whereas Ito et al. (2000b) imply that *Eupatorium* s.s. can be divided into three 'morphological species groups', one of which is the '*Eutrochium* group'.

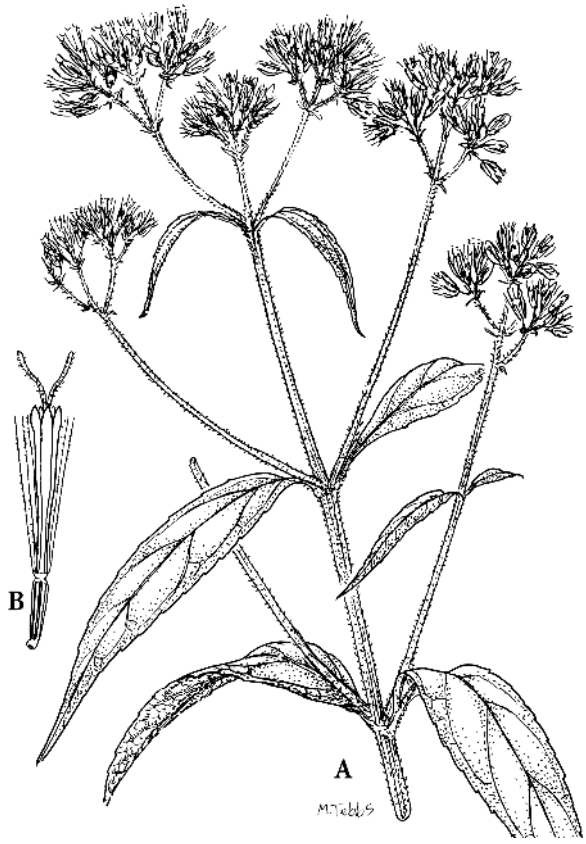

Fig. 110. Compositae-Eupatorieae. *Austroeupatorium inulifolium* (Eupatoriinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

1485. *Austroeupatorium* R.M. King & H. Rob.

Fig. 110

Austroeupatorium R.M. King & H. Rob., Phytologia 19: 433 (1970).

Eupatorium L. sect. *Austroeupatorium* (R.M. King & H. Rob.) Cabrera (1991).

Erect herbs or subshrubs. Leaves opposite below, often subopposite or alternate above, lamina ovate to narrowly oblong, usually crenulate to serrulate. Capitula in a flattened corymbose panicle. Phyllaries c. 12–18, 2–3-seriate, mostly unequal; receptacle flat or slightly convex. Florets 9–23, fragrant; corollas white, rarely lilac, narrowly funnelform with rather narrow tube, glands on outer surface; lobes c. 1.5 times as long as wide, without stomata; lower part of filaments slender and flexuous; anther collar narrowly cylindrical; apical anther appendages ovate-oblong, longer than wide, style base not enlarged, densely puberulous; style filiform. Achenes prismatic, 5-ribbed; carpopodium distinct; pappus setae 30–40, slender, barbellate, persistent, apical cells often enlarged, with rounded tips. n = 10. Thirteen species, southern South America, one species adventive in palaeotropics.

1486. *Stomatanthes* R.M. King & H. Rob.

Stomatanthes R.M. King & H. Rob., Phytologia 19: 430 (1970); Robinson, Phytologia 20: 334–337 (1970), reg. rev.

Perennial herbs or subshrubs. Leaves alternate, opposite or ternate, lamina elliptical or oblanceolate to ovate or orbicular, entire to markedly dentate. Inflorescence usually pyramidal to thyrsoid-particulate, sometimes corymbose. Phyllaries 4–12, distant to weakly subimbricate, 2–3-seriate, unequal to subequal; receptacle scarcely convex. Florets 4–11; corollas white, funnelform or nearly tubular, glabrous or glanduliferous with few to many hairs outside; lobes as long as wide to nearly 1.5 times as long as wide; lower parts of filaments short, thick, straight; anther collars cylindrical;

apical anther appendages ovate or slightly shorter than wide; style base lacking basal node, covered with numerous hairs; arms linear to filiform or with clavate tips, papillose at least below, tips when greatly enlarged with smooth surfaces. Achenes prismatic, 5–8-ribbed; carpopodium usually distinct; pappus setae uniseriate, numerous, barbellate, persistent, apical cells with obtuse or acute tips. $n = 10$. Sixteen species, eastern, central and southern Africa, Brazil, Paraguay, Uruguay.

The results of nuclear ITS sequencing of *Eupatorium* s.l. by Schmidt and Schilling (2000) suggest that '*Stomatanthes* appeared to be more closely related to *Praxelinae* (*Chromolaena*) than it is to any member of the *Liatrinae–Eupatorium* clade'. This is not supported, however, by its morphology. It is retained here in the *Eupatoriinae*.

1487. *Hatschbachiella* R.M. King & H. Rob.

Hatschbachiella R.M. King & H. Rob., Phytologia 23: 393 (1972).

Eupatorium L. sect. *Gyptis* (Cass.) Cabrera (1991), p.p.

Erect herbs or subshrubs. Leaves opposite or alternate, lamina elliptical to narrowly elliptical, entire to remotely serrulate. Inflorescence diffuse, with corymbose panicles at tips of leafy branches. Phyllaries 12–15, weakly subimbricate, 2–3-seriate, unequal; receptacle flat. Florets 10–12; corollas white, narrowly funnelform with a narrow basal tube, glanduliferous on outer surface; lobes c. 1.5 times as long as wide, with or without hairs on outer surface; filaments in lower part slender and flexuous; anther collars cylindrical; apical anther appendages ovate, as long as or longer than wide; style base not or slightly enlarged, with a few hairs; arms linear to narrowly clavate, distinctly papillose. Achenes prismatic, 5-ribbed, sometimes stipitate below; carpopodium distinct; pappus setae c. 30–40, barbellate, persistent, with slender tips, apical cells acute. $n = 10$. Two species, Argentina, Brazil, Paraguay, Uruguay.

XXX.9. Subtribe Liatrinae R.M. King & H. Rob. (1980).

Erect perennial herbs with rosulate basal leaves at least in early stages, or small shrubs. Leaves alternate. Inflorescence terminal on stems or branches, thyrsoid or corymbose to pseudospicate, capitula clustered, sessile or pedicellate; phyllaries few-(2–5)seriate, usually distinctly subimbricate, gradate, persistent; receptacle flat or slightly convex, epaleaceous or with a few paleae, glabrous. Florets 4–80; corollas funnelform; lobes shortly triangular to linear-oblong, mammillose or papillose inside; apical anther appendages slightly wider than long to longer than wide, often truncate or retuse at tip, style base not enlarged, glabrous; arms filiform or linear, not or scarcely broadened above, densely mamillose or short-papillose. Achenes prismatic, usually 8–10-ribbed, rarely 5-ribbed, usually setuliferous with setulae divided nearly to base, with only glands in *Hartwrightia*; carpopodium indistinct; pappus of many, capillary, barbellate to plumose, 1–3-seriate setae, with pointed apical cells, or lacking.

Schilling and Cox (2001) have provided an analysis of DNA sequence data which was used as the basis for the arrangement of genera in the present account.

Key to the Genera

1. Pappus absent; achenes 5-ribbed, glanduliferous, setulae absent **1493. *Hartwrightia***
– Pappus of capillary setae; achenes 8–10-ribbed, setulae few to many 2
2. Shrubs; leaves of mature stems not or scarcely reduced in size in upper parts; pappus setae 60–70, barbellate, outer series shorter and more slender **1488. *Garberia***
– Erect perennial herbs with basal rosettes (at least, initially) and reduced upper leaves; pappus setae 12–40, barbellate or subplumose to plumose 3
3. Pappus setae plumose or subplumose; inflorescence spiciform or racemose; receptacles epaleaceous; corollas often pubescent inside, corolla lobes narrowly lanceolate to linear-oblong; plants with corm-like or deeply penetrating root systems **1489. *Liatris***
– Pappus setae barbellate; inflorescence corymbose or thyrsoid; receptacles paleaceous (paleae often few); corollas glabrous inside, corolla lobes triangular to oblong; plants with fibrous roots 4
4. Pappus setae uniseriate; apical anther appendages obtuse to rounded **1491. *Trilisia***
– Pappus setae ± biseriate; apical anther appendages distinctly retuse 5
5. Phyllaries 15–40, distinctly imbricate, 3–4-seriate; achenes densely setuliferous; florets 12–35 **1490. *Carphephorus***
– Phyllaries 5–10, loosely overlapping, 2–3-seriate; achenes sparsely short-setuliferous, moderately to densely glandular-punctate; florets 5–10 **1492. *Litrisa***

Genera of Liatrinae

1488. *Garberia* A. Gray

Garberia A. Gray, Proc. Acad. Nat. Sci. Philadelphia 1879: 379 (1879).

Small erect shrubs, glandular-punctate. Leaves initially rosulate at base, lamina viscid, spathulate to spathulate-obovate or rounded-obovate, entire, often slightly retuse. Inflorescence a corymbose panicle. Phyllaries c. 15, subimbricate, c. 3-seriate, markedly unequal; receptacle slightly convex, epaleaceous. Florets 5; corollas pink to purplish, narrowly funnelform with slightly campanulate throat, glabrous on both surfaces; lobes 4–5 times as long as wide, longer than throat; inner surface densely and rather antrorsely short-papillose, outer surface smooth; anther collars short-cylindrical; apical anther appendages large, slightly longer than wide, somewhat retuse at tips; style arms long-linear, densely short-papillose. Achenes prismatic, c. 10-ribbed, densely setuliferous; carpopodium lacking; pappus setae c. 60–70, 2–3-seriate, basally barbellate and distally scabrid, persistent, outer setae somewhat shorter and narrower, apical cells acute. $n = 10$. One species, *G. heterophylla* (Bartram) Merr. & F. Harper, USA.

1489. *Liatris* Gaertn. ex Schreber

Liatris Gaertn. ex Schreber, Gen. Pl. 7: 542 (1791), nom. cons.; Gaiser, Rhodora 48: 165–183, 216–263, 273–326, 331–382, 393–412 (1946), rev.; Nesom, Sida 21, 3: 1305–1321 (2005), rev.

Erect perennial herbs. Leaf lamina linear, elliptic or oblanceolate, entire. Inflorescence cymose, usually spiciform or racemiform. Phyllaries c. 20–25, subimbricate, 3–5-seriate, mostly persistent; receptacle nearly flat, epaleaceous. Florets 3–80; corollas usually purple, sometimes lavender or white, broadly to narrowly funnelform, usually glandular-punctate on outer surface and rarely with uniseriate hairs, inner surface often with hairs near insertion of filaments or on lobes; corolla lobes linear-lanceolate to linear-oblong, c. 3–4 times as long as wide, densely mamillose or short-papillose on at least distal part of inner surface, smooth on outer surface, anther collars broadly cylindrical or slightly broadened below; apical anther appendages usually oblong-ovate and as long as wide or short and obsolete; style arms narrowly linear to scarcely broadened distally, flattened, densely mamillose, often with glands on inner surface or with septate hairs on upper shaft and abaxially on lower half of arms. Achenes prismatic, c.10-ribbed, densely setuliferous; carpopodium lacking; pappus setae c. 12–40, 1–2-seriate, plumose or markedly barbellate, persistent, barbellate and fimbriate on both lateral and outer surfaces, apical cells acute. $n = 10, 20, 30$. Forty-one species and several hybrids, Canada, Mexico, USA. Five sections are recognized (Nesom 2005). Many species cultivated.

1490. *Carphephorus* Cass.

Carphephorus Cass., Bull. Soc. Philom. Paris 1816: 198 (1816); Correa & Wilbur, J. Elisha Mitchell Sci. Soc. 85: 79–91 (1969), rev.; Cronquist, Vasc. Fl. SE U.S. 1: i–xvi, 1–261 (1980), rev.

Erect, scapose, perennial herbs. Leaf lamina linear to linear-lanceolate or oblanceolate, entire. Inflorescence an open flat-topped corymbose cyme. Phyllaries c. 15–40, distinctly subimbricate, c. 3–5-seriate, markedly unequal, mostly or totally persistent; receptacle slightly convex, usually with a few paleae. Florets c. 12–35, fragrant; corollas lavender to purple, funnelform or with narrowly campanulate throat, usually with glands on outer surface, or glabrous, glabrous on inner surface; lobes c. 1.5–2.5 times as long as wide, densely short-papillose on inner surface, smooth on outer surface; anther collars short-cylindrical, slightly constricted above; apical anther appendages medium-sized to large, ovate-oblong, as long as wide, distinctly retuse at tip; style narrowly linear, rather densely high-mamillose or short-papillose. Achenes prismatic, c. 10-ribbed, moderately to densely setuliferous and often with glands; carpopodium lacking; pappus setae c. 35–40, 2–3-seriate, barbellate (sometimes coarsely so), somewhat unequal, congested, apical cells acute. $n = 10$. Four species, USA.

1491. *Trilisa* (Cass.) Cass.

Trilisa (Cass.) Cass., Dict. Sci. Nat. 26: 228 (1827); Small, Fl. SE U.S.: 1170–1171 (1903), key.

Erect perennial herbs. Leaves sometimes extremely aromatic, lamina oblanceolate to obovate or rather narrowly elliptic, somewhat succulent, entire or coarsely few-dentate, obtuse to short-acute. Inflorescence cymose, corymbose or thyrsoid in form. Phyllaries c. 6–12, distant to weakly subimbricate, c. 2-seriate, slightly unequal to subequal, inner not deciduous; receptacle slightly convex, usually epaleaceous, or with 1 or 2 paleae. Florets 4–10(–15); corollas pink to purplish, narrowly funnelform, with numerous glands on outer surface, glabrous inside; lobes c. 1.25–1.5 times as long as wide, densely short-papillose on inner surface; anther collar cylindrical; apical anther appendages large, slightly longer than wide,

rounded to scarcely retuse at tip; style arms filiform, densely short-papillose. Achenes prismatic, c. 8-ribbed; carpopodium lacking; pappus setae usually uniseriate, c. 3–5, persistent, barbellate, with narrower setae sometimes between and slightly outside of larger setae, apical cells acute. $n = 10$. Two species, USA.

1492. *Litrisa* Small

Litrisa Small, Bull. Torrey Bot. Club 51: 392 (1924).

Erect, perennial herbs. Leaf lamina somewhat fleshy, oblanceolate, entire, narrowly acute to acuminate. Inflorescence a flat-topped corymbose cyme. Phyllaries 5–10, weakly subimbricate, 2–3-seriate, somewhat unequal, mostly persistent, with hairs and glands on outer surface; receptacle slightly convex, usually glabrous or with 1 or 2 paleae. Florets 5–10; corollas purple, narrowly funnelform, with a few glands on outer surface, glabrous inside; lobes c. 1.5 times as long as wide, inner surface mamillose, outer surface with numerous glands and some hairs; anther collars short-cylindrical, somewhat narrowed above; apical anther appendages large, ovate, as long as wide, retuse at tip; style arms narrowly linear, densely short-papillose, without glands or hairs. Achenes prismatic, 8–10-ribbed, setuliferous and glandular; carpopodium lacking; pappus setae c. 35, barbellate, persistent, c. 2-seriate, apical cells acute. $n = 10$. One species, *L. carnosa* Small, USA.

1493. *Hartwrightia* A. Gray ex S. Watson

Hartwrightia A. Gray ex S. Watson, Proc. Amer. Acad. Arts 23: 764 (1888).

Erect perennial herbs. Leaf lamina elliptic-oblanceolate to elliptical, usually entire, rarely with a large tooth or small lobe. Inflorescence an open corymbose often flat-topped cyme. Phyllaries c. 12–15, essentially distant, mostly subequal, persistent; receptacle slightly convex, often with a few phyllaries inside outermost florets. Florets 7–10; corollas pink, blue or white, broadly funnelform, with short and rather indistinct basal tube, with broad and slightly campanulate throat, glandular punctae numerous on outer surface; lobes about as long as wide or slightly longer, densely short-papillose on inner surface, slightly mamillose outside near margins; anther collar short-cylindrical; apical anther appendages oblong, slightly wider than long, truncate or retuse apically, with median groove adaxially; style arms short, linear, densely short-papillose. Achenes prismatic to obpyramidal, 5-ribbed, glanduliferous, lacking setulae; carpopodium lacking; pappus usually lacking, rarely a single hair-like glanduliferous seta. $n = 10$. One species, *H. floridana* A. Gray ex S. Watson, USA.

XXX.10. Subtribe Praxeliinae R.M. King & H. Rob. (1980).

Erect to subscandent, annual to perennial herbs or subshrubs. Leaves mostly opposite, lamina entire to serrate, sometimes dissected, ovate or oblong to linear. Inflorescence laxly cymose to thyrsoid-paniculate, rarely monocephalic on long erect pedicels, phyllaries imbricate, totally deciduous; receptacle slightly convex to highly conical, with or without paleae. Florets 5–65; corollas white, blue, lavender or purple, peripheral florets sometimes with enlarged outer lobes; lobes usually longer than wide, usually densely papillose on inner surface; anther collar usually 5 times as long as wide, usually distinctly broadened in lower half; apical anther appendages usually longer than wide, sometimes shorter, or obsolete; style base usually not enlarged, glabrous; arms usually narrowly linear and densely papillose. Achenes biconvex to trigonous or prismatic, 2–5-ribbed; carpopodium usually distinct; pappus setae uniseriate, usually numerous, capillary, barbellate, sometimes only 5–8, with or without intermixed smaller setae, or pappus reduced to fringe of short unequal setae, apical cells usually sharply acute.

Key to the Genera

1. Achene compressed and with 2 marginal ribs — 2
– Achene usually prismatic, usually 5-ribbed — 3
2. Pappus of 5 long equal setae; marginal florets zygomorpic with longer outer lobes; ribs densely long-setuliferous — **1499. *Eitenia***
– Pappus of short unequal barbellate setae; florets all actinomorphic; ribs sparsely short-setuliferous — **1496. *Eupatoriopsis***
3. Pappus setae 5; corolla lobes spreading and appearing salverform — **1498. *Praxeliopsis***
– Pappus setae numerous, usually long and capillary, rarely short and unequal; corolla lobes erect or ascending — 4
4. Pappus setae short and unequal — **1497. *Lomatozona***
– Pappus setae long and equal or subequal — 5
5. Receptacle conical — **1494. *Praxelis***
– Receptacle flat to slightly convex — 6
6. Style arms linear; pappus setae scarcely broadened or tapering; apical anther appendages large and usually much longer than wide — **1495. *Chromolaena***

– Style arms broadened towards apices; pappus setae somewhat broadened at apices; anther appendages shorter than wide **1500. *Osmiopsis***

Genera of Praxeliinae

1494. *Praxelis* Cass.

Praxelis Cass., Dict. Sci. Nat. 43: 261 (1826).
Eupatorium sect. *Praxelis* (Cass.) Benth. ex Baker (1876).

Erect to decumbent annual or perennial herbs or subshrubs. Leaves opposite or whorled, lamina ovate to elliptical or filiform, subentire to sharply serrate. Capitula solitary on long erect peduncles to laxly thyrsoid or rather densely corymbose, usually campanulate. Phyllaries 15–25, 3–4-seriate, unequal, gradate, outer falling first; receptacle highly conical, glabrous. Florets 25–30; corollas white, blue or lavender, narrowly funnelform or with cylindrical throat and slightly narrower basal tube, outer surface mostly smooth, with a few glands; lobes 1.5–3 times as long as wide, densely long-papillose on inner surface, usually with some projecting cells on outer surface at tip; anther collars with enlarged bases, narrowed above; apical anther appendages slightly longer than wide to distinctly longer than wide, often toothed at tip; style base not enlarged; arms long, narrowly linear, more broadened in distal half, densely long-papillose. Achenes slightly to strongly obcompressed, 3–4-ribbed, sparsely setuliferous; carpopodium distinct, broad, highly asymmetrical; pappus setae c. 40, persistent, not or scarcely broadened distally. $2n$ = 30, 48, 51, c. 80. Sixteen species, South America, one species adventive in Asia and Australia.

1495. *Chromolaena* DC. Fig. 111

Chromolaena DC., Prodr. 5: 133 (1836).
Eupatorium sect. *Cylindrocephala* DC. (1836).
Eupatorium sect. *Osmia* (Sch. Bip.) Benth. ex Baker (1876).
Eupatorium sect. *Chromolaena* (DC.) Benth. ex Baker (1876).

Erect to somewhat scandent perennial herbs, subshrubs or shrubs. Leaves usually opposite, lamina mostly ovate or triangular to elliptical, sometimes linear, subentire to lobed. Capitula usually thyrsoid to candelabriform or on laxly to densely corymbose branches, rarely solitary on long erect peduncles. Phyllaries 18–65, 4–6-seriate, markedly unequal, gradate, often with expanded herbaceous or coloured tips; receptacle flat to slightly convex, glabrous, sometimes paleaceous. Florets 6–75; corollas white, blue, lavender or purple, rather cylindrical with scarcely narrower base, outer surface smooth below lobes, with few to many short-stalked glands, often with rather stiff hairs; lobes slightly to distinctly longer than wide; usually densely papillose on inner surface, or smooth (subgenus *Osmiella* R.M. King & H. Rob.); anther collars usually broader below, narrowed above, or not broadened below (subgenus *Osmiella*); apical anther appendages large, oblong, c. 1.5 times as long as wide, entire or crenulate at tip; style base not enlarged; arms narrowly linear to slightly broadened distally, slightly mamillose to densely long-papillose. Achenes prismatic, (3–)5-ribbed, with setulae mostly on ribs; carpopodium distinct, short-cylindrical or narrowed below; pappus setae c. 40, slender, persistent, not

Fig. 111. Compositae-Eupatorieae. *Chromolaena morii* (Praxelinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

or scarcely broadened distally. n = 10, 20, 29, c. 40, 50. Circa 165 species, New World tropics and subtropics, one species a pantropical weed.

King and Robinson (1987) noted two subgenera and provided characters in their generic description to separate species of subgenus *Osmiella*. Concern is growing in many tropical countries over the alarming spread of the weed *Chromolaena odorata* (e.g. Zachariades et al. 2002). The taxonomy and distribution of this species has been well documented by Gautier (1992).

1496. *Eupatoriopsis* Hieron.

Eupatoriopsis Hieron., Bot. Jahrb. Syst. 18 (Beibl. 43): 46 (1893).

Erect annual herbs. Leaves opposite, lamina ovate to rather elliptical, serrate, short-acute. Inflorescence laxly cymose. Phyllaries c. 12–14, weakly subimbricate, c. 1–2-seriate, slightly unequal to subequal, mostly membranaceous or scarious, outer somewhat persistent; receptacle very highly conical to columnar, glabrous. Florets c. 30; corollas lilac, short-funnelform, with very short basal tube, glabrous on outer surface below lobes; corolla lobes broadly triangular, about as long as wide, tips and inner surface densely long-papillose, outer surface with glands; anther collars expanded below, narrower above; apical anther appendages narrower than thecae, subquadrate; style base not enlarged; arms narrowly linear, slightly broadened in distal half, densely papillose. Achenes broadly obcompressed, slightly obcordate, usually with 2 distinctly setuliferous ribs; carpopodium distinct, asymmetrical; pappus setae uniseriate, c. 18–20, very short, unequal, persistent. One species, *E. hoffmanniana* Hieron., Brazil.

1497. *Lomatozona* Baker

Lomatozona Baker in Mart., Fl. Brasil. 6, 2: 198 (1876); King & Robinson, Phytologia 44: 455–462 (1979), key.

Erect perennial herbs or subshrubs, covered with minute stipitate glands. Leaves opposite, lobed to deeply dissected, lower surface with very large sessile globular glands. Inflorescence laxly cymose. Phyllaries c. 25, markedly imbricate, c. 3–4-seriate, markedly unequal, gradate; receptacle slightly convex, with or without paleae. Florets 10–27; corollas white or bluish, narrowly funnelform, with occasional glands on outer surface; corolla lobes triangular to rather oblong, up to 1.5 times longer than wide, densely papillose on inner surface, or outer lobes of peripheral florets longer; anther collars short, slightly broader below; apical anther appendages large, oblong-ovate, longer than wide; style base not enlarged; arms filiform, densely papillose. Achenes prismatic, mostly 5-ribbed, setuliferous; carpopodium lacking or poorly developed; pappus setae uniseriate, 15–22, short, unequal, persistent, barbellate. Four species, Brazil.

1498. *Praxeliopsis* G.M. Barroso

Praxeliopsis G.M. Barroso, Arch. Jard. Bot. Rio de Janeiro 9: 176 (1949).

Erect annual (or possibly short-lived perennial) herbs, essentially glabrous. Leaves alternate, sessile, linear, entire. Inflorescence laxly cymose, pedicels very long. Phyllaries c. 20–25, imbricate, c. 3-seriate, markedly unequal; receptacle conical, glabrous. Florets c. 16; corollas lilac, hypocrateriform, with elongate narrowly funnelform basal tube, glabrous on both surfaces; throat very short and spreading; lobes unequal, 1.5–3 times as long as wide, densely papillose on inner surface; anthers borne slightly below bases of lobes, exserted above the spreading lobes; anther collars short and broad, broader below; apical anther appendages rudimentary or lacking; style base enlarged; arms filiform, densely papillose. Achenes prismatic, 5-ribbed, with numerous long setulae mostly on ribs; carpopodium small, distinct, symmetrical; pappus setae 5, stout, coarsely barbellate, persistent, narrowed distally. One species, *P. mattogrossensis* G.M. Barroso, Brazil.

1499. *Eitenia* R.M. King & H. Rob.

Eitenia R.M. King & H. Rob., Phytologia 28: 282 (1974).

Erect annual or short-lived perennial herbs. Leaves opposite, lamina ovate, coarsely serrate to sublobate, acute. Inflorescence a rather lax broadly cymose panicle. Phyllaries c. 22–35, imbricate, 3–4-seriate, markedly unequal, lanceolate, outer falling first; receptacle highly conical, glabrous. Florets c. 40–50; corollas violet or white, narrowly funnelform, with long cylindrical throat; lobes strongly unequal, with outer lobes of peripheral florets much longer and wider, all lobes oblong, densely long-papillose on inner surface, long-papillose and with few glands on outer surface; anther collars distinctly broadened in lower part; apical anther appendages narrowly oblong, c. 1.5 times as long as wide; style base not enlarged; arms filiform, densely long-papillose. Achenes

obcompressed, usually with 2 or rarely 3 ribs, ribs densely long-setuliferous; carpopodium distinct, asymmetrical; pappus uniseriate, of usually 2–8 stout scabrid persistent setae, sometimes interspersed with weaker setae, narrowed distally. Two species, Brazil.

1500. *Osmiopsis* R.M. King & H. Rob.

Osmiopsis R.M. King & H. Rob., Phytologia 32: 250 (1975).

Weak scandent shrubs. Leaves opposite, lamina ovate to lanceolate often with lobed bases, upper margins entire. Capitula numerous, terminal on lateral branches, in small corymbose clusters. Phyllaries c. 20, imbricate, 4–5-seriate, markedly unequal, gradate, mostly broadly oblong; receptacle flat to slightly convex on distal surface, glabrous. Florets 18–26; corollas white, funnelform with a short, broadly cylindrical base, sparsely glandular on outer surface below lobes; lobes as long as wide to 1.5 times as long as wide, smooth on both surfaces, densely glandular on outer surface; anther collars slightly broader below; apical anther appendages semicircular, wider than long; style base not enlarged; style arms narrowly linear with slightly broadened tips, sharply short-papillose. Achenes short-prismatic, slightly narrowed below, 5-ribbed, with few glands and short setulae; carpopodium distinct, short-cylindrical; pappus uniseriate, setae c. 25–30, stout, persistent, somewhat broadened distally. One species, *O. plumerii* (Urban & Ekman) R.M. King & H. Rob., Haiti.

XXX.11. Subtribe Gyptidinae R.M. King & H. Rob. (1980).

Erect perennial herbs, subshrubs, shrubs or small trees; leaves opposite to spirally inserted, rarely rosulate (*Bishopiella*). Inflorescence terminal on leafy branches or rarely scapose. Capitula clustered; phyllaries distant to weakly subimbricate, persistent; receptacle scarcely convex to strongly conical, paleaceous or epaleaceous, glabrous or pubescent. Florets usually numerous, rarely fewer than 10 per capitulum; corolla lobes often papillose on inner surface; apical anther appendages very short to longer than wide, sometimes deeply cleft at apex; style base often not enlarged and glabrous, sometimes with enlarged node or pubescent or both; arms usually linear, usually densely mamillose or papillose. Achenes usually 5-ribbed or rarely winged; carpopodium distinct, indistinct or apparently absent; pappus usually of many capillary setae, sometimes very short, rarely lacking or reduced to 5 fragile setae, sometimes with enlarged round-tipped apical cells. The greatest concentration of genera is in Brazil, especially in Northeast Brazil.

Gyptidinae s.l., currently containing 29 genera, constitute a somewhat problematic subtribe and is, without doubt, polyphyletic. The only full account of Gyptidinae s.l. is that of King and Robinson (1987). Hind (1999, 2000) believes that there are at least three distinct groups of genera, each representing a separate subtribe – the '*Gyptis* group' (genera 1501–1519), the '*Agrianthus* group' (genera 1520–1527) and the '*Litothamnus* group' (genera 1528 & 1529). Some support for such division of the subtribe is provided by the phytochemical studies by Bohlmann et al. (1980a, b, 1981a, b, c, d, 1982a, b, 1984a, b).

Key to the Genera

1. Plants rosulate; inflorescence scapiform; leaves fleshy **1527. *Bishopiella***
– Plants with leafy stems, not rosulate; inflorescence corymbose, cymose, paniculate, or of solitary capitula, but never scapiform; leaves coriaceous or herbaceous, if fleshy, then plants trees 2
2. Pappus of plumose or markedly barbellate setae, or absent and corollas densely pubescent, pubescence obscuring lobes 3
– Pappus barbellate, rarely simple, if absent, then corollas lacking dense pubescence, or pubescence not obscuring lobes 4
3. Corollas densely pubescent on throat and lobes; stems distinctly ribbed; leaves sessile or with narrow petioles; apical anther appendages rounded **1510. *Trichogonia***
– Corollas glandular-punctate distally; stems scarcely striate; leaves with distinctly winged petioles; apical anther appendages deeply cleft **1511. *Trichogoniopsis***
4. Plants with leaves inserted in dense spiral; leaves not usually progressively smaller upwards 5
– Plants with often lax opposite, or occasionally alternate leaves; leaves decreasing markedly in size upwards on plants 13
5. Receptacle paleaceous; leaves scale-like, small, usually imbricate and with broad cuneate bases 6
– Receptacle epaleaceous; leaves usually medium to large, membranous or coriaceous, sometimes fleshy, spreading, usually with narrowed bases or distinct petioles, or if leaves small and scale-like, then imbricate 7
6. Phyllaries biseriate with inner shorter than outer, all deciduous; inflorescence overtopped by upper leaves; corollas glabrous; leaves lacking obvious secondary venation; stems glabrous; style arms linear-filiform; pappus absent **1521. *Catolesia***
– Phyllaries (2–)3–5-seriate, gradate with inner longer than outer, persistent; inflorescences overtopping

leaves; corollas glandular-punctate or stipitate-glandular (sometimes sparsely so); leaves with obvious prominent secondary venation; stems variously pubescent; style arms clavate; pappus of setae with pectinate to subplumose margins, rarely absent (and if so, capitula sessile to very shortly pedicellate) **1520. *Agrianthus***

7. Leaves small and scale-like, imbricate **1520. *Agrianthus***
– Leaves medium to large, membranous or coriaceous, or if small, then linear and closely adpressed to stem with long eglandular hairs or with long stipitate-glandular hairs 8
8. Leaves glabrous 9
– Leaves variously pubescent 10
9. Leaves fleshy; achenes setuliferous, at least below apical callus; phyllaries scarcely longer than achenes, corollas well exserted above involucre **1429. *Morithamnus***
– Leaves not fleshy; achenes completely glabrous; phyllaries considerably longer than achenes, corollas ± included within involucre **1523. *Bahianthus***
10. Leaves narrowly linear and closely adpressed to stem **1522. *Arrojadocharis***
– Leaves narrowly elliptic, ovate to obovate or oblanceolate 11
11. Achenes markedly winged; leaves stipitate-glandular and eglandular-pubescent **1524. *Semiria***
– Achenes ribbed; leaves eglandular-pubescent 12
12. Style shaft pubescent; corollas stipitate-glandular; apical anther appendages shorter than wide **1526. *Stylotrichium***
– Style shaft glabrous; corollas glandular-punctate; apical anther appendages as long as or longer than wide **1525. *Lasiolaena***
13. Leaves coriaceous, sometimes fleshy, glabrous, sessile to subsessile 14
– Leaves membranous, thin, glabrous or variously pubescent, petiolate 15
14. Leaves elliptical to obovate, glabrous, distinctly fleshy, usually stoutly petiolate; achenes 5-ribbed; plants large shrubs or smallish trees of wooded *restinga* or coastal dunes; NE Brazil (Bahia) **1528. *Litothamnus***
– Leaves orbicular or ovate, short-pubescent and distinctly glandular-punctate, very short-petiolate; achenes 7–10-ribbed; plants shrubby but never tree-like, of upland *campos*; southern and central Brazil **77. *Vittetia***
15. Achenes with stipitate or long-attenuate bases 16
– Achenes of ± uniform diameter or only slightly narrowed towards base 19
16. Pappus of short-laciniate or subplumose flattened setae about 1/2 to 2/3 length of corollas; style base pubescent **1512. *Platypodanthera***
– Pappus of long capillary barbellate setae at least as long as corollas; style base glabrous 17
17. Capitula large, florets 30–100; receptacle conical or highly convex; achene ribs pale; many species in Brazil, 1 species widespread in South America **1515. *Campuloclinium***
– Capitula small to medium, florets < 50; receptacle flat or slightly convex; achene ribs concolorous with body; Bolivia, southern Brazil, Paraguay, Peru 18
18. Inner phyllaries much shorter than florets; pedicels long; anther cylinder visible and usually partially exserted from corolla throat; style arms linear; style base lacking basal node; glandular punctae, when present, clear or light-coloured; southern Brazil, Paraguay **1516. *Macropodina***
– Inner phyllaries equalling or slightly shorter than florets; pedicels short; anther cylinder wholly obscured and included well within corolla throat; style arms clavate; style base with basal node; corolla lobes, phyllaries and underside of leaves with conspicuous, often dark, amber-coloured glandular punctae; Bolivia, Peru **1513. *Neocuatrecasia***
19. Carpopodium procurrent on base of achene ribs 20
– Carpopodium annular, short-cylindrical, stopper-shaped or indistinct or obsolete, but not procurrent on ribs 22
20. Achenes completely glabrous; corolla lobes pilose; apical anther appendages bilobed to emarginate, shorter than wide **1506. *Diacranthera***
– Achenes glandular-punctate or setuliferous; corolla lobes glandular-punctate; apical anther appendages entire, rounded to acute, as long as or longer than wide 21
21. Achenes setuliferous; style base with swollen basal node, pubescent **1505. *Dasycondylus***
– Achenes glandular-punctate; style base lacking basal node, glabrous **1504. *Barrosoa***
22. Pappus setae with blunt, sometimes inflated apices 23
– Pappus setae with acute apices 25
23. Phyllaries with distinct, pubescent appendages; carpopodium stopper-shaped; Argentina, Bolivia, southern Brazil, Paraguay, Uruguay **1503. *Urolepis***
– Phyllary apices attenuate or acute but never appendaged; carpopodium indistinct 24
24. Corollas markedly widening above a short tube; leaves ascending; Argentina and southern Brazil **1502. *Gyptidium***
– Corollas narrowly funnelform; leaves spreading; Mexico and USA (Texas) **1517. *Conoclinium***
25. Achenes glabrous, lacking glandular punctae or eglandular setulae 26
– Achenes setuliferous, sometimes sparsely so, with or without or glandular punctae 27
26. Corolla lobes glabrous outside; leaves glabrous, usually viscid; phyllaries ± biseriate and conspicuously shorter than florets; carpopodium essentially annular with 'crenulate' upper margin; leaves concolorous; plants of coastal dunes of Bahia, Brazil **1509. *Prolobus***
– Corolla lobes pubescent outside; leaves conspicuously discolorous and densely tomentose beneath; phyllaries 3–4-seriate and slightly shorter than florets; carpopodium stopper-shaped with distinct upper rim; leaves discolorous; plants of the paramos of the northern Andes (Colombia, Venezuela) **1519. *Lourteigia***
27. Phyllary apices densely pubescent and appearing expanded; corolla lobes with hairs on outer surface; leaf bases acute to acuminate; northern Argentina, southern Brazil, Paraguay, Uruguay **1501. *Gyptis***
– Phyllary apices attenuate or acute, not expanded; corolla lobes glabrous or scattered glandular-punctate on outer surface; leaf bases truncate 28
28. Leaf margins crenate; corollas lacking glandular punctae; florets 20–30; carpopodium with setuliferous up-

per margin; Brazil, Colombia, Venezuela **1507. *Conocliniopsis***

– Leaf margins serrate or biserrate; corollas glandular-punctate; florets ≤ 10, and pedicels uniform throughout, or 40–70, with pedicels enlarged and fistulose beneath involucre; upper margin of carpopodium lacking setulae and distinct or indistinct 29

29. Florets ≤ 10; pedicels short, but uniform throughout; carpopodium broadly stopper-shaped with distinct upper margin; Bolivia, Brazil, Paraguay **1508. *Bejaranoa***

– Florets 40–70; pedicels conspicuous, enlarged/swollen and fistulose distally/beneath involucre; carpopodium indistinct and not markedly delimited above; Mexico and southern USA **1518. *Tamaulipa***

XXX.11. a. Gyptis Group

1501. *Gyptis* (Cass.) Cass.

Gyptis (Cass.) Cass., Dict. Sci. Nat. 16: 10 (1820); King & Robinson, Phytologia 21: 22–25 (1971), key.
Eupatorium L. sect. *Gyptis* (Cass.) Cabrera (1991).

Perennial herbs. Leaves opposite, often becoming alternate above, lamina ovate to bipinnatifid, serrulate to deeply dissected. Inflorescence subscapose, usually densely corymbose or cymose above. Phyllaries 2–3-seriate, 16–25, weakly subimbricate, subequal, with apical pubescence; receptacle flat, glabrous. Florets 4–26; corollas narrowly funnelform, white, pink or violet; lobes about as long as wide or slightly longer, strongly papillose on both surfaces, with hairs and often glands on outer surface, margin often with 2-celled teeth, anther collars short-cylindrical, only slightly expanded below; apical anther appendages ovate, twice as long as wide, style base not enlarged, usually glabrous; arms narrowly linear to filiform, densely papillose. Achenes prismatic, 5-ribbed, surfaces densely setuliferous; carpopodium very short or vestigial; pappus setae uniseriate, c. 20–30, persistent, apical cells subacute or acute. $n = 10$. Seven species, Argentina, Brazil, Paraguay, Uruguay.

1502. *Gyptidium* R.M. King & H. Rob.

Gyptidium R.M. King & H. Rob., Phytologia 23: 310 (1972).

Erect annual herbs. Leaves opposite, sometimes alternate above, lamina ovate to lanceolate, crenulate. Inflorescence cymose to subcymose, capitula sessile to long-pedicellate. Phyllaries 2–3-seriate, c. 25, distant to weakly subimbricate, subequal, persistent; receptacle conical, hirsute or with narrow paleae. Florets 50–80; corollas white or pale lilac, with very narrow basal tube; throat narrowly campanulate, smooth on both surfaces; lobes not or only slightly longer than wide, outer surface mostly smooth, inner surface slightly to strongly papillose; anther collars elongate, narrow; apical anther appendages ovate, longer than wide; style base not enlarged, glabrous; arms linear, densely papillose with papillae 1–2 times as long as wide. Achenes prismatic, 4–5-ribbed, glanduliferous; carpopodium obsolete; pappus setae uniseriate, c. 28, persistent, apical cells with rounded and sometimes dilated tips. Two species, Argentina, Brazil.

1503. *Urolepis* (DC.) R.M. King & H. Rob.

Urolepis (DC.) R.M. King & H. Rob., Phytologia 21: 304 (1971).
Eupatorium sect. *Urolepis* (DC.) Benth. (1876).

Coarse, erect annual herbs or subshrubs. Leaves opposite, lamina broadly deltoid, dentate or denticulate. Inflorescence a corymbose or subcymose panicle. Phyllaries c. 50, weakly subimbricate, 3–4-seriate, equal or subequal, inner phyllaries attenuate into long densely pubescent appendage; receptacle subglobose, densely short-pubescent. Florets 100–150; corollas pink, with long narrow basal tube; throat funnelform below, becoming cylindrical above, with outer surface of tube and throat glabrous; lobes slightly longer than wide, with a few short-stalked glands externally, smooth on inner and outer surface, extreme tips of lobes papillose; anther collars slender; apical anther appendages ovate-triangular, longer than wide; style base not enlarged, glabrous; arms densely papillose with very long antrorsely imbricate papillae. Achenes prismatic, 4–5-ribbed with occasional short-stalked glands; carpopodium large; pappus setae uniseriate, c. 20, barbellate, persistent, enlarged distally. $n = 10$. One species, *U. hecatantha* (DC.) R.M. King & H. Rob., Argentina, Bolivia, Brazil, Paraguay, Uruguay.

1504. *Barrosoa* R.M. King & H. Rob.

Barrosoa R.M. King & H. Rob., Phytologia 21: 26 (1971).

Erect perennial herbs. Leaves opposite, sometimes alternate above, lamina lanceolate to broadly ovate, serrate to crenulate. Inflorescence densely corymbose. Phyllaries c. 15–25, distant, usually biseriate, subequal; receptacle conical, glabrous, strongly foveolate. Florets 20–55; corollas funnelform, white, pink, blue or purple; throat smooth; lobes slightly longer than wide, papillose on both

surfaces, outer surface with hairs and glands; anther collars short; apical anther appendages subquadrate to oblong, about as long as wide; style base not enlarged, glabrous; arms densely short-papillose. Achenes prismatic, 5-ribbed, sparsely glanduliferous; carpopodium distinct, procurrent on to lower part of achene ribs; pappus setae 25–30, persistent, slender, barbellate, apical cells acute or subacute. $n = 10$, c. 30. Nine species, South America.

1505. *Dasycondylus* R.M. King & H. Rob.

Dasycondylus R.M. King & H. Rob., Phytologia 24: 188 (1972); King & Robinson, Phytologia 24: 187–191 (1972), key.

Erect or spreading subshrubs or shrubs, sometimes subscandent. Leaves opposite, lamina ovate to oblong, entire to serrate. Inflorescence a corymbose panicle. Phyllaries c. 15–25, subimbricate, 3–4-seriate, unequal, inner somewhat deciduous, outer often broad; receptacle conical, glabrous to sparsely pilose, strongly foveolate. Florets 20–60; corollas white, narrowly funnelform; lobes about as long to twice as long as wide, inner surface smooth, outer slightly papillose, glanduliferous and short-pubescent; anther collars short, slightly swollen; apical anther appendages ovate, longer than wide; style base enlarged, densely hirsute; arms slightly clavate distally, slightly mamillose. Achenes prismatic, 5-ribbed, sparsely setuliferous above; carpopodium distinct, procurrent on to lower part of achene ribs, pappus setae uniseriate, c. 30–40, persistent, barbellate, apical cells narrowly obtuse to acute. Eight species, Bolivia, Brazil, Peru.

1506. *Diacranthera* R.M. King & H. Rob.

Diacranthera R.M. King & H. Rob., Phytologia 24: 192 (1972); King & Robinson, Phytologia 24: 192–194 (1972), key.

Perennial herbs or subshrubs. Leaves opposite, lamina ovate to elliptical, crenulate to serrulate. Inflorescence slightly to strongly cymose with many branches. Phyllaries c. 25, distant, biseriate, subequal; receptacle broadly convex, glabrous. Florets 50–65; corollas pinkish, narrowly funnelform; lobes slightly longer than wide, inner surface smooth to slightly mamillose, outer with a few glands, with or without hairs; anther collars short, narrowly cylindrical; apical anther appendages bilobed, shorter than wide; style base slightly enlarged, densely hirsute; style arms linear to slightly clavate, scarcely mamillose. Achenes prismatic, 5-ribbed, glabrous; carpopodium shortly procurrent on to ribs of achene; pappus setae uniseriate, c. 35, persistent, not enlarged at tips, apical cells acute. Two species, Brazil.

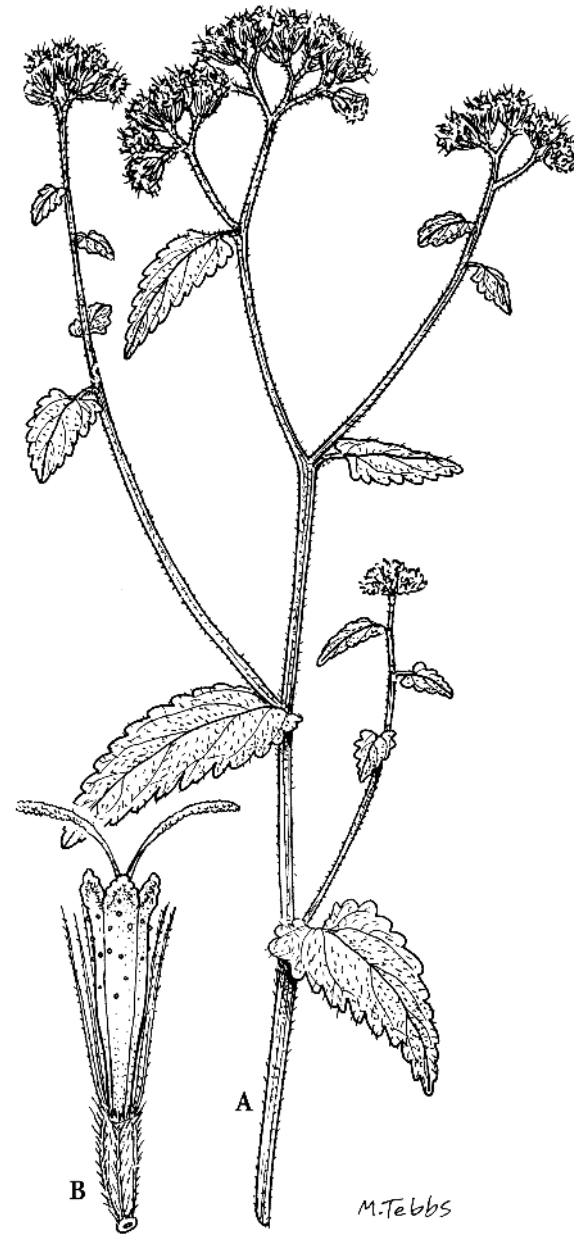

Fig. 112. Compositae-Eupatorieae. *Conocliniopis prasiifolia* (Gyptidinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

1507. *Conocliniopsis* R.M. King & H. Rob. Fig. 112

Conocliniopsis R.M. King & H. Rob., Phytologia 23: 308 (1972).

Erect subshrubs or shrubs. Leaves opposite, few alternate above, lamina ovate, strongly crenate. Inflorescence a dense corymbose panicle or cyme; phyllaries 12–16, distant, subequal, c. 3-seriate, persistent; receptacle high-conical, glabrous, strongly foveolate. Florets 20–30; corollas blue or lavender, narrowly funnelform, outer surface glanduliferous, inside glabrous; lobes twice as long as wide, inner surface mamillose, outer surface somewhat papillose distally; anther collars elongate, narrow; apical anther appendages ovate, longer than wide; style base not enlarged, glabrous; arms filiform, scarcely broader distally, densely papillose. Achenes prismatic, 4–5-ribbed, setuliferous; carpopodium very prominent with projecting setuliferous upper rim; pappus setae uniseriate, 30–35, persistent, barbellate, apical cells acute to subacute. n = 10, 30. One species, *C. prasiifolia* (DC.) R.M. King & H. Rob., Brazil, Colombia, Venezuela.

1508. *Bejaranoa* R.M. King & H. Rob.

Bejaranoa R.M. King & H. Rob., Phytologia 40: 52 (1978); King & Robinson, Phytologia 40: 51–53 (1978), key.

Erect subshrubs or shrubs. Leaves alternate or sometimes opposite, lamina ovate or ovate-lanceolate, serrate to doubly serrate. Inflorescence terminal with densely corymbose branches. Phyllaries 8–15, subimbricate, c. 4-seriate, unequal and somewhat gradate, persistent; receptacle flat to minutely conical, glabrous or subglabrous. Florets 4–10; corollas white to pale lavender, narrowly funnelform, glabrous inside, outside with glands above; lobes scarcely longer than wide, inner surface smooth, outer densely glanduliferous and minutely papillose near tip, lateral margins somewhat thickened; anther collars short-cylindrical; apical anther appendages oblong, longer than wide; style base not enlarged, glabrous; arms linear, slightly minutely mamillose, slightly broadened distally. Achenes prismatic, 5-ribbed, narrowed below, setuliferous and glandular; carpopodium short, with distinct upper rim; pappus setae uniseriate, c. 30–55, persistent, barbellate, apical cells acute or sometimes truncate. n = 10. Two species, Bolivia, Brazil, Paraguay.

1509. *Prolobus* R.M. King & H. Rob.

Prolobus R.M. King & H. Rob., Phytologia 50: 386 (1982).

Erect shrubs. Leaves mostly opposite, becoming alternate above, lamina ovate, coarsely serrate. Inflorescence cymose, with ascending branches, often extra-axillary. Phyllaries c. 12–15, slightly subimbricate, ± biseriate, subequal, receptacle flat or slightly convex, glabrous. Florets c. 12–14; corollas pale violet, glanduliferous above on outer surface, tube broadly cylindrical; throat narrowly funnelform; lobes slightly longer than wide, inner surface mamillose below, apex of outer surface forming prominent hump, anther collar cylindrical; apical anther appendages oblong, scarcely longer than wide; style base not enlarged, glabrous; arms narrowly linear, short-mamillose. Achenes prismatic, 5-ribbed, glabrous or with 1–2 setulae above; carpopodium with distinct crenulate upper margin; pappus setae uniseriate, 25–30, persistent, outer surfaces not flattened nor smooth, apical cells narrow, subacute. One species, *P. nitidulus* (Baker) R.M. King & H. Rob., Brazil.

1510. *Trichogonia* (DC.) Gardner

Trichogonia (DC.) Gardner, London J. Bot. 5: 459 (1846); Barroso, Arch. Jard. Bot. Rio de Janeiro 11: 7–18 & est. 1–13 (1951), reg. rev.

Erect perennial herbs or subshrubs. Leaves usually alternate, opposite in some species at least below, lamina linear to broadly cordate, usually crenulate to crenate. Inflorescence a lax to dense cymose or corymbose panicle. Phyllaries 10–25, distant, ± biseriate, subequal to equal; receptacle flat to slightly convex, glabrous. Florets 10–60; corollas pink, purple or white, narrowly funnelform, basal tube sometimes narrow and elongate, limb with dense pubescence on upper throat and lobes; lobes wider than long to slightly longer than wide, inner surface smooth, outer surface densely pubescent and with few glands; anther collars usually rather narrowly cylindrical; apical anther appendages slightly shorter to distinctly longer than wide, with rounded or retuse tip, style base not enlarged, glabrous; style arms linear or clubbed at tip, densely papillose or mamillose except on clubbed tips. Achenes prismatic, 5-ribbed, setuliferous at least on ribs; carpopodium a small rim; pappus setae uniseriate, usually c. 14–30, plumose or strongly barbellate, persistent, in some species some or all achenes epappose, apical cells acute. n = 10. Thirty species, Bolivia, Brazil, Colombia, Paraguay, Venezuela.

1511. *Trichogoniopsis* R.M. King & H. Rob.

Trichogoniopsis R.M. King & H. Rob., Phytologia 24: 180 (1972); Soares Nunes, Bradea 3: 129–138 (1981), part. key.

Erect perennial herbs or subshrubs. Leaves alternate or opposite, lamina ovate, serrate. Inflorescence a lax cymose or corymbose panicle. Phyllaries c. 18–20, distant, biseriate, subequal; receptacle flat or shallowly convex, glabrous. Florets 25–50; corollas white, narrowly funnelform, outer surface with few or no hairs above; lobes c. 1.5 times as long as wide, inner surface smooth, outer smooth and glanduliferous; anther collars narrow; apical anther appendages ovate, shorter than wide, strongly retuse to bilobed; style base not enlarged, glabrous; arms long-clavate, slightly mamillose. Achenes prismatic, 5-ribbed, with a narrow stipitate base, setuliferous; carpopodium small; pappus setae uniseriate, c. 30, plumose, persistent, mostly smooth on outer surface, apical cells narrow-acute. $n = 10$. Four species, Brazil.

1512. *Platypodanthera* R.M. King & H. Rob.

Platypodanthera R.M. King & H. Rob., Phytologia 24: 189 (1972); Hind, Kew Bull. 54: 927–932 (2000), key to subspp.

Erect or ascending, rarely procumbent, annual or perennial herbs or subshrubs. Leaves usually alternate, lamina ovate to lanceolate, serrate. Inflorescence a lax cymose or subcorymbose panicle with elongate basal internodes; phyllaries biseriate, c. 35, distant, mostly subequal; receptacle low-conical, glabrous. Florets 40–130; corollas pink or lavender, rarely white, narrowly funnelform, glabrous; lobes slightly longer than wide, smooth on both surfaces; anther collars short, greatly expanded below; apical anther appendages slightly shorter than wide, truncate; style base not enlarged, glabrous, arms long- and rather broad-clavate, smooth. Achenes prismatic, 5-ribbed, setuliferous; carpopodium narrowly annuliform; pappus setae uniseriate, 15–20, congested, rather broad, coarsely barbellate to subplumose, of various lengths, mostly half to two-thirds as long as corolla, smooth on outer surface, apical cells acute. $n = 10$. One species, *P. melissifolia* (DC.) R.M. King & H. Rob., Brazil.

1513. *Neocuatrecasia* R.M. King & H. Rob.

Neocuatrecasia R.M. King & H. Rob., Phytologia 20: 332 (1970); Robinson, Novon 12: 388–392 (2002), key.

Erect to procumbent perennial herbs. Leaves usually opposite, lamina ovate to deltoid or narrowly oblong, entire or dentate to deeply lobed. Inflorescence a lax to rather dense corymbose or cymose panicle; phyllaries ± biseriate, c. 10, distant, subequal; receptacle convex, glabrous. Florets 17–50; corollas white, with narrow basal tube, with abruptly expanded usually elongate and campanulate throat; cells of limb oblong with sinuous lateral walls; lobes longer than wide, inner surface densely papillose; outer surface smooth with a few hairs; anther collars short; apical anther appendages ovate, longer than wide; style base enlarged, hairy; arms long-clavate, densely papillose. Achenes prismatic, 5-ribbed, densely setuliferous; carpopodium short-cylindrical to annuliform; pappus setae uniseriate, c. 20–30, usually persistent and contiguous, apical cells acute. Twelve species, Bolivia, Peru.

1514. *Vittetia* R.M. King & H. Rob.

Vittetia R.M. King & H. Rob., Phytologia 29: 122 (1974); King & Robinson, Phytologia 49: 281–283 (1981), rev.
Eupatorium L. sect. *Macropodina* (R.M. King & H. Rob.) Cabrera (1991), p.p.

Erect shrubs or subshrubs. Leaves opposite or alternate, subsessile, lamina orbicular to broadly ovate or oblong, entire to crenate-serrate. Inflorescence an ascending multi-branched corymbose panicle. Phyllaries ± biseriate, c. 10–15, distant, subequal, receptacle flat, glabrous to minutely puberulous. Florets 10–12; corollas white to pink, narrowly funnelform or with narrow basal tube and rather campanulate limb; lobes slightly longer than wide, smooth on both surfaces, with glands on outer surface; anther collar short-cylindrical; apical anther appendages ovate, as long as or slightly longer than wide; style base not enlarged, glabrous; arms narrowly to broadly linear or narrowly clavate, densely sharply papillose. Achenes prismatic, 7–10-ribbed, glanduliferous and with non-glandular hairs; carpopodium small; pappus setae uniseriate, 30–65, persistent, apical cells sharply acute. $n = 10$. Two species, Brazil.

1515. *Campuloclinium* DC.

Campuloclinium DC., Prodr. 5: 136 (1836).
Eupatorium sect. *Campuloclinium* (DC.) Benth. (1876).

Erect coarse herbs or subshrubs. Leaves opposite or alternate, lamina ovate to narrowly oblong. Inflorescences corymbose, capitula few to many, moderate-sized or often large. Phyllaries 2–3-seriate, c. 15–30, distant to weakly subimbricate,

subequal; receptacle highly rounded to conical, with small raised scars, glabrous. Florets 30–100; corollas pink, lavender or purple, narrowly funnelform, basal tube somewhat constricted above nectary; lobes usually slightly wider than long, with mamillose or papillose cells on inner surface, slightly to strong1y papillose and with glands and often hairs outside; anther collar short-cylindrical; apical anther appendages oblong, about as long as wide to c. 1.5 times wider than long; style base not to distinctly enlarged, with few to many hairs or glabrous; arms broadly linear, flat, slightly mamillose to papillose. Achenes elongate, prismatic, with 5 strongly setuliferous ribs and few to many glands; carpopodium greatly enlarged; pappus setae uniseriate, c. 25–40, persistent, coarsely barbellate, usually elongate or sometimes short, apical cells subacute to acute. n = 10. Fourteen species, Argentina, Bolivia, Brazil, Colombia, Guatemala, Honduras, Mexico, Paraguay.

1516. *Macropodina* R.M. King & H. Rob.

Macropodina R.M. King & H. Rob., Phytologia 24: 173 (1972).

Eupatorium L. sect. *Macropodina* (R.M. King & H. Rob.) Cabrera (1991).

Erect subshrubs or shrubs. Leaves usually opposite, becoming alternate above, lamina ovate, serrulate. Inflorescence a lax cyme. Phyllaries 3–4-seriate, c. 18–40, weakly subimbricate, narrowly elliptical to linear, outer distinctly shorter; receptacle flat to slightly convex, glabrous. Florets (20–)25–30(–50); corollas pale blue, narrowly funnelform, basal tubes elongate; lobes c. 3 times as long as wide, smooth on both surfaces, outer surface with small glands; anther collar cylindrical; apical anther appendages ± quadrate, slightly longer than wide; style base not or only very slightly enlarged, sparsely to densely hirsute, arms linear, smooth to slightly mamillose. Achenes prismatic, 5–6 mm long with long basal stipe, 5-ribbed, sometimes minutely spiculiferous on ribs; carpopodium somewhat broader than stipe of achene; pappus setae uniseriate, c. 25–30, barbellate, persistent, apical cells subacute to acute. Three species, Brazil, Paraguay.

1517. *Conoclinium* DC.

Conoclinium DC., Prodr 5: 135 (1836).

Erect, rhizomatous, perennial herbs. Leaves opposite, lamina ovate to deltoid-ovate, crenate to bipinnatifid. Inflorescence laxly cymose below, with densely cymose branches. Phyllaries 2–3-seriate, c. 25, distant, mostly subequal, lanceolate; receptacle highly conical, glabrous or rarely pubescent. Florets 50–70; corollas blue or white, narrowly funnelform, with glands on outer surface; basal tube not constricted above nectary; lobes slightly longer than wide, inner surface with short bulging cells, mamillose to short-papillose, outer surface papillose in distal half, anther collars cylindrical, often narrow; apical anther appendages ovate to ± quadrate, about as long as wide; style base not enlarged, glabrous; arms narrowly linear to filiform, slightly broadened distally, densely papillose. Achenes prismatic, 5-ribbed, glabrous or with a few scattered glands, rarely setuliferous above; carpopodium usually obsolete, rarely distinct and asymmetrical; pappus setae uniseriate, c. 30, barbellate, persistent, often with slightly to distinctly enlarged tips, apical cells obtuse to rounded. n = 10. Four species, Mexico, USA (south-western and eastern Texas).

1518. *Tamaulipa* R.M. King & H. Rob.

Tamaulipa R.M. King & H. Rob., Phytologia 22: 154 (1971).

Erect woody shrubs. Leaves opposite, lamina deltoid, subserrate to dentate. Inflorescences terminal, corymbose; peduncles usually short, slightly broadened and fistulose distally. Phyllaries 2–3-seriate, 30–35, distant to slightly subimbricate, outer unequal, inner subequal; receptacle convex to low-conical, glabrous. Florets 40–70; corollas pale blue, narrowly funnelform, mostly glabrous on outer surface; lobes about as long as wide, smooth on both surfaces, with glands on outer surface; anther collar narrowly cylindrical; apical anther appendages oblong to ovate, slightly longer than wide; style base not enlarged, glabrous; arms broadly linear, smooth to slightly mamillose. Achenes prismatic, 5–6-ribbed, setuliferous; carpopodium sometimes indistinct, very narrow, somewhat confluent with broadened bases of ribs; pappus setae uniseriate, c. 35, barbellate, persistent, capillary, apical cells acute to subacute. n = 10. One species, *T. azurea* (DC.) R.M. King & H. Rob., Mexico, USA (Texas).

1519. *Lourteigia* R.M. King & H. Rob.

Lourteigia R.M. King & H. Rob., Phytologia 21: 28 (1971).

Small to medium-sized subshrubs or shrubs, sometimes procumbent. Leaves opposite, lamina

ovate to narrowly elliptical, crenulate to serrate, lower surface often white-tomentose. Inflorescence terminal, densely corymbose. Phyllaries 3–4-seriate, c. 20–25, weakly to moderately subimbricate, unequal; receptacle convex, rarely slightly conical, glabrous or with minute hairs. Florets 20(–40); corollas lilac, blue, purple or greenish white, funnelform, tube narrowed above nectary; lobes slightly longer than wide, smooth on most of both surfaces; papillose near margins, outer surface densely puberulous and with few to many glandular punctae; anther collar narrowly cylindrical; apical anther appendages ovate to oblong, slightly longer than wide; style base not enlarged, glabrous; arms long-subclavate, densely papillose. Achenes prismatic, 5-ribbed, strongly constricted above, narrowed below, sparsely setuliferous to subglabrous; carpopodium prominent, usually asymmetrical; pappus setae uniseriate, c. 30, inserted on an easily detached callus, slender, barbellate, persistent on callus, apical cells acute. $n = 10$. Circa 11 species, Colombia, Venezuela.

XXX.11. b. Agrianthus Group

1520. *Agrianthus* Mart. ex DC.

Agrianthus Mart. ex DC., Prodr. 5: 125 (1836); Mattfeld, Notizbl. Bot. Gart. Berlin-Dahlem 8: 428–451 (1923), rev.; Hind, Kew Bull. 245–277 (1993), key.

Erect many-branched shrubs. Leaves usually densely spirally inserted, lamina elliptical to oblong-lanceolate or subulate. Inflorescence terminal on branches, abrupt, a dense cluster of sessile or subsessile capitula. Phyllaries c. 18–40, distant to weakly subimbricate, c. 3-seriate, subequal, lanceolate; receptacle convex to conical, glabrous, sometimes with scattered narrow paleae. Florets 20–45; corollas usually pink or white, rarely purplish, narrowly funnelform, with resin ducts along veins in throat; lobes slightly longer than wide, mamillose to slightly papillose on inner surface, with slightly to strongly papillose apical cap on outer surface; anther collars prominent, cylindrical to flattened; apical anther appendages usually longer than wide, apices truncate or obtuse and sometimes retuse; style base not enlarged, glabrous, shaft glabrous, rarely glandular-punctate; arms narrowly clavate, strongly mamillose. Achenes prismatic, 5-ribbed, somewhat curved, setuliferous and glandular; carpopodium annuliform, usually procurrent on to bases of ribs; pappus rarely absent or rapidly caducous, usually uniseriate, with 20–40 narrow sometimes subplumose segments, flattened on outer surface, apical cells mostly acute. Eight species, Brazil.

1521. *Catolesia* D.J.N. Hind

Catolesia D.J.N. Hind, Kew Bull. 55: 942 (2000).

Poorly branched shrubs. Leaves densely spiralled, sessile, longest surrounding inflorescences and equalling or overtopping capitula, entire, slightly involute, apices acute, hooked upwards. Inflorescence terminal, corymbose; involucre campanulate, phyllaries biseriate, distant, outer persistent, inner deciduous or easily falling; receptacle convex, smooth, glabrous, paleaceous, paleae scattered and often indistinguishable from inner phyllaries. Corolla pink; tube glabrous, expanding gradually from base to lobes; lobes narrowly triangular, apices swollen inside and curved inwards, surfaces mammillose outside; apical anther appendages triangular, less than twice as long as wide, apices rounded, basal anther appendages rounded; anther collars prominent and distinctly wider than filaments; style base lacking node, glabrous, shaft glabrous, arms linear-filiform to very slightly clavate, short-papillose. Achenes 5-ribbed, sparsely setuliferous towards pale apical callus; carpopodium annular, slightly procurrent on to base of ribs; pappus absent, or rarely minute abortive setae initials on apical callus. One species, *C. mentiens* D.J.N. Hind, Brazil.

1522. *Arrojadocharis* Mattf.

Arrojadocharis Mattf., Notizbl. Bot. Gart. Berlin-Dahlem 10: 1053 (1930); King & Robinson, Phytologia 44: 463–465 (1979), rev.

Annual or short-lived perennial herbs or shrubs. Leaves spirally inserted, sessile; lamina linear. Inflorescence of solitary capitula or lax corymbs terminating leafy branches. Phyllaries c. 20, distant, 2–3-seriate, subequal, narrowly lanceolate, receptacle highly conical, paleaceous in lower part. Florets c. 50–60; corollas pink, funnelform, with small glands on outer surface; lobes slightly longer than wide, mamillose on inner surface, papillose on most of outer surface; anther collars cylindrical; apical anther appendages mostly half to two-thirds as long as wide, style base not enlarged, glabrous, shaft glabrous, arms clavate, mamillose. Achenes prismatic, 5-ribbed, somewhat curved, setuliferous and with occasional glands; carpopodium cylin-

drical or annuliform; pappus variable, absent or of c. 25 short or long setae, apical cells acute. Two species, Brazil.

1523. ***Bahianthus*** R.M. King & H. Rob. Fig. 113

Bahianthus R.M. King & H. Rob., Phytologia 23: 312 (1972).

Erect shrubs or small trees, viscid. Leaves densely spirally inserted, with distinct narrow petioles, lamina obovate, remotely serrate, obtuse or truncate. Inflorescence a corymbose panicle. Capitula hemispherical; phyllaries 18–20, ± subimbricate, c. 3-seriate, somewhat unequal to subequal, linear to lanceolate; receptacle flat to slightly convex, glabrous. Florets 15–22; corollas pink or white, narrowly funnelform to subcylindrical, tubes scarcely narrower than throat, resin ducts narrow and solitary along veins of throat; lobes as long as wide or slightly longer, glandular outside, papillose towards tip, mamillose on inner surface; apical anther appendages oblong-ovate, about as long as wide; style base not enlarged, glabrous, arms filiform with slightly clavate tips, densely patently papillose. Achenes prismatic, 4–5-ribbed, sparsely glandular; carpopodium enlarged, procurrent on lower part of achene ribs; pappus setae uniseriate, c. 30 persistent, shortly ciliate-dentate, flattened on outer surface, apical cells narrowly rounded. n = 10. One species, *B. viscosus* (Spreng.) R.M. King & H. Rob., Brazil.

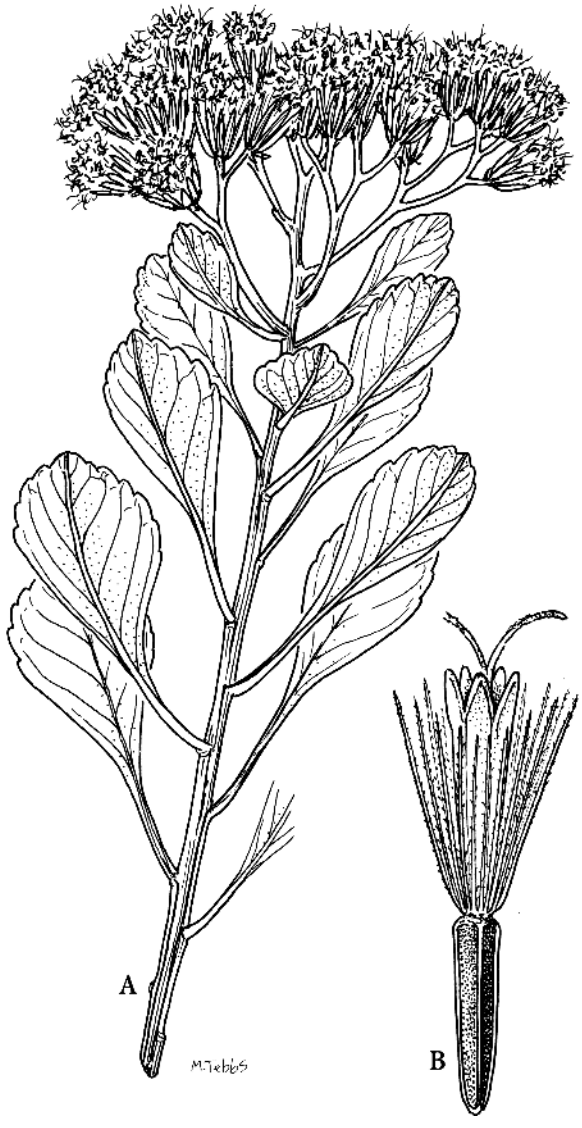

Fig. 113. Compositae-Eupatorieae. *Bahianthus viscosus* (Gyptidinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

1524. ***Semiria*** D.J.N. Hind Fig. 114

Semiria D.J.N. Hind, Kew Bull. 54: 425 (1999).

Moderately branched small tree. Leaves sessile, spirally inserted. Inflorescence terminal, of few to several capitula; involucres campanulate; phyllaries biseriate, subimbricate or eximbricate; receptacle convex, glabrous, epaleaceous. Florets c. 40, hermaphrodite; corollas pink, corolla tube cylindrical narrowing slightly towards base, glandular-punctate throughout and stipitate-glandular towards base; lobes mamillose inside, glandular-punctate outside; apical anther appendages obtuse to rotund, truncate or emarginate, basal appendages rounded or absent; anther collar markedly dilated; style base lacking basal node but enlarged, glabrous; shaft glabrous, arms linear, short-papillose. Achenes 5-winged, sparsely glandular-punctate, rarely sparsely stipitate-glandular, wings with lighter-coloured margins, glabrous; carpopodium ± annuliform, upper part procurrent on wing bases; pappus usually of 5 uniseriate subequal ascending to spreading setae, rarely absent, setae capillary, fragile, sometimes caducous, usually smooth, rarely sparsely barbellate towards apices, apices acute. One species, *S. viscosa* D.J.N. Hind, Brazil.

1525. ***Lasiolaena*** R.M. King & H. Rob. Fig. 115

Lasiolaena R.M. King & H. Rob., Phytologia 24: 185 (1972); Hind, Kew Bull. 54: 915–925 (2000), rev.

Erect shrubs. Leaves inserted in a dense spiral, short-petiolate, lamina narrowly to broadly obovate, serrulate above, obtuse or shortly acute.

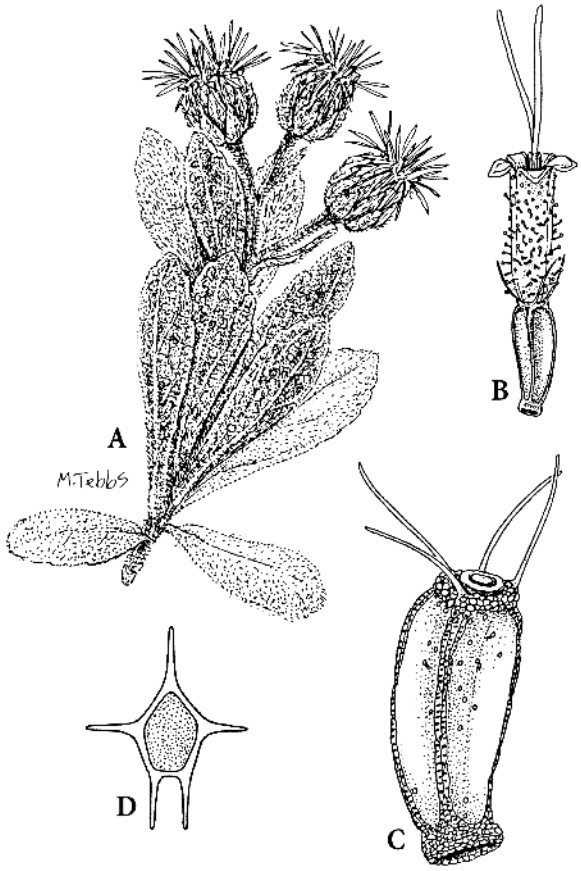

Fig. 114. Compositae-Eupatorieae. *Semiria viscosa* (Gyptidinae). **A** Flowering shoot. **B** Floret. **C** Achene. **D** Achene cross-section. (Drawings by Margaret Tebbs)

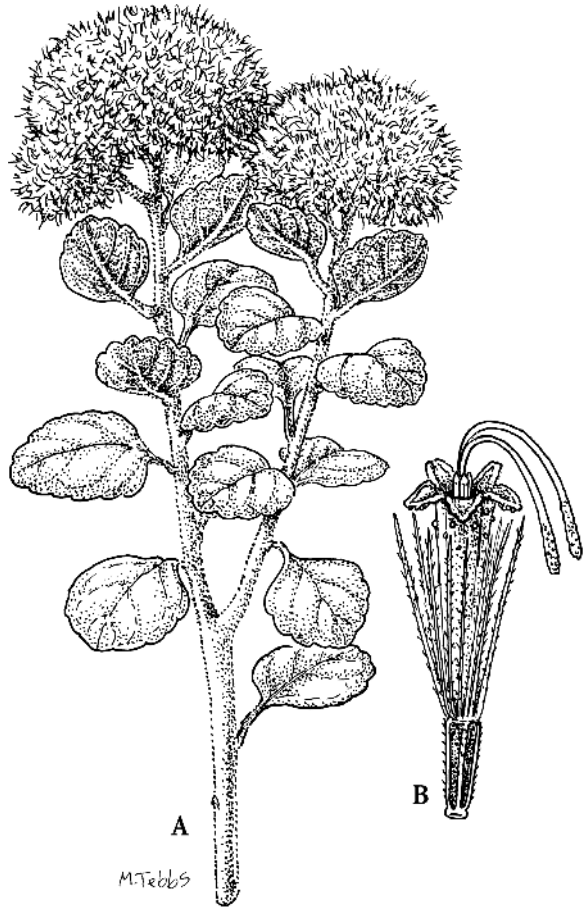

Fig. 115. Compositae-Eupatorieae. *Lasiolaena morii* (Gyptidinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

Inflorescence densely corymbose on tips of leafy branches. Phyllaries c. 20, weakly subimbricate, 2–3-seriate, mostly subequal, oblong-lanceolate, receptacle distinctly conical, pilose with a few hairs, epaleaceous. Florets 18–45; corollas narrowly funnelform, with scattered small glands on outer surface; lobes slightly to distinctly papillose on both surfaces, with or without hairs on outer surface; anther collars cylindrical to slightly flattened; apical anther appendages two-thirds as long as wide to slightly longer than wide, apices truncate to obtuse, sometimes emarginate; style base not enlarged, glabrous; shaft glabrous; arms linear, slightly mamillose to short-papillose. Achenes prismatic, 5-ribbed, bearing setulae and glands; carpopodium annuliform; pappus setae uniseriate, 20–40, persistent, congested, setae flattened throughout with barbellate to almost laciniate margins, apical cells sometimes with rounded tips. Six species, Brazil.

1526. *Stylotrichium* Mattf. Fig. 116

Stylotrichium Mattf. in Pilger, Notizbl. Bot. Gart. Berlin-Dahlem 8: 436 (1923); Bautista et al., Brittonia 52: 213–217 (2000), key.

Erect shrubs. Leaves densely spirally inserted, lamina narrowly obovate to orbicular, with prominent reticulate venation beneath. Inflorescence abruptly corymbose to subumbellate on tips of leafy branches; phyllaries c. 25, ± biseriate, distant, subequal, oblanceolate; receptacle distinctly conical, glabrous, epaleaceous. Florets c. 25–50; corollas white, short-funnelform, with stalked glands below lobes, outer surfaces of lobes glandular-punctate; lobes about as long as wide, mamillose on inner surface, papillose on most of outer surface; anther collars cylindrical; anther thecae reddish in most species; apical anther appendages about half as long as wide, truncate or

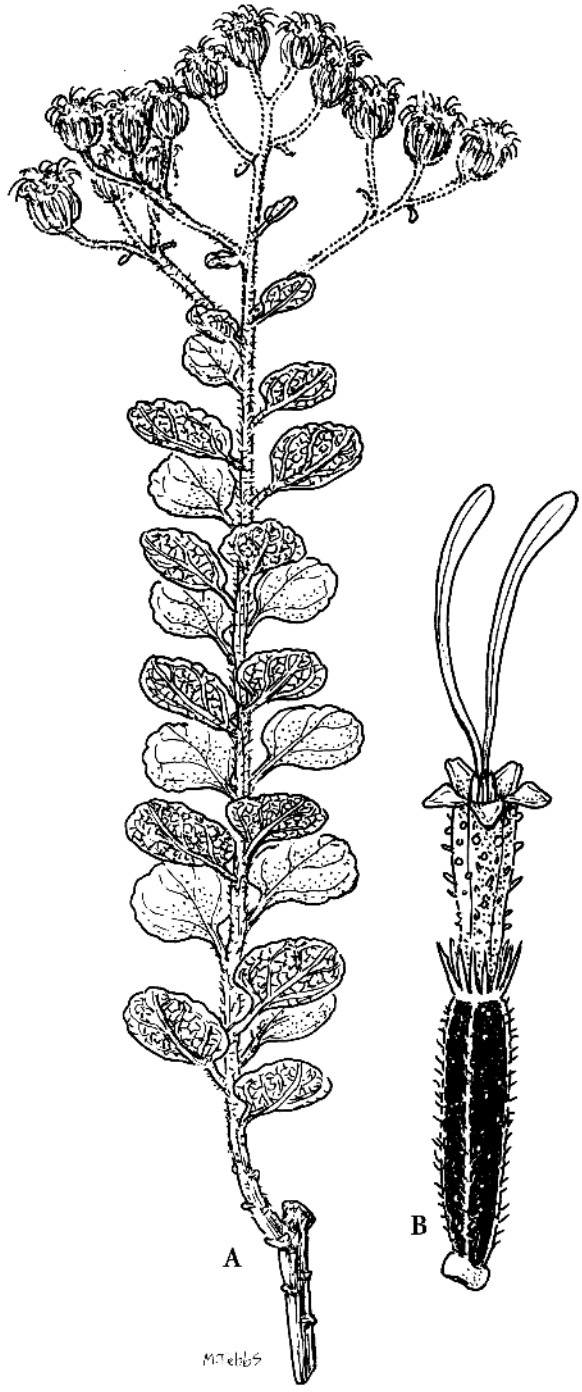

Fig. 116. Compositae-Eupatorieae. *Stylotrichium rotundifolium* (Gyptidinae). **A** Flowering shoot. **B** Achene. (Drawings by Margaret Tebbs)

emarginate at apex; style base not enlarged, glabrous; shaft and bases of arms densely pubescent with hairs and glands; arms with clavate tips, densely papillose below tips. Achenes prismatic, 5-ribbed, with setulae and occasional glands; carpopodium cylindrical or annuliform; pappus setae absent or uniseriate, 20–25, persistent, short, laterally densely fringed, apical cells often blunt. Five species, Brazil.

1527. *Bishopiella* R.M. King & H. Rob.

Bishopiella R.M. King & H. Rob., Phytologia 48: 418 (1981).

Acaulescent, scapose, annual or short-lived perennial herbs or subshrubs. Leaves forming rosette, lamina fleshy, oblanceolate, entire, narrowly obtuse. Inflorescence scapiform, a small, few-branched cyme. Phyllaries ± biseriate, c. 20, distant, equal or subequal, linear-lanceolate; receptacle highly conical, glabrous. Florets c. 40–50; corollas white, shortly funnelform from a broad, tapering, scarcely narrowed base, outer surface with a few short-stalked glands; lobes as long as wide, strongly mamillose on inner surface, outer surface papillose near margins and apex, anther collar short-cylindrical; apical anther appendages about half as long as wide, broadly rounded to truncate at tip; style base not enlarged, glabrous; arms broadly linear to strap-shaped, slightly broader distally, mamillose, essentially smooth at tip. Achenes short-prismatic, 5-ribbed, with many long setulae; carpopodium narrowly annuliform; pappus setae uniseriate, c. 35, persistent, somewhat flattened and margins coarsely barbellate to almost subplumose, apical cells sharply acute. One species, *B. elegans* R.M. King & H. Rob., Brazil.

XXX.11. c. Litothamnus Group

1528. *Litothamnus* R.M. King & H. Rob.

Litothamnus R.M. King & H. Rob., Phytologia 44: 80 (1979); Holmes, Phytologia 81: 385–390 (1997), rev.

Erect glabrous shrubs or small trees with subfleshy stems and leaves. Leaves opposite, lamina elliptical to slightly obovate, entire. Inflorescences corymbose, with opposite branches. Phyllaries 12–15, distant, ± biseriate, subequal, often with reddish tips; receptacle flat, glabrous. Florets (5–)15–25; corollas white, narrowly funnelform, sparsely glandular-puberulous on outer surface; lobes slightly longer than wide, inner surface mamillose; outer surface papillose; anther collar short-cylindrical; apical anther appendages oblong, slightly longer than wide; style base not enlarged, glabrous; arms linear, densely and patently papillose. Achenes prismatic, 5-ribbed,

glabrous or with few minute gland-tipped hairs above; carpopodium annuliform; pappus setae ± biseriate, c. 30, persistent, densely barbellate, congested, apical cells sharply acute. $n = 10$. Two species, Brazil.

1529. *Morithamnus* R.M. King, H. Rob. & G.M. Barroso

Morithamnus R.M. King, H. Rob. & G.M. Barroso, Phytologia 44: 452 (1979).

Erect shrubs or trees, with candelabra-like branching, viscid. Leaves opposite or alternate, lamina obovate to oblanceolate, entire (very rarely crenulate), obtuse or acute. Inflorescence abruptly terminal on branches; phyllaries c. 35, distant, biseriate, herbaceous, linear to narrowly lanceolate, with narrow apices, inner persistent; receptacle flat to slightly convex, glabrous. Florets c. 25–100; corollas pink or white, narrowly funnelform; tubes broad, gradually broadened into cylindrical throat; resin ducts of throat paired along veins; lobes ovate-oblong, smooth inside, outside with glands and sometimes minutely crested; anther collar short-cylindrical; apical anther appendages oblong-ovate; style base not enlarged, glabrous; arms filiform, densely papillose. Achene prismatic, 5-ribbed, moderately to densely setuliferous on upper part of ribs; carpopodium short-cylindrical; pappus setae uniseriate, 20–25, capillary or irregularly shortened, persistent, outer surfaces flattened at base, margins barbellate, apical cells sharply acute. Two species, Brazil.

XXX.12. Subtribe Disynaphiinae R.M. King & H. Rob. (1978).

Perennial herbs, more usually shrubs or small trees; leaves opposite or spirally inserted, lamina usually entire or serrate to serrulate, rarely pinnately or bipinnately lobed. Inflorescences terminal, usually densely corymbose or paniculate. Capitula mostly short-pedicellate; involucres narrowly cylindrical; phyllaries subimbricate, most or all usually persistent; receptacle scarcely convex, glabrous, epaleaceous. Florets 5; corolla lobes smooth or nearly smooth on inner surface; style base glabrous, lacking basal node; arms linear, distinctly and usually densely papillose. Achenes 5-angled, body mostly glabrous, sometimes angles sparsely setuliferous; carpopodium obsolete to annuliform or short-cylindrical; pappus uniseriate, usually of many straight capillary setae, very rarely few and hooked, sometimes with enlarged round-tipped apical cells.

Key to the Genera

1. Leaves pinnately or bipinnately lobed; style arm appendages with long narrow papillae **1530. *Acanthostyles***
– Leaves simple; style arm appendages short-papillose 2
2. Inflorescences densely paniculate **1531. *Raulinoreitzia***
– Inflorescences densely corymbose 3
3. Outer phyllaries as long as inner (and often dark coloured) **1534. *Grazielia***
– Phyllaries in gradate series 4
4. Phyllaries variously pubescent; leaves usually densely spirally inserted **1532. *Disynaphia***
– Phyllaries glabrous 5
5. Leaf venation prominent; pedicels glabrous; plants usually viscid/viscous; lamina ovate-elliptic, broadly lanceolate or obovate **1535. *Symphyopappus***
– Leaf venation, especially midrib, insculpate; pedicels pubescent; plants never viscid; lamina narrow-lanceolate or linear **1533. *Campovassouria***

Genera of Disynaphiinae

1530. *Acanthostyles* R.M. King & H. Rob.

Acanthostyles R.M. King & H. Rob., Phytologia 22: 111 (1971).

Erect shrubs. Leaves opposite, lamina narrowly lobed to pinnately dissected. Inflorescence a long pyramidal panicle. Phyllaries c. 25, c. 4-seriate, with glands on outer phyllaries, otherwise glabrous, receptacle slightly convex, glabrous. Corollas narrowly funnelform, purple-lilac; lobes c. 1.5 times as long as wide, with inner surface smooth, outer surface glanduliferous; anther collar elongate, cylindrical; apical anther appendages oblong to triangular, longer than wide; style arms long-linear, with stigmatic papillae elongate and forming a brush. Achenes prismatic, 4–5-ribbed, setuliferous; carpopodium indistinct or minutely annuliform; pappus setae uniseriate, c. 30–40, persistent, densely divaricately barbellate on margins and outer surface, not enlarged at apex, apical cells acute. $n = 10$. One species, *A. buniifolius* (Hook. & Arn.) R.M. King & H. Rob., Argentina, Bolivia, Brazil, Paraguay, Uruguay.

1531. *Raulinoreitzia* R.M. King & H. Rob.

Raulinoreitzia R.M. King & H. Rob., Phytologia 22: 113 (1971).

Eupatorium L. sect. *Raulinoreitzia* (R.M. King & H. Rob.) Cabrera (1991).

Erect shrubs. Leaves opposite, lamina elliptical to linear, serrulate. Inflorescence a pyramidal, often pendulous, panicle. Phyllaries c. 4-seriate, c. 15–20, markedly unequal, glabrous; receptacle slightly convex, glabrous. Corolla white, narrowly funnelform; lobes about as long as wide to longer than wide, smooth on inner surface; anther collar narrowly cylindrical; apical anther appendages triangular, slightly longer than wide; style arms linear, short-papillose or highly mamillose. Achenes prismatic, 4–5-ribbed, mostly glabrous; carpopodium short-cylindrical to stopper-shaped; pappus setae uniseriate, c. 30, persistent, scabrid mostly on margins, apices broadened with inflated round-tipped apical cells. n = 10. Three species, Brazil, Bolivia, Peru, Argentina, Paraguay, Uruguay.

1532. *Disynaphia* Hook. & Arn. ex DC. Fig. 117

Disynaphia Hook. & Arn. ex DC., Prodr. 7: 267 (1838).
Eupatorium sect. *Dysinaphia* [sic!] [= *Disynaphia*] (Hook. & Arn. ex DC.) Cabrera (1991).

Erect shrubs or subshrubs. Leaves alternate, usually densely spirally inserted, lamina linear to oblong or oblanceolate, entire to minutely serrulate. Inflorescence corymbose-paniculate. Phyllaries c. 11–15, 2–3(–4)-seriate, unequal, pubescent on outer surface, receptacle slightly convex or flat, glabrous to slightly pubescent. Corollas broadly tubular below, slightly broadening above, purple, pink or white; lobes as long as wide or longer, smooth to slightly mammillose on inner surface; anther collar short; anther base hastate, in a few species with bases as long as collar; apical anther appendages large, as long as wide, often notched at tip. Achenes prismatic, 4–5-ribbed, glabrous to slightly glanduliferous, in a few species setuliferous; carpopodium indistinct; pappus setae uniseriate, c. 35, persistent on callus, often falling as unit with callus, apical cells acute. n = 10. Sixteen species, Argentina, Brazil, Paraguay, Uruguay.

1533. *Campovassouria* R.M. King & H. Rob.

Campovassouria R.M. King & H. Rob., Phytologia 22: 121 (1971).
Eupatorium L. sect. *Campovassouria* (R.M. King & H. Rob.) Cabrera (1991).

Erect shrubs or subshrubs. Leaves opposite to alternate, usually closely spaced, lamina narrowly lanceolate to narrowly oblong or linear, entire to serrulate. Inflorescence densely corymbose-paniculate. Involucre cylindrical, phyllaries c. 12, 3–4-seriate, unequal and gradate, phyllaries eventually deciduous; receptacle flat, glabrous. Corollas narrowly funnelform, lavender to purple; lobes as long as wide, smooth on inner surface; anther collar cylindrical; anther thecae with short rounded bases; apical anther appendages broadly ovate to oblong, style arms narrowly linear, with dense, short, acute papillae. Achenes prismatic, 5-ribbed, slightly glanduliferous; carpopodium distinct, cylindrical; pappus setae uniseriate, c. 30–35, congested, persistent on callus, sometimes falling as unit with callus, apical cells acute. n = 10. One species, *C. cruciata* (Vell.) R.M. King & H. Rob., Argentina, Brazil, Bolivia, Paraguay, Uruguay.

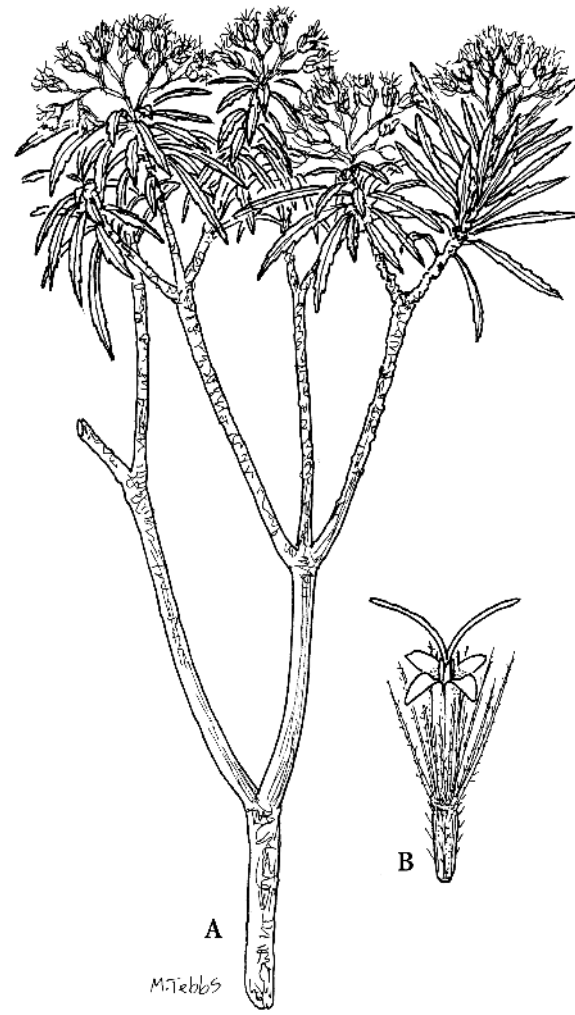

Fig. 117. Compositae-Eupatorieae. *Disynaphia praeficta* (Disynaphiinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

1534. ***Grazielia*** R.M. King & H. Rob.

Grazielia R.M. King & H. Rob., Phytologia 23, 3: 305 (1972).
Eupatorium section *Dimorpholepis* G.M. Barroso (1950).
Dimorpholepis (G.M. Barroso) R.M. King & H. Rob. (1971), non *Dimorpholepis* A. Gray (1852).

Coarse, mostly erect, herbs, subshrubs or shrubs. Leaves opposite, lamina ovate to lanceolate, sometimes pinnately to bipinnately dissected into narrow segments, often serrate. Inflorescence densely corymbose. Phyllaries c. 15, 3–4-seriate; unequal, with strongly differentiated, darker, linear basal bracts in distinct outer series; receptacle flat or slightly convex, glabrous. Corollas with broadly tubular bases, slightly broadening above, white, rose, lilac or purple; lobes longer than wide, mostly smooth on inner surface; anther collar short, cylindrical; anther thecae with short-pointed bases; apical anther appendages longer than wide; style base not enlarged, glabrous: style arms linear, not or scarcely broadened distally, densely short-papillose. Achenes prismatic, 4–5-ribbed, often with a few short-stalked glands and short setulae; carpopodium obsolete or short-cylindrical, procurrent upwards on lower part of achene ribs; pappus setae c. 20–30, congested, barbellate, persistent, tapering to a sharp point, apical cells acute. n = 10. Eleven species, Argentina, Brazil, Paraguay, Uruguay.

1535. ***Symphyopappus*** Turcz. Fig. 118

Symphyopappus Turcz., Bull. Soc. Imp. Naturalistes Moscou 21: 583 (1848).
Eupatorium L. sect. *Symphyopappus* (Turcz.) Cabrera (1991).

Erect shrubs or small trees, often viscid. Leaves opposite, sometimes becoming alternate near inflorescence, lamina ovate-lanceolate, serrate. Inflorescence rather densely corymbose. Phyllaries 3–4(–5)-seriate, c. 15, inner unequal and gradate, substramineous, usually mostly persistent; receptacle flat or slightly convex, glabrous or with numerous stiff hairs. Corollas with broadly tubular base, slightly broadening above, rarely narrowly funnelform throughout, white, rose or purple-pink; lobes slightly longer than wide to twice as long as wide, inner surface smooth, apices papillose outside and often sparsely glandular, outer surface otherwise glabrous; anther collar short, cylindrical; bases of anther thecae pointed; apical anther appendages large, triangular, twice as long as wide; style arms linear, covered with crowded, short, erect papillae. Achenes short-prismatic, 4–5-ribbed, glabrous or sparsely short stipitate-glandular; carpopodium short-cylindrical, procurrent on lower part of ribs; pappus setae biseriate, c. 40, congested, persistent on callus, often falling as unit with callus, setae tapering to sharp points, apical cells acute to obtuse, rarely with uncinate apices. n = 10. Twelve species, Brazil.

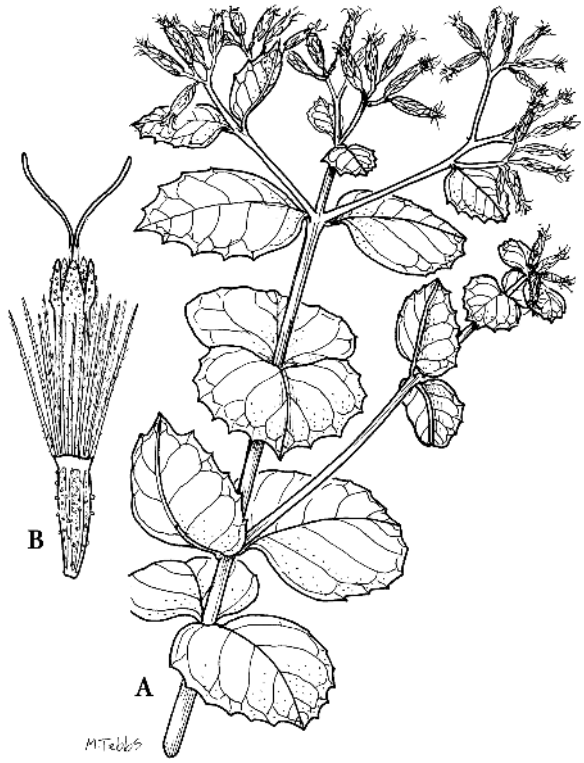

Fig. 118. Compositae-Eupatorieae. *Symphyopappus decussatus* (Disynaphiinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

XXX.13. Subtribe Ayapaninae R.M. King & H. Rob. (1980).

Erect or repent annual or perennial herbs or subshrubs, rarely vines, leaves opposite, sometimes becoming alternate above, rarely alternate throughout. Inflorescence terminal on leafy branches. Capitula clustered; phyllaries usually distinctly subimbricate, gradate, persistent; receptacle slightly convex, rarely columnar, usually glabrous, more rarely paleaceous or with hairs. Florets 3–300; corolla lobes usually smooth; apical anther appendage usually as long as wide, rarely reduced or lacking; style base with enlarged

node, with or without hairs; style arms linear to tapering, rarely broadened apically, smooth to strongly papillose. Achenes prismatic with 5 ribs; carpopodium distinct, strongly demarcated; pappus rarely absent, usually of many capillary setae, sometimes reduced in number, rarely short, with pointed apical cells.

Fig. 119. Compositae-Eupatorieae. *Ayapana amygdalina* (Ayapaninae). **A** Flowering shoot with leaf. **B** Floret. (Drawings by Margaret Tebbs)

Key to the Genera

1. Receptacle paleaceous 2
– Receptacle epaleaceous 4
2. Capitula on short pedicels and congested in dense cymes **1547. *Lepidesmia***
– Capitula distinctly pedicellate and arranged in panicles 3
3. Receptacle highly conical; florets many (> 100) per capitulum; anther appendages slightly longer than wide **1548. *Isocarpha***
– Receptacle low-conical; florets few (c. 12) per capitulum; anther appendages lacking **1546. *Parapiqueria***
4. Pappus of a single seta or setae short or lacking 5
– Pappus of 5 or more regularly arranged long and persistent setae 7
5. Pappus present and of one long and persistent seta; leaves 3-partite **1545. *Monogereion***
– Pappus lacking or of one or few deciduous setae; leaves simple 6
6. Plants erect or decumbent herbs; leaves petiolate; corolla lobes with a few short hairs; pappus lacking or of a few short deciduous setae **1543. *Alomiella***
– Plants repent herbs; leaves sessile; corolla lobes glabrous and papillose inside; pappus reduced to an annular ring, sometimes with a single short seta **1544. *Siapaea***
7. Pappus of few setae (5–10) **1542. *Gymnocondylus***
– Pappus of several to many setae (18–30) 8
8. Plants epiphytic vines; style arms with markedly dilated apices **1539. *Gongrostylis***
– Plants terrestrial; style arms linear or filiform 9
9. Corolla with conspicuously constricted basal tube **1541. *Condylidium***
– Corollas funnelform or narrow and tubular 10
10. Scandent shrubs; inflorescences with distinct cymose branching **1540. *Heterocondylus***
– Herbs or subshrubs; inflorescences corymbose or paniculate and often only with dense cymose terminal branching 11
11. Anther cylinder included well within corolla tube; florets 5–40 per capitulum; style base with pubescent node **1536. *Ayapana***
– Anther cylinder visible in corolla throat 12
12. Corolla tube funnelform; corollas pink to violet; florets 25–150 per capitulum; style base with glabrous or pubescent node **1537. *Ayapanopsis***
– Corolla tube very narrow and tubular; corollas white; florets 150–300 per capitulum; style base with glabrous node **1538. *Polyanthina***

Genera of Ayapaninae

1536. *Ayapana* Spach Fig. 119

Ayapana Spach, Hist. Nat. Vég. Phan. 10: 290 (1841); King & Robinson, Phytologia 34: 57–66 (1976), key.

Erect perennial herbs. Leaves mostly opposite, very rarely spiralled, lamina narrowly ovate to elliptical, entire to serrulate. Inflorescence laxly paniculate, with laxly or densely corymbose to

subcymose branches. Phyllaries 15–35, subimbricate, 4–5-seriate, lanceolate; receptacle convex, glabrous. Florets 5–40; corollas white or pink, narrowly funnelform to nearly tubular, glabrous on inner surface, with glands on outer surface of lobes; lobes short- to long-triangular, smooth on inner surface; anther collar slender; apical anther appendages triangular to oblong, slightly longer than wide; style base glabrous; arms filiform or with short tapering recurved appendages, densely long-papillose. Achenes prismatic, 5-ribbed, with setulae mostly on ribs; carpopodium stopper-shaped; pappus setae c. 20–40, slender, barbellate, persistent. n = 8, 10, 17, 18. Sixteen species, neotropics.

1537. *Ayapanopsis* R.M. King & H. Rob.

Ayapanopsis R.M. King & H. Rob., Phytologia 24: 382 (1972).

Erect perennial herbs or subshrubs. Leaves opposite, lamina elliptical or ovate to deltoid, acute to acuminate, serrate to nearly entire. Inflorescence a corymbose panicle with corymbose to weakly cymose branches. Phyllaries 30–50, subimbricate, 3–4-seriate, narrowly oblong to lanceolate; receptacle slightly convex, glabrous to minutely pilulose. Florets 35–150; corollas pink to violet, narrowly funnelform; lobes as long as wide or longer, outer surface usually glanduliferous, sometimes with non-glandular hairs, inner smooth, anther collar cylindrical; apical anther appendages ovate, 0.6–1.5 times as long as wide; style base glabrous to densely hirtellous; arms linear, almost smooth to slightly mamillose. Achenes prismatic to fusiform, 5-ribbed, setuliferous and stipitate-glandular; carpopodium short-cylindrical; pappus setae c. 15–40, barbellate, persistent. Seventeen species, South America.

1538. *Polyanthina* R.M. King & H. Rob.

Polyanthina R.M. King & H. Rob., Phytologia 20: 213 (1970).

Erect perennial herbs. Leaves opposite, sometimes alternate above, serrate. Inflorescence a lax thyrsoid or pyramidal panicle with denser cymose branches. Phyllaries c. 40–50, subimbricate, 2–3-seriate, lanceolate; receptacle slightly convex, shortly puberulous. Florets c. 200–300; corollas white, very narrowly tubular, glabrous on inner and outer surface; lobes longer than wide; filaments inserted at staggered levels on corolla tube; anther collar slender; apical anther appendages triangular to ovate, slightly longer than wide; style base glabrous; arms filiform, not tapered, shortly mamillose. Achenes prismatic, 5-ribbed, glabrous except for a few setulae near the top; carpopodium stopper-shaped or cylindrical; pappus setae c. 25, barbellate, persistent. n = 10. One species, *P. nemorosa* (Klatt) R.M. King & H. Rob., South America.

1539. *Gongrostylus* R.M. King & H. Rob.

Gongrostylus R.M. King & H. Rob., Phytologia 24: 387 (1972).

Slender epiphytic vines, sparingly branched. Leaves opposite, lamina ovate, remotely serrate. Inflorescences mostly axillary, corymbose with cymose branches. Phyllaries c. 25, subimbricate, c. 3-seriate, ovate to lanceolate or linear-lanceolate; receptacle slightly convex, glabrous. Florets c. 20; corollas white, very narrowly funnelform, mostly glabrous with glands on outer surface of lobes; lobes slightly longer than wide, smooth on both surfaces; anther collar elongate; apical anther appendages short, only half as long as wide; style base densely hirsute; arms narrow and slightly mamillose below, greatly enlarged and smooth distally in broadened and thickened fusiform tip. Achenes prismatic, 5-ribbed, glabrous; carpopodium a distinct short cylinder with prominent upper rim; pappus setae uniseriate, c. 30, barbellate, persistent, scarcely narrowed towards tips. One species, *G. costaricensis* (Kuntze) R.M. King & H. Rob., Colombia, Costa Rica, Ecuador, Panama.

1540. *Heterocondylus* R.M. King & H. Rob.

Heterocondylus R.M. King & H. Rob., Phytologia 24: 389 (1972).
Eupatorium L. sect. *Heterocondylus* (R.M. King & H. Rob.) Cabrera (1991).

Erect to subscandent perennial herbs or subshrubs. At least lower leaves opposite, upper alternate in some species, lamina ovate to narrowly oblong or panduriform, entire to serrate. Inflorescence pyramidal to distinctly cymose; capitula large, sometimes nodding. Phyllaries c. 15–30, subimbricate, 3–5-seriate, oblong to lanceolate; receptacle flat, glabrous. Florets 20–80; corollas white to pink or reddish-purple, narrowly funnelform; cells of limb elongate with mostly sinuous lateral walls; lobes usually distinctly longer than wide, smooth on both

surfaces, glabrous to sparsely glanduliferous on outer surface; anther collar often thickened above; apical anther appendage ovate to oblong, slightly longer than wide; style base glabrous or hirtellous; arms linear to broadly linear, smooth to short-mamillose. Achenes prismatic or fusiform, 4–5-ribbed, with short setulae or glands; carpopodium distinct, stopper-shaped; pappus setae c. 20–30, barbellate, persistent, apices not enlarged or only gradually dilated. n = c. 20. Thirteen species, Central and South America.

1541. *Condylidium* R.M. King & H. Rob.

Condylidium R.M. King & H. Rob., Phytologia 24: 380 (1972).

Erect to decumbent perennial herbs or subshrubs. Leaves opposite, lamina ovate to ovate-lanceolate, bluntly serrate to subentire, short-acuminate. Inflorescence thyrsoid-paniculate, with laxly and divaricately cymose branches. Phyllaries 15, subimbricate, in 5 ranks and 3 series, suborbicular to narrowly lanceolate; receptacle flat to slightly convex, glabrous. Florets 5–6; corollas white, with a short constricted basal tube, with abruptly and rather narrowly campanulate limb; lobes slightly longer than wide, smooth on both surfaces; lower filament rather short, collar almost as long, cylindrical; apical anther appendage slightly longer than wide; style base densely short-hirsute; arms linear, densely long-papillose. Achenes prismatic, 5-ribbed, ribs setuliferous; carpopodium asymmetrical, contorted and slightly tapering; pappus setae c. 30–40, slender, barbellate, persistent. n = 10. Two species, neotropics.

1542. *Gymnocondylus* R.M. King & H. Rob.

Gymnocondylus R.M. King & H. Rob., Phytologia 24: 393 (1972).

Erect perennial herbs. Leaves opposite, lamina ovate, crenulate, scarcely acuminate. Inflorescence a laxly corymbose cyme. Phyllaries c. 50, distant, 2–3-seriate, unequal, narrowly lanceolate to linear; receptacle slightly convex, glabrous. Florets 60–80; corollas white, narrowly funnelform, basal tube very narrow below; lobes about twice as long as wide, smooth on inner and outer surface, outer surface densely hirsute; anther collar slender; apical anther appendages triangular, 1.5 times as long as wide; style bases glabrous, arms very narrowly clavate, densely papillose. Achenes fusiform, 5-ribbed, setuliferous in upper part; carpopodium stopper-shaped; pappus setae uniseriate, c. 5–10, barbellate, persistent, enlarged distally. One species, *G. galeopsifolius* (Gardner) R.M. King & H. Rob., Brazil.

1543. *Alomiella* R.M. King & H. Rob.

Alomiella R.M. King & H. Rob., Phytologia 24: 395 (1972).

Erect to decumbent perennial herbs. Leaves opposite to subopposite, lamina broadly ovate, serrate, acute. Inflorescence laxly cymose. Phyllaries 20–30, subimbricate, 3-seriate, unequal, elliptical to oblong, receptacle flat, glabrous. Florets c. 40; corollas white, narrowly funnelform, glabrous below on both surfaces, veins greatly thickened in tube and throat; lobes about as long as wide, smooth on inner and outer surfaces, outer surface with a few small twin-hairs; anther collar cylindrical, slightly enlarged; apical anther appendages ovate, slightly longer than wide; style base glabrous, arms linear, densely papillose with narrow spreading papillae. Achenes prismatic, 5-ribbed, glabrous or setuliferous; carpopodium short stopper-shaped; pappus absent or of short deciduous setae. Two species, Brazil.

1544. *Siapaea* Pruski

Siapaea Pruski, Brittonia 48: 190 (1996).

Herbs. Stems repent, usually rooting at nodes. Leaves opposite, simple, lamina elliptic-lanceolate, serrate, acute. Inflorescence terminal, cymose, few-headed; phyllaries 1–2-seriate, few, distant, subequal; receptacle convex to conical, glabrous, epaleaceous. Florets several, hermaphrodite; corollas cream, corolla tube glabrous, corolla-lobes papillose; anther cylinder included within throat, apical anther appendages ovate, short, basal anther appendages rounded; style base appressed-pubescent, shaft glabrous, arms filiform. Achenes 4–5-ribbed, glabrous; carpopodium poorly developed; pappus reduced to a ring, sometimes with a single short bristle. One species, *S. liesneri* Pruski, Venezuela.

1545. *Monogereion* G.M. Barroso & R M. King

Monogereion G.M. Barroso & R.M. King, Brittonia 23: 118 (1971).

Erect, short-lived perennial herbs or subshrubs. Leaves mostly alternate, basal leaves opposite, lamina ovate, usually deeply lobed to tripartite. Inflorescence diffuse, with capitula laxly cymosely dis-

posed on ends of leafy branches. Phyllaries c. 15, weakly subimbricate, 2–3-seriate, somewhat unequal to subequal, lanceolate, receptacle slightly convex, glabrous. Florets c. 25–30; corollas white, narrowly funnelform, with hairs near base of tube, near tips of lobes and on entire upper two-thirds of inner surface of lobes; lobes c. 1.5 times as long as wide, smooth on both surfaces; anther collars slender; apical anther appendages ovate, about as long as wide; style base glabrous; arms with linear densely papillose appendages. Achenes somewhat fusiform, 5-ribbed, setuliferous; carpopodium distinct, very shortly stopper-shaped; pappus of a single long scabrid persistent seta and a fringe of numerous short narrow squamellae. One species, *M. carajensis* G.M. Barroso & R.M. King, Brazil.

1546. *Parapiqueria* R.M. King & H. Rob.

Parapiqueria R.M. King & H. Rob., Phytologia 47: 111 (1980).

Small, erect, annual or short-lived perennial herbs. Leaves opposite, upper subopposite to alternate, lamina linear. Inflorescence very diffuse with many capitula, branches rather thyrsoid-paniculate. Phyllaries c. 10, distant, ± biseriate, subequal, persistent, oblong, narrowly bicostate; receptacle conical, paleaceous with paleae similar to phyllaries. Florets c. 12; corollas white, with a short glabrous basal tube, limb broadly campanulate, with a short throat; lobes 4–5, oblong-ovate, c. 1.5 times as long as wide, smooth on inner surface, outer surface with 1–2 short glands; anther collars narrowly cylindrical; apical anther appendages lacking; style base scarcely enlarged, distinctly pilosulous; arms short, tapering, short-papillose. Achenes subfusiform, 5-ribbed, glabrous; carpopodium shortly stopper-shaped; pappus absent. One species, *P. cavalcantei* R.M. King & H. Rob., Brazil.

1547. *Lepidesmia* Klatt

Lepidesmia Klatt, Bull. Herb. Boissier 4: 479 (1896).

Erect perennial herbs. Leaves opposite, lamina rather fleshy, lanceolate to linear-lanceolate, entire to subentire, blunt. Inflorescence terminal, with elongate lower internodes, ending in dense cymes. Phyllaries c. 15, subimbricate, c. 2–3-seriate, unequal, lanceolate; receptacle slightly convex to flat, paleaceous; paleae lanceolate, similar to phyllaries but more scarious and more acute. Florets 3–7; corollas white, narrowly funnelform, glabrous below, with a few glands on lobes; lobes c. 1.5 times as long as wide, smooth on inner surface; anther collar slender; apical anther appendage oblong-ovate, slightly longer than wide; style base glabrous; arms narrowly tapering, densely long-papillose. Achenes prismatic, 4–5-ribbed, with few to many setulae mostly on ribs; carpopodium cylindrical; pappus a corona of short setae. $n = 10$. One species, *L. squarrosa* Klatt, Colombia, Cuba, Venezuela.

Aristeguieta (1964) included the genus in tribe Heliantheae along with *Isocarpha*.

1548. *Isocarpha* R. Br.

Isocarpha R. Br., Trans. Linn. Soc. London 12: 110 (1817); Keil & Stuessy, Syst. Bot. 6: 258–287 (1981), rev.

Erect annual or perennial herbs. Leaves opposite or alternate, lamina narrowly elliptical, entire to serrulate, narrowly acute. Inflorescence a lax, sometimes leafy panicle. Phyllaries c. 10–15, distant, ± biseriate, subequal to equal, elliptical to lanceolate, mostly strongly ribbed; receptacle highly conical to columnar, paleaceous, paleae similar to phyllaries. Florets > 100; corollas white to pink, usually narrowly funnelform with a distinct short basal tube, rarely cylindrical, glands on outer surface mostly on tube and lobes; lobes somewhat longer than wide, mostly smooth on inner surface, rarely papillose distally and marginally on inner surface; filaments usually inserted well above base, anther collar cylindrical; apical anther appendage triangular to oblong, slightly longer than wide; style base glabrous or papillose; arms rather short, sometimes slightly tapering, often spreading or strongly coiled, densely long-papillose. Achenes prismatic, 5-ribbed, glabrous or setuliferous; carpopodium short, stopper-shaped; pappus absent. $n = 10$. Five species, southern USA to Brazil.

XXX.14. Subtribe Alomiinae Less. (1832).

Subtribe Kuhniinae B.L. Rob. (1913).

Erect annual or perennial herbs or shrubs, sparingly to densely branched, leaves opposite or alternate, sometimes densely spiralled, usually petiolate. Inflorescence terminal on leafy branches, sometimes diffuse. Capitula usually clustered, rarely solitary, usually pedicellate, phyllaries usually distinctly subimbricate, gradate, persistent; receptacle flat or slightly convex, epaleaceous, usually glabrous. Florets 2–100; corollas usually

tubular; lobes usually smooth; anther appendage usually as long as wide; style base with or without enlarged node, node when present usually with hairs; style arms long-clavate, both thickened and broadened distally, rarely narrow, usually smooth. Achenes prismatic to obcompressed, 4–10-ribbed; carpopodium distinct, with little or no projecting upper rim, often asymmetrical; pappus setae usually many, capillary, sometimes flattened on outer surface, sometimes plumose, rarely few, winged, or absent. The generic concept applied here follows King and Robinson (1987, 1995), rather than Turner (1988, 1990, 1991a, 1994, 1995) and Turner et al. (1991).

Key to the Genera

1. Pappus lacking 2
– Pappus present, although sometimes deciduous 3
2. Florets 4–5 per capitulum; corollas glabrous or glandular-punctate; achenes with papillate setulae; Mexico **1558. *Alomia***
– Florets 40–50 per capitulum; corollas with numerous hairs and glandular punctae; achenes glabrous; Brazil **1568. *Planaltoa***
3. Style base with distinctly enlarged basal node 4
– Style base lacking distinctly enlarged basal node 14
4. Pappus setae easily deciduous, often caducous; Brazil **1567. *Leptoclinium***
– Pappus persistent 5
5. Pappus setae of two different sizes 6
– Pappus setae equal or subequal 7
6. Florets 4 per capitulum; leaves usually alternate; longer pappus setae alternating with shorter; Brazil (Goiás) **1566. *Goyazianthus***
– Florets 6–8 per capitulum; leaves opposite; longest pappus setae above ribs of achene; Brazil (Ceará, Piauí) **1563. *Dissothrix***
7. Leaves narrowly linear and inserted in dense spirals **1565. *Pseudobrickellia***
– Leaves usually ovate or oblong and opposite or whorled 8
8. Achenes 8–10-ribbed **1549. *Brickellia***
– Achenes 5-ribbed 9
9. Shrubs; leaf venation pinnate; phyllaries with rounded or obtuse apices; style base with glabrous or pubescent node 10
– Herbs or subshrubs; leaves usually 3-veined from or near to base; phyllaries mostly acute; style base with pubescent node 11
10. Leaves abruptly short-petiolate, lamina oblong-ovate, relatively small; inflorescence with ascending branchlets; achenes densely glanduliferous; Peru **1569. *Crossothamnus***
– Leaves attenuate to a stout petiole, lamina elliptical, medium sized; inflorescence with spreading branchlets; achenes with few glands or glands lacking; Colombia **1571. *Condylopodium***
11. Leaves with spiny lobes **1550. *Barroetea***
– Leaves without spiny lobes 12
12. Corolla throats flared; corolla lobes and style arms densely papillate **1551. *Phanerostylis***
– Corolla throats tubular or narrow funnelform; corolla lobes and style arms ± smooth 13
13. Inflorescences with laxly ascending branches; florets 10–30(–75) per capitulum; carpopodium relatively large and contorted; USA (Texas), Mexico **1553. *Flyriella***
– Inflorescences with spreading branches; florets 3–12 per capitulum; carpopodium relatively small and short-cylindrical; South America **1564. *Austrobrickellia***
14. Pappus setae basally flattened or pappus of squamellae or awns 15
– Pappus of capillary setae 17
15. Pappus of 5 awns **1554. *Ageratella***
– Pappus of alternating awns and squamellae 16
16. Leaves petiolate with distinct lamina, mostly opposite; achenes prismatic with short ascending setulae **1557. *Pleurocoronis***
– Leaves sessile, linear, mostly alternate; achenes fusiform with long spreading setulae on ribs **1556. *Malperia***
17. Achenes moderately to densely long stipitate-glandular **1559. *Dyscritogyne***
– Achenes short stipitate-glandular or setuliferous 18
18. Leaf lamina bases attenuate 19
– Leaf lamina bases truncate or cordate 21
19. Corollas glandular-punctate outside; achenes 5–6-ribbed; South America **1570. *Helogyne***
– Corollas eglandular outside; achenes 7–10-ribbed; USA, Mexico 20
20. Leaves sessile, opposite, linear or squamulose; phyllaries 4- or > 4-seriate **1555. *Asanthus***
– Leaves petiolate, opposite or whorled; phyllaries 2–3-seriate **1561. *Steviopsis***
21. Pappus setae plumose, united at base **1562. *Carminatia***
– Pappus setae barbellate, free at base 22
22. Florets 9–18 per capitulum; corollas tubular; achenes with long, spreading setulae **1560. *Kyrsteniopsis***
– Florets 25–35 per capitulum; corollas funnelform; achenes with short setulae **1552. *Brickelliastrum***

Genera of Alomiinae

1549. *Brickellia* Elliott

Brickellia Elliott, Sketch Bot. S. Carolina 2: 290 (1824); Robinson, Mem. Gray Herb. 1: 1–151 (1917), rev.

Erect annual or perennial herbs, subshrubs or shrubs. Leaves opposite or alternate, lamina linear, lanceolate, ovate, deltoid or lobate, usually dentate. Capitula usually clustered in leafy thyrsoid panicle, sometimes corymbose or cymose, rarely solitary and nodding on long peduncles. Phyllaries 14–45, subimbricate, 5–6-seriate, usually gradate, unequal; receptacle flat to slightly convex. Florets c. 4–100; corollas usually white to cream-coloured,

sometimes purplish, tubular or rarely narrowly funnelform; lobes as long as wide to twice as long as wide, smooth on both surfaces; anther collars slender to slightly thickened; apical anther appendages slightly longer than wide; style base with distinct enlarged node, covered with dense contorted hairs; style arms long-clavate. Achenes prismatic, 10-ribbed, setuliferous; carpopodium distinct, slightly to greatly longer on outer surface; pappus setae uniseriate, 10–80, persistent, flattened on outer surfaces, barbellate to densely plumosely fringed on lateral margins, apical cells acute. $n = 9$. Circa 100 species, New World.

1550. *Barroetea* A. Gray

Barroetea A. Gray, Proc. Amer. Acad. Arts 15: 29 (1880).

Annual or short-lived perennial herbs. Leaves opposite, lamina deltoid, serrate to dentate, with prickles on tip and teeth. Inflorescence a panicle. Phyllaries c. 4-seriate, c. 20–25, subimbricate, unequal; receptacle flat to convex, glabrous. Florets c. 15–35; corollas white, tubular; lobes more than twice as long as wide, smooth on both surfaces; anther collars very slender, elongate; apical anther appendages oblong, blunt, slightly longer than wide; style base enlarged, covered with contorted hairs; arms long-clavate, surface smooth to slightly mamillose. Achenes slightly to strongly obcompressed, constricted below pappus, 4-ribbed, setuliferous; carpopodium distinct, broad, strongly asymmetrical; pappus setae uniseriate, c. 16–30, persistent, flattened on outer surface, densely pectinately fringed on lateral margins; apical cells acute. $n = 9$. Seven species, Mexico.

1551. *Phanerostylis* (A. Gray) R.M. King & H. Rob.

Phanerostylis (A. Gray) R.M. King & H. Rob., Phytologia 24: 70 (1972).

Erect to decumbent or rhizomatous, annual or perennial herbs. Leaves opposite, lamina ovate to narrowly oblong. Inflorescence sparsely branched or capitula solitary on long erect peduncles. Phyllaries c. 30–50, subimbricate, 3–7-seriate, unequal, spreading with age; receptacle flat or slightly convex, glabrous. Florets 25–50; corollas white or pale pink, with slender basal tube, throat funnelform; lobes scarcely longer than wide to half again as long as wide, papillose on both surfaces; anther collars short to rather elongate; apical anther appendages slightly shorter to distinctly longer than wide; style base enlarged, covered with rather long, rather straight hairs; arms long-clavate, fleshy, enlarged part densely covered with small papillae. Achenes prismatic, 4–5-ribbed, scabrid with minute setulae; carpopodium distinct, nearly symmetrical to asymmetrical; pappus setae uniseriate, c. 25, persistent, essentially smooth on outer surface, apical cells very slender, narrowly acute. $n = 9$. Five species, Mexico.

1552. *Brickelliastrum* R.M. King & H. Rob.

Brickelliastrum R.M. King & H. Rob., Phytologia 24: 63 (1972).

Erect to decumbent subshrubs. Lower leaves opposite, upper often alternate, lamina ovate to triangular, slightly pungent, crenate-serrate. Inflorescence corymbose to pyramidally paniculate. Phyllaries c. 4-seriate, c. 25, subimbricate, unequal; receptacle slightly convex, glabrous. Florets 25–35; corollas white, narrowly and evenly funnelform from base; lobes slightly longer than wide, smooth on both surfaces; anther collars rather short, slender; apical anther appendages oblong, slightly longer than wide; style base not enlarged, glabrous; arms very narrowly and long-clavate, slightly mamillose, nearly smooth. Achenes prismatic, mostly 5–7-ribbed, scabrous with short setulae; carpopodium distinct, shortly rounded; pappus setae c. 25, somewhat deciduous, barbellate, slightly flattened on outer surface, apical cells strongly acute. $n = 10$. Two species, Mexico and USA (Texas).

1553. *Flyriella* R.M. King & H. Rob.

Flyriella R.M. King & H. Rob., Phytologia 24: 67 (1972); Baker & Turner, Sida 11: 300–317 (1986), rev.

Perennial herbs to subshrubs, erect or decumbent. Leaves usually opposite, sometimes alternate above, lamina ovate to deltoid, serrate. Inflorescence a laxly branched panicle. Phyllaries c. 30, subimbricate, c. 3-seriate, unequal, usually lanceolate, or c. 40, with enlarged foliaceous-tipped outer phyllaries; receptacle flat, glabrous. Florets usually 10–30 (to c. 75); corollas white, tubular to scarcely funnelform, mostly glabrous, cells of limb mostly elongate with sinuous lateral walls; lobes scarcely to distinctly longer than wide, smooth on both surfaces, outer surface with few glands, sometimes with short hairs, anther collars narrow; apical anther appendages

oblong-ovate, slightly longer than wide; style base enlarged, densely hirsute, with erect or somewhat curved hairs; arms long-clavate, smooth. Achenes prismatic, 5-ribbed, setuliferous; carpopodium distinct, cylindrical or asymmetrical; pappus setae uniseriate, 20–40, capillary, barbellate, narrowed distally, slightly flattened and barbellate on outer surface, persistent, apical cells obtuse to acute. $n = 10$. Four species, Mexico, USA.

1554. *Ageratella* A. Gray ex S. Watson

Ageratella A. Gray ex S. Watson, Proc. Amer. Acad. Arts 22: 419 (1887); Turner, Phytologia 78: 204–208 (1995), rev.

Erect subshrubs or shrubs. Leaves alternate or sometimes opposite below, lamina ovate, obovate, linear or linear-oblanceolate, entire to lobed. Inflorescence a loose racemose or narrowly thyrsoid panicle. Phyllaries c. 18–20, distant, 4–5-seriate, unequal, somewhat ranked, short-ovate to lanceolate; receptacle slightly convex, glabrous. Florets 15; corollas whitish, tubular, somewhat constricted above, with glands on outer surface on tube and lobes and especially on base of throat; lobes more than twice as long as wide, smooth on both surfaces; anther collars slender; apical anther appendages about twice as wide as long; style base not enlarged, glabrous, arms long and narrowly clavate, with surface mamillate on lower part of appendage, becoming smoother above. Achenes prismatic, 5-ribbed, with short setulae; carpopodium short stopper-shaped; pappus of 4–5 persistent, scabrid awns, winged below, apical cells acute. One species, *A. microphylla* (Sch. Bip.) A. Gray ex S. Watson, Mexico.

1555. *Asanthus* R.M. King & H. Rob.

Asanthus R.M. King & H. Rob., Phytologia 24: 66 (1972).

Erect subshrubs. Lower leaves opposite, upper sometimes alternate, sometimes reduced and scale-like, lamina narrowly lanceolate to linear. Inflorescence thyrsoid-paniculate with densely corymbose branches. Phyllaries c. 20–25, 4- or > 4-seriate, subimbricate; receptacle flat, glabrous. Florets 8–14; corollas whitish, tubular and slightly constricted above to minimally funnelform, with sparse minute glands externally; lobes 2–3 times as long as wide, smooth on both surfaces; anther collars cylindrical; apical anther appendages oblong, slightly longer than wide or longer; style bases not enlarged, glabrous; arms long and narrowly clavate, slightly mamillose below, usually becoming smooth above. Achenes long-prismatic, c. 10-ribbed, ribs with short setulae; carpopodium short stopper-shaped; pappus setae 1–3-seriate, 20–100, persistent, barbellate on margins and outer surface, apical cells strongly acute. Three species, Mexico, USA.

1556. *Malperia* S. Watson

Malperia S. Watson, Proc. Amer. Acad. Arts 24: 54 (1889); King, Rhodora 69, 777: 35–47 [43–45] (1967), rev.

Erect annual herbs. Leaves opposite below, alternate above, lamina linear, entire. Inflorescence a loose cymose panicle. Phyllaries 20–25, subimbricate, c. 3-seriate, strongly unequal; receptacle flat, glabrous. Florets c. 20–30; corollas white, narrowly tubular, with scattered small glands on outer surface; lobes scarcely spreading, c. 1.5 times as long as wide, smooth on both surfaces; apical anther appendages oblong-ovate, slightly longer than wide; style base not enlarged, glabrous; arms narrow and long-clavate, scarcely mamillose. Achenes somewhat fusiform, 5-ribbed, with spreading setulae on ribs; carpopodium somewhat asymmetrical; pappus uniseriate, of long awns with winged bases and intervening short squamellae, persistent, awns scabrid, becoming barbellate distally, with apical cells sharply acute. $n = 10$. One species, *M. tenuis* S. Watson, Mexico, USA.

1557. *Pleurocoronis* R.M. King & H. Rob.

Pleurocoronis R.M. King & H. Rob., Phytologia 12: 468 (1966); King, Rhodora 69: 35–47 [34–43] (1967), rev.

Erect, small, usually spreading shrubs. Leaves opposite, alternate above, lamina minutely rhomboid to broadly deltoid or cordiform in outline, slightly to deeply toothed or incised to bipinnatifid. Capitula solitary or in lax to rather dense corymbose or subcymose panicles. Phyllaries 30–35, subimbricate, 3–4-seriate, outer short-ovate with small herbaceous tips, inner lanceolate; receptacle flat or slightly convex, epaleaceous, glabrous. Florets 25–30; corollas white, tubular, with scattered minute glands on outer surface; anther collars cylindrical; apical anther appendages ovate to oblong, c. 15 times as long as wide; style base not enlarged, glabrous; arms long and sometimes rather broadly clavate, slightly mamillose. Achenes prismatic, 4–5-ribbed, setulose; carpopodium slightly asymmetrical; pappus setae uniseriate, 3–6, long, barbellate, persistent, with intervening

short erosely dentate squamellae, apical cells of setae sharply acute. $n = 9$. Three species, Mexico, USA.

1558. *Alomia* Kunth

Alomia Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. (ed. folio) 4: 119 (1818).

Erect to decumbent short-lived perennial herbs. Leaves opposite, lamina usually ovate, upper leaves sometimes elliptical or lanceolate, usually serrate or dentate. Inflorescence rather lax, weakly to strongly cymose panicles. Phyllaries 25–30, subimbricate, 2–4-seriate, unequal to subequal; receptacle broadly convex, without paleae, glabrous. Florets 40–50; corollas white, tubular or with narrowly campanulate throat, with minute scattered glands on outer surface; lobes longer than wide, smooth or nearly smooth on both surfaces; anther collars cylindrical; apical anther appendages ovate, about as long as wide; style base not enlarged, glabrous; arms scarcely thickened to long and narrowly clavate, slightly mamillose to densely short-papillose. Achenes prismatic, 5-ribbed, with short blunt twin-hairs; carpopodium cylindrical; pappus absent. $n = 10$. Five species, Mexico.

1559. *Dyscritogyne* R.M. King & H. Rob.

Dyscritogyne R.M. King & H. Rob., Phytologia 22: 158 (1971).

Erect perennial herbs. Leaves opposite to alternate, lamina broadly to narrowly ovate, subserrulate to serrate, acute. Inflorescence a loose pyramidal or corymbose panicle. Phyllaries c. 33–40, subimbricate, c. 4–6-seriate, strongly unequal, mostly persistent; receptacle flat to slightly convex, glabrous. Florets 11–16; corollas white or pink, tubular, with scattered minute glands on outer surface, sometimes with sparse hairs inside near base of throat; lobes scarcely longer than wide, smooth on both surfaces; anther collars cylindrical or narrow below; apical anther appendages oblong to ovate, about as long as wide; style base not enlarged, glabrous or with a few minute papillae; arms long-clavate or strap-shaped, fleshy, nearly smooth. Achenes prismatic to rather fusiform, 4–5-ribbed, densely punctate- or stipitate-glandular; carpopodium indistinct; pappus setae 1–2-seriate, c. 35–40, persistent, barbellate on margins and outer surface, apex not or slightly broadened, apical cells acute. Two species, Mexico.

1560. *Kyrsteniopsis* R.M. King & H. Rob.

Kyrsteniopsis R.M. King & H. Rob., Phytologia 22: 146 (1971).
Pseudokyrsteniopsis R.M. King & H. Rob. (1973).

Erect subshrubs or shrubs. Leaves opposite, lamina ovate to deltoid, entire to dentate or denticulate. Inflorescence a lax leafy thyrsoid panicle, with laxly to densely corymbose branches. Phyllaries 20–25, subimbricate, c. 3–4-seriate, strongly unequal, spreading when dry; receptacle slightly convex, glabrous. Florets 9–18; corollas greenish white or cream-white, narrowly tubular to minimally funnelform, with glands on outer surface of tube and lobes or glabrous on tube with some glands on lobes; lobes slightly longer than wide, slightly spreading, smooth on both surfaces; anther collars narrowly cylindrical; apical anther appendages oblong to ovate, slightly longer than wide, style base not enlarged, glabrous; arms linear to scarcely long-clavate, rounded on outer surface, scarcely or not mamillose. Achenes prismatic, 5-ribbed, with setulae mostly on ribs, often with stipitate glands; carpopodium distinct; pappus setae uniseriate, 25–45, barbellate, persistent, apical cells acute. $n = 10$. Five species, Guatemala, Mexico.

1561. *Steviopsis* R.M. King & H. Rob.

Steviopsis R.M. King & H. Rob., Phytologia 22: 156 (1971).

Erect coarse herbs. Leaves usually opposite or verticillate, alternate above, lamina ovate to narrowly lanceolate, serrulate, narrowly acute to acuminate. Inflorescence a loose often leafy pyramidal or corymbose panicle, branches ascending. Phyllaries 20–30, distant to weakly subimbricate, c. 2–3-seriate, with some shorter exterior bracts; receptacle slightly convex, glabrous. Florets 15–20; corollas greyish pink to purplish, tubular to narrowly funnelform, glabrous on outer surface; lobes 1.2–2 times longer than wide, spreading, smooth on both surfaces; anther collars broadly cylindrical; apical anther appendages oblong, slightly longer than wide; style base not enlarged, glabrous; arms long and narrowly clavate, fleshy, somewhat flattened, slightly mamillose to smooth. Achenes prismatic, 5–10-ribbed, densely to sparsely setuliferous, with few to many short-stalked glands; carpopodium indistinct; pappus setae uniseriate, c. 25–30, often coarsely barbellate, persistent, not flattened nor smooth on outer surface, apices not broadened, apical cells acute. Four species, Mexico.

King and Robinson's (1971, 1972, 1987) concept of *Steviopsis* was expanded by Turner (1988) to include both *Asanthus* and *Dyscritogyne*. Turner (1994) also considered the newly described *Brickelliastrum villarrealii* R.M. King & H. Rob. part of his expanded *Steviopsis*. All four genera are kept separate here.

1562. *Carminatia* Moç. ex DC.

Carminatia Moç. ex DC., Prodr. 7: 267 (1838).

Erect annual herbs. Leaves opposite, lamina deltoid to broadly ovate, dentate. Inflorescence spiciform, with capitula solitary or clustered at nodes along spike. Phyllaries c. 20, subimbricate, c. 3-seriate, lanceolate to linear; receptacle flat, glabrous. Florets c. 10–11; corollas white, rather tubular, either slightly broader or slightly narrower above, glabrous on outer surface or with a few minute glands above, veins greatly thickened towards base; lobes slightly shorter or slightly longer than wide, smooth on both surfaces; anther collars slender; apical anther appendages slightly longer than wide; style base not enlarged, glabrous; arms narrowly linear to scarcely long-clavate, surface slightly mamillose. Achenes prismatic, 5-ribbed, minutely setuliferous; carpopodium strongly differentiated; pappus setae c. 9–13, often deciduous in groups with narrowly fused bases, flattened on outer surface, plumose, apical cells acute. $n = 10$. Three species, Mexico and USA (Arizona).

1563. *Dissothrix* A. Gray

Dissothrix A. Gray, Hooker's J. Bot. Kew Gard. Misc. 3: 223 (1851).

Erect annual herbs. Leaves opposite, lamina ovate-lanceolate, serrate. Inflorescence a loose leafy thyrsoid panicle with cymose branches. Phyllaries c. 15, subimbricate, c. 3-seriate; receptacle flat, glabrous. Florets 6–8; corollas whitish, tubular, somewhat constricted above, glands dense at tips of lobes, very sparse elsewhere on outer surface, veins distinctly thickened below; lobes smooth on both surfaces; anther collars slender; apical anther appendages longer than wide; style base enlarged, with numerous thin-walled hairs; arms with long narrow mamillose bases on appendages, with broad elongate clavate smooth tips. Achenes prismatic, 5-ribbed, with short setulae; carpopodium stopper-shaped; pappus setae uniseriate, persistent, barbellate, of two distinct types, c. 5 longer thicker setae above ribs of achene, c. 18 shorter narrower unequal setae above areas between ribs, apical cells of longer setae obtuse, apical cells of others mostly short-acute. One species, *D. imbricata* (Gardner) B.L. Rob., Brazil.

Known only from the type collections.

1564. *Austrobrickellia* R.M. King & H. Rob.

Austrobrickellia R.M. King & H. Rob., Phytologia 24: 72 (1972).

Eupatorium sect. *Austrobrickellia* (R.M. King & H. Rob.) Cabrera (1995).

Erect or spreading to arching subshrubs or shrubs. Leaves opposite, lamina ovate, entire to sharply dentate. Inflorescence a lax leafy thyrsoid panicle, branches densely corymbose at tips. Phyllaries c. 6–20, subimbricate, 2–4-seriate, ovate to lanceolate; receptacle flat to slightly convex, glabrous. Florets 3–12; corollas greenish white to purple, tubular, sometimes with slight constrictions above and near base, glabrous on outer surface or with few minute glands on lobes; lobes about twice as long as wide, erect, smooth on both surfaces; anther collars cylindrical, sometimes short; apical anther appendages oblong, 1.25–1.5 times as long as wide; style base enlarged, with numerous scarcely distorted ascending hairs; arms long-clavate, mostly smooth. Achenes prismatic, 5-ribbed, with setulae often nearly restricted to ribs, with or without glands on sides; carpopodium shortly stopper-shaped; pappus setae uniseriate, 30–35, persistent, barbellate, with flattened mostly uninterrupted band along middle of outer surface, margins rather densely scabrid, apical cells mostly obtuse, sometimes narrowly rounded. $n = 10$. Three species, Argentina, Bolivia, Brazil, Paraguay.

1565. *Pseudobrickellia* R.M. King & H. Rob.

Fig. 120

Pseudobrickellia R.M. King & H. Rob., Phytologia 24: 74 (1972); Hind, Fl. Pico das Almas 260–261 (1996), key.

Small trees or erect, often somewhat fasciculated shrubs. Leaves densely spirally inserted, lamina narrowly linear, glabrous. Inflorescence terminal on leafy branches, densely corymbose to somewhat pyramidal. Phyllaries 12–18, subimbricate, 3–4-seriate, oblong to lanceolate; receptacle flat, epaleaceous (with a few marginal paleae?), glabrous. Florets 2–4(–8?); corollas greenish white, tubular or minimally funnelform, glabrous on outer surface; lobes c. twice as long as wide, erect, smooth on both surfaces; anther collars broadly

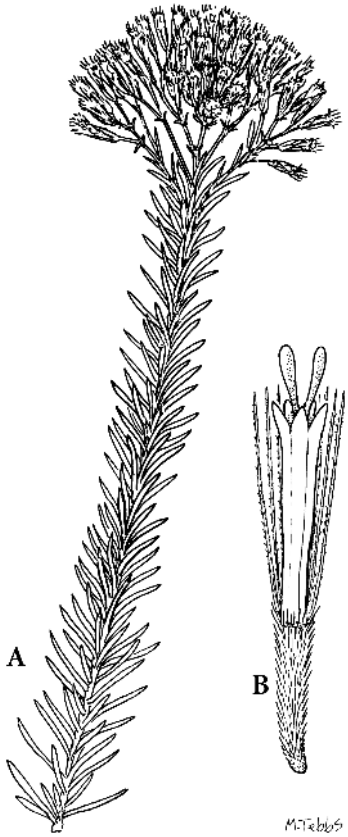

Fig. 120. Compositae-Eupatorieae. *Pseudobrickellia brasiliensis* (Alomiinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

cylindrical; apical anther appendages broadly ovate, about as long as wide; style base enlarged, hirsute with short, contorted, blunt-tipped hairs; arms long-clavate, flattened only on inner surface, scarcely mamillose below, smooth apically. Achenes prismatic, 5–10-ribbed, distinctly setuliferous; carpopodium narrowly annuliform to short stopper-shaped; pappus setae c. 35, barbellate, persistent, ± biseriate, some outer setae shorter, outer surfaces with median glabrous band. Two species, Brazil.

1566. *Goyazianthus* R.M. King & H. Rob.

Goyazianthus R.M. King & H. Rob., Phytologia 37: 461 (1977).

Erect cinereo-puberulous and glandular-punctate subshrubs. Primary leaves usually alternate, branch leaves and bracts of inflorescence usually opposite, lamina narrowly oblong-oblanceolate, entire, with rounded and apiculate tips. Inflorescence thyrsoid-paniculate, with subcymose branches. Phyllaries 15–16, subimbricate, c. 4-seriate, mostly in 4 distinct ranks; receptacle flat, glabrous. Florets 4; corollas creamy white, tubular, narrower above, with numerous glands on outer surface; lobes about twice as long as wide, smooth on both surfaces; filaments inserted near basal fourth of corolla, lower parts short, anther collars slightly thickened; apical anther appendages oblong-ovate, about as long as wide; style base enlarged, densely pubescent with short contorted hairs; arms clavate, fleshy, mamillose below, becoming smooth above. Achenes prismatic, c. 7-ribbed, densely setuliferous and glanduliferous; carpopodium short stopper-shaped; pappus setae c. 50, persistent, dimorphic, with outer smaller series in most gaps between larger inner setae, densely barbellate on margins, with few short free cell apices on outer surface, apical cells acute. $n = 20$. One species, *G. tetrastichus* (B.L. Rob.) R.M. King & H. Rob., Brazil.

1567. *Leptoclinium* Benth. & Hook. f.

Leptoclinium Benth. & Hook. f., Gen. Pl. 2: 244 (1873).

Erect shrubs. Leaves alternate, imbricate, lamina broadly lanceolate, entire. Inflorescence of small terminal corymbose panicles. Phyllaries c. 12, subimbricate, c. 3-seriate, narrowly ovate to oblong-ovate; receptacle flat to slightly convex, glabrous. Florets 5; corollas creamy white, tubular, glabrous; lobes over twice as long as wide; anther collars short-cylindrical; apical anther appendages about as long as wide; style base enlarged, with dense cluster of short contorted hairs; arms broad- and long-clavate, with inner surface flattened, mamillose below, smooth on broadest parts, stigmatic lines marginal or submarginal. Achenes prismatic, 5-ribbed, glabrous; carpopodium stopper-shaped; pappus setae apparently uniseriate, numerous, usually caducous, apical cells short-acute. One species, *L. trichotomum* (Gardner) Benth. ex Baker, Brazil.

1568. *Planaltoa* Taub.

Planaltoa Taub., Bot. Jahrb. Syst. 21: 454 (1896); King & Robinson, Monogr. Syst. Bot. 22: i–xii, 1–581 (1987), key.

Erect, densely hirtellous subshrubs or shrubs. Leaves alternate, imbricate, lamina lanceolate to oblong-elliptical, minutely serrulate, margins sometimes reflexed. Inflorescence terminal, densely corymbose or thyrsoid; capitula sessile in

small bracteolate clusters. Phyllaries 5–7, weakly subimbricate, ± biseriate, subequal; receptacle flat, glabrous. Florets 3–5; corollas pink, tubular or minimally funnelform, outer surface densely pubescent with eglandular hairs, stipitate glandular hairs, or short-stalked glands; lobes nearly twice as long as wide or longer, somewhat mamillose, with or without hairs on inner surface; anther collar short; apical anther appendages slightly wider than long to longer than wide, style base scarcely enlarged, densely pubescent with long scarcely contorted hairs; arms long and narrowly clavate with papillae below, becoming mamillose to smooth above, or linear and densely papillose. Achenes prismatic, 5–6-ribbed, glabrous, abruptly constricted at base; carpopodium indistinct; pappus lacking. $n = 10$. Two species, Brazil.

1569. ***Crossothamnus*** R.M. King & H. Rob.

Crossothamnus R.M. King & H. Rob., Phytologia 24: 77 (1972); King & Robinson, Phytologia 78: 381–383 (1995), key.

Erect shrubs. Leaves opposite to alternate, lamina ovate, serrulate to subserrulate. Inflorescence thyrsoid-paniculate, with branches rather densely corymbose. Phyllaries c. 20, 3–4-seriate, strongly subimbricate, oblong. Florets c. 10; corollas white, slightly funnelform, slightly narrowed above, glanduliferous on outer surface; lobes slightly longer than wide, smooth on both surfaces; anther collars broadly cylindrical; apical anther appendages oblong, 1.25 times as long as wide; style base enlarged, smooth to papillose; arms long-clavate, slightly mamillose below, smooth above, flattened only on inner surface. Achenes prismatic, 5–7-ribbed, densely glanduliferous with short-stipitate glands, rarely setuliferous; carpopodium short-cylindrical; pappus setae uniseriate, c. 35, persistent, barbellate, without flattened outer surfaces, apices somewhat broadened, apical cells obtuse. $n = 10$. Four species, Colombia, Ecuador, Peru.

1570. ***Helogyne*** Nutt.

Helogyne Nutt., Trans. Amer. Philos. Soc. n.s. 7: 449 (1841).

Erect subshrubs or shrubs. Leaves alternate, lamina small, elliptical to lanceolate, entire. Inflorescence a dense rather pyramidal or thyrsoid panicle or sometimes diffuse and leafy. Phyllaries c. 10–30, usually subimbricate, 2–5-seriate, rarely distant and subequal; receptacle slightly convex, glabrous. Florets 5–18; corollas white, pink, purple, or according to some descriptions, yellow, tubular and somewhat constricted above or funnelform, with many minute glands on outer surface, at least on lobes; lobes smooth on both surfaces; anther collars cylindrical; apical anther appendage slightly longer than wide; style base not enlarged, rarely scarcely broadened, glabrous; style arms long-clavate, flattened on inner surface, minutely mamillose to slightly papillose to tip, rarely smooth above. Achenes prismatic, 5–6-ribbed, usually with both setulae and numerous minute glands; carpopodium stopper-shaped to short-cylindrical; pappus setae uniseriate, c. 20–30, persistent, barbellate to plumose on margins, free cell apices reduced or lacking along middle of outer surface, apical cells acute. Eight species, Argentina, Bolivia, Chile, Peru.

1571. ***Condylopodium*** R.M. King & H. Rob.

Condylopodium R.M. King & H. Rob., Phytologia 24: 397 (1972); Diaz-Piedrahita & Mendez-Ramirez, Revista Acad. Colomb. Ci. Exact. 25: 17–19 (2001), key.

Erect to subscandent shrubs. Leaves opposite, lamina broadly elliptical, entire to remotely serrulate. Inflorescence broadly pyramidally paniculate. Phyllaries 20–30, subimbricate, c. 4–5-seriate, inner deciduous; receptacle slightly convex, puberulous. Florets c. 10–12; corollas greenish white, minimally narrowly funnelform, with glands above on outer surface; lobes c. 1.5 times as long as wide, erect, smooth on both surfaces, anther collars cylindrical, poorly demarcated at base; apical anther appendages oblong-ovate, slightly longer than wide, style base enlarged, with or without somewhat contorted hairs; arms scarcely to distinctly long-clavate, mamillose below, in broader forms becoming smooth at tip. Achenes prismatic, 5-ribbed, with sparse setulae or minute glands on sides; carpopodium shortly stopper-shaped; pappus setae uniseriate, 30–40, barbellate, persistent, contiguous, with broadened apices, apical cells obtuse. Four species, Colombia.

XXX.15. Subtribe Critoniinae R.M. King & H. Rob. (1980).

Perennial herbs, erect or scandent shrubs, or small trees. Leaves mostly opposite, sometimes alternate. Inflorescence terminal, lateral or rarely axillary, usually with corymbose branches; capitula clustered, pedicellate or sessile; phyllaries weakly

to strongly subimbricate or imbricate, usually gradate, inner usually deciduous; receptacle flat to slightly convex, rarely conical, paleaceous or epaleaceous. Florets 1–300; corollas usually funnelform, sometimes tubular or with campanulate throat, glabrous or sometimes with hairs on inner surface; corolla lobes smooth on both surfaces; anther collar cylindrical, less than 5 times as long as wide, rarely very short; apical anther appendages often as long as wide or longer, less often half as long as wide or less, rarely lacking; style base not enlarged, glabrous; style arms filiform or linear to distinctly clavate, mamillose or distally smooth, rarely distinctly short-papillose. Achenes prismatic to fusiform, 5-ribbed; carpopodium usually distinct, sometimes procurrent along ribs; pappus rarely squamiform or absent, setae usually uniseriate, many, capillary, barbellate, apices not to greatly expanded, apical cells obtuse to sharply acute.

Key to the Genera

1. Plants rosulate or subrosulate and inflorescences scapose or scapiform (peduncle or stipe rarely with one or two leaf-like bracts) 2
– Plants coarse herbs to small trees with leafy stems 3
2. Capitula with 9–10 florets; pappus setae about as long as corollas; apical anther appendages vestigial; top of corolla tube conspicuously constricted and tube distinctly inflated; eastern Cuba **1577. *Ciceronia***
– Capitula with 30–50 florets; pappus a low crown of deeply laciniate scales; apical anther appendages large, nearly as long as wide; top of corolla tube slightly narrowed; central Cuba **1576. *Antillia***
3. Individual capitula single-flowered and aggregated into spherical clusters; leaves mostly alternate 4
– Individual capitula with 3 or 4 florets; leaves opposite or alternate 5
4. Pappus of squamellae **1591. *Mexianthus***
– Pappus of capillary setae **1592. *Neohintonia***
5. Pappus absent; plants coastal epiphytic herbs or shrubs **1611. *Tuberostylis***
– Pappus usually present; plants terrestrial herbs, shrubs, trees or vines 6
6. Leaves distinctly alternate (except sometimes at base) 7
– Leaves mostly opposite or subopposite 8
7. Leaves densely spirally inserted, short-petiolate; phyllaries strongly subimbricate, margins markedly scarious; stems and leaves lacking stipitate glands; capitula sessile in spiciform inflorescences, with 6–8 florets; Peru **1585. *Nothobaccharis***
– Leaves remote, with slender petioles; phyllaries distant, margins herbaceous; stems and leaves with numerous stipitate glands; capitula pedicellate in corymbose inflorescences with 30–60 florets; Argentina, Bolivia **1584. *Bishovia***
8. Capitula densely clustered and sessile in leaf axils **1609. *Uleophytum***
– Capitula not sessile nor clustered in leaf axils 9
9. Receptacles with many paleae; capitula with 100–300 florets **1582. *Eupatoriastrum***
– Receptacle with few paleae or epaleaceous; capitula with 4–70 florets (up to 100 in *Aristeguietia*) 10
10. Leaves bipinnate; Haiti, Dominican Republic **1578. *Eupatorina***
– Leaves not dissected, rarely pinnately lobed 11
11. Phyllaries distant or weakly subimbricate in up to 3 rather irregular series 12
– Phyllaries subimbricate or imbricate in 4 or more gradate series, inner phyllaries sometimes easily deciduous 17
12. Apical anther appendages absent, often appearing as two minute lobes; phyllaries distant **1605. *Ophryosporus***
– Apical anther appendages distinct, 1/3 as long as wide or longer; phyllaries weakly subimbricate 13
13. Corolla lobes as long as wide, glabrous or subglabrous on outer surface; plants scandent; Brazil (Bahia) **1586. *Santosia***
– Corolla lobes not distinctly longer than wide, densely glandular-punctate on outer surface; plants erect or subscandent herbs or shrubs 14
14. Corolla tube basally constricted with throat distinctly expanded near base; Argentina, Paraguay **1589. *Chacoa***
– Corolla tube broadly cylindrical, expanded gradually into funnelform throat 15
15. Capitula sessile in dense spherical clusters **1583. *Sphaereupatorium***
– Capitula not sessile in dense spherical clusters 16
16. Receptacle with some paleae; shrubs with strongly pinnately veined elliptical leaves **1590. *Idiothamnus***
– Receptacle epaleaceous; herbs or shrubs with pinnately or 3-veined leaves of various shapes **1581. *Koanophyllon***
17. Lower leaf surfaces and phyllaries both densely tomentose or villous; eastern Cuba **1587. *Grisebachianthus***
– Lower leaf surfaces and phyllaries glabrous, glandular-punctate, puberulous or sparsely to moderately pubescent or tomentose but never both similarly so 18
18. Apical anther appendages shorter than wide, truncate to bilobed; style arms often with abruptly enlarged apices 19
– Apical anther appendages about as long as wide or longer, usually with rounded apices, rarely retuse; style arms with abruptly enlarged apices in some *Critonia* and *Cronquistianthus* 24
19. Corollas pubescent on inner surface; inflorescence with strongly ascending mostly subopposite to alternate branches; apical anther appendages bilobed; style arm apices not clavate; Argentina, Brazil **1608. *Neocabreria***
– Corollas usually glabrous on inner surface; inflorescence with numerous spreading opposite branches; apical anther appendages usually truncate 20

20. Pappus setae slender, mostly separate; anther thecae reddish; outer phyllaries usually persistent, phyllaries often whitish **1579. *Fleischmanniopsis***
– Pappus setae stout, contiguous; anther thecae not reddish; inner phyllaries often easily deciduous, phyllaries never whitish 21
21. Corollas funnelform; leaf lamina sparsely to densely pubescent **1581. *Koanophyllon***
– Corollas cylindrical and not wider at lobes than at base; leaf lamina glabrous (without evident hairs!) 22
22. Leaves with numerous glandular punctae on lower surface; phyllaries 7–8-seriate **1575. *Adenocritonia***
– Leaves glabrous and lacking glandular punctae, sometimes with internal cavities appearing as translucent spots along veins or in areolae; phyllaries 5–6-seriate 23
23. Anther filaments inserted near base of corolla; achenes and corollas glabrous; Jamaica, Cuba **1574. *Urbananthus***
– Anther filaments inserted well above corolla base; achenes sparsely glandular-punctate and setuliferous, corolla lobes glandular-punctate outside; Mexico, Guatemala, Honduras, El Salvador **1575. *Critoniadelphus***
24. Leaves with translucent or lens-like internal secretory pockets when viewed against light, lacking glandular punctae; coarse vines and shrubs **1572. *Critonia***
– Leaves lacking secretory pockets, often with glandular punctae 25
25. Style arm appendages broad and fleshy, often rather strap-shaped and wrinkled when dry; Andean plants 26
– Style arm appendages not prominently broadened 29
26. Achenes glabrous or with eglandular setulae, lacking glandular punctae 27
– Achenes with numerous glandular punctae, lacking eglandular setulae 28
27. Inflorescences with mostly alternate ascending branches; phyllary apices acute; carpopodium symmetrical with little or no upper rim **1595. *Aristeguietia***
– Inflorescence with many spreading opposite branches; phyllaries apices rounded; carpopodium asymmetrical with distinct upper rim **1606. *Cronquistianthus***
28. Phyllaries many-ribbed; carpopodium cylindrical and procurrent on ribs; pappus setae flattened and smooth on outer surface, especially near base **1599. *Grosvenoria***
– Phyllaries 2–4-ribbed; carpopodium annuliform or short stopper-shaped with straight upper edge; pappus setae not flattened on outer surface **1598. *Badilloa***
29. Pappus setae with markedly dilated spinose apices; capitula with 50–70 florets **1610. *Amboroa***
– Pappus setae without or with only slightly dilated apices; capitula with 5–35 florets 30
30. Leaves with numerous yellowish vermiform hairs when young; corollas with large spreading lobes from apex of narrowly cylindrical basal tube and throat **1600. *Corethamnium***
– Leaves lacking yellowish vermiform hairs; corolla lobes not appearing to spread directly from tube 31
31. Capitula all with distinct, sometimes elongate, pedicels 32
– Capitula at least partially sessile or subsessile in clusters 35
32. Inner phyllaries persistent; pappus setae fragile; inflorescences with prominently spreading opposite branches 33
– Inner phyllaries easily deciduous; pappus setae persistent; inflorescences with ascending often alternate branches 34
33. Pappus setae slightly but distinctly dilated at apices; capitula with 18–35 florets; corollas glabrous; Central America **1593. *Peteravenia***
– Pappus setae not broadened at apices; capitula with 10–12 florets; corolla lobes glandular-punctate outside; South America **1588. *Lorentzianthus***
34. Leaf lamina 3-veined from base; most capitula with large foliose bract at base; Mexico **1580. *Viereckia***
– Leaf lamina pinnately veined with ascending veins; capitula without foliose bract at base; Brazil, Uruguay **1603. *Malmeanthus***
35. Pappus setae barbellate below and tapering to a smooth apex in distal half **1597. *Austrocritonia***
– Pappus setae lacking smooth tapering distal halves, barbellate throughout and sometimes with broadened or dilated apices 36
36. Leaves elliptical with widely spreading pinnate venation 37
– Leaves mostly ovate with ascending or 3-veined secondary venation 38
37. Leaves stiffly coriaceous, glandular-punctate and scabrid on both surfaces; phyllaries partly pubescent; corolla lobes with sclerified apices on outer surface; capitula with c. 10 florets; style arms wider than thick; Colombia **1602. *Imeria***
– Leaves thinly coriaceous, glabrous above, paler beneath; phyllaries sparsely pubescent or glabrous; corolla lobes lacking sclerified apices; capitula with 6–7 florets; style arms narrowed above stigmatic area becoming terete and filiform; Venezuela **1601. *Castanedia***
38. Corolla lobes 2–3 times longer than wide, throat pubescent inside; apices of pappus setae dilated **1607. *Steyermarkina***
– Corolla lobes about as long as wide, throat glabrous inside; apices of pappus setae not enlarged 39
39. Carpopodium clearly procurrent on to base of ribs; petiole more than one third the length of lamina; style arms slender and terete above stigmatic area **1594. *Critoniella***
– Carpopodium not markedly extending upwards on to base of ribs; petioles usually less than a quarter the length of lamina; style arms slightly flattened and broadened 40
40. Inflorescences with thyrsoid-paniculate branches; most phyllaries easily deciduous; receptacle strongly convex, ± hemispherical; involucres campanulate; plants scandent; Peru **1604. *Hughesia***
– Inflorescence branches with dense glomerate clusters of capitula; most phyllaries usually persistent; receptacle flat; involucres cylindrical; plants erect or arching herbs; Colombia, Ecuador, Peru **1596. *Asplundianthus***

Genera of Critoniinae

1572. *Critonia* P. Browne

Critonia P. Browne, Civ. Nat. Hist. Jamaica: 490 (1756).

Coarse subshrubs to small trees or woody vines or climbers. Leaves opposite, lamina elliptical to broadly ovate, entire to serrate. Inflorescences usually thyrsoid-paniculate, with branches opposite and usually spreading at 90° angles; involucres usually cylindrical to fusiform. Phyllaries c. 20–25, subimbricate to weakly imbricate, 4–6-seriate, unequal, gradate, all but outer easily deciduous; receptacle flat to slightly convex, glabrous. Florets 4–12; corollas whitish, tubular or narrowly funnelform, glabrous outside or rarely a few glands on lobes; lobes oblong to long-triangular, erect to slightly spreading, smooth on inner surface, sometimes roughened at tip outside; anther collar moderately narrow; style base not enlarged, glabrous, arms filiform to slightly spathulate, smooth to slightly mamillose. Achenes prismatic, 3-ribbed, glabrous or setuliferous; carpopodium a narrow rim or short cylinder; pappus setae uniseriate, 25–35, persistent, congested, apices slightly enlarged and more densely barbellate, apical cells usually acute. n = 10. Forty-three species, Central and South America, Greater Antilles.

1573. *Critoniadelphus* R.M. King & H. Rob.

Critoniadelphus R.M. King & H. Rob., Phytologia 22: 52 (1971).

Erect shrubs to small trees. Leaves opposite, lamina elliptical to broadly lanceolate, entire to serrulate. Inflorescences pyramidally paniculate, involucres cylindrical to narrowly campanulate. Phyllaries 25–30, strongly subimbricate to imbricate, 5–6-seriate, unequal, gradate, glabrous, inner deciduous; receptacle flat, glabrous. Florets 3–8; corollas white, tubular to minimally funnelform, glabrous below lobes, lobes equilaterally triangular, smooth on inner surface, glandular-punctate on outer; anther collar rather long-cylindrical; style base not enlarged, glabrous, arms distinctly broadened at apex, flattened, mostly mamillose, becoming smooth apically. Achenes prismatic, 5-ribbed, sparsely setuliferous and glanduliferous; carpopodium symmetrical, short-cylindrical; pappus setae uniseriate, c. 30–35, contiguous, persistent, not broadened distally, apical cells acute. Two species, El Salvador, Guatemala, Honduras, Mexico.

1574. *Urbananthus* R.M. King & H. Rob.

Urbananthus R.M. King & H. Rob., Phytologia 22: 55 (1971).

Erect shrubs or small trees. Leaves opposite, lamina elliptical, entire to subserrulate, short- to long-acuminate. Inflorescence pyramidally paniculate; capitula cylindrical to narrowly campanulate. Phyllaries c. 20–30, 5–6-seriate, unequal, gradate, inner deciduous; receptacle usually slightly convex, glabrous. Florets 4–10; corollas white, tubular, glabrous, lobes oblong to oblong-ovate, mostly erect, smooth on inner surface; anther collars cylindrical; style base not enlarged, glabrous, arms with minutely spathulate tips, mamillose except at tips. Achenes prismatic, 5-ribbed with somewhat thickened ribs, glabrous; carpopodium distinct; pappus setae uniseriate, c. 30, persistent, contiguous, not broadened at tips, apical cells acute. Two species, Cuba, Jamaica.

1575. *Adenocritonia* R.M. King & H. Rob.

Adenocritonia R.M. King & H. Rob., Phytologia 33: 281 (1976); Robinson, Phytologia 71: 176–180 (1991), key.

Erect shrubs. Leaves opposite, lamina ovate, apex narrowly acuminate and entire, intervening margins serrulate to serrate. Inflorescence a broad corymbose cyme with densely corymbose branches. Phyllaries strongly subimbricate, 6–7-seriate, markedly unequal, lower persistent, broadly ovate, inner 12–15, 3–4-seriate, somewhat deciduous, narrowly oblong; receptacle slightly convex, glabrous. Florets 5; corollas white, tubular, base slightly inflated, glabrous outside below lobes; lobes about as long as wide, inner surface smooth with short-oblong cells, outer with numerous glands; anther collars cylindrical; style base not enlarged, glabrous, arms distinctly and shortly spathulate at tip. Achenes prismatic, 5-ribbed, glabrous or sparsely glandular-punctate; carpopodium short-cylindrical; pappus setae uniseriate, c. 30–35, persistent, contiguous, not noticeably broadened at tips, apical cells acute. Three species, Guatemala, Jamaica, Mexico.

1576. *Antillia* R.M. King & H. Rob.

Antillia R.M. King & H. Rob., Phytologia 21: 398 (1971).

Erect subrosulate perennial herbs, subscapose. Leaves mostly opposite, lamina oblanceolate with tapering base, crenate-lobate. Inflorescence scapose, with few ascending mostly elongate branches above. Capitula broadly campanulate;

phyllaries c. 25, distant to very weakly subimbricate, 2–3-seriate, mostly subequal, persistent; receptacle slightly convex, glabrous. Florets c. 40–50; corollas white (?), funnelform, with scattered minute glands and short rather pointed hairs on outer surface of throat and lobes; lobes slightly longer than wide, smooth on both surfaces; anther collars cylindrical; style base not enlarged, glabrous, arms narrowly linear, slightly broader at tip, mamillose except at tip. Achenes prismatic, 7–8-ribbed, setuliferous mostly on ribs; carpopodium distinct; pappus a short crown of deeply laciniate scales, marginal cells of scales acute. One species, *A. brachychaeta* (B.L. Rob.) R.M. King & H. Rob., Cuba.

1577. *Ciceronia* Urban

Ciceronia Urban, Repert. Spec. Nov. Reg. Veg. 21: 324 (1925).

Perennial rosulate herbs. Leaves densely inserted, spiralled or perhaps partially opposite, lamina oblanceolate, lobate-crenate. Inflorescence scapiform, with few slender branches distally. Phyllaries c. 10, weakly subimbricate, c. 3-seriate, subequal, persistent; receptacle flat, glabrous. Florets 9–10; corollas lavender, with short broad basal tube shortly constricted above, throat broad and short-funnelform with slightly campanulate base, sparsely glandular-punctate on outer surface, densely on outer surfaces of lobes; lobes about as long as wide, smooth on both surfaces; anther collars cylindrical; style base not enlarged, glabrous, arms with stigmatic portion slightly broadened, then narrowing and broadening distally and smooth at apex. Achenes prismatic, c. 8 ribbed, densely setuliferous mostly on ribs, glandular-punctate mostly between ribs; carpopodium distinct; pappus setae uniseriate, c. 45, barbellate, persistent, with tips of teeth and apical cells blunt. One species, *C. chaptalioides* Urban, Cuba.

1578. *Eupatorina* R.M. King & H. Rob.

Eupatorina R.M. King & H. Rob., Phytologia 21: 396 (1971).

Erect perennial calcicolous herbs. Leaves opposite, larger congested at base, decrescent and increasingly remote above, lamina deeply bipinnatifid with small rounded to oblong ultimate segments, fern-like. Inflorescence a lax thyrsoid panicle, with branches ending in lax cymes; pedicels slender. Phyllaries c. 12, moderately subimbricate, 2–3-seriate, unequal, gradate, persistent or with a few inner deciduous; receptacle flat to slightly convex, glabrous. Florets 13–20; corollas blue, lavender or pale purple, narrowly funnelform, outer surface with numerous glandular punctae mostly on lobes and at slightly constricted top of basal tube, lobes about as long as wide, smooth on both surfaces, anther collars narrow; style base not enlarged, glabrous, arms only slightly broadened at tips, mamillose except at tips. Achenes prismatic, 4–5-ribbed, setuliferous; carpopodium distinct; pappus setae uniseriate, c. 40, persistent, contiguous, apical cells short-acute. One species, *E. sophiifolia* (L.) R.M. King & H. Rob., Dominican Republic, Haiti.

1579. *Fleischmanniopsis* R.M. King & H. Rob.

Fleischmanniopsis R.M. King & H. Rob., Phytologia 21: 402 (1971); King & Robinson, Phytologia 36: 193–200 (1977), key.

Erect perennial herbs. Leaves opposite, lamina ovate-lanceolate, usually serrate. Inflorescence a rather diffuse corymbose to thyrsoid panicle with densely corymbose branchlets. Phyllaries c. 15–20, markedly subimbricate, 3–5-seriate, markedly unequal, gradate, inner usually persistent; receptacle flat or slightly convex, glabrous. Florets 5–10; corollas white, narrowly funnelform without distinct constriction at top of basal tube, nearly glabrous outside, rarely with few hairs inside near bases of filaments; lobes about as long as wide, smooth on both surfaces, with short papillae only at tips; anther collar slender; style base not enlarged, glabrous, arms rather abruptly spathulate at tips, slender bases of appendages short-papillose, becoming mamillose near tips. Achenes prismatic, 4- or 5-ribbed, ribs with very few to many setulae; carpopodium distinct; pappus setae uniseriate, c. 30–40, persistent, contiguous to somewhat separate, apical cells acute, sometimes distorted. $n = 10$. Five species, El Salvador, Guatemala, Mexico.

1580. *Viereckia* R.M. King & H. Rob.

Viereckia R. M. King & H. Rob., Phytologia 31: 118 (1975).

Erect moderately branched shrubs. Leaves opposite, lamina deltoid, serrulate, sharply acute. Inflorescence terminal, with small rather corymbose clusters; capitula few, usually with 1 or 2 foliose bracts immediately below involucre. Phyllaries c. 20, subimbricate, 4–5-seriate, unequal,

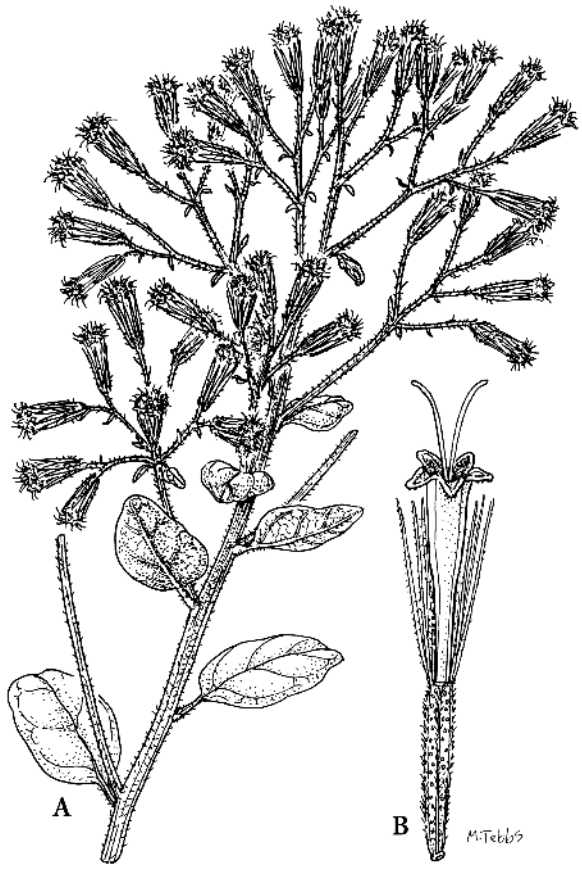

Fig. 121. Compositae-Eupatorieae. *Koanophyllon adamantium* (Critoniinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

gradate, 2–4-costate, inner easily deciduous; receptacle slightly convex, glabrous to scarcely puberulous. Florets 10–12; corollas whitish (?), narrowly funnelform, glabrous; lobes about twice as long as wide, smooth on both surfaces; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms linear, not broadened distally, mamillose or shortly papillose. Achenes prismatic, 5-ribbed, setulae mostly on ribs, a few minute glands at upper end; carpopodium distinct; pappus setae uniseriate, c. 30–35, slender, persistent, slightly broadened distally, apical cells acute. One species, *V. tamaulipasensis* R.M. King & H. Rob., Mexico.

1581. *Koanophyllon* Arruda Fig. 121

Koanophyllon Arruda, Diss. Pl. Brazil: 38? (1810).
Eupatorium L. sect. *Laevia* Cabrera (1991).

Shrubs or small trees, rarely vines. Leaves opposite, rarely alternate, lamina broadly lanceolate to elliptical, entire to serrate, rarely irregularly lobed. Inflorescences pyramidally paniculate to corymbose. Phyllaries 7–16, distant to strongly subimbricate, usually weakly subimbricate, 2–4-seriate, unequal to subequal, mostly spreading at maturity, inner sometimes deciduous; receptacle flat to slightly convex, glabrous, epaleaceous. Florets 5–20; corollas whitish to greenish yellow, rarely violet, funnelform with broadly cylindrical basal tube; lobes as wide as long to 1.5 times as long as wide, smooth on both surfaces, with numerous clustered short-capitate glands and sometimes a few hairs on outer surface; anther collars cylindrical; style base not enlarged, glabrous, arms usually distinctly broadened and becoming smooth apically, without glands. Achenes prismatic, 5-ribbed, ribs and upper surfaces bearing setulae, with few or no glands; carpopodium distinct; pappus setae uniseriate, c. 30–35, persistent, usually rather stout, usually long, rarely short or lacking, apical cells acute. n = 10, 20. Circa 120 species, neotropics.

1582. *Eupatoriastrum* Greenm.

Eupatoriastrum Greenm., Proc. Amer. Acad. Arts 39: 93 (1903).

Erect perennial herbs or subshrubs. Leaves opposite, lamina deltoid or broadly ovate, serrate, basal sometimes deeply lobed. Inflorescence a very lax thyrsoid panicle. Phyllaries c. 50, weakly to moderately subimbricate, 3–5-seriate, unequal to subequal, rather persistent; receptacle strongly convex, paleaceous. Florets 100–300; corollas pink, purple, red or whitish, narrowly funnelform, inner and outer surfaces of throat glabrous; lobes about as long as wide, smooth on both surfaces, with clustered short-stipitate glands on outer surface, with or without hairs outside; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms filiform with scarcely to distinctly broadened tips, weakly mamillose except at expanded tips. Achenes prismatic, 4–5-ribbed, with numerous setulae on sides; carpopodium distinct; pappus setae uniseriate, 15–35, slender, persistent to ± deciduous, with non-contiguous bases, apical cells acute. n = 16. Four species, Costa Rica, El Salvador, Guatemala, Mexico.

1583. *Sphaereupatorium* (O. Hoffm.) Kuntze ex B.L. Rob.

Sphaereupatorium (O. Hoffm.) Kuntze ex B.L. Rob., Contr. Gray Herb. n.s. 61: 24 (1920).
Eupatorium sect. *Sphaereupatorium* O. Hoffm. (1897).

Erect perennial herbs or shrubs. Leaves opposite, lamina broadly ovate, shallowly mucronate-dentate, acuminate. Inflorescence laxly thyrsoid-paniculate, with branches and branchlets at right angles; capitula sessile in terminal globose clusters. Phyllaries c. 12–20, distant, 3–4-seriate, slightly unequal, ovate-lanceolate, partially deciduous; receptacle complex, with convex lobes, paleaceous or with interspersed phyllaries from incompletely separated capitula. Florets c. 11; corollas white, narrowly funnelform, with broadly cylindrical basal tube, outer surface sparsely glandular-punctate, inner surface glabrous; lobes about as long as wide, smooth on both surfaces, with small cluster of glands in middle of outer surface; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms spathulate distally, mamillose except at tips. Achenes prismatic, 5-ribbed, with a few setulae on ribs; carpopodium symmetrical; pappus setae uniseriate, c. 20, scarcely flexuous, persistent, not broadened distally, apical cells acute. One species, *S. scandens* (Gardner) R.M. King & H. Rob., Bolivia, Brazil.

1584. *Bishovia* R.M. King & H. Rob.

Bishovia R.M. King & H. Rob., Phytologia 39: 339 (1978).

Erect perennial herbs or subshrubs. Leaves alternate above, opposite near base, lamina ovate to broadly ovate, serrate to sublobate, acute. Inflorescence a diffuse somewhat leafy cyme. Phyllaries c. 25, distant to scarcely subimbricate, ± biseriate, subequal, distinctly bicostate on outer surface, persistent; receptacle flat to slightly convex, glabrous. Florets 30–60, fragrant; corollas lavender, narrowly funnelform, with cylindrical basal tube; lobes longer than wide, smooth on both surfaces, glabrous or with minute hairs or glands, anther collar narrowly cylindrical; style base not enlarged, glabrous, arms linear, only slightly enlarged distally, densely mamillose. Achenes prismatic, 5-ribbed, setuliferous and with small glands; carpopodium distinct; pappus setae uniseriate, c. 30–40, slender, persistent, contiguous, scarcely broadened distally, apical cells acute. n = c. 10. Two species, Argentina, Bolivia.

1585. *Nothobaccharis* R.M. King & H. Rob.

Nothobaccharis R.M. King & H. Rob., Phytologia 41: 397 (1979).

Erect shrubs. Leaves densely spirally inserted, lamina small, suborbicular to elliptical, dentate to crenate. Inflorescence a dense thyrsoid panicle, with branches usually spiciform; capitula crowded. Phyllaries c. 15, distinctly subimbricate, 3–4-seriate, markedly unequal, gradate, rather persistent; receptacle flat to slightly convex, glabrous. Florets 6–8; corollas whitish, narrowly funnelform, glabrous on inner and most of outer surfaces; lobes c. 1.5 times as long as wide, smooth on both surfaces, outer surface with cluster of short-stipitate glands in upper half; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms slightly enlarged distally, mamillose, becoming smooth at tips. Achenes prismatic, 5-ribbed, glanduliferous and sparsely setuliferous; carpopodium distinct; pappus setae uniseriate, c. 30–35, contiguous, persistent, slightly broadened and distinctly more barbellate distally, apical cells acute. One species, *N. candolleana* (Steud.) R.M. King & H. Rob., Peru.

1586. *Santosia* R.M. King & H. Rob.

Santosia R.M. King & H. Rob., Phytologia 45: 463 (1980).

Woody vines. Leaves opposite, lamina ovate to ovate-elliptical, subentire. Inflorescences elongate, terminal, thyrsoid panicles. Phyllaries c. 13, subimbricate, c. 3-seriate, unequal, inner rather easily deciduous; receptacle flat to slightly convex, glabrous. Florets 1–10; corollas white, narrowly funnelform, with broadly cylindrical base, essentially glabrous on outer surface; lobes more than twice as long as wide, smooth on both surfaces, with an occasional gland on outer surface; anther collar short-cylindrical; style base not enlarged, glabrous, arms linear to ± filiform, mamillose to short-papillose below, essentially smooth at slightly broadened tips. Achenes prismatic, 5-ribbed, sparsely setuliferous mostly on ribs; carpopodium forming a basal ring; pappus setae uniseriate, c. 20, persistent, broadened and somewhat flattened externally near base, sometimes slightly broadened distally, apical cells acute. One species, *S. talmonii* R.M. King & H. Rob., Brazil.

1587. *Grisebachianthus* R.M. King & H. Rob.

Grisebachianthus R.M. King & H. Rob., Phytologia 32: 268 (1975); Borhidi, Acta Bot. Acad. Sci. Hung. 29: 181–215 (1983), key.

Erect to spreading shrubs. Leaves opposite, lamina broadly elliptical or oblong to broadly ovate, entire to remotely subserrulate, rounded to shortly acute. Inflorescences terminal, cymose to

somewhat pyramidal; capitula in irregular congested glomerules. Phyllaries c. 15–25, markedly subimbricate, 4–5-seriate, congested, unequal, gradate, inner deciduous; receptacle flat, glabrous. Florets 12–60; corollas white to pink or purple, narrowly funnelform, glands on outer surface often restricted to lobes, glabrous on inner surface; lobes distinctly longer than wide, smooth on both surfaces; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms linear, slightly spathulate distally, mamillose to short-papillose except at tip. Achenes prismatic, 5-ribbed, sparsely setuliferous and glanduliferous; carpopodium short-cylindrical; pappus setae uniseriate, c. 20–30, rather stout, persistent, contiguous, not to scarcely broadened distally, apical cells obtuse to short-acute. Eight species, Cuba.

1588. ***Lorentzianthus*** R.M. King & H. Rob.

Lorentzianthus R.M. King & H. Rob., Phytologia 32: 273 (1975).

Erect shrubs. Leaves opposite, lamina ovate, often rather large, serrate, narrowly acuminate. Inflorescence a pyramidal panicle. Phyllaries c. 20, subimbricate, c. 5-seriate, unequal, gradate, stramineous; receptacle slightly convex, glabrous. Florets c. 10–12; corollas whitish to purple, narrowly funnelform with narrowly cylindrical basal tube, mostly glabrous outside below lobes, glabrous on inner surface; lobes smooth on both surfaces, with clustered short-stipitate glands on outer surface; anther collars narrowly cylindrical; style base not enlarged, glabrous, arms linear, not or scarcely broadened at tips, mamillose, becoming smooth at tip. Achenes prismatic with broad base, 5-ribbed, setuliferous on ribs; carpopodium annuliform; pappus setae uniseriate, 35–40, slender, rather fragile, tips not broadened, apical cells sharply acute. $n = 10$. One species, *L. viscidus* (Hook. & Arn.) R.M. King & H. Rob., Argentina, Bolivia.

1589. ***Chacoa*** R.M. King & H. Rob.

Chacoa R.M. King & H. Rob., Phytologia 32: 275 (1975).
Eupatorium L. sect. *Laevia* Cabrera (1991), p.p.

Erect flexuous shrubs. Leaves opposite, lamina ovate to deltoid, serrate. Inflorescences lax terminal pyramidal panicles. Phyllaries c. 15, very weakly subimbricate, appearing distant, c. 2-seriate, subequal, lanceolate to linear, rather persistent; receptacle flat to slightly convex, glabrous. Florets c. 20; corollas white, with slender basal tubes and narrowly campanulate limbs, glanduliferous on outer surface; lobes not longer than wide, smooth on both surfaces, numerous glands on outer surface; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms filiform, only slightly broadened near tips, short-papillose. Achenes prismatic, with somewhat narrowed bases, setuliferous and glanduliferous; carpopodium small; pappus setae uniseriate, c. 30, persistent, slender, contiguous, not broadened distally, apical cells sharply acute. One species, *C. pseudoprasiifolia* (Hassl.) R.M. King & H. Rob., Argentina, Brazil, Paraguay.

1590. ***Idiothamnus*** R.M. King & H. Rob.

Idiothamnus R.M. King & H. Rob., Phytologia 32: 277 (1975).

Erect spreading shrubs or small trees. Leaves opposite, lamina elliptical to ovate, narrowly acuminate, serrate to remotely subserrulate. Inflorescences terminal, corymbose. Phyllaries c. 14–21, subimbricate, c. 2–3-seriate, unequal to subequal, persistent; receptacle convex, with few paleae. Florets c. 12–20; corollas whitish to lavender, narrowly funnelform, with broadly cylindrical basal tube, glabrous on outer surface below lobes; lobes about 1–2 times as long as wide, smooth on both surfaces, with few to many short-stipitate glands on outer surface; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms filiform, scarcely broadened distally, slightly mamillose to smooth. Achenes prismatic, 5-ribbed, sparsely setuliferous; carpopodium distinct; pappus setae uniseriate, 20–30, slender, contiguous, mostly persistent, sometimes slightly broadened distally, apical cells acute. Four species, Argentina, Brazil, Peru, Venezuela.

1591. ***Mexianthus*** B.L. Rob.

Mexianthus B.L. Rob., Contr. Gray Herb. n.s. 80: 5 (1928).

Erect subshrub. Leaves alternate, lamina ovate, acuminate, serrate. Inflorescence a laxly thyrsoid leafy panicle, capitula in dense spherical glomerules at tips of branchlets. Phyllaries 3(5), 1–2-seriate, distant, subequal or with 1–2 shorter outer phyllaries, inner forming thin sheath around floret; receptacle minute, glabrous. Floret 1; corollas white; with short cylindrical basal tube and broadly funnelform to slightly campanulate limb, glabrous on outer surface below lobes; lobes about as long as wide, slightly mamillose on inner surface, smooth with clustered short-stipitate glands on outer surface; anther collar narrowly

cylindrical; style base not enlarged, glabrous, arms with minutely but distinctly spathulate tips, slightly mamillose below tips. Achenes rather fusiform, 5-ribbed, glabrous below, with a few setulae above; carpopodium indistinct; pappus of 5–7 laciniate squamellae. One species, *M. mexicanus* B.L. Rob., Mexico.

1592. *Neohintonia* R.M. King & H. Rob.

Neohintonia R.M. King & H. Rob., Phytologia 22: 143 (1971).

Scandent subshrubs or shrubs. Leaves alternate to subopposite or opposite, lamina ovate, serrulate, short-acuminate. Inflorescence a lax narrowly thyrsoid leafy panicle; heads sessile in spherical glomerules. Phyllaries 4–5, weakly subimbricate, in 2 subequal series, oblong, persistent; receptacle minute, glabrous. Florets 1 or rarely 2; corollas white, with broadly cylindrical base and funnelform throat, scattered glands on outer surface, more numerous on lobes; lobes as long as wide, smooth on both surfaces; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms with minutely but distinctly spathulate tips, slightly mamillose below tips, with glands along inner surface. Achenes prismatic, 5-ribbed, with setulae and a few glands on sides; carpopodium shortly stopper-shaped; pappus uniseriate, of c. 25 slender scabrid slightly deciduous scarcely contiguous bristles, not broadened at tips, apical cells acute. One species, *N. monantha* (Sch. Bip.) R.M. King & H. Rob., Mexico.

1593. *Peteravenia* R.M. King & H. Rob.

Peteravenia R.M. King & H. Rob., Phytologia 21: 394 (1971).

Erect coarse herbs or subshrubs. Leaves opposite, lamina broadly ovate to deltoid or oblong-elliptical, usually serrulate to serrate, short-acuminate. Inflorescence pyramidally paniculate, sometimes laxly branched. Involucre often pale or brightly coloured, broadly campanulate. Phyllaries c. 25, strongly subimbricate, 3–4-seriate, unequal, gradate, inner mostly persistent; receptacle broadly convex, glabrous. Florets 18–75; corollas white, lavender or purple, narrowly funnelform, with outer and inner surfaces glabrous; lobes as long as wide or longer, smooth on both surfaces; anther collar usually narrowly cylindrical; style base not enlarged, glabrous, arms linear, sometimes slightly spathulate at tip, short-papillose below, mamillose distally. Achenes prismatic, 4–5-ribbed, narrowed and sometimes long-stipitate below, setuliferous mostly on ribs; carpopodium shortly stopper-shaped; pappus setae uniseriate, c. 30, deciduous, slender and non-contiguous below, broadened distally, apical cells acute. $n = 10$, c. 17. Five species, Central America.

1594. *Critoniella* R.M. King & H. Rob.

Critoniella R.M. King & H. Rob., Phytologia 30: 224 (1975).

Erect herbs or shrubs. Leaves opposite, lamina ovate to broadly ovate, serrulate to serrate, acute to acuminate. Inflorescence a broadly corymbose to cymose panicle; capitula sessile on congested glomerulate branchlets. Involucres narrowly cylindrical; phyllaries c. 18–32, markedly subimbricate to imbricate, 4–6(–7)-seriate, markedly unequal, gradate, inner usually rather persistent; receptacle flat, glabrous. Florets 6–25; corollas white, lavender, bluish or purple, narrowly funnelform, glabrous on inner surface and outside below lobes; lobes as long as wide, smooth on both surfaces, with few glands on outer surface; anther collar narrowly cylindrical; style base not enlarged, glabrous, arm appendages terete and filiform, densely short-papillose. Achenes ± fusiform, 5-ribbed, sparsely to moderately setuliferous; carpopodium stopper-shaped; pappus setae uniseriate, c. 40, persistent, slender, narrowly tapering to tip, apical cells acute. $n = 10$. Six species, Colombia, Peru, Venezuela.

1595. *Aristeguietia* R.M. King & H. Rob.

Aristeguietia R.M. King & H. Rob., Phytologia 30: 218 (1975).

Erect to procumbent shrubs to small trees. Leaves opposite, lamina broadly ovate to linear, often oblong or elliptical, usually densely crenulate to dentate. Capitula few to many, corymbose, pedicellate. Phyllaries c. 25–70, strongly subimbricate, 4–6-seriate, unequal, gradate, mostly persistent; receptacle flat to slightly convex, rarely conical, glabrous. Florets 13–100; corollas bluish, lavender, purple or pink, narrowly funnelform, inner and usually outer surfaces glabrous, some species with few hairs or few to many small glands on lobes; lobes slightly longer than wide, smooth on both surfaces; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms broadly strap-shaped, often longitudinally folded, mamillose. Achenes prismatic, 5-ribbed, usually with setulae; carpopodium indistinct; pappus setae c.

30–45, 1–2-seriate, persistent, congested, scarcely spreading at maturity, not broadened distally, apical cells acute. n = 10. Twenty-one species, Chile, Colombia, Ecuador, Peru.

1596. *Asplundianthus* R.M. King & H. Rob.

Asplundianthus R.M. King & H. Rob., Phytologia 30: 224 (1975).

Erect to scandent shrubs or trees. Leaves opposite, lamina ovate to lanceolate, subserrate to serrate. Inflorescence usually corymbose-paniculate, capitula sessile in glomerules. Phyllaries c. 15–20, subimbricate, c. 3–5-seriate, markedly unequal, gradate, inner deciduous; receptacle flat, glabrous. Florets 6–10; corollas lilac, lavender or purple, narrowly funnelform, usually with glands on outer surface; lobes as long as wide, smooth on both surfaces; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms narrowly linear, mamillose. Achenes prismatic, 5-ribbed, glabrous or sparsely setuliferous, rarely with a few glands; carpopodium stopper-shaped; pappus setae c. 30–40, slender, persistent, tapering distally, apical cells acute. n = 10. Seven species, Colombia, Ecuador, Peru.

1597. *Austrocritonia* R.M. King & H. Rob.

Fig. 122

Austrocritonia R.M. King & H. Rob., Phytologia 31: 115 (1975).

Erect shrubs or small trees. Leaves opposite, lamina ovate to elliptical, entire or remotely serrulate to closely serrate. Inflorescence broadly corymbose; capitula sessile in clusters. Phyllaries 12–25, markedly subimbricate, c. 3–5, markedly unequal, gradate, inner easily deciduous; receptacle flat to slightly convex, glabrous. Florets 5 or c. 10; corollas white, narrowly funnelform, glabrous on inner and outer surfaces; lobes ± twice as long as wide, smooth on both surfaces, glabrous; anther collar cylindrical; style base not enlarged, glabrous, arms linear, mamillose. Achenes prismatic, 5-ribbed, glanduliferous or glabrous; carpopodium distinct, long-cylindrical; pappus setae usually uniseriate, c. 40–50, persistent, congested, narrowed and becoming essentially smooth distally, apical cells acute. n = 10. Four species, Brazil.

1598. *Badilloa* R.M. King & H. Rob.

Badilloa R.M. King & H. Rob., Phytologia 30: 230 (1975).

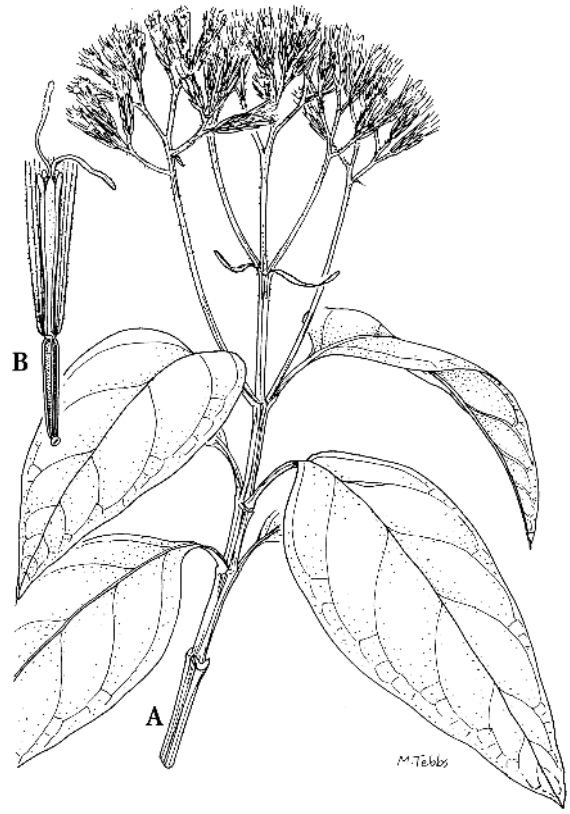

Fig. 122. Compositae-Eupatorieae. *Austrocritonia angulicaulis* (Critoniinae). **A** Flowering shoot. **B** Floret. (Drawings by Margaret Tebbs)

Erect shrubs, pubescent. Leaves opposite, lamina oblong to lanceolate, serrate to remotely subserrulate. Inflorescence corymbose. Phyllaries c. 16–25, markedly subimbricate, 4-seriate, markedly unequal, gradate, inner rather deciduous; receptacle flat to slightly convex, glabrous. Florets usually 4–10(–23); corollas white, lavender, pink or violet, narrowly funnelform, glabrous on inner surface and on outer surface of throat; lobes c. 1.5 times as long as wide, smooth on both surfaces, with glands or a few small hairs on outer surface near tips; anther collar usually broadly cylindrical; style base not enlarged, glabrous, arms broadly linear or strap-shaped, slightly mamillose. Achenes prismatic, 5-ribbed, body densely glandular-punctate; carpopodium short-cylindrical to annuliform; pappus setae uniseriate, c. 30–35, persistent, contiguous, not distinctly broadened nor flattened on outer surface at base, not or slightly broadened distally, apical cells acute. Ten species, Colombia, Ecuador, Peru, Venezuela.

1599. ***Grosvenoria*** R.M. King & H. Rob.

Grosvenoria R.M. King & H. Rob., Phytologia 30: 221 (1975).

Erect shrubs or small trees. Leaves opposite, lamina ovate to narrowly elliptical, entire to remotely serrate, sharply acute to short-acuminate. Inflorescence broadly corymbose paniculate. Phyllaries 12–15, markedly subimbricate, 3–5-seriate, markedly unequal, gradate, inner easily deciduous; receptacle flat to slightly convex, glabrous. Florets 5–10, fragrant; corollas pink to white, narrowly funnelform, with tube glabrous, without hairs on inner surface; cells of throat oblong with sinuous lateral walls; lobes c. 1.5 times as long as wide, smooth on both surfaces; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms very elongate, broadly linear, somewhat broader near tip, rounded to obtusely mamillose Achenes prismatic, 5-ribbed, glandular-punctate; carpopodium procurrent on to bases of ribs; pappus setae uniseriate, c. 30–40, persistent, congested, bases broadened and flattened, longer setae distinctly broadened distally, apical cells acute to obtuse. Four species, Ecuador, Peru.

1600. ***Corethamnium*** R.M. King & H. Rob.

Corethamnium R.M. King & H. Rob., Phytologia 39: 55 (1978).

Erect shrubs. Leaves opposite, lamina ovate to suborbicular, crenate-serrulate, short-obtuse to rounded. Inflorescence of dense small corymbose panicles on leafy branches. Phyllaries c. 16–18, subimbricate, c. 4–5-seriate, markedly unequal, gradate, mostly persistent; receptacle flat, glabrous. Florets c. 6; corollas white, with narrowly cylindrical tube and throat without external differentiation, with only lobes spreading, outer surface very sparsely glanduliferous, inner surface glabrous; lobes 3 times as long as wide, smooth on both surfaces; anther collars cylindrical; style base lacking basal node, glabrous, arms narrowly linear to filiform, terete distally, distinctly papillose. Achenes prismatic, 5-ribbed, glabrous or with very few small glands; carpopodium a short cylindrical ring without a distinct upper rim; pappus setae 1–2-seriate, c. 45, coarse, congested, persistent, less barbellate and narrowed distally, apical cells subacute. One species, *C. chocoensis* R.M. King & H. Rob., Colombia.

1601. ***Castanedia*** R.M. King & H. Rob.

Castanedia R.M. King & H. Rob., Phytologia 39: 58 (1978) ('*Castenedia*').

Erect shrubs. Leaves opposite, lamina elliptical or elliptical-oblong to slightly obovate, remotely serrulate, short-acute to obtuse. Inflorescence a dense corymbose panicle. Involucre cylindrical; phyllaries c. 25, subimbricate, c. 4-seriate, markedly unequal, gradate, inner easily deciduous; receptacle flat, glabrous. Florets 6–7; corollas white, narrowly funnelform, sparsely glanduliferous on narrow tube and on throat, more glands on lobes; lobes slightly longer than wide, smooth on both surfaces, anther collar cylindrical; style base not enlarged, glabrous, arms with broader stigmatic part, in appendage becoming filiform and terete with short papillae. Achenes prismatic, 5-ribbed, glabrous; carpopodium shortly stopper-shaped; pappus setae c. 60, congested, persistent, c. 2-seriate, narrowed distally, apical cells sharply acute. One species, *C. santamartensis* R.M. King & H. Rob., Colombia.

1602. ***Imeria*** R.M. King & H. Rob.

Imeria R.M. King & H. Rob., Phytologia 32: 271 (1975).

Erect slender shrubs or small trees. Leaves opposite, lamina thickly coriaceous to subcoriaceous, ovate to elliptical, entire or serrate, shortly acute to acuminate. Inflorescences terminal, corymbose, capitula sessile in dense clusters. Phyllaries c. 20–25, markedly subimbricate, 4–5-seriate, unequal, gradate, outer persistent, inner deciduous; receptacle slightly convex, sparsely hirsute. Florets 8–10; corollas rose-coloured or pink, narrowly funnelform, glabrous, lobes slightly longer than wide, smooth on inner surface, densely mamillose to papillose outside on the tips forming sclerified cap; anther collars shortly cylindrical; style base not enlarged, glabrous, arms linear, slightly mamillose. Achenes prismatic, 7–9-ribbed, glabrous; carpopodium very shortly cylindrical; pappus setae c. 50, 1–2-seriate, congested, subpersistent, longer setae broadened at tips, apical cells subacute to obtuse. One species, *I. memorabilis* (Maguire & Wurd.) R.M. King & H. Rob., Brazil, Venezuela.

1603. ***Malmeanthus*** R.M. King & H. Rob.

Malmeanthus R.M. King & H. Rob., Phytologia 47: 225 (1980).

Eupatorium L. sect. *Gyptis* (Cass.) Cabrera (1991), p.p.

Erect shrubs. Leaves opposite, lamina ovate, serrulate to subentire, scarcely acuminate. Inflorescences terminal, corymbose-paniculate, with ascending mostly alternate branching. Involucres

campanulate; phyllaries c. 20, strongly subimbricate, c. 4-seriate, markedly unequal, gradate, stramineous, inner easily deciduous; receptacle slightly convex, glabrous. Florets 5–22; corollas whitish, narrowly funnelform, with broad basal tube, glabrous; lobes about as long as wide to twice as long as wide, smooth, with or without sparse glands on outer surface; anther collar cylindrical; style base not enlarged, glabrous, arms narrowly linear, slightly to distinctly mamillose. Achenes prismatic, narrowed at base, 5-costate, setuliferous or glandular-punctate; carpopodium obsolete; pappus setae mostly uniseriate, c. 30–35, slender, persistent, not or scarcely broader and not more barbellate distally, apical cells acute. Three species, Argentina, Brazil, Paraguay, Uruguay.

1604. *Hughesia* R.M. King & H. Rob.

Hughesia R.M. King & H. Rob., Phytologia 47: 252 (1980).

Woody vines. Leaves opposite, lamina ovate, subentire, remotely and minutely serrulate, shortly acute, minutely acuminate. Inflorescences terminal on lateral branches, distinctly thyrsoid-paniculate with spreading branches; capitula sessile or subsessile in small clusters. Phyllaries c. 18, markedly subimbricate, c. 4-seriate, markedly unequal, gradate, inner easily deciduous; receptacle convex or hemispherical, glabrous. Florets c. 9; corollas purple in distal half when dry, narrowly funnelform with broadly cylindrical basal tubes, glabrous; lobes about as long as wide, smooth; anther collars cylindrical; style base not enlarged, glabrous, arms linear, densely mamillose or short-papillose. Achenes prismatic, 5-ribbed, with short setulae above, glabrous below; carpopodium short-cylindrical, slightly procurrent on to ribs; pappus setae uniseriate, c. 30, slender, persistent, not or scarcely broadened at tips, apical cells acute. One species, *H. reginae* R.M. King & H. Rob., Peru.

1605. *Ophryosporus* Meyen

Ophryosporus Meyen, Reise Erde 1: 402 (1834); Robinson, Proc. Amer. Acad. Arts 42: 17–27 (1906), rev.

Erect herbs or subshrubs, rarely scandent. Leaves usually opposite, lamina broadly lanceolate to elliptical, coarsely to scarcely serrate, acute to short-acuminate. Inflorescence corymbose or thyrsoid, with corymbose branches; lateral capitula sometimes from axils of lower phyllaries of central capitula. Phyllaries 4–8, distant, 1–2-seriate, mostly subequal, persistent; receptacle slightly convex, glabrous. Florets 3–12; corollas white, with constricted basal tube and narrowly funnelform or campanulate limb, usually glanduliferous outside, glabrous or rarely puberulous inside; lobes 1–2 times as long as wide, smooth; anther collar cylindrical; style base not enlarged, glabrous; style arms with strongly knob-like smooth tips, mamillose below. Achenes prismatic, 5-ribbed, with minutely gland-tipped hairs and/or setulae, base narrowed and sometimes striate; carpopodium slightly stopper-shaped; pappus of setae, broad laciniate scales, vestigial squamellae or lacking, setae barbellate to subplumose, persistent, not broadened distally, apical cells acute. $n = 10$. Thirty-seven species, Argentina, Bolivia, Brazil, Chile, Ecuador, Peru.

1606. *Cronquistianthus* R.M. King & H. Rob.

Cronquistianthus R.M. King & H. Rob., Phytologia 23: 410 (1972).

Erect or flexuous shrubs. Leaves opposite, lamina ovate or lanceolate to linear, entire to serrate, mostly acute, not acuminate. Inflorescence a terminal corymbose panicle. Phyllaries 12–25, markedly subimbricate, 3–5-seriate, markedly unequal, gradate, inner easily deciduous; receptacle flat, glabrous. Florets 8–18, fragrant; corollas white, lavender or bluish, narrowly funnelform with broadly cylindrical basal tube, outer surface glabrous or with few glands or scattered hairs, inner usually glabrous, rarely with small hairs; lobes as long as wide or slightly longer, smooth; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms broadly linear or narrowly linear with slightly dilated tips, short-papillose. Achenes prismatic, usually 5-ribbed, with few to many setulae predominantly on ribs, usually without glands; carpopodium distinct; pappus setae uniseriate, c. 30–35, persistent, contiguous, usually ± as long as corolla, more coarsely barbellate below, narrowed and sometimes nearly smooth at tips, apical cells acute. 20 species, Colombia, Ecuador, Peru.

Turner (1991b) did not accept *Cronquistianthus* other than as a group of species within *Eupatorium* s. lat.

1607. *Steyermarkina* R.M. King & H. Rob.

Steyermarkina R.M. King & H. Rob., Phytologia 22: 43 (1971).

Eupatorium L. sect. *Steyermarkina* (R.M. King & H. Rob.) Cabrera (1991).

Vines or flexuous shrubs. Leaves opposite, lamina ovate, entire, obtuse to acute. Inflorescence a lax thyrsoid panicle. Phyllaries c. 15–20, markedly subimbricate, 4–5-seriate, strongly unequal, gradate; receptacle convex to slightly conical, usually glabrous. Florets 3–5; corollas white, narrowly funnelform, outer surface glabrous or with minute glands or large hairs on base of throat and lobes, inner densely pilose on throat; lobes c. 2–4 times as long as wide, cut to below bases of anther sacs, smooth; anther collar narrowly cylindrical; style base not enlarged, glabrous, arms linear, mamillose. Achenes prismatic, 5–6-ribbed, densely short-setuliferous; carpopodium distinct, short; pappus setae mostly uniseriate, c. 30, slender, congested, persistent, slightly flattened on outer surface, longer setae distinctly broadened at tips, apical cells shortly to sharply acute. Four species, Brazil, Venezuela.

1608. *Neocabreria* R.M. King & H. Rob.

Neocabreria R.M. King & H. Rob., Phytologia 23: 151 (1972); King & Robinson, Phytologia 38: 424–428 (1978), key.
Eupatorium L. sect. *Gyptis* (Cass.) Cabrera (1991), p.p.
Eupatorium L. sect. *Heterocondylus* (R.M. King & H. Rob.) Cabrera (1991), p.p.

Erect subshrubs. Leaves opposite, lamina narrowly elliptical, closely serrulate to crenate-serrulate. Inflorescence a corymbose panicle. Phyllaries 25–30, strongly subimbricate, 3–4-seriate, markedly unequal, gradate, inner easily deciduous; receptacle flat to slightly convex, glabrous to densely hirsute. Florets 6–25; corollas white to rose-purple, narrowly funnelform, glabrous on outer surface, with numerous hairs on inner; lobes as long as wide or longer, smooth, glabrous or with sparse glands on outer surface, anther collar cylindrical; style base not enlarged, glabrous, arms broadly linear, almost smooth or distinctly mamillose. Achenes prismatic, 4–5-ribbed, with narrow base, setuliferous or glandular-punctate above; carpopodium indistinct; pappus setae uniseriate, 30–40, slender, contiguous, persistent, not broadened distally, apical cells acute. Five species, Argentina, Brazil, Paraguay.

1609. *Uleophytum* Hieron.

Uleophytum Hieron., Verh. Bot. Vereins Prov. Brandenburg 48: 198 (1906).

Woody vines. Leaves opposite, lamina broadly oblong-ovate, minutely denticulate, acuminate. Inflorescence of numerous capitula clustered in axils of leaves. Phyllaries c. 25, subimbricate, 3–4-seriate, unequal, gradate, mostly persistent; receptacle flat, glabrous. Florets c. 55–60; corollas whitish (?), narrowly funnelform, glabrous on inner and lower outside surfaces; lobes slightly longer than wide, smooth, with numerous glands clustered on outer surface; anther collar cylindrical; style base not enlarged, glabrous, arms narrowly linear, nearly filiform below, slightly broadened distally, mamillose. Achenes prismatic, 4–5-ribbed, glabrous except for few glands near top; carpopodium stopper-shaped; pappus setae uniseriate, c. 30, closely contiguous, persistent, not or slightly broader and not or slightly more barbellate distally, apical cells obtuse to short-acute. One species, *U. scandens* Hieron., Peru.

1610. *Amboroa* Cabrera

Amboroa Cabrera, Bol. Soc. Argent. Bot. 6: 91 (1956).

Small erect subshrubs or shrubs. Leaves opposite, lamina narrowly elliptical, remotely serrulate, sharply acute. Inflorescences on slender peduncles, with solitary capitula or a pair of sessile capitula. Phyllaries c. 25–40, markedly subimbricate, c. 4–5-seriate, unequal, gradate, inner persistent; receptacle convex, alveolate, glabrous. Florets 50–$\geq$80; corollas white, narrowly funnelform, with long cylindrical basal tube and rather cylindrical throat, glabrous; lobes short compared to length of corolla, longer than wide, smooth; anther collars cylindrical; style base not enlarged, glabrous, arms narrowly linear, becoming nearly filiform, with dense short-erect papillae. Achenes prismatic, 5–6-ribbed, glabrous; carpopodium indistinct; pappus setae uniseriate, c. 15–25, non-contiguous, slender, with bases broad and flattened, extremely slender and smooth for most of length, becoming greatly enlarged and subplumose distally with many large densely projecting obtuse or short-acute cells. Two species, Bolivia, Peru.

1611. *Tuberostylis* Steetz

Tuberostylis Steetz in Seemann, Bot. Voy. Herald 142 (1854).

Creeping to scandent herbs or shrubs. Leaves opposite, lamina slightly fleshy, glabrous, obovate to elliptical, entire to crenulate, obtuse to short-acuminate. Inflorescences terminal on lateral branches or sessile in axils of leaves; capitula sessile in small panicles or axillary fascicles. Phyl-

laries 25–30, subimbricate, 4–5-seriate, unequal, gradate, spreading at maturity or inner deciduous; receptacle flat or slightly convex, glabrous or with narrow paleae inside marginal florets. Florets c. 10–20; corollas white, narrowly tubular with slightly thickened base, glabrous on inner surface and lower outside surface; lobes 1–3 times as long as wide, smooth, mamillose at tips, a few minute glands on outer surface, anther collar cylindrical; style base not enlarged, glabrous, arms narrowly linear, slightly mamillose, slightly broadened distally. Achenes prismatic to cylindrical, 5-veined or 5-ribbed, whitish and strongly corticated when mature, glabrous; carpopodium short, indistinct; pappus absent. Two species, Colombia, Ecuador, Panama.

XXX.16. Subtribe Hebecliniinae R.M. King & H. Rob. (1980).

Erect perennial herbs or shrubs to small trees, never rosulate. Leaves usually opposite, often with long petioles; lamina often broad with rounded to cordate bases. Inflorescence laxly cymose to densely corymbose or thyrsoid-paniculate, with clustered capitula; phyllaries usually strongly subimbricate, gradate, with inner phyllaries easily deciduous, rarely distant and persistent; receptacle slightly convex to strongly hemispherical, usually epaleaceous, often with hairs. Florets 4–150; corollas narrowly funnelform, rarely with hairs inside of throat, cells of throat elongate with sinuous lateral walls; lobes triangular, usually about as long as wide, smooth on both surfaces; anther collar usually elongate, 5–10 times as long as wide, of even width; apical anther appendage usually longer than wide, style base not enlarged, glabrous; arms narrowly linear to filiform, mamillose to short-papillose, rarely with enlarged tips. Achenes prismatic, 5-ribbed; carpopodium annuliform to turbinate, procurrent on to ribs of achene; pappus setae usually uniseriate, rarely biseriate, usually of numerous capillary setae, usually persistent, apical cells sharply acute.

Key to the Genera

1. Receptacle paleaceous; florets numerous (c. 200) per capitulum **1618. *Matudina***
– Receptacle epaleaceous (rarely paleaceous in *Decachaeta*); florets few to many (4–80) per capitulum 2
2. Pappus absent or setae easily deciduous 3
– Pappus setae present and persistent 4
3. Pappus absent; receptacle glabrous; phyllaries ± biseriate **1616. *Erythradenia***
– Pappus present, setae deciduous; receptacle pubescent (rarely paleaceous); phyllaries 3–4-seriate **1615. *Decachaeta***
4. Phyllaries distant and subequal; achenes with a stipitate base **1613. *Amolinia***
– Phyllaries imbricate and gradate; achenes prismatic 5
5. Receptacle markedly convex to hemispherical; style arm appendages filiform **1612. *Hebeclinium***
– Receptacle slightly convex; style arm appendages linear to slightly clavate 6
6. Carpopodium symmetrical; receptacle sparsely to densely pubescent, rarely glabrous **1614. *Bartlettina***
– Carpopodium strongly asymmetrical; receptacle glabrous **1617. *Guayania***

Genera of Hebecliniinae

1612. *Hebeclinium* DC.

Hebeclinium DC., Prodr. 5: 136 (1836); Diaz Piedrahita & Mendez Ramirez, Revista Acad. Colomb. Ci. Exact. 24: 25–44 (2000), reg. rev.

Eupatorium section *Hebeclinium* (DC.) Benth. ex Baker (1876).

Large herbs or subshrubs. Leaves opposite, lamina broadly ovate to deltoid or lanceolate, usually crenate or serrate-pinnate. Inflorescence a lax cyme with widely spreading branches. Involucres broadly campanulate; phyllaries c. 25–40, 3–5-seriate, markedly unequal, outer persistent, inner deciduous; receptacle hemispherical, sclerified throughout, glabrous to densely hirsute. Florets (12–)20–80; corollas white or pink, outer surface glabrous below, inner surface of throat in some species with numerous hairs; lobes slightly longer than wide, usually with prominent multicellular uniseriate hairs and few glands on outer surface; anther collar usually slender; apical anther appendages large, ovate-triangular to oblong, slightly longer than wide; style arms narrowly filiform, terete, mamillose, sometimes somewhat broadened distally. Achenes narrowed below, 4–5-ribbed, sometimes setulose; carpopodium scarcely distinct; pappus setae uniseriate, c. 30–40, barbellate, slender, persistent, capillary, sometimes broadened distally. $n = 10$. Twenty species, neotropics.

1613. *Amolinia* R.M. King & H. Rob.

Amolinia R.M. King & H. Rob., Phytologia 24: 265 (1972).

Erect shrubs or small trees. Leaves opposite, lamina ovate, entire, narrowly acuminate. Inflorescence

a corymbose panicle. Involucres narrowly campanulate; phyllaries c. 15, ± distant, 2–3-seriate, slightly unequal, linear; receptacle slightly convex, usually short-pubescent. Florets 20–25; corollas white, with cylindrical basal tube, outer surface sparsely glanduliferous, inner surface smooth and glabrous; lobes ovate-triangular, anther collar slender and elongate; apical anther appendage large, oblong, slightly longer than wide; style arms narrowly linear, mamillose. Achenes elongate, 5-ribbed, densely glanduliferous and sparsely setuliferous; carpopodium very short; pappus setae uniseriate, c. 30 (40–50?), slender, barbellate, persistent, not broadened distally. n = 10. One species, *A. heydeana* (B.L. Rob.) R.M. King & H. Rob., Guatemala, Mexico.

1614. *Bartlettina* R.M. King & H. Rob.

Bartlettina R.M. King & H. Rob., Phytologia 22: 160 (1971).

Erect shrubs or small trees. Leaves opposite, lamina lanceolate to broadly ovate. Inflorescence usually corymbose-paniculate. Involucres broadly campanulate; phyllaries 3–5-seriate, c. 20–50, weakly to strongly subimbricate, inner deciduous; receptacle broadly convex, usually sparsely to densely pubescent. Florets 8–150; corollas white, lavender, blue or purple, inner surface glabrous; lobes triangular, outer surface usually densely puberulous, often glanduliferous; anther collars very elongate; apical anther appendage large, oblong-ovate to long-triangular, longer than wide; style arms narrowly linear, sometimes slightly broadened distally, nearly smooth to short-papillose. Achenes 5-ribbed, glabrous to sparsely setuliferous, rarely with glands; carpopodium slightly to distinctly enlarged, symmetrical; pappus setae 1–2-seriate, c. 30–40, slender, barbellate, persistent, rarely broadened distally. n = 10, 16. Circa 37 species, tropical Central and South America.

1615. *Decachaeta* DC.

Decachaeta DC., Prodr. 5: 133 (1836); King & Robinson, Brittonia 21: 275–284 (1969), rev.

Erect or arching subshrubs or shrubs. Leaves alternate or sometimes opposite, lamina elliptical, ovate or suborbicular, sometimes rather lobed, margins serrate or crenate, acuminate. Inflorescence a thyrsoid panicle, usually leafy. Involucres campanulate; phyllaries 3–4-seriate, c. 10–15, subimbricate; receptacle slightly to strongly convex, sometimes hirsute. Florets 4–30; corollas white, sometimes bluish, narrowly funnelform, with cylindrical basal tube, outer surface glabrous or sparsely glanduliferous; lobes triangular; anther collar rather narrow, often long; apical anther appendage short, much wider than long, margin strongly reflexed; style arms narrowly linear, slightly broadened distally, mamillose. Achenes 4–5-ribbed, with numerous setulae mostly on ribs; carpopodium short-cylindrical or stopper-shaped; pappus setae uniseriate, c. 10–30, slender, barbellate, somewhat deciduous, often distinctly dilated distally. n = 16. Seven species, Costa Rica, Guatemala, Mexico, Panama.

1616. *Erythradenia* (B.L. Rob.) R.M. King & H. Rob.

Erythradenia (B.L. Rob.) R.M. King & H. Rob., Brittonia 21: 285 (1969).

Erect or arching subshrubs, with numerous reddish or yellowish glandular punctae. Leaves alternate, lamina broadly ovate, often with lobed dentate margins, shortly and often broadly acuminate. Inflorescence an elongate leafy thyrsoid panicle with sessile or subsessile capitula in small clusters. Involucres short, broadly campanulate; phyllaries c. 10, weakly subimbricate, ± biseriate, somewhat unequal, persistent; receptacle slightly convex, glabrous. Florets c. 6; corollas white, with broadly cylindrical basal tube, outer surface glanduliferous, inner glabrous; lobes triangular, about as long as wide, with numerous glands on outer surface; anther collar narrowly cylindrical; apical anther appendage very short, much wider than long, reflexed; style arm appendages narrowly linear, slightly broader distally, mamillose. Achenes 5-ribbed, setuliferous; carpopodium a narrow rim, not procurrent on to ribs; pappus setae obsolete, short, barbellate, persistent, scarcely distinguishable from setulae of achene ribs. n = 16. One species, *E. pyramidalis* (B.L. Rob.) R.M. King & H. Rob., Mexico.

1617. *Guayania* R.M. King & H. Rob.

Guayania R.M. King & H. Rob., Phytologia 21: 302 (1971); Pruski, Fl. Venez. Guayana 3: 293–295 (1997), rev.

Erect perennial herbs or shrubs. Leaves opposite, lamina elliptical to broadly ovate, serrate. Inflorescences strongly cymose, ultimate branchlets with clusters of sessile or subsessile capitula. Involucres campanulate; phyllaries c. 12–25, subimbricate, ± 3–4-seriate, unequal, rather persistent; receptacle convex to hemispherical, glabrous. Florets

5–25; corollas bluish-white, lavender or white, with cylindrical basal tube, outer surface glabrous below lobes, inner glabrous; lobes triangular, outer surface densely short-pubescent; anther collars slender; apical anther appendage large, triangular, longer than wide; style arm appendages filiform, essentially terete, densely short-papillose. Achenes 5-ribbed, glabrous or with few setulae; carpopodium strongly asymmetrical; pappus setae uniseriate, c. 30–40, slender, barbellate, persistent, narrowed distally. Five species, Brazil, Colombia, Guyana, Venezuela.

1618. ***Matudina*** R.M. King & H. Rob.

Matudina R.M. King & H. Rob., Phytologia 26: 171 (1973).

Coarse sprawling to erect calciphilous subshrubs or shrubs. Leaves opposite, lamina broadly ovate, dentate-lobate. Inflorescences subcymose. Capitula broadly campanulate; subinvolucral bracts and phyllaries c. 75–125, 5–6-seriate, subequal, narrowly lanceolate; receptacle broadly convex, paleaceous. Florets c. 200; corollas white, nearly cylindrical, with throat slightly constricted above, glabrous except for few glands on outer surface of lobes; lobes small compared to length of corolla, about as long as wide, smooth on inner and most of outer surface: anther collar slender; apical anther appendages large, oblong, slightly longer than wide, not retuse or grooved; style arms narrowly linear, slightly broadened distally, ± mamillose, apex obtuse. Achenes narrowly fusiform, 5-ribbed, with short setulae mostly on ribs; carpopodium symmetrical, shortly stopper-shaped; pappus setae uniseriate, c. 15–22, slender, barbellate, noncontiguous or scarcely contiguous, rather easily deciduous, broadened and more barbellate distally. $n = 16$. One species, *M. corvi* (McVaugh) R.M. King & H. Rob., Mexico.

XXX.17. Subtribe Neomirandeinae R.M. King & H. Rob. (1980).

Large herbs or shrubs to small trees, epiphytic or humicolous. Leaves opposite or whorled, lamina deltoid or aceriform to elliptical or oblong, often slightly fleshy, entire to coarsely lobed and dentate. Inflorescence a broadly cymose or corymbose panicle, with clustered capitula; phyllaries c. 9–28, strongly subimbricate, 3–4-seriate, gradate, ecostate, inner somewhat deciduous, outer persistent; receptacle flat or slightly convex, without paleae, with or without hairs. Florets 2–28; corollas white to reddish purple, narrowly funnelform, with or without hairs inside throat; lobes triangular to narrowly oblong, smooth on both surfaces; anther collar elongate, 5–10 times as long as wide, of even width; apical anther appendages longer than wide; style base with or without enlargement, glabrous; style arms narrowly linear, not strongly clavate at tip. Achenes prismatic, 5-ribbed; carpopodium short; pappus setae numerous, persistent, capillary, apical cells obtuse to acute.

Bremer et al. (1994) suggested that the subtribe be synonymized with Hebecliniinae, to date the only author to have done so. Turner (1997) left the 'Hebeclinium group' and the 'Neomirandea group' separate. We retain the two separate in this account.

Only one genus:

1619. ***Neomirandea*** R.M. King & H. Rob.

Neomirandea R.M. King & H. Rob., Phytologia 19: 360 (1970); King & Robinson, Phytologia 19: 305–310 (1970), rev.; King & Robinson, Ann. Missouri Bot. Gard. 62: 888–1004 (1976), reg. rev.; Scott, Systematic studies of *Neomirandea* (Asteraceae–Eupatorieae). Unpubl. Ph.D. Thesis, Univ. Austin Texas (1985), rev.

Characters of the subtribe. $n = 17$, 20, c. 24, 25. Twenty-eight species, Colombia, Costa Rica, Ecuador, Mexico, Panama.

Asteroid Genus of Uncertain Placement

C. Jeffrey

1620. ***Symphyllocarpus*** Maxim.

Symphyllocarpus Maxim., Prim. Fl. Amur.: 151, t. 8, f. 1 (1859); Smol'yaninova, Bot. Mat. Gerb. Bot. Inst. Komarova 20: 282–288 (1960), morph., syst.

Annual herb; leaves alternate, lanceolate, apically 1–3-denticulate, glabrous. Capitula congested 2–4 together in the stem bifurcations, globose, heterogamous, disciform to minutely radiate. Phyllaries subuniseriate, equal, imbricate, membranous, margins transparent. Receptacle flat, paleate. Outer florets pistillate, numerous in several series; corolla filiform, tubular or minutely radiate, (2–)3(–4)-lobed, pale yellow. Inner florets few (6–20), perfect; corolla with campanulate 4-lobed limb, anthers ecalcarate, shortly caudate, apically rounded to truncate, unappendaged; style arms short, ob-

long, with sweeping hairs extending to shortly below the bifurcation; ovary adnate to 1 or 2 of the receptacular scales. Achenes homomorphic, terete, smooth, glandular and sparsely pilose with long, apically divergent twin hairs, adnate to 1 or rarely 2 of the receptacular scales. Pappus absent. One species, *S. exilis* Maxim., north-east Asia.

The lack of palynological, carpological and molecular data precludes the assignment of this undoubtedly Asteroid genus to a more definite systematic position. Smol'yaninova made it the type of its own subtribe of Inuleae which would now be placed in Gnaphalieae, where the genus would undoubtedly be anomalous.

Selected Bibliography to Compositae

Ahlstrand, L. 1988. Embryology of Calenduleae (Compositae). Nordic J. Bot. 5: 79–97.

Ahlstrand, L. 1992. Contributions to the embryology of Arctotideae (Compositae). The genera *Dymondia* Compton, *Cullumia* R. Br., *Didelta* L'Herit. and *Heterolepis* Cass. Comp. Newslett. 22: 1–4.

Albach, D.C., Soltis, P.S., Olmstead, R.G. 2001. Phylogenetic analysis of Asteridae based on sequences of four genes. Ann. Missouri Bot. Gard. 88: 163–212.

Alvarenga, S.A.V., Ferreira, M.J.P., Rodrigues, G.V., Emerenciano, V.P. 2005. A general survey and some taxonomic implications of diterpenes in the Asteraceae. Bot. J. Linn. Soc. 147: 291–308.

Anderberg, A.A. 1982. The genus *Anvillea* (Compositae). Nordic J. Bot. 2: 297–305.

Anderberg, A.A. 1985. The genus *Iphonia* (Compositae-Inuleae). Nordic J. Bot. 5: 169–194.

Anderberg, A.A. 1989. Phylogeny and reclassification of the tribe Inuleae (Asteraceae). Canad. J. Bot. 67: 2277–2296.

Anderberg, A.A. 1991a. Taxonomy and phylogeny of the tribe Gnaphalieae (Asteraceae). Opera Bot. 104: 1–195.

Anderberg, A.A. 1991b. Taxonomy and phylogeny of the tribe Inuleae (Asteraceae). Pl. Syst. Evol. 176: 75–123.

Anderberg, A.A. 1991c. Taxonomy and phylogeny of the tribe Plucheeae (Asteraceae). Pl. Syst. Evol. 176: 145–177.

Anderberg, A.A., Eldenäs, P., Bayer, R.J., Englund, M. 2005. Evolutionary relationships in the Asteraceae tribe Inuleae (incl. Plucheeae) evidenced by DNA sequences of ndhF; with notes on the systematic position of some aberrant genera. Organism Diversity Evol. 5: 135–146.

Aristeguieta, L. 1964. *Lepidesmia*. Compositae. In: Lasser, T. (ed.) Flora de Venezuela, vol. 10, 2. Caracas: Inst. Botanico, pp. 529–531.

Ariza Espinar, L., Cerana, M.M. 1986. Contribucion al conocimiento de las especies de *Stevia* (*Asteraceae*) del centro de Argentina. Bol. Acad. Nac. Ci. Cordoba 57: 381–400.

Baagøe, J. 1980. SEM studies in ligules of Lactuceae (Compositae). Bot. Tidsskr. 75: 199–217.

Babcock, E.B., Stebbins, G.L. 1943. Systematic studies of Cichoroideae. Univ. Calif. Publ. Bot. 18: 227–240.

Badillo, V.M. 1992. Anotaciones adicionales al género *Tamananthus* Badillo (Heliantheae-Asteraceae). Ernstia 2: 17–19.

Bain, J.F., Tyson, S., Bray, D.F. 1997. Variation in pollen wall ultrastructure in New World Senecioneae (Asteraceae), with special reference to *Packera*. Canad. J. Bot. 75: 730–735.

Baldwin, B.G. 2003a. A phylogenetic perspective on the origin and evolution of Madiinae. In: Carlquist, S., Baldwin, B.G., Carr, G.D. (eds) Tarweeds & silverswords: evolution of the Madiinae (Asteraceae). St. Louis: Missouri Botanical Garden Press, pp. 193–228.

Baldwin, B.G. 2003b. Characteristics and diversity of Madiinae. In: Carlquist, S., Baldwin, B.G., Carr, G.D. (eds) Tarweeds & silverswords: evolution of the Madiinae (Asteraceae). St. Louis: Missouri Botanical Garden Press, pp. 17–52.

Baldwin, B.G., Wessa, B.L. 2000a. Origin and relationships of the tarweed–silversword lineage (Compositae–Madiinae). Amer. J. Bot. 87: 1890–1908.

Baldwin, B.G., Wessa, B.L. 2000b. Phylogenetic placement of *Pelucha* and new subtribes in Helenieae sensu stricto (Compositae). Syst. Bot. 25: 522–538.

Baldwin, B G., Wessa, B.L., Panero, J.L. 2002. Nuclear rDNA evidence for major lineages of helenioid Heliantheae (Compositae). Syst. Bot. 27: 161–198.

Baldwin, B.G., Wessa, B.L., Panero, J.L. 2003. Evolutionary insights from a putative taxonomic garbage can. Tribe Helenieae revisited and revised. Comp. Newslett. 40: 8.

Barclay, H.S., Earle, F.R. 1965. The search for new industrial crops. V. The South African Calenduleae (Compositae) as a source of new oil seeds. Econ. Bot. 19: 33–43.

Barkley, T.M. 1999. The segregates of *Senecio*, s.l., and *Cacalia*, s.l., in the flora of North America north of Mexico. Sida 18: 661–672.

Batygina, T.B., Yakovlev, M.B. 1987. Comparative embryology of flowering plants. Davidiaceae-Asteraceae (in Russian). Leningrad: Izdat. Nauka, 391 pp.

Bayer, R.J., Cross, E.W. 2002. A reassessment of tribal affinities of the enigmatic genera *Printzia* and *Isoetopsis* (Asteraceae), based on three chloroplast sequences. Austral. J. Bot. 50: 677–686.

Bayer, R.J., Puttock, C.F. 1999. Molecular systematics of southern hemisphere Gnaphalieae. In: Anon. (ed.) XVI International Botanical Congress Abstracts. St. Louis: Missouri Botanical Garden, p. 17.

Bayer, R.J., Starr, J.R. 1998. Tribal phylogeny of the Asteraceae based on two non-coding chloroplast sequences, the *trn*L intron and *trn*L/*trn*F intergenic spacer. Ann. Missouri Bot. Gard. 85: 242–256.

Bayer, R.J., Puttock, C.F., Kelchner, S.A. 2000. Phylogeny of South African Gnaphalieae (Asteraceae) based on two non-coding chloroplast sequences. Amer. J. Bot. 87: 259–272.

Bayer, R.J., Greber, D.G., Bagnall, N.H. 2002. Phylogeny of Australian Gnaphalieae (Asteraceae) based on chloroplast and nuclear sequences, the *trn*L intron,

the *trn*L/*trn*F intergenic spacer, *mat*K and ETS. Syst. Bot. 27: 801–814.

Bayer, R.J., Breitwieser, I., Dillon, M., Koekemoer, M., Ward, J. 2003. Phylogeny of the Gnaphalieae based on three cpDNA sequences. Comp. Newslett. 40: 8.

Beck, J.B., Nesom, G.L., Calie, P.J., Baird, G.I., Small, R.L., Schilling, E.E. 2004. Is subtribe Solidagininae (Asteraceae) monophyletic? Taxon 53: 691–698.

Bentham, G. 1873a. Compositae. In: Bentham, G., Hooker, J.D., Genera Plantarum, vol. II, 1. London: Lovell Reeve, pp. 163–533 (plus Addenda et Corrigenda).[1]

Bentham, G. 1873b. Notes on the classification, history and geographical distribution of Compositae. J. Linn. Soc., Bot. 13: 335–577.

Berry, P.E., Calvo, R.N. 1989. Wind pollination, self-incompatibility and shifts in pollination systems in the high Andean genus *Espeletia* (Asteraceae). Amer. J. Bot. 76. 1602–1614.

Bierner, M.W. 2001. Taxonomy of *Hymenoxys* subgenus *Picradenia* and a conspectus of the subgenera of *Hymenoxys* (Asteraceae: Helenieae: Tetraneurinae). Lundellia 4: 37–63.

Blackmore, S. 1981. Palynology and intergeneric relationships in subtribe Hyoseridinae (Compositae: Lactuceae). Bot. J. Linn. Soc. 82: 1–13.

Blackmore, S. 1982. Palynology of subtribe Scorzonerinae (Compositae: Lactuceae) and its taxonomic significance. Grana 21: 149–160.

Blackmore, S. 1986. The identification and taxonomic significance of lophate pollen in the Compositae. Canad. J. Bot. 64: 3101–3112.

Blackmore, S., Persson, V. 1996. Palynology and systematics of the Crepidinae (Compositae: Lactuceae). In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 111–122.

Blake, S.F. 1935. The genus *Chionopappus* of Bentham (Asteraceae). J. Wash. Acad. Sci. 25: 488–493.

Bohlmann, F., Jakupovic, J. 1990. Progress in the chemistry of the Vernonieae (Compositae). Pl. Syst. Evol. suppl. 4: 3–43.

Bohlmann, F., Burkhardt, T., Zdero, C. 1973. Naturally occurring acetylenes. London: Academic Press.

Bohlmann, F., Zdero, C., King, R.M., Robinson, H. 1980a. New helangiolides from *Conocliniopsis prasiifolia*. Phytochemistry 19: 1547–1549.

Bohlmann, F., Zdero, C., Robinson, H., King, R.M. 1980b. Guaianolides from *Agrianthus pungens*. Phytochemistry 19: 1873–1874.

Bohlmann, F., Abraham, W.-R., Robinson, H., King, R.M. 1981a. Heliangiolides and other constituents from *Bejaranoa semistriata*. Phytochemistry 20: 1639–1642.

Bohlmann, F., Jakupovic, J., King, R.M., Robinson, H. 1981b. New germacranolides, guaianolides and rearranged guaianolides from *Lasiolaena santosii*. Phytochemistry 20: 1613–1622.

Bohlmann, F., Suwita, A., Robinson, H., King, R.M. 1981c. Six guaianolides from *Stylotrichium rotundifolium*. Phytochemistry 20: 1887–1890.

Bohlmann, F., Zdero, F., Pickard, J., Robinson, H., King, R.M. 1981d. New types of sesquiterpene lactones and other constituents from *Trichogonia* species. Phytochemistry 20: 1323–1333.

Bohlmann, F., Singh, P., King, R.M., Robinson, H. 1982a. New guaianolides from *Pseudostifftia kingii*. Phytochemisty 21: 1171–1172.

Bohlmann, F., Jakupovic, J., Schuster, A., King, R.M., Robinson, H. 1982b Guaianolides and homoditerpenes from *Lasiolaena morii*. Phytochemistry 21, 1: 161–165.

Bohlmann, F., Zdero, C., King, R.M., Robinson, H. 1984a Heliangiolides and bejaranolides from *Conocliniopsis prasiifolia*. Phytochemistry 23, 7: 1509–1511.

Bohlmann, F., Zdero, C., Jakupovic, J., Gerke, T., Wallmeyer, M., King, R.M., Robinson, H. 1984b Neus Sesquiterpenlactone und Rosan-Derivate aus *Trichogonia*-Arten. Liebigs Ann. Chem. 1984: 162–185.

Bohm, B.A., Stuessy, T.F. 1995. Flavonoid chemistry of Barnadesioideae (Asteraceae). Syst. Bot. 20: 22–27.

Bohm, B.A., Stuessy, T.F. 2001. Flavonoids of the sunflower family (Asteraceae). Berlin Heidelberg New York: Springer.

Bolick, M.R. 1978. Taxonomic, evolutionary and functional considerations of Compositae pollen ultrastructure and sculpture. Pl. Syst. Evol. 130: 209–218.

Bremer, K. 1987. Tribal interrelationships of the Asteraceae. Cladistics 3: 210–253.

Bremer, K. 1993. New subtribes of the Lactuceae (Asteraceae). Novon 3: 328–330.

Bremer, K. 1994. Asteraceae. Cladistics & classification. Portland, OR: Timber Press.

Bremer, K. 1996. Major clades and grades of the Asteraceae. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 1–7.

Bremer, K., Gustafsson, M.H.G. 1997. East Gondwana ancestry of the sunflower alliance of families. Proc. Natl Acad. Sci. U.S.A. 94: 9188–9190.

Bremer, K., Humphries, C.J. 1993. Generic monograph of the Asteraceae-Anthemideae. Bull. Nat. Hist. Mus. London 23: 71–177.

Bremer, K., Jansen, R.K. 1992. A new subfamily of the Asteraceae. Ann. Missouri Bot. Gard. 79: 414–415.

Bremer, K., Anderberg, A.A., Karis, P.O., Lundberg, J. 1994. Tribe Eupatorieae. In: Bremer, K. (ed.) Asteraceae. Cladistics & classification. Portland, OR: Timber Press, pp. 625–680.

Brouillet, L., Allen, G., Semple, J.C., Ito, M. 2001. ITS phylogeny of North American asters (Asteraceae: Astereae). In: Proceedings Botany 2001, ASPT/BSA/IOPB Joint Meeting, Albuquerque, New Mexico, 12–16 August 2001.

Brown, K.S. 1984. Adult-obtained pyrrolizidine alkaloids defend ithomine butterflies against a spider predator. Nature 309: 707–709.

Brown, G.K., Clark, W.D. 1981. Chromosome numbers in South American *Haplopappus* Cass. (Compositae). Amer. J. Bot. 68: 1218–1221.

Brown, G.K., Clark, W.D. 1982. Taxonomy of *Haplopappus* sect. *Gymnocoma* (Compositae). Syst. Bot. 7: 199–213.

[1] The authorship of genera described or combined in Bentham and Hooker's 'Genera Plantarum' (1873) has been variously referred to as Benth. (1873), Benth. in Benth. & Hook. f. (1873) or Benth. & Hook. f. (1873).

Bruhl, J.J., Quinn, C.J. 1990. Cypsela anatomy in the Cotuleae (Asteraceae: Anthemideae). Bot. J. Linn. Soc. 102: 37–59.

Bruhl, J.J., Quinn, C.J. 1991. Floral morphology and a reassessment of affinities in the 'Cotuleae' (Asteraceae). Austral. Syst. Bot. 4: 637–654.

Cabrera, A.L. 1937. Revisión del genero *Chaetanthera* (Compositae). Revista Mus. La Plata ser. 2, 1(3): 87–210.

Cabrera, A.L. 1954. Compuestas sudamericanas nuevas o críticas, II. Notas del Museo, Universidad Nacional de Eva Peron 17, 84: 71–80.

Cabrera, A.L. 1959. Revisión del género *Dasyphyllum* (Compositae). Revista Mus. La Plata, Secc. Bot. 9: 21–100.

Cabrera, A.L. 1961. Compuestas Argentinas. Clave para la determinación de los géneros. Revista Mus. Argent. Ci. Nat., Bot. 2: 291–362.

Cabrera, A.L. 1965. Revision del genero *Mutisia* (Compositae). Opera Lilloana 13: 1–227.

Cabrera, A.L. 1971. Revision del genero *Gochnatia* (Compositae). Revista Mus. La Plata, Secc. Bot. 12: 1–160.

Cabrera, A.L. 1977. Mutisieae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, vol. 2. London: Academic Press, pp. 1039–1066.

Cabrera, A.L. 1978. Flora de la Provincia de Jujuy, vol. 10. Buenos Aires: INTA.

Cabrera, A.L. 1982. Revisíon del género *Nassauvia* (Compositae). Darwiniana 24: 283–379.

Cabrera, A.L. 1996. *Compositae* III, Asteroideae, Eupatorieae. In: Flora of Paraguay, vol. 25. Missouri Botanical Garden and Conservatoire et Jardin botaniques de la Ville de Genève, Geneva.

Cabrera, A.L., Freire, S.E. 1997. *Stevia*. In: Espinar, L.A. (co-ord.) Flora Fanerogâmica Argentina, fasc. 47. 280. Asteraceae, parte 8. Tribu II. Eupatorieae. Cordoba: ProFlora Conicet.

Cabrera, A.L., Freire, S.E. (compilers) 1999. Eupatorieae in Asteraceae. In: Zuloaga, O., Morrone, O. (eds) Catálogo de las plantas vasculares de la República Argentina, II. Monogr. Syst. Bot. 75.

Cabrera, A.L., Klein, R.M. 1989 (1991). Tribo Eupatorieae. Compostas 4. In: Reitz, R. (ed.) Flora ilustrada Catarinense. Part 1. Monografia. Itajaí, Brazil: Herbário Barbosa Rodrigues.

Candolle, A.P. de 1836. Ordo CII: Compositae [part 1]. Prodr. 5: 4–706. Paris: Treuttel et Würtz.

Canne, J.M. 1977. A revision of the genus *Galinsoga* (Compositae: Heliantheae). Rhodora 79: 319–389.

Carlquist, S. 1959. Studies on Madiinae: anatomy, cytology, and evolutionary relationships. Aliso 4: 171–236.

Carlquist, S. 1960. Wood anatomy of Cichorieae (Compositae). Trop. Woods 112: 65–91.

Carlquist, S. 1966. Wood anatomy of Compositae: a summary with comments on factors controlling wood evolution. Aliso 6: 25–44.

Carlquist, S. 1976. Tribal interrelationships and phylogeny of the Asteraceae. Aliso 8: 465–492.

Cassini, H. 1819. Sixième mémoire sur la famille des Synanthérées, contenant les caractères des tribus. J. Phys. Chim. Hist. Nat. Arts 88: 150–163, 189–204.

Cassini, H. 1823. Liabon. In: Cuvier, G. (ed.) Dictionnaire des Sciences Naturelles 26: 203–211. Reprinted in King, R.M., Dawson, H.W. (eds) 1975, Cassini on Compositae. New York: Oriole Editions.

Cassini, H. 1825. Oligacte. In: Cuvier, G. (ed.) Dictionnaire des Sciences Naturelles 36: 16–18. Reprinted in King, R.M., Dawson, H.W. (eds) 1975, Cassini on Compositae. New York: Oriole Editions.

Cassini, H. 1829. Tableau synoptique des Synanthérées. Ann. Sci. Nat. Paris 17: 387–423.

Cassini, H. 1830. Zyegee. In: Cuvier, G. (ed.) Dictionnaire des Sciences Naturelles 60: 560–619. Reprinted in King, R.M., Dawson, H.W. (eds) 1975, Cassini on Compositae. New York: Oriole Editions.

Cerana, M.M., Ariza Espinar, L. 1995. Sobre la presencia de domacios en *Mikania* (Asteraceae). Kurtziana 24: 7–18.

Chase, M.W., Soltis, D.E., Olmstead, R.G., Morgan, D., Les, D., Mischler, B.D., Duvall, M.R., Price, R.A., Hills, H.G., Qia, Y., Kron, K.A., Rettig, J.A., Conti, E., Palmer, J.D., Manhart, J.R., Sytsma, K.J. Michaels, H.J., Kress, W.J., Donoghue, M.J., Clark, W.-D., Hendren, M., Gaut, B.S., Jansen, R.K., Kim, K.-J, Wimpee, C.F., Smith, J.F., Furnier, G.R., Strauss, S., Xiang, Q., Plunkett, G.M., Soltis, P.S., Swensen, S., Eguiarte, L.E., Learn, G.H. Jr., Barrett, S.C.H., Graham, S., Dayanadan, S., Albert, V.A. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbc* L. Ann. Missouri Bot. Gard. 80: 528–580.

Clark, W.D. 1979. The taxonomy of *Hazardia* (Compositae: Astereae). Madroño 26: 105–127.

Claßen-Bockhoff, R. 1992. Florale Differenzierung in komplex organisierten Asteraceen-Köpfen. Flora 186: 1–22.

Claßen-Bockhoff, R. 1996. Functional units beyond the level of the capitulum and cypsela in Compositae. In: Caligari, P.D., Hind, D.J.N. (eds) Compositae: biology & utilization. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 2. Royal Botanic Gardens, Kew, pp. 129–160.

Claßen-Bockhoff, R., Froebe, H., Langerheins, D. 1989. Die Infloreszenzstruktur von *Gundelia tournefortii* L. (Asteraceae). Flora 182: 463–479.

Cronquist, A.J. 1955. Phylogeny and taxonomy of the Compositae. Amer. Midl. Naturalist 53: 478–511.

Cross, E.W., Quinn, C.J., Wagstaff, S.J. 2002. Molecular evidence for the polyphyly of *Olearia* (Astereae: Asteraceae). Pl. Syst. Evol. 235: 99–120.

Cuatrecasas, J. 1970. Reinstatement of the genus *Llerasia* (Compositae). Biotropica 2: 39–45.

Cuatrecasas, J. 1976. A new subtribe in the Heliantheae (Compositae): Espeletiinae. Phytologia 35: 42–61.

D'Arcy, W. 1975. Conspectus of the Panamanian Compositae. In: Woodson, R.E., Schery, R.W. et al. (eds) Flora of Panama, vol. Family 184, pp. 845–846. Compositae. Ann. Missouri Bot. Gard. 62: 835–1321.

DeJong, D.C., Beaman, J.H. 1963. The genus *Olivaea* (Compositae, Astereae). Brittonia 15: 86–92.

DeVore, M.L., Stuessy, T.F. 1995. The place and time of the origin of the Asteraceae, with additional comments on the Calyceraceae and Goodeniaceae. In: Hind, D.J.N., Jeffrey, C., Pope, G.V. (eds) Advances in Compositae systematics. Royal Botanic Gardens, Kew, pp. 23–40.

Dillon, M.O., Hensold, N. (compilers) 1993. Asteraceae. In: Brako, L., Zarruchi, J.L. (eds) Catalogue of the flow-

ering plants and gymnosperms of Peru. Monogr. Syst. Bot. 45: 103–189.

Dittrich, M. 1977. Cynareae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, vol. 2. London: Academic Press, pp. 999–1015.

Dittrich, M. 1996. Die Bedeutung morphologischer und anatomischer Achänen-Merkmale für die Systematik der Tribus Echinopseae Cass. und Carlinae Cass. Boissiera 51: 5–102.

Eldenäs, P., Anderberg, A.A., Källersjö, M. 1998. Molecular phylogenetics of the tribe Inuleae s.str. (Asteraceae) based on ITS sequences of nuclear ribosomal DNA. Pl. Syst. Evol. 210: 159–173.

Eldenäs, P., Källersjö, M., Anderberg, A.A. 1999. Phylogenetic placement and circumscription of tribes Inuleae s.str. and Plucheeae (Asteraceae): evidence from sequences of chloroplast gene *ndh*F. Mol. Phylog. Evol. 13: 50–58.

Erbar, C., Leins, P. 1995. Portioned pollen release and the syndromes of secondary pollen presentation in the Campanulales-Asterales complex. Flora 190: 323–338.

Erbar, C., Leins, P. 2000. Some interesting features in the capitulum and flower of *Arnoldoa macbrideana* Ferreyra (Asteraceae, Barnadesioideae). Bot. Jahrb. Syst. 122: 503–515.

Eriksson, T. 1991. The systematic position of the *Blepharispermum* group (Asteraceae–Heliantheae). Taxon 40: 33–39.

Eriksson, T. 1992. The genus *Blepharispermum* (Asteraceae, Heliantheae). Pl. Syst. Evol. 182: 149–227.

Eriksson, T. 1993. The genus *Athroisma* (Asteraceae, Heliantheae). Bot. J. Linn. Soc. 119: 101–184.

Feinbrun-Dothan, N. 1977. Flora Palaestina, vol. 3. Jerusalem: Israel Academy of Sciences and Humanities.

Ferreyra, R. 1995. Flora of Peru. Family Asteraceae. VI. Fieldiana, Bot. 35: 87–90.

Fioretto, A., Alfani, A. 1988. Anatomy of succulence and CAM in 15 species of *Senecio*. Bot. Gaz. 149: 142–152.

Fiori, A., Paoletti, G. 1895–1899. Iconographia florae italicae. Padova: Tipografia Antoniana.

Folch, R. 1986. La vegetació dels Països Catalans. Barcelona: Ketres.

Font Quer, P. 1962. Plantas medicinales. El Dioscórides renovado. Barcelona: Labor.

Francisco-Ortega, J., Santos-Guerra, A., Hines, A., Jansen, R.K. 1997. Molecular evidence for a Mediterranean origin of the Macaronesian endemic genus *Argyranthemum* (Asteraceae). Amer. J. Bot. 84: 1595–1613.

Freire, S.E., Katinas, L. Sancho, G. 2002. *Gochnatia* (Asteraceae, Mutisieae) and the *Gochnatia* complex: taxonomic implications from morphology. Ann. Missouri Bot. Gard. 89: 524–550.

Funk, V.A., Chan, R.A. 2003. A brief survey of the phylogeny of the Arctoteae (Compositae: Cichorioideae s.s.). Comp. Newslett. 40: 13–14.

Funk, V.A., Robinson, H. (compilers) 1996. Asteraceae. In: Boggan, J., Funk, V.A., Kelloff, C., Hoff, M., Cremers, G., Feuillet, C. (eds) Checklist of the plants of the Guianas (Guyana, Surinam, French Guiana), 2nd edn. Washington, DC: Smithsonian Institution.

Funk, V.A., Robinson, H. 2001. A bully new genus from the Andes (Compositae: Liabeae). Syst. Bot. 26: 216–225.

Funk, V.A., Chan, R., Keeley, C. 2004. Insights into the evolution of the tribe Arctoteae (Compositae: subfamily Cichorioideae *s. s.*) using *trn*L, *ndh*F, and ITS. Taxon 53: 637–655.

Funk, V.A., Bayer, R.J., Keeley, S., Chan, R., Watson, L., Gemeinholzer, B., Schilling, E.E., Panero, J.L., Baldwin, B.G., Garcia-Jacas, N.T., Susanna, A., Jansen, R.K. 2005. Everywhere but Antarctica: using a supertree to understand the diversity and distribution of the Compositae. In: Friis, I., Balslev, H. (eds) Plant diversity and complexity patterns – local, regional and global dimensions. Proceedings International Symposium, Royal Danish Academy of Sciences and Letters, Copenhagen, 25–28 May 2003. Biol. Skr. 55: 343–373.

Gadek, P.A., Bruhl, J.J., Quinn, C.J. 1989. Exine structure in the 'Cotuleae' (Anthemideae, Asteraceae). Grana 28: 163–178.

Galetto, L. 1995. Estudios sobre el nectar y los nectarios en *Hyaloseris rubricunda* y *Barnadesia odorata* (Asteraceae–Mutisieae). Darwiniana 33: 127–133.

Gamerro, J.C. 1990. Identidad de *Pseudostifftia* con *Moquinia* (Compositae) y consideracions sobre la ubicacion tribal del taxon. Darwiniana 30: 123–136.

Garcia-Jacas, N. 1992. Estudi taxonòmic i biosistemàtic de les espècies ibériques i nord-africanes del gènere *Centaurea* sect. *Acrocentron* subsect. *Orientales*. Diss., University of Barcelona.

Garcia-Jacas, N., Susanna, A., Ilarlsan, R. 1996. Aneuploidy in the Centaureinae (Compositae): is $n = 7$ the end of the series? Taxon 45: 39–42.

Garcia-Jacas, N., Susanna, A., Mozaffarian, R., Ilarslan, R. 2000. The natural delimitation of *Centaurea* (Asteraceae: Cardueae): ITS sequence analysis of the *Centaurea jacea* group. Pl. Syst. Evol. 223: 185–199.

Garcia-Jacas, N., Susanna, A., Garnatje, T., Vilatersana, R. 2001. Generic delimitation and phylogeny of the subtribe Centaureinae (Asteraceae): a combined nuclear and chloroplast DNA analysis. Ann. Bot. London 87: 503–515.

Garcia-Jacas, N., Garnatje, T., Susanna, A., Vilatersana, R. 2002. Tribal and subtribal delimitation and phylogeny of the Cardueae (Asteraceae): a combined nuclear and chloroplast DNA analysis. Mol. Phylog. Evol. 22: 51–64.

Garg, S., Sastry, T.C.S. 1996. Indian Compositae in foods and flavours – a review. In: Caligari, P.D.S., Hind, D.J.N. (eds) Compositae: biology & utilization. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 2. Royal Botanic Gardens, Kew, pp. 361–382.

Gautier, L. 1992. Taxonomy and distribution of a tropical weed: *Chromolaena odorata* (L.) R. King & H. Robinson. Candollea 47: 645–662.

Giuliano, D.A. 2001. Clasificación infragenérica de las especies argentinas de *Baccharis* (Asteraceae, Astereae). Darwiniana 39: 131–154.

Goertzen, L.R., Cannone, J.J., Gutell, R.R., Jansen, R.K. 2003. ITS secondary structure derived from comparative analysis: implications for sequence alignment and phylogeny of Asteraceae. Mol. Phylog. Evol. 29: 216–234.

Graham, A. 1996. A contribution to the geologic history of the Compositae. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind,

Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 123–140.
Grashoff, J. 1974. Novelties in *Stevia* (Compositae: Eupatorieae). Brittonia 26: 347–384.
Grau, J. 1980. Die Testa der Mutisieae und ihre systematische Bedeutung. Mitt. Bot. Staatssamml. München 16: 269–332.
Grau, J., Hopf, H. 1985. Das Endosperm der Compositae. Bot. Jahrb. Syst. 107: 251–268.
Greger, H. 1977. Anthemideae – chemical review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae. London: Academic Press, pp. 851–898.
Gustafsson, M.H.G., Bremer, K. 1995. Morphology and phylogenetic relationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae and related families (Asterales). Amer. J. Bot. 82: 250–265.
Gustafsson, M.H.G., Backlund, A., Bremer, B. 1996. Phylogeny of the Asterales sensu lato based on *rbc*L sequences with particular reference to the Goodeniaceae. Pl. Syst. Evol. 199: 217–242.
Gustafsson, M.H.G., Pepper, A.S.-R., Albert, V.A., Källersjö, M. 2001. Molecular phylogeny of the Barnadesioideae (Asteraceae). Nordic J. Bot. 21: 149–160.
Gutterman, Y., Ginott, S. 1994. Long-term protected 'seed bank' in dry inflorescences of *Asteriscus pygmaeus*: achene dispersal mechanism and germination. J. Arid Environ. 26: 149–163.
Häffner, E. 2000. On the phylogeny of the subtribe Carduinae (tribe Cardueae, Compositae). Englera 21: 1–209.
Häffner, E., Hellwig, F. 1999. Phylogeny of the tribe Cardueae (Compositae) with emphasis on subtribe Carduinae: an analysis based on ITS sequence data. Willdenowia 29: 27–39.
Hansen, H.V. 1985a. A taxonomic revision of the genus *Gerbera* (Compositae, Mutisieae) sections *Gerbera*, *Parva*, *Piloselloides* (in Africa) and *Lasiopus*. Opera Bot. 78: 1–36.
Hansen, H.V. 1985b. Notes on *Gerbera* sect. *Pseudoseris* (Compositae-Mutisieae). Nordic J. Bot. 5: 451–453.
Hansen, H.V. 1988. A taxonomic revision of the genera *Gerbera* sect. *Isanthus*, *Leibnitzia* (in Asia), and *Uechtritzia* (Compositae, Mutisieae). Nordic J. Bot. 8: 61–76.
Hansen, H.V. 1990. Phylogenetic studies in the *Gerbera*-complex (Compositae, tribe Mutisieae, subtribe Mutisiinae). Nordic J. Bot. 9: 469–485.
Hansen, H.V. 1991a. SEM – studies and general comments on pollen in tribe Mutisieae (Compositae) sensu Cabrera. Nordic J. Bot. 10: 607–623.
Hansen, H.V. 1991b. Phylogenetic studies in Compositae tribe Mutisieae. Opera Bot. 109: 1–50.
Hansen, H.V. 1997. Studies in the Goodeniaceae and the Brunoniaceae with a discussion of their relationship to Asteraceae and Calyceraceae. Nordic J. Bot. 17: 495–510.
Harling, G. 1995. The genus *Jungia* L. fil. (Compositae-Mutisieae). Acta Regiae Soc. Sci. Litt. Gothob. Bot. 4: 1–133.
Harris, E.M. 1995. Inflorescence and floral ontogeny in Asteraeae: a synthesis of historical and current concepts. Bot. Rev. 61: 93–275.
Harris, E.M. 1999. Capitula in the Asteridae: a widespread and varied phenomenon. Bot. Rev. 65: 348–369.
Hartman, R.L. 1990. A conspectus of *Machaeranthera* (Asteraceae: Astereae). Phytologia 68: 439–465.
Hegnauer, R. 1977. The chemistry of the Compositae. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae. London: Academic Press, pp. 283–335.
Heinrich, M. 1996. Ethnobotany of Mexican Compositae: an analysis of historical and modern sources. In: Caligari, P.D.S., Hind, D.J.N. (eds) Compositae: biology & utilization. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 2. Royal Botanic Gardens, Kew, pp. 475–503.
Hellwig, F.H. 1990. Die Gattung *Baccharis* L. (Compositae–Astereae) in Chile. Mitt. Bot. Staatssamml. München 29: 1–456.
Hellwig, F.H. 1993. The genera *Pingraea* Cass. and *Neomolina* Hellwig (Compositae–Astereae). Candollea 48: 203–219.
Hellwig, F.H. 1996. Taxonomy and evolution of Baccharidinae (Compositae). In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 575–590.
Hendry, G.A.F. 1996. Fructan and the ecology and evolution of the Compositae. In: Caligari, P.D.S., Hind, D.J.N. (eds) Compositae: biology & utilization. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 2. Royal Botanic Gardens, Kew, pp. 121–128.
Herz, W. 1977. Sesquiterpene lactones in the Compositae. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, vol. 2. London: Academic Press, pp. 337–357.
Heywood, V.H., Humphries, C.J. 1977. Anthemideae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae. London: Academic Press, pp. 851–898.
Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) 1977. The biology and chemistry of the Compositae. London: Academic Press.
Hind, D.J.N. 1999. A new genus, *Semiria* (Compositae: Eupatorieae) and a discussion of its affinities within the subtribe Gyptidinae of Bahia, Brazil. Kew Bull. 54: 425–435.
Hind, D.J.N. 2000. A new genus, *Catolesia* (Compositae: Eupatorieae), and a discussion of its affinities within the subtribe Gyptidinae of Bahia, Brazil. Kew Bull. 55: 941–948.
Hitchcock, C.L., Cronquist, A., Ownbey, M., Thompson, J.W. 1959. Vascular plants of the Pacific Northwest, vol. 5. Compositae. Seattle: University of Washington Press, 349 pp.
Hoffmann, O. 1894. Compositae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, IV. Leipzig: Engelmann, pp. 87–391.
Holmes, W.C. 1991. Dioecy in *Mikania* (Compositae: Eupatorieae). Pl. Syst. Evol. 175: 87–92.
Huang, Y.-P., Ling, Y.-R. 1996. Economic Compositae in China. In: Caligari, P.D.S., Hind, D.J.N. (eds) Compositae: biology & utilization. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 2. Royal Botanic Gardens, Kew, pp. 431–451.

Humbert, H. 1962. 189ème Famille – Composées, tome 2. In: Flore de Madagascar et des Comores. Paris: Typ. Firmin-Didot., pp. 339–622.

Iljin, M. 1960. Species novae generis *Jurinea* Cass. ex Asia Media (in Russian). Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 20: 344–355.

Ito, M., Yahara, T., King, R.M., Watanabe, K., Oshita, S., Yokoyama, J., Crawford, D.J. 2000a. Molecular phylogeny of Eupatorieae (Asteraceae) estimated from cpDNA RFLP and its implication for the polyploid origin hypothesis of the tribe. J. Pl. Res. 113: 91–96.

Ito, M., Watanabe, K., Kita, Y., Kawahara, T., Crawford, D.J., Yahara, T. 2000b. Phylogeny and phytogeography of *Eupatorium* (Eupatorieae, Asteraceae): insights from sequence data of the nrDNA ITS regions and cpDNA RFLP. J. Pl. Res. 113: 79–89.

Jansen, R.K. 1991. Phylogeny and character evolution in the Asteraceae based on chloroplast DNA restriction site mapping. Syst. Bot. 16: 98–115.

Jansen, R.K., Kim, K.-J. 1996. Implications of chloroplast DNA data for the classification and phylogeny of the Asteraceae. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 317–339.

Jansen, R.K., Palmer, J.D. 1987. A chloroplast DNA inversion marks an ancient evolutionary split in the sunflower family (Asteraceae). Proc. Natl Acad. Sci. U.S.A. 84: 5818–5822.

Jansen, R.K., Palmer, J.D. 1988. Phylogenetic implications of chloroplast DNA restriction site variation in the Mutisieae (Asteraceae). Amer. J. Bot. 75: 753–766.

Jansen, R.K., Michaels, H.J., Palmer, J.D. 1991. Phylogeny and character evolution in the Asteraceae based on chloroplast DNA restriction site mapping. Syst. Bot. 16: 98–115.

Jeffrey, C. 1966. Notes in Compositae. I. The Cichorieae in East Tropical Africa. Kew Bull. 18: 427–486.

Jeffrey, C. 1967. Notes on Compositae. II. The Mutisieae in East Tropical Africa. Kew Bull. 21: 177–223.

Jeffrey, C. 1978. Compositae. In: Heywood, V.H. (ed.) Flowering plants of the world. New York: Mayflower Books, pp. 263–268.

Jeffrey, C. 1986. The Senecioneae in East Tropical Africa. Kew Bull. 41: 873–943.

Jeffrey, C. 1992. The tribe Senecioneae (Compositae) in the Mascarene Islands with an annotated world check-list of the genera of the tribe. Kew Bull. 47: 49–109.

Jeffrey, C. 2002. Systematics of Compositae at the beginning of the 21st century (in Russian). Bot. Zhurn. (Moscow & Leningrad) 87, 11: 1–15.

Jeffrey, C. 2004. Systema Compositarum (Asteracearum) nova (in English). Bot. Zhurn. (Moscow & Leningrad) 89, 12: 1817–1822.

Jepson, W.L. 1901. A flora of Western Middle California. Berkeley, CA: Encina.

Jones, S.B. 1977. Vernonieae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, vol. 2. London: Academic Press, pp. 503–521.

Kadereit, J.W. 1989. Chloroplast DNA, cladistics and the phylogeny of the Asteraceae. Bot. Acta 102: 7–10.

Karis, P.O. 1992. *Hoplophyllum* DC., the sister group to *Eremothamnus* O. Hoffm. (Asteraceae)? Taxon 41: 193–198.

Karis, P.O. 1993a. The Heliantheae sensu lato (Asteraceae), clades and classification. Pl. Syst. Evol. 188: 139–195.

Karis, P.O. 1993b. Morphological phylogenetics of the Asteraceae-Asteroideae, with notes on character evolution. Pl. Syst. Evol. 186: 69–93.

Karis, P.O. 1998. *Apostates* Lander (Asteraceae-Astereae), transferred to the Heliantheae sensu lato. Bot. Jahrb. Syst. 120: 131–135.

Karis, P.O. 2006. Morphological data indicates two major clades of the subtribe Gorteriinae (Asteraceae-Arctotideae). Cladistics 22:199–221.

Karis, P.O., Ryding, O. 1994a. Tribe Heliantheae. In: Bremer, K. (ed.) Asteraceae. Cladistics & classification. Portland, OR: Timber Press, pp. 559–624.

Karis, P.O., Ryding, O. 1994b. Tribe Helenieae. In: Bremer K. (ed.) Asteraceae. Cladistics & classification. Portland, OR: Timber Press, pp. 521–558.

Karis, P.O., Källersjö, M., Bremer, K. 1992. Phylogenetic analysis of the Cichorioideae (Asteraceae) with emphasis on the Mutisieae. Ann. Missouri Bot. Gard. 79: 416–427.

Karis, P.O, Eldenäs, P., Källersjö, M. 2001. New evidence for the systematic position of *Gundelia* L. with notes on delimitation of Arctoteae (Asteraceae). Taxon 50: 105–114.

Katinas, L. 2000. Implications of morphological phylogenetics for the placement of the genera *Adenocaulon* and *Eriachaenium* (Asteraceae). Pl. Syst. Evol. 223: 229–250.

Keeley, S.C., Chan, K. 2003. The Vernonieae: searching for a new paradigm. Comp. Newslett. 40: 19.

Keeley, S.C., Jansen, R.K. 1991. Evidence from chloroplast DNA for the recognition of a new tribe, the Tarchonantheae, and the tribal placement of *Pluchea* (Asteraceae). Syst. Bot. 16: 173–181.

Keeley, S.C., Jansen, R.K. 1995. Chloroplast DNA restriction site variation in the Vernonieae (Asteraceae), an initial appraisal of the relationship of New and Old World taxa and the monophyly of *Vernonia*. Pl. Syst. Evol. 193: 249–265.

Kilian, N. 1997. Revision of *Launaea* Cass. (Compositae, Lactuceae, Sonchinae). Englera 17: 1–478.

Kim, K.-J., Jansen, R.K. 1995. *ndh*F sequence evolution and the major clades in the sunflower family. Proc. Natl Acad. Sci. U.S.A. 92: 10379–10383.

Kim, K.-J., Jansen, R.K., Wallace, R.S., Michaels, H.J., Palmer, J.D. 1992. Phylogenetic implications of *rbc*L sequence variation in the Asteraceae. Ann. Missouri Bot. Gard. 79: 428–445.

Kim, H.-G., Keeley, S.C., Vroom, P.S., Jansen, R.K. 1998. Molecular evidence for an African origin of the Hawaiian endemic *Hesperomannia* (Asteraceae). Proc. Natl Acad. Sci. U.S.A. 95: 15440–15445.

Kim, S.-C., Crawford, D.J., Jansen, R.K., Santos Guerra, A. 1999a. The use of a non-coding region of chloroplast DNA in phylogenetic studies of the subtribe Sonchinae (Asteraceae: Lactuceae). Pl. Syst. Evol. 215: 85–99.

Kim, S.-C., Crawford, D.J., Francisco-Ortega, J., Santos Guerra, A. 1999b. Adaptive radiation and genetic differentiation in the woody *Sonchus* alliance (Aste-

raceae: Sonchinae) in the Canary Islands. Pl. Syst. Evol. 215: 101–118.
Kim, H.-G., Loockerman, D.J., Jansen, R.K. 2002. Systematic implications of *ndh*F sequence variation in the Mutisieae (Asteraceae). Syst. Bot. 27: 598–609.
Kim, H.-G., Funk, V.A., Vlasek, A., Zimmer, E. 2003. A phylogeny of the Munnoziinae (Compositae, Liabeae): circumscription of *Munnozia* and a new placement of *M. perfoliata*. Pl. Syst. Evol. 239: 171–185.
Kimball, R.T., Crawford, D.J. 2004. Phylogeny of Coreopsideae (Asteraceae) using ITS sequences suggests lability in reproductive characters. Mol. Phylog. Evol. 33: 127–139.
King, R.M., Robinson, H. 1970. Studies in the Eupatorieae (Compositae). XIX. New combinations in *Ageratina*. Phytologia 19: 208–229.
King, R.M., Robinson, H. 1971. Studies in the Eupatorieae (Asteraceae). LIX. A new genus, *Steviopsis*. Phytologia 22: 156–157.
King, R.M., Robinson, H. 1972. Studies in the Eupatorieae (Asteraceae). LXXVII. Additions to the genus *Steviopsis*. Phytologia 24: 60–62.
King, R.M., Robinson, H. 1978. Studies in the Eupatorieae (Asteraceae). CLXVIII. Additions to the genus *Ageratina*. Phytologia 38: 323–355.
King, R.M., Robinson, H. 1987. The genera of Eupatorieae (Asteraceae). Missouri Bot. Gard. Monogr. Syst. Bot. 22: 1–581.
King, R.M., Robinson, H. 1995. Generic limits in the Alomiinae (Eupatorieae–Asteraceae), and new combinations in *Brickelliastrum* and *Barroetea*. Phytologia 78: 124–126.
King, R.M., Kyhos, D.W., Powell, A.M., Raven, P.H., Robinson, H. 1976. Chromosome numbers in Compositae. XIII. Eupatorieae. Ann. Missouri Bot. Gard. 63: 862–888.
Koopman, W.J.M., Guetta, E., van de Wiel, C.C.M. et al. 1998. Phylogenetic relationships among *Lactuca* (Asteraceae) species and related genera based on ITS-1 DNA sequences. Amer. J. Bot. 85: 1517–1530.
Kornkven, A.B., Watson, L.E., Estes, J.R. 1998. Phylogenetic analysis of *Artemisia* sect. *Tridentatae* (Asteraceae) based on sequences from internal transcribed spacers (ITS) of nuclear ribosomal DNA. Amer. J. Bot. 85: 1787–1795.
Kornkven, A.B., Watson, L.E., Estes, J.R. 1999. Molecular phylogeny of *Artemisia* sect. *Tridentatae* (Asteraceae) based on chloroplast DNA restriction site variation. Syst. Bot. 24: 69–84.
Lack, H.W. 1979. The subtribe Hypochoeridinae (Asteraceae, Lactuceae) in the tropics and the southern hemisphere. In: Larsen, K., Holm-Nielsen, L.B. (eds) Tropical botany. London: Academic Press, pp. 265–276.
Lammers, T.G. 1992. Circumscription and phylogeny of the Campanulales. Ann. Missouri Bot. Gard. 79. 358–413.
Lander, N.S. 1994. *Olearia*. In: Harden, G.J. (ed.) Flora of New South Wales, vol. 3. New South Wales University Press.
Lane, M.A. 1996. Pollination biology of Compositae. In: Caligari, P.D.S., Hind, D.J.N. (eds) Compositae: biology & utilization. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 2. Royal Botanic Gardens, Kew, pp. 61–80.
Lane, M.A., Hartman, R.L. 1996. Reclassification of North American *Haplopappus* (Compositae: Astereae) completed: *Rayjacksonia* gen. nov. Amer. J. Bot. 83: 356–370.
Lane, M.A., Morgan, D.R., Suh, Y.-B., Simpson, B.B., Jansen, R.K. 1996. Relationships of North American genera of Astereae, based on chloroplast DNA restriction site data. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 49–77.
Lee, J., Baldwin, B.G., Gottlieb, L.D. 2003. Phylogenetic relationships among the primarily North American genera of Cichorieae (Compositae) based on analysis of 18S–26S nuclear rDNA ITS and ETS sequences. Syst. Bot. 28: 616–626.
Leins, P. 1970. Die Pollenkörner und Verwandtschaftsbeziehungen der Gattung *Eremothamnus* (Asteraceae). Mitt. Bot. Staatssamml. München 7: 369–376.
Leins, P. 1971. Pollensystematische Studien an Inuleen, vol. 1. Tarchonanthinae, Plucheinae, Inulinae, Buphthalminae. Bot. Jahrb. Syst. 91: 91–146.
Leins, P., Erbar, C. 1987. Studien zur Blütenentwicklung an Compositen. Bot. Jahrb. Syst. 108: 381–401.
Leins, P., Erbar, C. 1990. On the mechanisms of secondary pollen presentation in the Campanulales–Asterales complex. Bot. Acta 103: 87–92.
Leins, P., Erbar, C. 2000. Die frühesten Entwicklungsstadien der Blüten bei den Asteraceae. Bot. Jahrb. Syst. 122: 503–515.
Leins, P., Thyret, G. 1971. Pollen phylogeny and taxonomy exemplified by an African Asteraceae group. Mitt. Bot. Staatssamml. München 10: 280–286.
Lersten, N.R., Curtis, J.D. 1985. Distribution and anatomy of hydathodes in Asteraceae. Bot. Gaz. 146: 106–114.
Lessing, C.F. 1832. Synopsis generum Compositarum, earumque dispositionis novae tentamen monographus multarum capensium interjectis. Berlin: Duncker & Humblot.
Liu, J.-Q., Gao, T.-G., Chen, Z.-D., Lu, A.-M. 2002. Molecular phylogeny and biogeography of the Qinghai-Tibet Plateau endemic *Nannoglottis* (Asteraceae). Mol. Phylog. Evol. 23: 307–325.
Loockerman, D.J., Turner, B.L., Jansen, R.K. 2003. Phylogenetic relationships within the Tageteae (Asteraceae) based on nuclear ribosomal ITS and chloroplast *ndh*F gene sequences. Syst. Bot. 28: 191–207.
Lowrey, T., Urbatsch, L. 2003. Phylogenetic studies in the Astereae: the need for generic redelimitation and a reasonable subtribal classification. Comp. Newslett. 40: 25.
Lundin, R. 2006. *Nordenstamia* Lundin (Compositae-Senecioneae), a new genus from the Andes of South America. Comp. Newslett. 44: 14–18.
Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl. J. Pl. Sci. 164: 553–578.
Marticorena, C., Parra, O. 1975. Morfología de los granos de polen de *Hesperomannia* Gray y *Moquinia* DC. (Compositae–Asteraceae). Estudio comparativo con generos afines. Gayana 29: 3–22.
McKenzie, R.J., Barker, N.P. Samuel, J., Muller, E.M., Skinner, A.K.W. 2005. Morphology of cypselae in subtribe Arctotidinae (Compositae-Arctotideae) and its taxo-

nomic implications. Ann. Missouri Bot. Gard. 92: 569–594.
McVaugh, R. 1984. Compositae. In: Anderson, W.R. (ed.) Flora Novo-Galiciana, vol. 12. Ann Arbor: University of Michigan Press.
Meiri, L., Dulberger, R. 1986. Stamen filament structure in the Asteraceae: the anther collar. New Phytol. 104: 693–701.
Merxmüller, H., Leins, P., Roessler, H. 1977. Inuleae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, vol. 1. London: Academic Press, pp. 577–602.
Metcalfe, C.R., Chalk, L. 1950. Anatomy of the Dicotyledons. Oxford: Oxford University Press.
Michaels, H.J.K., Scott, K.M., Olmstead, R.G., Szaro, T., Jansen, R.K., Palmer, J.D. 1993. Interfamilial relationships of the Asteraceae: insights from *rbc*L sequence variation. Ann. Missouri Bot. Gard. 80: 742–751.
Morgan, D.R. 2003. nrDNA external transcribed spacer (ETS) sequence data, reticulate evolution, and the systematics of *Machaeranthera* (Asteraceae). Syst. Bot. 28: 179–190.
Morgan, D.R., Hartman, R.L. 2003. A synopsis of *Machaeranthera* (Asteraceae: Astereae), with recognition of segregate genera. Sida 20: 1387–1416.
Muschler, R. 1911. Compositae africanae novae, I. Bot. Jahrb. Syst. 46: 51–124.
Nash, D.L., Williams, L.O. 1976. Flora of Guatemala, vol. 12. Fieldiana, Bot. 24: 1–603.
Nesom, G.L. 1989. Infrageneric taxonomy of New World *Erigeron* (Compositae: Astereae). Phytologia 67: 67–93.
Nesom, G.L. 1990. Taxonomy of the *Erigeron pringlei* group (Asteraceae: Astereae). Phytologia 69: 227–235.
Nesom, G.L. 1993. Taxonomic infrastructure of *Solidago* and *Oligoneuron* (Asteraceae: Astereae) and observations on their phylogenetic position. Phytologia 75: 1–44.
Nesom, G.L. 1994a. *Erigeron pattersonii* (Asteraceae: Astereae), a new species from Nuevo Leon, Mexico. Phytologia 76: 96–100.
Nesom, G.L. 1994b. Taxonomic dispersal of Australian *Erigeron* (Asteraceae: Astereae). Phytologia 76: 143–159.
Nesom, G.L. 1994c. Subtribal classification of the Astereae (Asteraceae). Phytologia 76: 193–274.
Nesom, G.L. 1994d. Review of the taxonomy of *Aster* sensu lato (Asteraceae: Astereae), emphasizing New World species. Phytologia 77: 141–297.
Nesom, G.L. 1998 (2000). Full constitution of the Australian genus *Pappochroma* (Asteraceae: Astereae). Phytologia 85: 276–279.
Nesom, G.L. 2000a. New subtribes for North American Astereae (Asteraceae). Sida 19: 263–268.
Nesom, G.L. 2000b. Generic conspectus of the tribe Astereae in North America, Central America, the Antilles, and Hawaii. Sida Bot. Misc. 20: i–viii, 1–100.
Nesom, G.L. 2005. Infrageneric classification of *Litaris* (Asteraceae: Eupatorieae). Sida 21, 3: 1305–1321.
Nesom, G.L., Noyes, R.D. 1999. Notes on sectional delimitations in *Erigeron* (Asteraceae: Astereae). Sida 18: 1161–1165.
Nesom, G.L., Noyes, R.D. 2000. *Batopilasia* (Asteraceae: Astereae), a new genus from Chihuahua, Mexico. Sida 19: 79–84.
Nesom, G.L., Robinson, H., Granda Paucar, A. 2001. A new species of *Chiliotrichopsis* (Asteraceae: Astereae) from Peru. Brittonia 53: 430–434.
Nijs, H.C.M. den, Menken, S.B.J. 1996. Relations between breeding system, ploidy level and taxonomy in some advanced sections of *Taraxacum*. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 665–677.
Nordenstam, B. 1977. Senecioneae and Liabeae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, vol. 2. London: Academic Press, pp. 799–830.
Nordenstam, B. 1978. Taxonomic studies in the tribe Senecioneae (Compositae). Opera Bot. 44: 1–83.
Nordenstam, B. 1994a. Tribe Calenduleae. In: Bremer, K. (ed.) Asteraceae. Cladistics & classification. Portland, Timber Press, pp. 365–376.
Nordenstam, B. 1994b. New combinations in the Calenduleae. Comp. Newslett. 25: 46–49.
Nordenstam, B. 1996. Recent revision of Senecioneae and Calenduleae systematics. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Kew: Royal Botanic Gardens, pp. 591–596.
Nordenstam, B. 2004. Two new species of *Osteospermum* (Compositae-Calenduleae) from Southwestern Cape Province, South Africa. Edinburgh J. Bot. 60: 259–265.
Nordenstam, B. 2006a. Additions to the genus *Jacobaea* Mill. (Compositae-Senecioneae). Comp. Newslett. 44: 12–13.
Nordenstam, B. 2006b. New combinations in *Nordenstamia* (Compositae-Senecioneae) from Argentina, Bolivia, Peru and Ecuador. Comp. Newslett. 44: 19–23.
Nordenstam, B. 2006c. *Canariothamnus* B. Nord., a new genus of the Compositae-Senecioneae, endemic to the Canary Islands. Comp. Newslett. 44: 24–31.
Nordenstam, B. 2006d. Generic revisions in the tribe Calenduleae (Compositae). Comp. Newslett. 44: 38–49.
Nordenstam, B. 2006e. New genera and combinations in the Senecioneae of the Greater Antilles. Comp. Newslett. 44: 74–93.
Nordenstam, B. 2006f. *Ignurbia*, a new genus of the Asteraceae-Senecioneae from Hispaniola. In: Sipman, H., Raus, Th., Kilian, N. (eds) Festschrift Werner Greuter. Willdenowia spec. vol. 31, 1, pp. 463–468.
Nordenstam, B., Pelser, P.B. 2005. *Dauresia* and *Mesogramma*: one new and one resurrected genus of the Asteraceae-Senecioneae from Southern Africa. Comp. Newslett. 42: 74–88.
Nordenstam, B., Källersjö, M., Eldenäs, P. 2006. *Nephrotheca*, a new monotypic genus of the Compositae-Calenduleae from the southwestern Cape. Province Comp. Newslett. 44: 32–37.
Norlindh, T. 1943. Studies in the Calenduleae, I. Monograph of the genera *Dimorphotheca*, *Castalis*, *Osteospermum*, *Gibbaria* and *Chrysanthemoides*. Lund: Gleerup.

Norlindh, T. 1960. Additions to the monograph on *Osteospermum*. Bot. Notiser 113: 385–399.

Norlindh, T. 1962. Studies in *Calendula maderensis* DC. With a discussion on the delimitation of *Calendula* L. from *Gibbaria* Cass. and *Osteospermum* L. Bot. Notiser 115: 437–445.

Norlindh, T. 1977. Calenduleae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae. London: Academic Press, pp. 961–987.

Noyes, R.D. 2000. Biogeographical and evolutionary insights on *Erigeron* and allies (Asteraceae) from ITS sequence data. Pl. Syst. Evol. 220: 93–114.

Noyes, R.D., Rieseberg, L.H. 1999. ITS sequence data support a single origin for North American Astereae (Asteraceae) and reflect deep geographical division in *Aster* s.l. Amer. J. Bot. 86: 398–412.

Oberprieler, Ch. 2001. Phylogenetic relationships in *Anthemis* (Compositae, Anthemideae) based on nrDNA ITS sequence variation. Taxon 50: 745–762.

Oberprieler, Ch. 2002. A phylogenetic analysis of *Chamaemelum* Miller (Compositae, Anthemideae) and related genera based upon nrDNA ITS and cpDNA *trn*L/*trn*F IGS sequence variation. Bot. J. Linn. Soc. 138: 255–273.

Oberprieler, C. 2004a. On the taxonomic status and the phylogenetic relationships of some unispecific Mediterranean genera of *Compositae-Anthemideae*. I. *Brocchia*, *Endopappus*, and *Heliocauta*. Willdenowia 34: 39–57.

Oberprieler, C. 2004b. On the taxonomic status and the phylogenetic relationships of some unispecific Mediterranean genera of *Compositae-Anthemideae*. II. *Daveaua*, *Leococyclus*, and *Nananthea*. Willdenowia 34: 341–350.

Oberprieler, C. 2005. Temporal and spatial diversification of Circum-Mediterranean *Compositae-Anthemideae*. Taxon 54: 951–966.

Oberprieler, Ch., Vogt, R. 2000. The position of *Castrilanthemum* Vogt & Oberprieler and the phylogeny of Mediterranean Anthemideae (Compositae) as inferred from nrDNA ITS and cpDNA *trn*L/*trn*F IGS sequence variation. Pl. Syst. Evol. 225: 145–170.

Oberprieler, Ch., Vogt, R. 2002. *Cladanthus* Cass., p. 197. In: Greuter, W., Raus, Th. (eds) Med-Checklist Notulae, 21. Willdenowia 32: 195–208.

Olmstead, R.G., Bremer, K., Scott, R.M., Palmer, J.D. 1993. A parsimony analysis of the Asteridae sensu lato based on *rbc*L sequences. Ann. Missouri Bot. Gard. 80: 700–722.

Ortiz, S., Paiva, J.A.R., Rodríguez-Oubiña, J. 1996. An outline of the genus *Anisopappus* Hook. & Arn. (Compositae). Anales Jard. Bot. Madrid 54: 378–391.

Palmer, J.H. 1996. Floral initiation and production in the oil-seed sunflower. In: Caligari, P.D.S., Hind, D.J.N. (eds) Compositae: biology & utilization. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 2. Royal Botanic Gardens, Kew, pp. 161–178.

Panero, J.L. 2005. New combinations and infrafamilial taxa in the Asteraceae. Phytologia 87: 1–14.

Panero, J.L., Funk, V.A. 2002. Toward a phylogenetic subfamilial classification for the Compositae (Asteraceae). Proc. Biol. Soc. Wash. 115: 909–922.

Panero, J.L., Jansen, R.K., Clevinger, J.A. 1999. Phylogenetic relationships of the subtribe Ecliptinae (Asteraceae: Heliantheae) based on chloroplast DNA restriction site data. Amer. J. Bot. 86: 413–427.

Panero, J.L., Baldwin, B.G., Schilling, E.E., Clevinger, J.A. 2001a. Molecular phylogenetic studies of members of tribes Helenieae, Heliantheae and Eupatorieae (Asteraceae). 1. Introduction. In: Osborn, J.M. (prog. dir.) Botany 2001, Abstracts, part 3. Systematics. St. Louis, MO: Botanical Society of America.

Panero, J.L., Baldwin, B.G., Schilling, E.E., Clevinger, J.A. 2001b. Molecular phylogenetic studies of members of tribes Helenieae, Heliantheae and Eupatorieae (Asteraceae). 2. Tribal/generic relationships. In: Osborn, J.M. (prog. dir.) Botany 2001, Abstracts, part 3. Systematics. St. Louis, MO: Botanical Society of America.

Panero, J.L., Baldwin, B.G., Schilling, E.E., Clevinger, J.A. 2001c. Molecular phylogenetic studies of members of tribes Helenieae, Heliantheae and Eupatorieae (Asteraceae). 3. General systematics and proposed taxonomic changes in current classification. In: Osborn, J.M. (prog. dir.) Botany 2001, Abstracts, part 3. Systematics. St. Louis, MO: Botanical Society of America.

Pelser, P.B., Veldkamp, J.-F., van der Meijden R. 2006. New combinations in *Jacobaea* Mill. (Asteraceae: Senecioneae). Comp. Newslett. 44: 1–11.

Petit, D.P. 1997. Generic interrelationships of the Cardueae (Compositae): a cladistic analysis of morphological data. Pl. Syst. Evol. 207: 173–203.

Petit, D.P. 1998. Le genre *Echinops* L. (Compositae, Cardueae). I. Position phylétique et interprétation de l'incapitulescence. Candollea 43: 467–481.

Petit, D.F., Mathez, J., Qaid, H. 2000. Phylogeny of the Cardueae (Asteraceae) based on analysis of morphological and palynological characters. Bocconea 13: 41–53.

Pittman, A.B., Bates, V. 1989. A new species of *Polymnia* (Compositae: Heliantheae) from the Ouchita mountain region of Arkansas. Sida 13: 481–486.

Poljakov, P.P. 1967. Origin and classification of the Compositae (in Russian). Akad. Nauk Kazakh. S.S.R. Inst. Bot., 335 pp.

Powell, A.M. 1969. Taxonomy of *Perityle* section *Pappothrix* (Compositae-Peritylinae). Rhodora 71: 58–93.

Powell, A.M. 1972. Taxonomy of *Amauria* (Compositae-Peritylinae). Madroño 21: 516–525.

Powell, A.M. 1973. Taxonomy of *Perityle* section *Laphamia* (Compositae-Helenieae-Peritylinae). Sida 5: 61–128.

Powell, A.M. 1974. Taxonomy of *Perityle* section *Perityle* (Compositae-Peritylinae). Rhodora 76: 229–306.

Powell, A.M., Turner, B.L. 1974. A generic conspectus of the subtribe Peritylinae (Asteraceae-Helenieae) and reassessment of its tribal position. Amer. J. Bot. 61: 87–93.

Praglowski, J., Grafström, E. 1980. The pollen morphology of the tribe Calenduleae with reference to taxonomy. Bot. Notiser 133: 177–188.

Proksch, P., Kunze, A. 1996. Chemosystematic evidence from prenylated acetophenones – conclusions at the tribal, inter- and intrageneric level. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 295–305.

Pullaiah, T. 1983. Studies in the embryology of Senecioneae (Compositae). Pl. Syst. Evol. 142: 61–70.
Rauscher, J.T. 2002. Molecular phylogenetics of the *Espeletia* complex (Asteraceae): evidence from nrDNA ITS sequences of the closest relatives of an Andean adaptive radiation. Amer. J. Bot. 89: 1074–1084.
Reese, H. 1989. Die Entwicklung von Perikarp und Testa bei Calenduleae und Arctotideae (Asteraceae) – ein Beitrag zur Systematik. Bot. Jahrb. Syst. 110: 325–419.
Reitbrecht, F. 1974. Fruchtanatomie und Systematik der Anthemideae (Asteraceae). Diss. philosophischen Fakultät, Universität Wien, 160 S.
Reveal, J.L. 1997. Early suprageneric names in Asteraceae. Comp. Newslett. 30: 29–45.
Roberts, R.P., Urbatsch, L.E. 2004. Molecular phylogeny of *Chrysothamnus* and related genera (Asteraceae, Astereae) based on nuclear ribosomal 3′ ETS and ITS sequence data. Syst. Bot. 29: 199–215.
Robins, D.J. 1977. Senecioneae – chemical review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae. London: Academic Press, pp. 831–850.
Robinson, B.L. 1930a. Observations on the genus *Stevia*. Contr. Gray Herb. n.s. 90: 36–58, pl. 1.
Robinson, B.L. 1930b. The stevias of the Argentine republic. Contr. Gray Herb. n.s. 90: 58–79.
Robinson, B.L. 1930c. The stevias of Paraguay. Contr. Gray Herb. n.s. 90: 79–90.
Robinson, B.L. 1930d. The stevias of North America. Contr. Gray Herb. n.s. 90: 90–160.
Robinson, B.L. 1931a. The stevias of Colombia. Contr. Gray Herb. n.s. 96: 28–36.
Robinson, B.L. 1931b. The stevias of Venezuela. Contr. Gray Herb. n.s. 96: 37–43.
Robinson, B.L. 1931c. The stevias of Ecuador. Contr. Gray Herb. n.s. 96: 43–49.
Robinson, B.L. 1932a. The stevias of Peru. Contr. Gray Herb. n.s. 100: 20–36.
Robinson, B.L. 1932b. The stevias of Bolivia. Contr. Gray Herb. n.s. 100: 36–39.
Robinson, H. 1977. An analysis of the characters and relationships of the tribes Eupatorieae and Vernonieae (Asteraceae). Syst. Bot. 2: 199–208.
Robinson, H. 1978a. Studies in the Heliantheae (Asteraceae). XIV. Validation of subtribes. Phytologia 41: 39–44.
Robinson, H. 1978b. Studies in the Heliantheae (Asteraceae). XII. Re-establishment of the genus *Smallanthus*. Phytologia 39: 47–53.
Robinson, H. 1979. Two new genera of the Vernonieae (Asteraceae) from Brazil, *Heterocypsela* and *Pseudostifftia*. Phytologia 44: 442–450.
Robinson, H. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). Smithsonian Contr. Bot. 51: 1–102.
Robinson, H. 1983a. A generic review of the tribe Liabeae (Asteraceae). Smithsonian Contr. Bot. 54: 1–69.
Robinson, H. 1983b. Studies in the Liabeae (Asteraceae). XVI. New taxa from Peru. Phytologia 54: 62–65.
Robinson, H. 1984. Style rotation in the Asteraceae. Taxon 33: 400–404.
Robinson, H. 1990a. Notes on *Sinclairia* and *Liabellum* in Mesoamerica (Liabeae: Asteraceae). Phytologia 69: 57–60.
Robinson, H. 1990b. A redelimitation of *Microliabum* Cabrera (Asteraceae: Liabeae). Syst. Bot. 15: 736–744.
Robinson, H. 1992. Observations on the unique form of sweeping hairs on the styles of the Eremothamneae (Asteraceae). Taxon 41: 199–200.
Robinson, H. 1994. Notes on the tribes Eremothamneae, Gundelieae and Moquinieae, with comparisons of their pollen. Taxon 43: 33–44.
Robinson, H. 1996. The status of generic and subtribal revisions in the Vernonieae. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 511–529.
Robinson, H. 1997. New species of *Aphanactis* in Ecuador and Bolivia and new combinations in *Selloa* (Heliantheae: Asteraceae). Brittonia 49: 71–78.
Robinson, H. 1999a. Revisions of Paleotropical Vernonieae (Asteraceae). Proc. Biol. Soc. Wash. 112: 220–247.
Robinson, H. 1999b. Generic and subtribal classification of American Vernonieae. Smithsonian Contr. Bot. 89: i–iv, 1–116.
Robinson, H. (compiler) 1999c. Eupatorieae in Asteraceae. In: Jørgensen, R.M., León-Yánez, S. (eds) Catalogue of vascular plants of Ecuador. Monogr. Syst. Bot. 75: 260–314.
Robinson, H., Brettell, R.D. 1972. Tribal revisions in the Asteraceae. I. The relationship of *Geissolepis*. Phytologia 24: 299–301.
Robinson, H., Brettell, R.D. 1973a. Tribal revisions in the Asteraceae. III. A new tribe, Liabeae. Phytologia 25: 404–407.
Robinson, H., Brettell, R.D. 1973b. Tribal revisions in the Asteraceae. V. The relationship of *Rigiopappus*. Phytologia 26: 69–70.
Robinson H., Brettell, R.D. 1973c. Tribal revisions in the Asteraceae. VIII. A new tribe, Ursinieae. Phytologia 26: 76–86.
Robinson, H., Brettell, R.D. 1973d. Tribal revisions in the Asteraceae. X. The relationship of *Plagiocheilus*. Phytologia 26: 159–162.
Robinson, H., Brettell, R.D. 1974. Studies in the Liabeae (Asteraceae). II. Preliminary survey of the genera. Phytologia 28: 43–63.
Robinson, H., Funk, V.A. 1987. A phylogenetic analysis of *Leiboldia*, *Lepidonia*, and a new genus *Stramentopappus* (Vernonieae: Asteraceae). Bot. Jahrb. Syst. 108: 213–228.
Robinson, H., Kahn, B. 1986. Trinervate leaves, yellow flowers, tailed anthers, and pollen variation in *Distephanus* Cassini (Vernonieae: Asteraceae). Proc. Biol. Soc. Wash. 99: 493–501.
Robinson, H., Marticorena, C. 1986. A palynological study of the Liabeae (Asteraceae). Smithsonian Contr. Bot. 64: i–iv, 1–50.
Robinson, H., Moore, A.J. 2004. New species and new combinations in *Rhysolepis* (Asteraceae: Heliantheae). Proc. Biol. Soc. Wash. 117: 423–446.
Robinson, H., Powell, A.M., King, R.M., Weedin, J.F. 1985. Chromosome numbers in Compositae. XI. Liabeae. Ann. Missouri Bot. Gard. 72: 469–479.
Robinson, H., Powell, A.M., Carr, G.D., King, R.M., Weedin, J.F. 1989. Chromosome numbers in Composi-

tae. XVI. Eupatorieae II. Ann. Missouri Bot. Gard. 76: 1004–1011.
Ross-Craig, S. 1962. Drawings of British plants, vol. 17. London: Bell & Hyman.
Ross-Craig, S. 1963. Drawings of British plants, vol. 18. London: Bell & Hyman.
Rydberg, P.A. 1927. Carduaceae, Liabeae, Neurolaeneae, Senecioneae (pars). N. Amer. Flora 34: 289–360.
Ryding, O., Bremer, K. 1992. Phylogeny, distribution, and classification of the Coreopsideae (Asteraceae). Syst. Bot. 17: 649–659.
Sáenz, A.A. 1981. Anatomía y morfología de frutos de Heliantheae. Darwiniana 23: 37–117.
Sandwith, N.Y. 1956. Contributions to the flora of tropical America. LXI. Notes on *Philoglossa*. Kew Bull. 1956: 289–293.
Schilling, E.E., Cox, P.B. 2001. Abstract 555. Systematic analysis of *Liatrinae* (*Asteraceae*). In: Osborn, J.M. (prog. dir.) Botany 2001, Abstracts, part 3. Systematics. St. Louis, MO: Botanical Society of America.
Schilling, E.E., Panero, J.L. 2002. A revised classification of subtribe Helianthinae (Asteraceae-Heliantheae). 1. Basal lineages. Bot. J. Linn. Soc. 140: 65–76.
Schilling, E.E., Panero, J.L., Cox, P.B. 1999. Chloroplast DNA restriction data support a narrowed interpretation of *Eupatorium* (Asteraceae). Pl. Syst. Evol. 219: 209–233.
Schmidt, G.J., Schilling, E.E. 2000. Phylogeny and biogeography of *Eupatorium* (Asteraceae: Eupatorieae) based on nuclear ITS sequence data. Amer. J. Bot. 87: 716–726.
Seaman, F.C. 1982. Sesquiterpene lactones as taxonomic characters in the Asteraceae. Bot. Rev. 48: 121–592.
Seaman, F.C., Funk, V.A. 1983. Cladistic analysis of complex natural products: developing transformation series from sesquiterpene lactone data. Taxon 32: 1–27.
Sell, P.D. 1975. Taxonomic and nomenclatural notes on the Compositae subfamily Cichorioideae. Bot. J. Linn. Soc. 71: 236–274.
Sennikov, A.N., Illarinova, I.D. 2001. The morphological and anatomical structure of the achenes of species of the genus *Hieracium* (Asteraceae) and related genera (in Russian). Bot. Zhurn. (Moscow & Leningrad) 86, 3: 37–59.
Shannon, R.K., Wagner, W.L. 1997. *Oparanthus* revisited. In: Lorence, D. (ed.) Botanical results of the 1988 Fatu Hiva Expedition to the Marquesas Islands. Allertonia 7: 273–295.
Shih, C., Chen, Y.L. 1996. *Faberiopsis* Shih et Y.L. Chen, genus novum familiae Compositarum sinensium. Acta Phytotax. Sin. 34: 438–439.
Short, P.S., Wilson, K.E., Nailon, J. 1989. Notes on the fruit anatomy of Australian members of the Inuleae (Compositae). Muelleria 7: 57–79.
Skottsberg, C. 1937. Die Flora der Desventuradas Inseln (San Felix und San Ambrosio). Göteb. Kungl. Vetensk. Vitterh. Samh. Handl. ser. 5 B 5: 1–88.
Skvarla, J.J., Turner, B.L., Patel, V.C., Tomb, A.S. 1977. Pollen morphology in the Compositae and in morphologically related families. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae. London: Academic Press, pp. 141–265.
Smith, C.R., Wilson, T.L., Melvin, E.H., Wolff, I.A. 1960. Dimorphecolic acid – a unique hydroxydienoid fatty acid. J. Amer. Chem. Soc. 82: 1417–1421.
Solbrig, O.T. 1977. Chromosomal cytology and evolution in the family Compositae. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae. London: Academic Press, pp. 267–281.
Stebbins, G.L. 1953. A new classification of the tribe Cichorieae, family Compositae. Madroño 12: 65–81.
Stix, E. 1960. Pollenmorphologische Untersuchungen an Compositen. Grana Palynol. 2: 41–114.
Strother, J.L. 1977. Tageteae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, vol. 2. London: Academic Press, pp. 769–783.
Strother, J.L. 1986. Renovation of *Dyssodia* (Composiate: Tageteae). Sida 11: 371–378.
Strother, J.L., Panero, J.L. 1994. Chromosome studies: Latin American Compositae. Amer. J. Bot. 81: 770–775.
Stuessy, T.F. 1977. Heliantheae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, vol. 2. London: Academic Press, pp. 621–671.
Stuessy, T.F., Garver, D. 1996. The defensive role of pappus in heads of Compositae. In: Caligari, P.D.S., Hind, D.J.N. (eds) Compositae: biology & utilization. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 2. Royal Botanic Gardens, Kew, pp. 81–91.
Stuessy, T.F, Spooner, D.M. 1988. The adaptive and phylogenetic significance of receptacular bracts in the Compositae. Taxon 37: 114–126.
Stuessy, T.F., Sang, T., DeVore, M.L. 1996. Phylogeny and biogeography of the subfamily Barnadesioideae with implications for early evolution of Compositae. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 463–490.
Susanna, A., Garcia-Jacas, N., Soltis, D.E., Soltis, P.S. 1995. Phylogenetic relationships in tribe Cardueae (Asteraceae) based on ITS sequences. Amer. J. Bot. 82: 1056–1068.
Susanna, A., Garcia-Jacas, N., Hidalgo, O., Vilatersana, R., Garnatje, T. 2006. The Cardueae (Compositae) revisited: insights from a ITS, trnL-trnF and matK nuclear and chloroplast DNA analysis. Ann. Missouri Bot. Gard. 93:150–171.
Suyama, C. 2001. A new naturalized plant, *Gymnocoronis spilanthoides* DC. (in Japanese). J. Phytogeogr. Taxon. 49: 183–184.
Swenson, U. 1995. Systematics of *Abrotanella*, an Amphipacific genus of Asteraceae (Senecioneae). Pl. Syst. Evol. 197: 149–193.
Swenson, U., Bremer, K. 1999. On the circumscription of the Blennospermatinae (Asteraceae, Senecioneae) based on *ndh*F sequence data. Taxon 48: 7–14.
Tadesse, M., Crawford, D.J., Smith, E.B. 1995. Comparative capitular morphology and anatomy of *Coreopsis* L. and *Bidens* L. (Compositae) including a review of generic boundaries. Brittonia 47: 61–91.
Tadesse, M., Crawford, D.J., Kim, S.-C. 2001. A cladistic analyses of morphological features in *Bidens* L. and *Coreopsis* L. (Asteraceae: Heliantheae) with notes on generic delimitation and systematics. In: Friis, I., Ryding, O. (eds) Biodiversity research in the Horn of Africa

region. Biologiske Skrifter, The Royal Danish Academy of Sciences and Letters, Copenhagen, pp. 85–102.

Tegel, F. 2002. Die Testaepidermis der Lactuceae (Asteraceae) – ihre Diversität und systematische Bedeutung. Diss., Universität München (http://edoc.ub.uni-muenchen.de/archive/00000104/01/Tegel_Friedrich.pdf).

Thiele, M. 1988. Bau und Funktion des Antheren-Griffel-Komplexes der Compositen. Diss. Bot. 117, 169 pp. Stuttgart: J. Cramer.

Tomb, A.S. 1976. Pollen morphology in tribe Lactuceae (Compositae). Grana 15: 79–89.

Tomb, A.S. 1977. Lactuceae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae. London: Academic Press, pp. 1067–1079.

Torrell, M., Garcia-Jacas, N., Susanna, A., Vallès, J. 1999. Phylogeny in *Artemisia* (Asteraceae, Anthemideae) inferred from nuclear ribosomal DNA (ITS) sequences. Taxon 48: 721–736.

Turner, B.L. 1980. La taxonomía del género *Aphanactis* (Asteraceae-Heliantheae). Bol. Soc. Argent. Bot. 19: 33–44.

Turner, B.L. 1987a. Submergence of the genera *Caterothamnus* and *Oaxacania* into *Hofmeisteria* (Eupatorieae, Asteraceae). Phytologia 63: 415–416.

Turner, B.L. 1987b. Taxonomy of *Carphochaete* (Asteraceae–Eupatorieae). Phytologia 64, 2: 145–162.

Turner, B.L. 1988. Submergence of the genera *Asanthus* and *Discritogyne* within *Steviopsis* (Asteraceae, Eupatorieae), including new combinations. Phytologia 64: 259–262.

Turner, B.L. 1989. Revisionary treatment of the genus *Sinclairia*, including *Liabellum* (Asteraceae, Liabeae). Phytologia 67: 168–206.

Turner, B.L. 1990. A new species of *Steviopsis* (Asteraceae: Eupatorieae) from Nuevo Leon, Mexico. Phytologia 68: 410–412.

Turner, B.L. 1991a. *Brickellia sonorana* (Asteraceae), a new species from México belonging to the subgenus *Phanerostylis*. Phytologia 71: 51–56.

Turner, B.L. 1991b. Recension of the *Cronquistianthus* group of *Eupatorium* (Asteraceae). Phytologia 70: 158–177.

Turner, B.L. 1994. Taxonomic status of *Brickelliastrum villarrealii* R.M. King & H. Robins. (Asteraceae, Eupatorieae). Phytologia 76: 389–390.

Turner, B.L. 1995. Synopsis of *Ageratella* (Asteraceae, Eupatorieae). Phytologia 78: 204–208.

Turner, B.L. 1997. Eupatorieae. In: Turner, B.L. (ed.) The Compositae of Mexico. A systematic account of the family Asteraceae, vol. 1. Phytologia Mem. 11: i–iv, 1–272.

Turner, B.L., Powell, A.M. 1977. Helenieae – systematic review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae. London: Academic Press, pp. 699–737.

Turner, B.L., Powell, A.M., Cuatrecasas, J. 1967. Chromosome numbers in the Compositae. XI. Peruvian species. Ann. Missouri Bot. Gard. 54: 172–177.

Turner, B.L., Kim, K.J., Norris, J. 1991. Taxonomic status of *Barroetea glutinosa* (Asteraceae, Eupatorieae) and its allies: morphological evidence for the transfer of *Barroetea* to *Brickellia*. Phytologia 71: 38–50.

Urbatsch, L.E., Roberts, R.P. 2004. New combinations in the genus *Gundlachia* and four new genera of Astereae (Asteraceae) from northern Mexico and the southern United States. Sida 21: 243–257.

Urbatsch, L.E., Roberts, R.P., Karaman, V. 2003. Phylogenetic evaluation of *Xylothamia*, *Gundlachia*, and related genera (Asteraceae, Astereae) based on ETS and ITS nrDNA sequence data. Amer. J. Bot. 90: 634–649.

Urtubey, E., Stuessy, T.F. 2001. New hypotheses of phylogenetic relationships in Barnadesioideae (Asteraceae) based on morphology. Taxon 50: 1043–1063.

Urtubey, E., Tellería, M.C. 1998. Pollen morphology of the subfamily Barnadesioideae (Asteraceae) and its phylogenetic and taxonomic significance. Rev. Palaeobot. Palynol. 104: 19–37.

Valadon, L.R.G. 1977. Arctoteae and Calenduleae – chemical review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, vol. 2. London: Academic Press, pp. 989–998.

Vallès, J., Blanché, C., Bonet, M.À., Agelet, A., Muntané, J., Raja, D., Parada, M. 1996. A contribution to the ethnobotany of the Asteraceae in Catalonia. In: Caligari, P.D.S., Hind, D.J.N. (eds) Compositae: biology & utilization. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 2. Royal Botanic Gardens, Kew, pp. 453–466.

Vallès, J., Torrell, M., Garnatje, T., Garcia-Jacas, N., Vilatersana, R., Susanna, A. 2003. The genus *Artemisia* and its allies: phylogeny of the subtribe Artemisiinae (Asteraceae, Anthemideae) based on nucleotide sequences of nuclear ribosomal DNA internal transcribed spacers (ITS). Pl. Biol. 5: 274–284.

Velez, M.C. 1981. Karpologische Untersuchungen an amerikanischen Astereae (Compositae). Mitt. Bot. Staatssamml. München 17: 1–170.

Vezey, E.L., Watson, L.E., Skvarla, J.J., Estes, J.R. 1994. Plesiomorphic and apomorphic pollen structure characteristics of Anthemideae (Asteroideae: Asteraceae). Amer. J. Bot. 81: 648–657.

Viswanathan, M.V., Singh, H.B. 1996. Potential industrial uses of some less-known Asteraceae of India. In: Caligari, P.D.S., Hind, D.J.N. (eds) Compositae: biology & utilization. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 2. Royal Botanic Gardens, Kew, pp. 643–659.

Voytenko, V.F. 1989a. Heterocarpy (heterodiaspory) in angiospermous plants: analysis of the concept, classification, terminology (in Russian). Bot. Zhurn. (Moscow & Leningrad) 74: 281–297.

Voytenko, V.F. 1989b. The typology and evolution of forms of heterocarpy in the tribe Lactuceae (Asteraceae) (in Russian). Bot. Zhurn. (Moscow & Leningrad) 74: 1241–1257.

Voytenko, V.F., Oparina, S.N. 1990. Comparative analysis of anatomical structure of fruits in heterocarpous representatives of the tribe Lactuceae (Asteraceae) (in Russian). Bot. Zhurn. (Moscow & Leningrad) 75, 3: 299–314.

Wagenitz, G. 1997. The impact of molecular methods on the systematics of angiosperms. Bot. Acta 110: 274–281.

Wagenitz, G., Hellwig, F.H. 1996. Evolution of characters and phylogeny of the Centaureinae. In: Hind, D.J.N., Beentje, H.J. (eds) Compositae: systematics. Proceedings of the International Compositae Conference, Kew, 1994 (D.J.N. Hind, Editor-in-Chief), vol. 1. Royal Botanic Gardens, Kew, pp. 491–510.

Wagenitz, G., Dittrich, M., Damboldt, J. 1982. *Centaurothamnus*, eine neue Gattung der Compositae-Cardueae in Arabien. Candollea 37: 101–115.

Wagner, H. 1977. Cynareae – chemical review. In: Heywood, V.H., Harborne, J.B., Turner, B.L. (eds) The biology and chemistry of the Compositae, vol. 2. London: Academic Press, pp. 1017–1038.

Wagstaff, S.J., Breitwieser, I. 2002. Phylogenetic relationships of New Zealand Asteraceae inferred from ITS sequences. Pl. Syst. Evol. 231: 203–224.

Wagstaff, S.J., Breitwieser, I. 2004. Phylogeny and classification of *Brachyglottis* (Senecioneae, Asteraceae): an example of rapid species radiation in New Zealand. Syst. Bot. 29: 1003–1010.

Walsh, N.G. 1999. *Centipeda*. In: Walsh, N.G., Entwisle, T.J. (eds) Flora of Victoria, vol. 4. Dicotyledons, Cornaceae to Asteraceae. Melbourne: Inkata Press, pp. 720–723.

Walsh, N.G., Entwisle, T.J. (eds) 1999. Flora of Victoria, vol. 4. Melbourne: Inkata Press.

Watanabe, K., King, R.M., Tetsukaza, Y., Ito, M., Yokoyama, J., Suzuki, T., Crawford, D.J. 1995. Chromosomal cytology and evolution in Eupatorieae (Asteraceae). Ann. Missouri Bot. Gard. 82: 581–592.

Watson, L.E., Evans, T.M. 1999. Phylogeny and biogeography of the tribe Anthemideae. In: Anon. (ed.) XVI International Botanical Congress, Abstracts, p. 358. St. Louis: Missouri Botanical Garden.

Watson, L.E., Evans, T.M., Boluarte, T. 2000. Molecular phylogeny of tribe Anthemideae (Asteraceae), based on chloroplast gene *ndh*F. Mol. Phylog. Evol. 15: 59–69.

Watson, L.E., Bates, P.L., Evans, T.M., Unwin, M.M., Estes, J.R. 2002. Molecular phylogeny of subtribe Artemisiinae (Asteraceae), including *Artemisia* and its allied and segregate genera. BMC Evol. Biol. 2: 17.

Weddell, H.A. 1855–1857. Chloris Andina, vol. 1. Paris: P. Bertrand.

Weitz, F.M. 1989. A revision of the genus *Corymbium* (Asteraceae). S. African J. Bot. 55: 598–629.

Werker, E. 1997. Seed anatomy. In: Handbuch der Pflanzenanatomie, X. 3. 1. Berlin: Bornträger, 424 pp.

Whitton, J., Wallace, R.S., Jansen, R.K. 1995. Phylogenetic relationships and patterns of character change in the tribe Lactuceae (Asteraceae) based on chloroplast DNA restriction site variation. Canad. J. Bot. 73: 1058–1073.

Wilson, P.G. 1992. The *Lawrencella* complex (Asteraceae: Gnaphalieae: Angianthinae) of Australia. Nuytsia 8: 361–377

Wood, A.R., Nordenstam, B. 2004. An interesting new species of *Osteospermum* (Asteraceae-Calenduleae) from the western Cape Province, South Africa, providing a link to the genus *Chrysanthemoides*. S. African J. Bot. 69: 572–578.

Wulff, A.F., Hunziker, J.H., Escobar, A. 1996. Estudios cariologicos en Compositae, VII. Darwiniana 34: 213–231.

Wussow, J.R., Urbatsch, L.E., Sullivan, G.A. 1985. *Calea* (Asteraceae) in Mexico, Central America, and Jamaica. Syst. Bot. 10: 241–267.

Yahara, T., Kawahara, T., Crawford, D.J., Ito, M., Watanabe, K. 1989. Extensive gene duplication in diploid *Eupatorium* (Asteraceae). Amer. J. Bot. 76: 1247–1253.

Zachariades, C., Muniappan, R., Strathie, L.W. (eds) 2002. Proceedings 5th International Workshop Biological Control and Management of *Chromolaena odorata*, Durban, South Africa, 23–25 October 2000. Pretoria: ARC-Plant Protection Research Institute, 186 pp.

Zardini, E.M. 1974. Sobre la presencia del genero *Gerbera* en America. Bol. Soc. Argent. Bot. 16: 103–108.

Zdero, C., Bohlmann, F. 1988. Macrolide diterpenes and other ent-labdanes from *Corymbium villosum*. Phytochemistry 27: 227–231.

Zdero, C., Bohlmann, F. 1990. Systematics and evolution within the Compositae, seen with the eyes of a chemist. Pl. Syst. Evol. 171: 1–14.

Zdero, C., Bohlmann, F., King, R.M., Robinson, H. 1986. Further 5-methyl coumarins and other constituents from the subtribe Mutisiinae. Phytochemistry 25: 509–516.

Zhang, X., Bremer, K. 1993. A cladistic analysis of the tribe Astereae (Asteraceae) with notes on their evolution and subtribal classification. Pl. Syst. Evol. 184: 256–283.

Zhao, Z., Skvarla, J.J., Jansen, R.K., DeVore, M.L. 2000. Phylogenetic implications of pollen morphology and ultrastructure in the Barnadesioideae (Asteraceae). Lundellia 3: 26–40.

Goodeniaceae[1]

Goodenovieae R. Br., Prodr.: 573 (1810), nom. cons.
Brunoniaceae R. Br. (1816).

R.C. Carolin

Herbs, subshrubs, shrubs or rarely scramblers, glabrous or hairy with simple or branched or glandular hairs, sometimes viscid and varnished with age. Leaves mostly spirally arranged, rarely opposite, often with an axillary tuft of hairs; blades simple, with entire to dentate or rarely lobed margins; stipules absent. Flowers in cymes, thyrses, racemes, spikes, subumbels or heads or rarely solitary. Sepals usually 5, rarely 3, sometimes connate, sometimes reduced to a rim or obsolete. Corolla tubular, usually slit on the adaxial side, often 2-lipped, sometimes fan-like, sometimes with a pouch or spur; lobes 5, often winged, often with auricles on margin of the adaxial slit which surround the indusium. Stamens 5, opposite the sepals, epigynous or epipetalous or apparently almost hypogynous; anthers free or connate, 2-locular, dehiscing through longitudinal slits. Ovary superior, half-inferior or inferior, usually 2-locular (often incompletely so), rarely 4-locular or apparently 1-locular; style usually entire with a hollow pollen-cup (indusium) usually enclosing the 2-fid or unlobed stigma, rarely 2–4-fid. Fruit a drupe, inferior nut, or capsule dehiscing through 2–4 valves, rarely separating transversely into 1-seeded woody articles. Seeds with or without endosperm, rarely with a caruncle; embryo terete or flattened.

Eleven genera and c. 440 species, mostly in the southern hemisphere, mainly Australia.

Vegetative Morphology. Most species in the family are either herbs, shrubs or subshrubs, with *Scaevola enantophylla* and *S. oppositifolia* being the only woody scramblers. *Scaevola spinescens* is thorny. Many of the herbs are relatively ephemeral, occurring in the more arid areas of Australia and becoming often very common after rain. Only a few species are large shrubs. Leaves are simple and arranged spirally in almost all species, with a variety of shapes, but opposite in *Scaevola enantophylla*.

Vegetative Anatomy. Carlquist (1969) gives a detailed account of the wood anatomy in the family. The species from drier habitats ("xeromorphic") tend to have short narrow vessels whilst those from wetter regions ("mesic") have long wider vessels. Abundant crystals, possibly of calcium oxalate, are usually found in species from drier regions. Libriform fibres have not been found in the family and there is a relative abundance of uniseriate rays. Krause (1912) notes the occurrence of medullary bundles in *Goodenia* spp., e.g. *G. ovata*, and describes them as leaf traces. Rajput and Carolin (1984) show that the cortical bundles in *Dampiera* are leaf bundles from the node(s) above, and that the number found in any cross-section is related to the phyllotaxis of that shoot. An illustration by Krause (1912) indicates that there may be a similar situation in *Lechenaultia*. Trichomes are widespread through the family, and in *Dampiera* these may be particularly dense. Carolin (1970) gives a detailed account of the types to be found, including glandular, stellate, simple, strigose and dendritic hairs. Groups of species within *Goodenia*, *Coopernookia* and *Scaevola* secrete a viscous fluid from glandular hairs on the leaves and stems, and in some of these species this secretion hardens to a varnish. Stomates are anomocytic.

Inflorescence Structure. There are two distinct types of inflorescence in the family (for a discussion of these types, see Carolin 1967). In *Goodenia*, *Scaevola*, *Coopernookia*, *Selliera*, *Verrauxia*, *Pentaptilon* and *Diaspasis*, the primitive form of the inflorescence is a thyrse without a terminal flower. More often, the reduction of each constituent axillary cyme to a single flower has resulted in a raceme or spike. In a number of *Goodenia* spp., the racemes are condensed into subumbels. In most *Velleia* spp., the condensation of the main axis and the expansion of each axillary cyme has given a very characteristic form to the

[1] Updated by J.W. Kadereit and M.H.G. Gustafsson.

plant. In *Dampiera*, *Lechenaultia*, *Anthotium* and *Brunonia*, the inflorescence is based on a cymo-panicle with a terminal flower (see also Rajput and Carolin 1988). Tightly condensed head-like inflorescences are found in *Brunonia australis*, *Dampiera wellsiana*, *D. eriocephala*, *D. dentata* and *Scaevola globosa*. These may elongate strongly when fruiting.

Flower Structure. Carolin (1959; 1966) has examined the flower structure in detail. In all genera, the petals are connate to some degree but, except for *Brunonia*, the corolla tube is slit to the base (or nearly so) on the adaxial side. In almost all species (*Brunonia* excluded), each corolla lobe has a thin but often large, brightly coloured wing on either side. In *Scaevola*, the flower is opened out on either side of this slit, exposing the pollen presentation apparatus and stigma, to form a fan-shaped corolla. In other genera, the adaxial corolla lobes are often folded around the indusium and, in some cases, the corolla is distinctly 2-lipped (e.g. most species of *Velleia*, *Dampiera* and *Lechenaultia*, and many of *Goodenia*) to such an extent that adaxial and abaxial corolla lobes may be different in colour (e.g. *Goodenia bicolor*). In many species of *Goodenia* and throughout *Dampiera* and *Velleia*, the lower part of the wings of the corolla lobes on either side of the slit are modified into auricles which enclose the indusium. Petal venation has been described by Gustafsson (1995), and petals were found to have three major veins meeting at the apex. These veins anastomose or not. The corolla shows a wide range of colours, particularly in *Lechenaultia* which has been developed as an horticultural plant. In most species, however, the corolla is various shades of yellow or blue. Stamens are epipetalous or free from the petals in *Velleia*. The anthers are free or connate and dehisce in the bud, and the pollen is deposited inside a cup at the top of the style (indusium) which grows up through the dehisced stamens (Brough 1927; Carolin 1960; Leins and Erbar 1989). The indusium (Fig. 123) may be equipped with hairs (e.g. *Goodenia*, *Velleia*), or it may be glabrous as in *Dampiera*. The pollen is presented in the indusium when the flower opens. However, pollen collection by the indusium is rather inefficient, and much pollen is also found around the auricles and on the outside of the indusium. The indusium is an outgrowth from the style (Carolin 1960) and surrounds the stigma initially, which eventually grows out of the cup to appear as a 2-lobed structure. In *Lechenaultia*, however, the pollen is presented entirely on the outside of the style and the stigmatic surface is on the upper surface of the style near the top. The homologies of the stylar parts of this genus are not clear. The ovary is superior, half-inferior or inferior. In *Goodenia*, the ovary is usually inferior but, in *G. macroplectra*, the sepals are free from the ovary and are inserted below it, whereas the corolla is at least partially adnate to the ovary and epigynous. Almost throughout the family the ovary consists of 3 zones: a basal 2-locular zone which may be very short, a middle 1-locular zone and an upper 2-locular zone (Carolin 1959; see also Leins and Erbar 1989). Ovules may be inserted in either of the 2 lower zones on axile or parietal placentas respectively. There is, however, anatomical evidence to suggest that the ovary is 4-carpellary (Carolin 1959, 1966). In *Scaevola porocarya*, there are 4 fertile locules whereas in

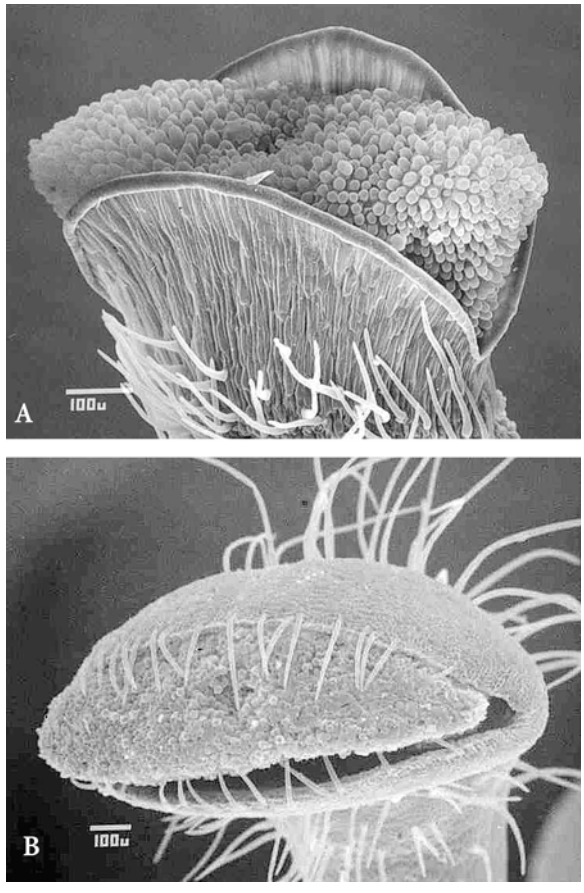

Fig. 123. Goodeniaceae. Stylar cup and stigma. **A** *Brunonia australis*. **B** *Selliera radicans*. (SEM photographs by C. Erbar and P. Leins)

many other species of *Scaevola* there are 2 fertile loculi and 2 sterile cavities. The homologies of the sterile cavities are unclear (Carolin 1966). The ontogenetic studies of Leins and Erbar (1989), however, do not appear to show any evidence for a 4-carpellate ovary.

Embryology. Early accounts of embryology include those of Rosén (1937, 1946), and a summary of embryological characters has been presented by Tobe and Morin (1996). The ovule is anatropous, unitegmic and tenuinucellar, and the integument is 16–20 cells thick. The embryo sac is of the Polygonum type and is surrounded by an endothelium except at the micropylar and chalazal ends. The embryo sac invades the chalazal tissue with a multicellular extension which does not seem to have the characteristics of a haustorium (Rosén 1937, 1946; Carolin, unpubl. data). In *Brunonia*, a suspensor haustorium has been claimed to exist by Rosén (1946) but this has been doubted by Tobe and Morin (1996). No haustorial endosperm is formed at either the micropylar or the chalazal end. The embryo develops according to the Solanad type (Rosén 1937, 1946). In *Goodenia*, *Velleia*, *Selliera*, *Scaevola*, *Diaspasis* and *Coopernookia*, the embryo is spathulate in shape, the cotyledons being wider than the radicle, but in *Dampiera*, *Lechenaultia* and *Anthotium* the embryo is terete (Carolin, unpubl. data). Endosperm formation is ab initio cellular or nuclear, and in *Brunonia* the endosperm is eventually confined to a band of crushed cells surrounding the embryo which has swollen cotyledons (Carolin, unpubl. data). Anther wall development is dicotyledonous, the endothecium is fibrous, and the tapetum glandular. Mature pollen grains are 2-celled.

Fruit and Seed. The fruits are mostly capsular but in a number of species, and throughout *Scaevola*, *Dampiera* and *Diapasis*, they are indehiscent. There is a fleshy mesocarp surrounding a hard endocarp in *Scaevola* sect. *Scaevola* whilst in *Scaevola* sects. *Xerocarpa*, *Dampera*, *Diaspasis*, and several species of *Goodenia*, the mesocarp is thin and more or less dry. In the indehiscent fruit of *Goodenia neogoodenia* and *Pentaptilon*, the endocarp is not thickened to any degree. In *Coopernookia*, the seed is obloid and carunculate and, in *Scaevola*, it is similar in shape but with a thin testa, being contained within the endocarp, and no caruncle is present. In *Goodenia* and related genera, the seed is variously flattened and has a wing or rim around the edge (Carolin 1966). In *Lechenaultia*, each seed is surrounded by a hardened inner portion of the pericarp and each of these single-seeded articles is dispersed separately (Morrison 1986).

Pollen Morphology. Pollen (Fig. 124) in the family is typically tricolporate (Duigan 1961; Gustafsson et al. 1997). Duigan (1961) distinguishes three types of pollen grain on the basis of surface pattern and the border of the pore. In *Goodenia* and *Brunonia*, the surface pattern is relatively coarse but in *Dampiera* it is very fine. *Goodenia* has a sexine which tapers gradually into the colpi whilst *Brunonia* has a sexine which forms two distinct ridges on either side of the colpi. Pollen grains in *Lechenaultia*, however, are porate and held together in one plane in rhomboidal tetrads. There are varying numbers of aborted grains in the tetrads, probably associated with

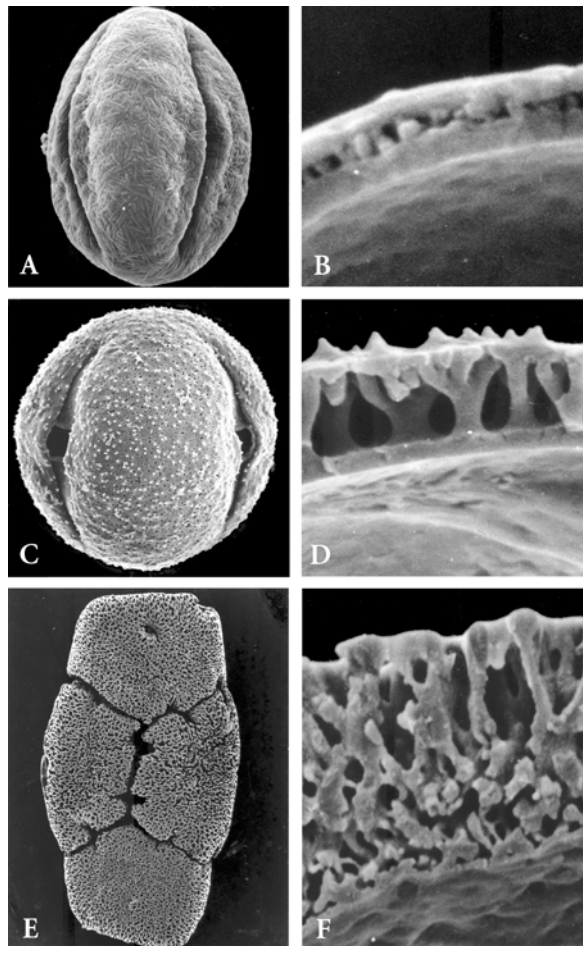

Fig. 124. Goodeniaceae. Pollen surface and exine structure. **A**, **B** *Dampiera*. **C**, **D** *Velleia*. **E**, **F** *Lechenaultia*. (SEM photographs by M. Gustafsson)

univalent formation at meiosis (Peacock 1959). Essentially, the three groups recognized by Duigan (1961) were also identified by Gustafsson et al. (1997), i.e. *Lechenaultia* with tetrads, *Anthotium-Dampiera* with tricolporate, rugulate grains with a thin infratectum and rounded ora, and the remaining genera (*Scaevola-Goodenia* group) with tricolporate, microspinulose grains with distally branched columellae (Fig. 124D) and lalongate ora. Within the latter group, *Brunonia* has ridges and depressions along the colpi.

Karyology. There are three distinct basic chromosome numbers in Goodeniaceae. *Coopernookia* alone has a base number of $x = 7$. The other genera can be divided into two groups: *Brunonia*, *Dampiera*, *Lechenaultia* and *Anthotium* with a base number of $x = 9$, and the remaining genera with a base number of $x = 8$. There are polyploid species within these groups, and in some species polyploid races (Peacock 1963; Peacock and Smith-White 1978).

Dispersal. Some species are clearly animal-dispersed because they have fleshy mesocarps, particularly the drupes of many *Scaevola* species. There is evidence, for instance, of emus eating the fruits of *S. tomentosa* and *S. spinencens*, the latter having the vernacular name of Emu Bush in parts of Western Australia. The littoral species *S. taccada* and *S. calendulacea* also have a fleshy mesocarp and may be dispersed by birds but, in *S. taccada*, part of the endocarp is ± corky and it may also float some distance in sea currents. *Selliera radicans* has a ± fleshy fruit containing seeds with a very mucilaginous border, which stick very effectively to animals (pers. obs.) and may be dispersed this way. Dispersal by seabirds may account for the trans-Pacific distribution of this species, which occurs in littoral salt-marshes as well as highland swamps. Many species of *Goodenia* have seeds with a mucilaginous border or wing, although it is doubtful if this structure attaches the seed to animals as effectively as that of *Selliera*. However, ants appear to be attracted to this border or wing in some cases, and here it might function as an elaiosome, e.g. the desert species *G. cycloptera* (pers. obs.; A.J. Beatty, pers. comm.). In some other *Goodenia* spp., the wing on the seed is scarcely mucilaginous and seems to function as a wind-dispersal agent, the seeds being blown for considerable distance across the bare soil of communities in the arid areas of Australia, e.g. *G. vilmorinae*, *G. triodiophila* (pers. obs.). In *Brunonia*, the single-seeded fruit is retained within the hardened hairy calyx tube which has persistent hairy lobes at the top, and this whole structure is dispersed by the wind. Many species of the family do not appear to have well-developed dispersal mechanisms, although little work has been done on most of them.

Reproductive Biology. Pollen is presented to the vector in or around the indusium (Fig. 123). It is deposited on the vector, usually an insect, as it probes to the bottom of the flower where the nectar is contained either in a single spur or pocket, as in *Goodenia*, *Velleia*, etc. (Carolin 1959), in several pockets as in *Dampiera*, or on the surface of the ovary (Carolin 1959). The hairs on and around the indusium are agitated by the vector, thus releasing the pollen onto its body (pers. obs.). There are a number of structures on the corolla which act as tactile guides for the vector. In *Coopernookia* these are large barbulae, which are often hairy in *Scaevola*; in *Goodenia* they are mostly surface hairs or large papillae, and in *Goodenia* sect. *Borealis* they are ridges; in *Dampiera*, they are sinuous ridges (Carolin et al. 1992). The vectors observed so far are mostly native bees and Lepidoptera. *Lechenaultia* sect. *Lechenaultia*, *Scaevola coccinea* and *S. glabra* show a bird-pollination syndrome, with well-developed corolla tubes and red, orange or rarely bright yellow or green flowers. The stigmatic initials later grow out of the indusium (expect in *Lechenaultia*) but it appears that, in at least some species, the pollen in the indusium is by that time non-viable (Brough 1927). All species examined are self-incompatible.

Phytochemistry. Inulin has been reported as a storage carbohydrate in the family. Seco-loganin, a simple seco-iridoid, has also been recorded. Alkaloids are also known and may be responsible for the use of members of the family as medicines by Australian natives.

Subdivision of and Relationships Within the Family. Relationships within the family have been investigated by Carolin (1959, 1978), Gustafsson et al. (1996) and Hansen (1997). In their analysis of *rbc*L sequence variation of all genera except *Pentaptilon*, albeit including only few species of the large genera, and considering morphological variation, Gustafsson et al. (1996) demonstrate the existence of four lineages. These

are (1) *Lechenaultia*, (2) *Anthotium* and *Dampiera*, (3) *Brunonia* and (4) the remaining genera (*Scaevola-Goodenia* group). *Brunonia*, often treated as a separate family, is well-nested within Goodeniaceae. In the *Scaevola-Goodenia* group, *Diaspasis* and *Scaevola* are successive sister genera to a well-supported clade of *Goodenia*, *Selliera*, *Coopernookia*, *Velleia* and *Verreauxia*, of which *Goodenia* may not be monophyletic. The four subgroups of the family can also be characterized in terms of pollen morphology (Gustafsson et al. 1997). The analysis by Gustafsson et al. (1996) confirms several but not all results of Carolin's (1978) earlier analysis, and some similarity can be seen between the morphology-based conclusions of Hansen (1997) and those of Gustafsson et al. (1996). Howarth et al. (2003) found that *Diaspasis* is deeply nested within *Scaevola*, while *Scaevola collaris* should be excluded from this genus because it is most closely related to species of *Goodenia*. Their results also indicated that *Verreauxia* and *Velleia* may be nested within *Goodenia*.

Affinities. Goodeniaceae have usually been placed in the Campanulales with Campanulaceae, Lobeliaceae, Compositae, Calyceraceae and Stylidiaceae. Carolin (1978) and Lammers (1992) have examined these relationships and suggest that this position be retained, after the removal of Stylidiaceae. Lammers (1992) also suggests that Menyanthaceae be included here. Indeed, on the basis of phytochemical data, he considers that Goodeniaceae, Compositae, Calyceraceae and Menyanthaceae form a well-defined clade, with Campanulaceae, Lobeliaceae (and Cyphiaceae) as the sister-group. Both molecular and morphological evidence (Morgan and Soltis 1993; Cosner et al. 1994; Gustafsson and Bremer 1995; Olmstead et al. 2000; Soltis et al. 2000; Bremer et al. 2001; Lundberg and Bremer 2003) confirms the existence of a well-supported Menyanthaceae, Goodeniaceae, Calyceraceae, Compositae clade, in which Goodeniaceae are sister to Calyceraceae/Compositae, and Menyanthaceae sister to these three families. This clade is part of the Asterales (APG II 2003).

Distribution and Habitats. The family is almost entirely southern hemisphere in distribution and most species are confined to Australia. They occur in a wide variety of habitats but mostly in more open communities, particularly in the arid and semi-arid parts of the continent, but also with significant numbers in the sclerophyll forests and heaths of the damper climate zones. Only a few species, such as *Scaevola enantophylla and S. glabra*, occur in rain forests. *Scaevola* is the most widespread genus outside Australia. Two strand species occur almost throughout the tropics: *Scaevola taccada* in the Indo-Pacific region, and *S. plumieri* in America, Africa and India. Restricted endemics are *Scaevola hainanensis* in southern China, *S. socotrensis* on Socotra and *S. wrightii* on Cuba. Many of the islands of the South Pacific have an endemic, inland, montane *Scaevola* species. New Caledonia and the Hawaiian islands each have several species, in both cases the result of three independent colonisations, one of which gave rise to a small evolutionary radiation in each of the archipelagos (Howarth et al. 2003). The largest genus, *Goodenia*, also occurs northwards from Australia, with *G. purpurascens*, *G. pumilia* and *G. armstrongiana* in New Guinea, *G. koningsbergeri* in Java, and *G. pilosa* in Indonesia and south-eastern Asia. *Selliera radicans* occurs in Australia, New Zealand and Chile. *Lechenaultia filiformis* is found in New Guinea and the Moluccas, and *Velleia spathulata* occurs in New Guinea.

Key to the Genera

1. Anthers connate 2
– Anthers free 6
2. Ovary superior **1. *Brunonia***
– Ovary inferior 3
3. Ovules and seeds more than 2; fruit dehiscent or fragmenting, rarely indehiscent and then the fruit beaked 4
– Ovules and seeds 1 or 2; fruit indehiscent, not beaked 5
4. Leaves all cauline; indusium 2-lipped **3. *Lechenaultia***
– Leaves cauline and basal; indusium not 2-lipped **2. *Antotium***
5. Corolla without auricles; hairs simple **7. *Diaspasis***
– Corolla with auricles; hairs branched, rarely absent **4. *Dampiera***
6. Ovules (and usually seeds) more than 2 per loculus 7
– Ovules and seeds 1 or 2 per loculus 11
7. Seeds ovoid, obloid or irregularly compressed, without a wing, rim or peripheral groove 8
– Seeds flattened or concave-compressed, with a wing, rim or peripheral groove 9
8. Corolla yellow **10. *Velleia***
– Corolla blue to pinkish or white **5. *Coopernookia***
9. Corolla lobes without wings; fruit ± fleshy, indehiscent **9. *Selliera***
– Corolla lobes winged; fruit a dry, dehiscent capsule 10
10. Flowers in thyrses, racemes, spikes or subumbels; ovary inferior or half-inferior (or superior to the sepals but the corolla fused to the top of the ovary in *Goodenia macroplectra*) **8. *Goodenia***

– Flowers in axillary dichasia often in the axils of basal leaves; ovary free from the corolla for most of its length **10. *Velleia***

11. Fruit a capsule **5. *Coopernookia***
– Fruit indehiscent, nut-like or soft-shelled with several seeds or a 1–2-seeded drupe 12

12. Ovary and fruit winged **11. *Pentaptilon***
– Ovary and fruit not winged 13

13. Style with stiff purplish hairs; corolla white, usually with violet spots **8. *Goodenia***
– Style with whitish hairs or glabrous (purplish bristles sometimes present on back of indusium); corolla without violet spots 14

14. Corolla blue to white **6. *Scaevola***
– Corolla yellow or brownish 15

15. Shrubs with alternate leaves or scramblers with opposite leaves **6. *Scaevola***
– Herbs with alternate or basal leaves 16

16. Plants hairy with unbranched cottony hairs or glabrous **8. *Goodenia***
– Plants hairy with branched and simple hairs **12. *Verreauxia***

Genera of Goodeniaceae

1. *Brunonia* Sm. ex R. Br. Fig. 125

Brunonia Sm. ex R. Br., Prodr.: 589 (1810).

Herbs or subshrubs. Leaves basal or alternate towards the base of the stem, ± villous. Flowers in heads, each flower with several hyaline bracts; heads surrounded by green involucral bracts. Sepals connate; tubes swollen towards the top when mature; lobes with long cilia. Petals 5, blue, connate; tube entire; lobes spreading, not winged, stamens epipetalous; anthers connate. Ovary superior, 1-locular; indusium scarcely compressed, erect, with scattered hairs and almost glabrous lips. Fruit a nut enclosed in the persistent calyx. Seeds ellipsoid, without conspicuous endosperm. $2n$ = 18, 36, 72. One species, *B. australis* Sm. ex R. Br., Australia south of the 17th parallel.

2. *Anthotium* R. Br.

Anthotium R. Br., Prodr.: 582 (1810).

Perennial glabrous herbs with 1 to many stems and a woody rootstock. Leaves mostly basal. Flowers sessile, arranged in compact monochasia condensed into heads; bracts and bracteoles leaf-like. Corolla 2-lipped, red to light blue or cream; tube slit nearly to the base adaxially; lobes winged; adaxial lobes with auricles on adjacent margins. Anthers coherent into a tube. Ovary inferior, 2-locular, with numerous ovules; indusium ± globular, glabrous or hairy; stigmatic surface within the indusium.

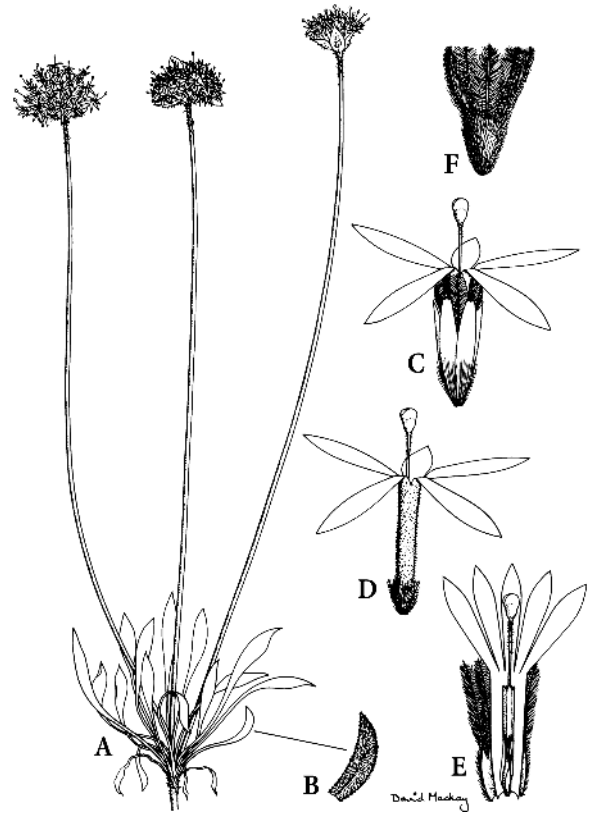

Fig. 125. Goodeniaceae. *Brunonia australis*. **A** Habit. **B** Leaf tip. **C** Flower, with bracts. **D** Flower, calyx removed. **E** Flower, longitudinal section. **F** Fruit with persistent sepals. (Illustrations by David Mackay in Carolin 1992; reproduced with permission from Flora of Australia)

Fruit a capsule with 4 valves. Three species, southwestern Australia.

3. *Lechenaultia* R. Br.

Lechenaultia R. Br., Prodr.: 581 (1810).
Latouria (Endl.) Lindley (1847).
Ericopsis C. Gardner (1923).

Perennial hairy or glabrous herbs or subshrubs with woody rootstock, often with suckers. Leaves sessile, linear or sometimes lanceolate to ovate. Flowers sessile, arranged in cymes; bracts and bracteoles usually leaf-like. Corolla 2-lipped, usually glabrous outside, variously hairy inside, red to blue, orange, white or yellow; tube slit adaxially or not; lobes winged, sometimes only slightly so. Anthers cohering into a tube. Ovary inferior, 2-locular, with numerous ovules; indusium 2-lipped, usually hairy; stigmatic surface on the upper side of the indusium. Fruit capsule-like, with 4 narrow valves. Each seed enclosed in an article which is

part of the hard endocarp. $2n = 18, 36$. Twenty-six to 27 species, south-western, central and northern Australia, one species extending to New Guinea.

Three sections: sect. *Lechenaultia*: corolla tube not slit; sect. *Patentes* D. Morrison: corolla tube slit adaxially, adaxial corolla lobes winged; sect. *Latouria* (Endl.) Benth.: corolla tube slit adaxially, adaxial corolla lobes usually not winged.

4. *Dampiera* R. Br.

Dampiera R. Br., Prodr.: 587 (1810); Rajput & Carolin, Telopea 3: 183–216 (1988), gen. class.

Subshrubs to many-stemmed perennial woody herbs or rosette herbs, sometimes with suckers, glabrous or with branched dendritic hairs. Flowers in racemes or thyrses which are sometimes condensed into heads, or in irregular cymo-panicles or apparently in clusters in the leaf axils. Sepals usually small or sometimes obsolete. Corolla 2-lipped, blue or yellow, rarely white or pink, usually hairy outside, often with ridges and calli inside; tube slit to the base adaxially and often laterally; lobes winged; adaxial lobes auriculate on adjacent margins. Anthers connate. Ovary inferior, 2–1-locular; indusium ± globular, usually with a glabrous orifice; stigmatic surface within the indusium. Ovules 1–2, sometimes bent or horseshoe-shaped. Fruit an inferior nut. $2n = 18, 36, 54$. About 66 species, Australia.Two sections: sect. *Linschotenia* (Vriese) Benth.: flowers in racemes, thyrses or heads; sect. *Dampiera*: flowers in cymo-panicles or apparently clustered in leaf axils.

5. *Coopernookia* Carolin

Coopernookia Carolin, Proc. Linn. Soc. New South Wales 92: 209 (1968).

Subshrubs with stellate and glandular hairs, often viscid and becoming varnished. Flowers in leafy thyrses or racemes, with small bracteoles; pedicels articulate. Corolla scarcely 2-lipped, with long, stiff, retrorse bristles inside, white to mauve or deep pink; tube slit to the base adaxially; lobes broadly winged, without auricles. Anthers free. Ovary inferior, incompletely 2-locular; indusium ± flattened, with long bristles on the lips. Ovules 2–8. Fruit a capsule with 2 valves. Seeds ovoid to obloid, glossy, carunculate, without a wing. $2n = 14$. Six species, South Australia.

6. *Scaevola* L.

Scaevola L., Mant. Pl. 2: 145 (1771); Carolin, Telopea 3: 477–515 (1990), gen. class.; Howarth et al., Amer. J. Bot. 90: 915–923 (2003), phylog.
Nigromnia Carolin (1974).

Perennial herbs, shrubs, scramblers or small trees. Leaves alternate or rarely opposite. Flowers in terminal or axillary thyrses, racemes, spikes or apparently cymes, bracteolate. Corolla blue, white, mauve or rarely yellow, slit on the adaxial side to the base and fan-shaped, rarely tubular; lobes usually winged. Anthers free. Ovary inferior, 1–4-locular, sometimes with 2 fertile loculi and 2 sterile cavities; ovules 1–4, indusium flattened, often pubescent and with stiff hairs on the lips. Fruit indehiscent; mesocarp fleshy, corky or ± dry; endocarp hard. Seeds ovoid, without wing or caruncle. $2n = 16, 32$. Circa 130 species, 70 endemic in Australia, the others throughout the Indo-Pacific region and more rarely in other tropical areas.

Three sections: sect. *Scaevola*: leaves alternate, fruit corky or fleshy, inflorescence continuing growth after flowering, Australia and Indo-Pacific; sect. *Enantiophyllum* Miq.: leaves opposite, fruit fleshy, inflorescence continuing growth after flowering, Australia; sect. *Xerocarpa* G. Don.: leaves alternate, fruit usually dry, inflorescence not continuing growth after flowering.

7. *Diaspasis* R. Br.

Diaspasis R. Br., Prodr.: 586 (1810).

Perennial with a tough rootstock, sprinkled with papillate hairs. Leaves sessile, linear. Flowers in terminal racemes, bracteolate. Sepals often unequal. Corolla slightly 2-lipped, white to pink or lavender or rarely yellowish; tube slightly slit adaxially; lobes winged. Anthers connate. Ovary inferior, 2-locular; indusium compressed laterally; ovules solitary in each loculus. Fruit dry, indehiscent; endocarp hard. $2n = 16$. One species, south-western Australia.

8. *Goodenia* Sm. Fig. 126

Goodenia Sm., Sec. Bot. New Holl.: 15 (1793); Carolin et al., Fl. Austral. (1992), rev.; Sage, Nuytsia 13: 367–377 (2000), key Australia.
Neogoodenia C. Gardner & A.S. George (1963).

Herbs or shrubs. Flowers in thyrses, racemes spikes or subumbels, bracteolate or ebracteolate. Sepals variously adnate to the ovary or free. Corolla adnate to the ovary, yellow, cream, pink, blue, pur-

Fig. 126. Goodeniaceae. *Goodenia macroplecta*. **A** Habit. **B** Flower. (Illustrations by David Mackay in Carolin et al. 1992; reproduced with permission from Flora of Australia)

plish on brownish red, usually pouched or sometimes spurred, usually bilabiate; tube slit to the base adaxially; lobes winged; adaxial lobes sometimes auriculate. Anthers free. Ovary usually inferior (the sepals may be free from the ovary, although the corolla is always at least partially adnate and the stamens are always epigynous), usually incompletely 2-locular; style simple or 2–4-fid; indusium usually with stiff bristles on the lips; ovules solitary to numerous. Fruit usually a capsule, rarely a small 1-seeded nut or a large, hard, 4-seeded drupe. Seeds compressed, usually winged. $2n$ = 16, 32, 48, 64. About 180 species, 178 in Australia, three extending to New Guinea and southern China; one endemic in Java.

Two subgenera: subg. *Monochila* (G. Don) Carolin: corolla white, usually with purplish spots near the base of the lobes, or pale pink, rarely yellow; subg. *Goodenia*: flowers yellow, cream, blue, purplish or brownish red.

9. *Selliera* Cav.

Selliera Cav., Anales Hist. Nat. 1: 41 (1799).

Glabrous creeping perennial, rooting at the nodes. Flowers in condensed axillary racemes or solitary in the leaf axils. Corolla whitish, tinged with red, not 2-lipped, without a pouch; tube slit to the base adaxially but not opening out, lobes erect, wingless or almost so. Anthers free. Ovary inferior, 2-locular; indusium compressed, with stiff bristles on the lips; ovules numerous. Fruit indehiscent or eventually splitting, slightly fleshy. Seeds compressed, with a mucilaginous wing. $2n$ = 16. One species, *S. radicans* Cav., Australia, New Zealand and Chile.

10. *Velleia* Sm.

Velleia Sm., Trans. Linn. Soc. London, Bot. 4: 217 (1798).

Herbs or slightly shrubby plants, usually with basal leaves. Flowers in branching cymes arising from the axils of the leaves. Sepals sometimes reduced to 3, usually adnate to the base of the ovary only. Corolla usually free from the ovary except at the base, 2-lipped, yellow to orange or pink to mauve or white; tube slit to the base adaxially; lobes winged; adaxial lobes auriculate. Anthers free. Ovary superior, incompletely 2-locular; indusium compressed, with stiff bristles on the lips; ovules several. Fruit a capsule with 2–4 valves. Seeds compressed, winged or with a thickened rim. $2n$ = 16. Twenty-one species, all in Australia, with one extending to New Guinea.

Three sections: sect. *Euthales* (R. Br.) Carolin: sepals 5, connate into a tube, south-western Australia; sect. *Menoceras* R. Br.: sepals 5, free or slightly connate at the base, southern Australia; sect. *Vellelia*: sepals 3, eastern Australia.

11. *Pentaptilon* E. Pritz.

Pentaptilon E. Pritz., Bot. Jahrb. Syst. 35: 564 (1905).

Erect herb with a basal stock. Leaves mostly basal, tomentose with branched hairs. Flowers in a terminal thyrse, bracteolate. Corolla 2-lipped, yellow, throat brownish red and with dense tuft of whitish hairs; tube slit to the base adaxially; lobes winged. Stamens free. Ovary inferior, winged, 2-locular; indusium compressed, with stiff white bristles on the lips; ovules several; fruit soft, indehiscent, with 3 large and 2 smaller ± bladdery wings alternating with the sepals. Seeds compressed, with a narrow

wing. One species, *P. careyi* E. Pritz., Western Australia.

12. *Verreauxia* Benth.

Verreauxia Benth., Fl. Austral. 4: 105 (1868).

Herbs or shrubs. Leaves basal or alternate, tomentose to villous with branched hairs. Flowers in loose or spike-like terminal thyrses. Corolla 2-lipped, yellow, brownish in the throat; tube slit to the base adaxially; lobes winged. Stamens free. Ovary inferior, 1-locular, with reddish or golden multicellular hairs between three of the sepaline ribs; indusium ± grooved, with short white bristles on the lips; ovule solitary. Fruit a compressed nut. Seeds flat, with an indistinct rim. Three species, southwestern Australia.

Selected Bibliography

APG (Angiosperm Phylogeny Group) II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436.

Bremer, K., Backlund, A., Sennblad, B., Swenson, U., Andreasen, K., Hjertson, M., Lundberg, J., Backlund, M., Bremer, B. 2001. A phylogenetic analysis of 100+ genera and 50+ families of euasterids based on morphological and molecular data with notes on possible higher level morphological synapomorphies. Pl. Syst. Evol. 229: 137–169.

Brough, P. 1927. Studies in the Goodeniaceae. I. The life history of *Dampiera stricta* R. Br. Proc. Linn. Soc. New South Wales 52: 471–498.

Carlquist, S. 1969. Wood anatomy of Goodeniaceae and the problem of insular woodiness. Ann. Missouri Bot. Gard. 56: 358–390.

Carolin, R.C. 1959. Floral structure and anatomy in the family Goodeniaceae Dumort. Proc. Linn. Soc. New South Wales 84: 252–255.

Carolin, R.C. 1960. The structures involved in the presentation of pollen to visiting insects in the order Campanulales. Proc. Linn. Soc. New South Wales 85: 197–205.

Carolin, R.C. 1966. Seeds and fruit of the Goodeniaceae. Proc. Linn. Soc. New South Wales 91: 58–83.

Carolin, R.C. 1967. The concept of the inflorescence in the order Campanulales. Proc. Linn. Soc. New South Wales 92: 7–26.

Carolin, R.C. 1970. The trichomes of the Goodeniaceae. Proc. Linn. Soc. New South Wales 96: 8–22.

Carolin, R.C. 1978. The systematic relationship of *Brunonia*. Brunonia 1: 9–29.

Carolin, R.C. 1980. Pattern of the seed surface of *Goodenia* and related genera. Austral. J. Bot. 28: 123–137.

Carolin, R.C. 1990. Nomenclatural notes, new taxa and systematic arrangement in the genus *Scaevola* and its synonyms. Telopea 3: 477–515.

Carolin, R.C. 1992. Brunoniaceae. In: Gorge, A. (ed.) Flora of Australia, vol. 35. Canberra: Australian Government Publishing Service, pp. 1–3.

Carolin, R.C., Rajput, M.T.M., Morrison, D. 1992. Goodeniaceae. In: George, A. (ed.) Flora of Australia, vol. 35. Canberra: Australian Government Publishing Service, pp. 4–351.

Cosner, M.E., Jansen, R.K., Lammers, T.G. 1994. Phylogenetic relationships in the Campanulales based on *rbc*L sequences. Pl. Syst. Evol. 190: 79–95.

Duigan, S.L. 1961. Studies of the pollen grains of plants native to Victoria, Australia. I. Goodeniaceae (including *Brunonia*). Proc. Roy. Soc. Victoria 74: 87–109.

Gustafsson, M.H.G. 1995. Petal venation in the Asterales and related orders. Bot. J. Linn. Soc. 118: 1–18.

Gustafsson, M.H.G., Bremer, K. 1995. Morphology and phylogenetic interrelationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and related families (Asterales). Amer. J. Bot. 82: 250–265.

Gustafsson, M.H.G., Backlund, A., Bremer, B. 1996. Phylogeny of the Asterales sensu lato based on *rbc*L sequences with particular reference to the Goodeniaceae. Pl. Syst. Evol. 199: 217–242.

Gustafsson, M.H.G., Grafström, E., Nilsson, S. 1997. Pollen morphology of the Goodeniaceae and comparisons with related families. Grana 36: 185–207.

Hansen, H.V. 1997. Studies in the Goodeniaceae and the Brunoniaceae with a discussion of their relationships to Asteraceae and Calyceraceae. Nordic J. Bot. 17: 495–510.

Howarth, D.G., Gustafsson, M.H.G., Baum, D.A., Motley, T.J. 2003. Phylogenetics of the genus *Scaevola* (Goodeniaceae): implication for dispersal patterns across the Pacific Basin and colonization of the Hawaiian Islands. Amer. J. Bot. 90: 915–923.

Krause, K. 1912. Goodeniaceae und Brunoniaceae. Pflanzenreich IV, 277, 277a. Leipzig: Engelmann.

Lammers, T.G. 1992. Circumscription and phylogeny of the Campanulales. Ann. Missouri Bot. Gard. 79: 388–413.

Leins, P., Erbar, C. 1989. Zur Blütenentwicklung und sekundären Pollenpräsentation bei *Selliera radicans* Cav. (Goodeniaceae). Flora 182: 43–56.

Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–578.

Morgan, D.R., Soltis, D.E. 1993. Phylogenetic relationships among members of Saxifragaceae *sensu lato* based on *rbc*L sequence data. Ann. Missouri Bot. Gard. 80: 631–660.

Morrison, D.A. 1986. Notes on the fruits of *Lechenaultia* (Goodeniaceae) with a new species from northern Australia. Telopea 3: 159–166.

Olmstead, R.J., Kim, K.-J., Jansen, R.K., Wagstaff, S.J. 2000. The phylogeny of the Asteridae sensu lato based chloroplast *ndh*F gene sequences. Mol. Phylog. Evol. 16: 96–112.

Peacock, W.J. 1959. Pollen tetrads in *Leschenaultia* (sic!). Proc. Linn. Soc. New South Wales 84: 271–277.

Peacock, W.J. 1963. Chromosome numbers and cytoevolution in the Goodeniaceae. Proc. Linn. Soc. New South Wales 88: 8–27.

Peacock, W.J., Smith-White, S. 1978. Cytogeography of *Brunonia australis* Sm. ex R. Br. Brunonia 1: 31–43.

Rajput, M.T.M., Carolin, R.C. 1984. Stem structure and vascularisation in *Dampiera* (Goodeniaceae). Proc. Linn. Soc. New South Wales 107: 479–485.

Rajput, M.T.M., Carolin, R.C. 1988. The genus *Dampiera* (Goodeniaceae): systematic arrangement, nomenclatural notes and new taxa. Telopea 3: 183–216.

Rosén, W. 1937. Beiträge zur Kenntnis der Embryologie der Goodeniaceen. Acta Hort. Göteb. 12: 1–10.

Rosén, W. 1946. Further notes on the embryology of the Goodeniaceae. Acta Hort. Göteb. 16: 235–249.

Soltis, D.E., Soltis, P.S., Chase, M.W., Mort, M.E., Albach, D.C., Zanis, M., Savolainen, V., Hahn, W.H., Hoot, S.B., Fay, M.F., Axtell, M., Swensen, S.M., Prince, L.M., Kress, W.J., Nixon, K.C., Farris, J.S. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbc*L, and *atp*B sequences. Bot. J. Linn. Soc. 133: 381–461.

Tobe, H., Morin, N.R. 1996. Embryology and circumscription of Campanulaceae and Campanulales: a review of literature. J. Pl. Res. 109: 425–435.

Menyanthaceae

Menyanthaceae Bercht. & J. Presl, Prir. Rostlin 1, 115: 1 (1823), nom. cons.

G. Kadereit

Glabrous perennial or rarely annual herbs with tufted rootstocks or horizontal creeping rhizomes. Leaves monomorphic or dimorphic, alternate, often forming a rosette, simple, linear to cordate or reniform, rarely 3-foliolate; margin entire, undulate, regularly or irregularly dentate or crenate; petioles mostly long, sometimes sheathing, stipules absent. Inflorescence a simple or branched cyme, raceme, panicle, umbel, head or cluster, or flowers in pairs or solitary. Flowers actinomorphic, (4)5-merous, either hermaphrodite and monomorphic or heterostylous, or in some species monoecious, dioecious, or gynodioecious. Sepals persistent, at least basally united. Corolla sympetalous, often deeply lobed, valvate or imbricate in bud, inner surface of petal lobes often fimbricate or crested, margins often fringed; petals white, pinkish or yellow, caducous. Stamens (4)5, alternating with the corolla lobes, filaments inserted near base of the corolla tube; anthers dorsifixed, bilocular, tetrasporangiate, mostly sagittate, opening by longitudinal slits; sometimes flowers with fringed scales alternating with the stamens. Ovary superior to semi-inferior, of two united carpels, unilocular; style of varying length or absent in one morph, 2-lobed, stigma papillate, lacerate or with secondary lobes. Separate nectaries or disc present at base of ovary. Ovules numerous, on two parietal, often intruding placentae, anatropous, unitegmic, tenuinucellate. Fruit a regularly or irregularly dehiscent or indehiscent capsule, or rarely a berry. Seeds few to many, sometimes winged, endosperm abundant.

An almost cosmopolitan family with five genera and c. 60 species.

Vegetative Morphology. All Menyanthaceae are herbs adapted to wet or aquatic habitats. They have either creeping rhizomes or tufted rootstocks bearing leaves, stolons, adventitious roots and one to several fertile culms. The adventitious roots are thick and spur-like, or slender and more or less straight. Leaves are monomorphic or, in many species of *Nymphoides*, dimorphic with small leaves arising from the tufted rootstocks and large floating leaves on the fertile culms. Petioles are erect or flexuose. In aquatic species, the leaf blades are raised above the water surface by erect, long petioles, or the petioles are flexuose and the leaf blades float on the water surface. The blades are mostly elliptic, ovate, rotund, cordate or reniform. *Menyanthes trifoliata* has trifoliolate leaves and *Liparophyllum gunnii* has linear leaves. Leaf blades are thin, thick, or slightly succulent. The margin is mostly entire, sometimes it is minutely (irregularly or regularly) dentate or crenate. *Nephrophyllidium crista-galli* has deeply crenate, reniform leaf blades. The petioles of some species are winged, and several species have membranous sheaths towards the base of the petioles.

Vegetative Anatomy. Leaves of Menyanthaceae are dorsiventral or isobilateral. On non-floating leaves, stomata of the Ranunculus type are usually present on both surfaces but they are confined to the upper surface of floating leaves. Hydathodes are often located at enlarged ends of veins at leaf margins. The mesophyll of the leaves and the cortex of the petioles and flower-bearing culms show characteristic systems of intercellular canals and spaces. Some species have branched, sclerenchymatous idioblasts (astrosclereids) which project into these air cavaties. The vascular bundles in the petiole are normally widely spaced and are either arranged in a circle, are scattered, or form one or two arcs with the median vascular bundle being considerably larger than the peripheral ones. The vascular bundles of the fertile culms and rhizomes are also widely spaced and isolated. Intraxylary phloem is absent in Menyanthaceae (Metcalfe and Chalk 1950, 1979).

Inflorescence and Flower Morphology. The fertile culms are leafless, uniphyllous or have several leaves. Many species have simple or

branched cymes. The flowers of most species of *Nymphoides* are aggregated in umbels, heads or clusters. *Nephrophyllidium* and several species of *Villarsia* have paniculate inflorescences. *Menyanthes* has racemes, and *Liparophyllum* has solitary flowers in the leaf axils. Bracts are present but small and inconspicuous whereas the corollas are large and attractive. Their display is often enhanced by a large array of outgrowths, e.g. membranous extensions, fringes of emergences, or ruffles on the margin or on the inner surface. In *Menyanthes trifoliata*, the emergences are located on the upper part of the adaxial side of the petals, and fill the space between petals and anthers. In *Nymphoides peltata*, the margin of the petals is extended by undulated stretches of thinner, translucent tissue (Erbar 1997). Armstrong (2002) found that the fringe of trichomes in some species of *Nymphoides* significantly increases the upward force of the flower when pulled under water or opened under water (e.g. *Nymphoides geminata*), and also increases the buoyancy of the flower when supporting the weight of a pollinator. In several species, emergences are also present above the nectary glands where they might protect the secretory tissue. In some dioecious species, clusters of yellow trichomes alternate with the non-polliniferous stamens of the female flowers (see below).

Embryology. Menyanthaceae have a secretory (glandular) anther tapetum, and pollen grains have three nuclei when shed. The ovary contains many anatropous, tenuinucellate ovules on parietal placentae. The development of the megaspore follows the Polygonum type. The innermost layer of the integument develops into a tapetum. The polar nuclei fuse early to form a central nucleus which is located in the centre of the embryosac. There are always three antipodes which degenerate early, often before the embryosac is fully developed. The endosperm is cellular, and there is no endosperm haustorium at either the micropylar or the chalazal end. Endosperm in mature seeds is copious, and embryogenesis follows the Asterid type. The testa is one cell thick and formed by the exotesta whereas the mesotesta and endotesta are crushed (Stolt 1921; Erbar 1997; Tobe and Morin 1996 and ref. therein).

Pollen Morphology. Nilsson (1973) described two pollen types for the family, these being the *Menyanthes* type and the *Villarsia* type. *Nephrophyllidium* and *Menyanthes* have the *Menyanthes* type, which is subprolate to prolate, tricolpate with each furrow with a single germ pore, and a striate to rugulose exine. *Liparophyllum*, *Nymphoides* and *Villarsia* have the *Villarsia* pollen type, which is oblate to suboblate, parasyncolpate with an isolated apocolpical area, and a spinulose, striate, rugulose or smooth exine. In heterostylous species, the number and size of pollen grains differ between morphs. For example, in *Menyanthes trifoliata* the pin anthers produce c. 2×10^3 pollen grains whereas the thrum anthers produce only half as many (0.96×10^3). Pin and thrum pollen grains measure c. 29.0 and c. 33.1 µm in diameter, respectively. Nic Lughadha and Parnell (1989) reported that, on average, 26.6% of thrum pollen was inviable. By contrast, only 5.6% of pollen grains were inviable in pin anthers.

Karyology. Postulated base numbers are $x = 9$ (*Menyanthes*, *Nymphoides*, *Villarsia*) and $x = 17$ (*Nephrophyllidium*). The chromosome number of *Liparophyllum* is unknown. Chromosome counts for *Villarsia* (11 species studied) and *Nymphoides* (ten species studied) show different ploidy levels, and diploid, tetraploid and hexaploid species occur in both genera (Ornduff 1970, 1974; Ornduff and Chuang 1988). Li et al. (2002) reported a triploid chromosome number ($2n = 27$) for *Nymphoides lungtanensis*.

Pollination and Reproductive Systems. Flowers of Menyanthaceae are large and showy with white, pinkish or yellow corollas. Their attractiveness is increased by fimbriae or crests on the inner surfaces of the petals, by fringed petal margins, and by fringed scales alternating with the stamens. Some species have sap marks. The flowers reward the visitors with nectar which is produced by five nectar glands or a nectar disc at the base of the ovary. As far as is known, Menyanthaceae flowers are visited by short-tongued insects, mainly various Apidae. In all *Nymphoides* species studied by Ornduff (1966), maturation of floral buds is underwater. Before anthesis, the buds are raised above the water level. The corolla withers after a few hours of flowering, the pedicels deflect, and fruit development takes place under water.

Dioecy occurs only in a few species of *Nymphoides*. Female flowers have vestigial stamens which alternate with clusters of staminode-like trichomes. Male flowers have an ovary which contains ovules but lacks a style or stigma.

Heterostyly is found in four of the five genera. *Menyanthes trifoliata* is self-incompatible with dimorphic heterostyly (Nic Lughadha and Parnell 1989), although at least one homostylous population is known from Greenland. *Nephrophyllidium crista-galli* is also distylous. In *Nymphoides*, distyly is common but also homostyly, dioecy and gynodioecy occur in several species. *Villarsia* shows homostyly and distyly, the latter combined with self-incompatibility in at least two species (Ornduff 1988), and with strongly dimorphic stigmas in pin and thrum flowers in most species (Dulberger and Ornduff 2000). *Liparophyllum gunnii* has monomorphic flowers and is self-compatible (Ornduff 1982).

Vegetative reproduction is common by branching and subsequent decay of older parts of the rhizome resulting in independent ramets. Plants can also regenerate from pieces of rhizome broken off mature plants and washed ashore. Stoloniferous species, e.g. many species of *Villarsia*, reproduce by rooting stolons which break off the mother plant.

Fruit and Seed. Most species of Menyanthaceae have dry fruits, only *Liparophyllum* has a fleshy berry. The dry fruits are capsules which open regularly or irregularly, or they are indehiscent. The latter is found in *Nymphoides*. In this genus, the infructescence is submerged and the fruits break off by decay of the pedicels. Seeds are released after fruit wall decay. *Villarsia* has four-valved capsules in which the valves can split secondarily. The seeds are orbicular, elliptic, ovate or discoid. Seed size varies in the range 0.4–5.2 mm, and seed colour from straw yellow, light brown, brown, dark brown to black. Seed surfaces are smooth, tuberculate or armed with trichomes of different shape. Outlines of epidermal cells, if not obscure, are narrowly rectangular, penta- or hexagonal, or interdigitate. The hilum is terminal or subterminal, and in some ant-dispersed species surrounded by a caruncle which is rich in lipids. Size, shape and ornamentation of mature seeds and caruncle characters have been shown to be useful for distinguishing species (Sivarajan et al. 1989; Aston 2003) but to be too variable to characterize genera (Chuang and Ornduff 1992).

Seed Dispersal. Most species are adapted to dispersal by water. The air-filled seed hairs of *Nymphoides* and *Villarsia* and the air-filled testa cells of *Menyanthes* as well as their hydrophobic seed surface result in good buoyancy. For example, the seeds of *Menyanthes trifoliata* can float for at least 15 months, remaining viable. The hooked hairs on the seeds of some species may serve epizoochory mainly by birds. Endozoochory may also play a certain role. It has been shown that the seeds of *Menyanthes trifoliata* are readily eaten by reindeer, snow bunting, mallard, various species of fish, and probably ducks (Ridley 1930; Chuang and Ornduff 1992). At least four Australian species of *Villarsia* are reported to be dispersed by ants (Berg 1975).

Phytochemistry. The chemical profile of Menyanthaceae includes iridoids (loganin), secoiridoids (seco-loganin, sweroside), iridoid alkaloids, and inulin in roots (Lammers 1992; Grayer et al. 1999). Bohm et al. (1986) studied the flavonoid chemistry of 23 species including all genera of the family. The 38 flavonoid glycosides observed in this study are derived mainly from kaempferol and quercetin. The majority of compounds occur as 3-O-glycosides involving glucose, galactose, arabinose or rhamnose. *Nephrophyllidium* is unique in having galactosylglucosides of kaempferol and quercetin, and the corresponding acylated derivatives. *Liparophyllum* has the same, simple aglycone profiles as some species of *Nymphoides* and *Villarsia*. Arabonosylglucosides occur only in *Liparophyllum* and nine species of *Nymphoides*.

Intergeneric Relationships. Lundberg and Bremer (2003), in a molecular and morphological analysis of Asterales, found that the genera of Menyanthaceae (except *Liparophyllum*, which was not included) form two well-supported lineages, one comprising *Villarsia* and *Nymphoides* and the other comprising the two monotypic genera *Nephrophyllidium* and *Menyanthes*. *Villarsia* and *Nymphoides* are also very similar to each other in morphological and pollen characters. They are separated by their different capsule morphology (and dispersal ecology). *Nephrophyllidium* and *Menyanthes* have the same pollen type. Flower, fruit and leaves of *Nephrophyllidium*, however, are similar to certain species of *Villarsia*. The flavonoid profile of *Nephrophyllidium* is unique in the family. *Menyanthes* is distinct from all other genera of the family by its trifoliolate leaves. Leaf and fruit morphology of *Liparophyllum* is different from that of all other genera. However, it is similar to *Villarsia* and *Nymphoides* in pollen morphology and flavonoid chemistry.

Affinities. The placement of Menyanthaceae has long been controversial (Bohm et al. 1986; Erbar 1997 and ref. therein). Traditionally, the family has been included in either Gentianales (e.g. Takhtajan 1987), Solanales (e.g. Cronquist 1981) or Cornales (Dahlgren 1989). Pollard and Amuti (1981) first recognized a similarity to Asterales/Campanulales on the basis of the presence of inulin as a storage compound. Lundberg and Bremer (2003, and ref. therein) substantiated the monophyly of Menyanthaceae and their placement in Asterales as sister group to a clade consisting of Goodeniaceae, Calyceraceae and Asteraceae. The monophyly of Menyanthaceae, Goodeniaceae, Calyceraceae and Asteraceae is further supported by the presence of petal lateral veins and of a thick and multilayered integument, and the absence of micropylar endosperm haustoria (Lundberg and Bremer 2003, and ref. therein).

Distribution and Habitat. The family contains aquatic and marshland herbs. *Menyanthes* is found in bogs, fens, lakes and rivers between sea level and 3,200 m altitude, where it grows along the margins of open water or in places flushed by telluric waters, e.g. peat with surface water flow. The main distribution area is circumpolar between 40°N and the Arctic Circle. It grows north of the Arctic Circle in Greenland, Norway, Alaska and probably Siberia. *Nymphoides* is distributed primarily in the tropics (13 spp. in Africa and Madagascar, 12 in Australia, nine in India, five in South America, three in Meso-America and the West Indies). Two species are indigenous to eastern North America, and *Nymphoides peltata* is the only Eurasian species. Most species of *Nymphoides* are true aquatics growing in ponds, lakes and rivers. *Nephrophyllidium* is distributed along the west coast of boreal North America (from British Columbia to Alaska), in mountain swamps of Japan and Korea, and in snowbeds of high mountains along the coast of the Sea of Japan. Twelve species of *Villarsia* are found in southern Australia. Only two species are distributed outside Australia, the one in the south-western Cape Province of South Africa, the other in south-eastern Asia. *Villarsia* occurs predominantly in wet, moist or boggy habitats such as swamps or swampy soils, lakes, stream edges, wetlands and shallow (seasonal) waters. It can rarely be found in aquatic habitats typical for *Nymphoides*.

Economic Importance. After studying nitrogen and phosphorus accumulation and cycling by *Nymphoides peltata*, Brock et al. (1983) concluded that the species has the potential to function as a nitrogen and phosphorus pump which regenerates sediment nutrients. Some species are cultivated as ornamentals, e.g. *Nymphoides cordata*. Several species of *Nymphoides* have been recorded as weeds in ricefields and irrigation channels.

Key to the Genera

1. Leaves trifoliolate, leaflets obovate or elliptic **2. *Menyanthes***
– Leaves simple, rounded, cordate, elliptic, ovate, reniform or linear 2
2. Leaves linear, slightly succulent; fruit a globose fleshy berry **1. *Liparophyllum***
– Leaves rounded, cordate, elliptic, ovate, kidney-shaped; fruit a capsule, regularly (septicidal or loculicidal) or irregularly dehiscent, or fruit indehiscent, dry 3
3. Leaves reniform with a deeply crenate margin **3. *Nephrophyllidium***
– Leaves rounded, cordate, elliptic, ovate, rarely reniform, margin entire, rarely minutely dentate-crenate 4
4. Fruit a valvate capsule **5. *Villarsia***
– Fruit indehiscent or opening irregularly **4. *Nymphoides***

Genera of Menyanthaceae

1. *Liparophyllum* Hook. f.

Liparophyllum Hook. f., London J. Bot. 6: 473 (1847).

Small creeping herbs with linear or spathulate, slightly succulent leaves aggregated at nodes. Flowers solitary in leaf axils on short and stout pedicels. Flowers hermaphrodite, 5-merous, monomorphic. Calyx with long, linear, acute lobes. Corolla subrotate, deeply lobed. Corolla lobes ovate, slightly hairy within, undulate. Ovary bottle-shaped, stigma subsessile, two-lobed, nectary glands absent. Fruit a globose, fleshy berry. Seeds broadly elliptic, compressed laterally, surface minutely wrinkled. One species, *L. gunnii* Hook. f., New Zealand and Tasmania in wetland communities at various elevations.

2. *Menyanthes* L. Fig. 127

Menyanthes L., Sp. Pl. 1: 145 (1753).

Perennial herbs with submersed sympodial rhizomes with adventitious roots and a tuft of leaves at the apex. Leaves trifoliolate, leaflets obovate or elliptic, petiole with membranous sheaths towards

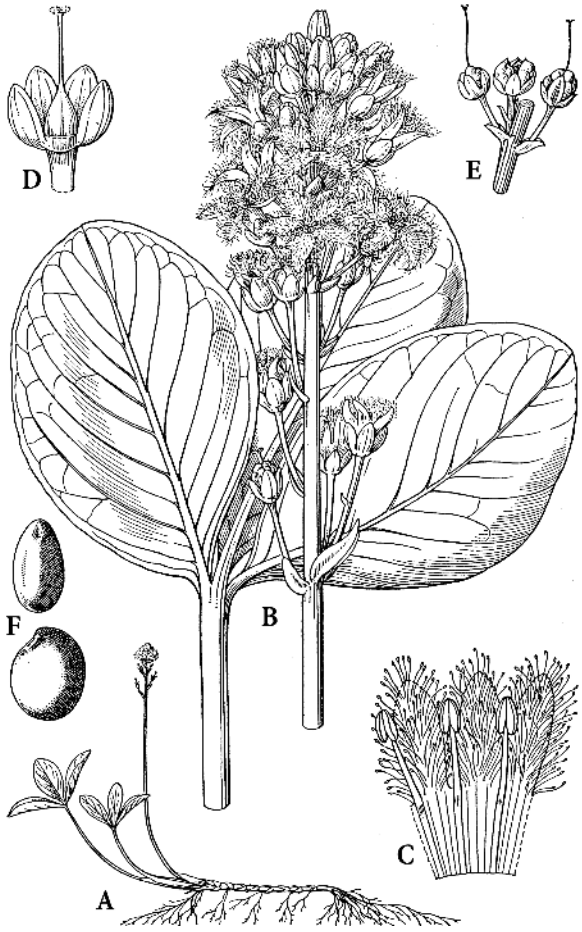

Fig. 127. Menyanthaceae. *Menyanthes trifoliata*. **A** Habit. **B** Inflorescence and leaf. **C** Adaxial view of part of corolla and androecium. **D** Calyx (one lobe removed) and ovary. **E** Part of infructescence. **F** Seeds. (Ross-Craig 1964)

the base. One racemose inflorescence on leafless scape from terminal bud of rhizome. Flowers hermaphrodite, 5-merous, distylous. Calyx lobed. Corolla broadly campanulate, deeply lobed, inside of lobes bearded with fimbriae. Ovary superior, with 5 nectary glands at the base, stigma capitate. Fruit a two-valved loculicidal capsule. Seeds numerous, broadly elliptic, compressed laterally, surface smooth. $2n = 54$. One species, *M. trifoliata* L., circumboreal mainly between 40°N and the Arctic Circle in lowland to montane bogs, fens, rivers and lakes.

3. *Nephrophyllidium* Gilg

Nephrophyllidium Gilg, in Engler & Prantl, Nat. Pflanzenfam. IV, 2: 105 (1895).
Fauria Makino (1904).

Perennial herbs with stout, creeping, leafy rhizome. Leaves erect, blades reniform, margin deeply crenate, petioles sheathing at base. One terminal culm bearing a paniculate cyme with 10–30 flowers. Flowers hermaphrodite, 5-merous, distylous. Calyx adnate to the ovary, with five lanceolate lobes. Corolla campanulate, deeply lobed, lobes induplicate in bud, midrib with distinct crest. Ovary semi-inferior, one-locular with five glands at the base. Style short or absent, stigma with two large semicircular lobes. Capsule cylindric, two-valved, valves two-lobed. Seeds broadly and asymmetrically elliptic, compressed laterally, surface smooth. $2n = 34$. One species, *F. crista-galli* (Menzies) Makino, north-eastern Asia (Japan, Korea) and Pacific coast of north-western North America.

4. *Nymphoides* Séguier

Nymphoides Séguier, Pl. Veron. 3: 121 (1754); Raynal, Adansonia II, 14: 227–270, 405–458 (1974), reg. rev.; Ornduff, Brittonia 21: 346–352 (1969), reg. rev.; Sivarajan & Joseph, Aquat. Bot. 45: 145–170 (1993), reg. rev.; Wood, J. Arnold Arb. 64: 431–445 (1983), reg. rev; Li et al., Taiwania 47: 246–258 (2002), reg. rev.
Limnanthemum S.G. Gmelin, p.p. (1769).

Perennial or rarely annual herbs with short, stout rhizome producing clusters of spur-like adventitious roots, stolons and leaves. Leaves monomorphic or dimorphic, rhizomatous leaves small, often spathulate with sheating petioles, floating leaves arising from fertile culms, blades rounded to cordate, margin entire. Flowers in cymose, umbel-like clusters. Flowers (4)5-merous, hermaphrodite and distylous or homostylous, or flowers unisexual and plants dioecious or gynodioecious. Calyx deeply lobed. Corolla rotate, deeply lobed, with five glandular, staminode-like tufts or fringes of trichomes near the base. Ovary superior or basally adnate to the perianth tube with five nectar glands at the base. Fruit a capsule, indehiscent or irregularly dehiscent. Seeds lenticular or globose, wingless, smooth or variously ornamented. $2n = 18, 36, 54$. About 40 species, cosmopolitan, mainly tropical and subtropical areas, aquatic plants in ponds, lakes and slow-flowing streams.

5. *Villarsia* Vent.

Villarsia Vent., Choix Plant: 9 (1803), nom. cons.; Aston, Muelleria 2: 3–63 (1969), reg. rev.

Perennial or annual herbs, with rootstock or creeping rhizome bearing leaves, sometimes stolons,

and one to several fertile culms. Leaves erect or floating, blades elliptic, ovate, rotund or reniform, margin entire to crenate-dentate, petioles winged or semi-sheathing towards the base. Inflorescence paniculate or flowers in clusters or heads. Flowers hermaphrodite, homo- or distylous. Calyx lobes distinct almost to the base, persistent. Corolla lobed, throat bearded with fimbriae, lobes with a broad margin and sometimes with a vertical keel on the inner surface. Ovary superior to semi-inferior, with 5 nectary glands at the base. Fruit a few- to many-seeded capsule, opening by four (or secondarily more) apical valves. Seeds smooth to tuberculate. $2n$ = 18, 36, 54. About 14 species, Australia, Cape region of South Africa (1 sp.) and south-eastern Asia (1–2 spp.).

Selected Bibliography

Armstrong, J.E. 2002. Fringe science: are the corollas of *Nymphoides* (Menyanthaceae) flowers adapted for surface tension interactions? Amer. J. Bot. 89: 362–365.

Aston, H.I. 2003. Seed morphology of Australian species of *Nymphoides* (Menyanthaceae). Muelleria 18: 33–65.

Berg, R.Y. 1975. Myrmecochorous plants in Australia and their dispersal by ants. Austral. J. Bot. 23: 475–508.

Bohm, B.A., Nicholls K.W., Ornduff, R. 1986. Flavonoids of the Menyanthaceae: intra- and interfamilial relationships. Amer. J. Bot. 73: 204–213.

Brock, Th.C.M., Bongaerts, M.C.M., Heijnen, G.J.M.A., Heijthuijsen, J.H.F.G. 1983. Nitrogen and phosphorus accumulation and cycling by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Aquat. Bot. 17: 189–214.

Chuang, T.I., Ornduff, R. 1992. Seed morphology and systematics of Menyanthaceae. Amer. J. Bot. 79: 1396–1406.

Cronquist, A. 1981. An integrated system of classification of flowering plants. New York: Columbia University Press.

Dahlgren, G. 1989. The last Dahlgrenogram. System of classification of dicotyledons. In: Tan, K. (ed.) The Davis and Hedge Festschrift. Edinburgh: University Press, pp. 249–260.

Dulberger, R., Ornduff, R. 2000. Stigma morphology in distylous and non-heterostylous species of *Villarsia* (Menyanthaceae). Pl. Syst. Evol. 225: 171–184.

Erbar, C. 1997. Fieberklee und Seekanne – Enzian- oder Aster-verwandt? Zur Blütenentwicklung und systematischen Stellung der Menyanthaceae. Bot. Jahrb. Syst. 119: 115–135.

Grayer, R.J., Chase, M.W., Simmonds M.S.J. 1999. A comparison between chemical and molecular characters for the determination of phylogenetic relationships among plant families: an appreciation of Hegnauer's "Chemotaxonomie der Pflanzen". Biochem. Syst. Ecol. 27: 369–393.

Lammers, T.G. 1992. Circumscription and phylogeny of the Campanulales. Ann. Missouri Bot. Gard. 79: 388–413.

Li, S.-P., Hsieh, T.-H., Lin, C.-C. 2002. The genus *Nymphoides* Séguir (Menyanthaceae) in Taiwan. Taiwania 47: 246–258.

Lundberg J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–578.

Metcalfe, C.R., Chalk, L. 1950. Anatomy of the dicotyledons, vol. II. Oxford: Clarendon Press, pp. 933–939.

Metcalfe, C.R., Chalk, L. 1979. Anatomy of the dicotyledons, ed. 2, vol. I. Oxford: Clarendon Press, pp. 190–221.

Nic Lughadha, E.M., Parnell, J.N. 1989. Heterostyly and gene-flow in *Menyanthes trifoliata* L. (Menyanthaceae). Bot. J. Linn. Soc. 100: 337–354.

Nilsson, S. 1973. Menyanthaceae. In: Nilsson, S. (ed.) World pollen and spore flora, vol. 2. Stockholm: Almquist & Wiksell, pp. 1–19.

Ornduff, R. 1966. The origin of dioecism from heterostyly in *Nymphoides* (Menyanthaceae). Evolution 20: 309–314.

Ornduff, R. 1970. Cytogeography of *Nymphoides* (Menyanthaceae). Taxon 19: 715–719.

Ornduff, R. 1974. Cytotaxonomic observations on *Villarsia* (Menyanthaceae). Austral. J. Bot. 22: 513–516.

Ornduff, R. 1982. Heterostyly and incompatibility in *Villarsia capitata* (Menyanthaceae). Taxon 31: 495–497.

Ornduff, R. 1988. Distyly and monomorphism in *Villarsia* (Menyanthaceae): some evolutionary considerations. Ann. Missouri Bot. Gard. 75: 761–767.

Ornduff, R., Chuang, T.I. 1988. Chromosome numbers of Western Australian species of *Villarisa* (Menyanthaceae). Pl. Syst. Evol. 161: 49–52.

Pollard, C.J., Amuti, K.S. 1981. Fructose oligosaccharides: possible markers of phylogenetic relationships among dicotyledonous plant families. Biochem. Syst. Evol. 9: 69–78.

Ridley, H.N. 1930. The dispersal of plants throughout the world. Ashford: Kent.

Ross-Craig, S. 1964. Drawings of British plants, vol. 20. London: Bell & Hyman.

Sivarajan, V.V., Chaw, S.-M., Joseph, K.T. 1989. Seed coat micromorphology of Indian species of *Nymphoides* (Menyanthaceae). Bot. Bull. Acad. Sin. 30: 275–283.

Stolt, K.A.H. 1921. Zur Embryologie der Gentianaceen und Menyanthaceen. Kungl. Svenska Vetenskaksakad. Handl. 61, 14: 3–56.

Takhtajan, A. 1987. Systema Magnoliophytorum. Leningrad: Nauka.

Tobe, H., Morin, N.R. 1996. Embryology and circumscription of the Campanulaceae and Campanulales: a review of literature. J. Pl. Res. 109: 425–435.

Pentaphragmataceae

Pentaphragmataceae J. Agardh, Theoria Syst. Pl.: 95 (1858), nom. cons.

T.G. Lammers

Perennial herbs, somewhat fleshy or succulent. Leaves alternate, simple, asymmetric at base, estipulate, petiolate. Inflorescences axillary or extra-axillary sympodial helicoid cymes; bracts conspicuous, membranous. Flowers tetracyclic, perfect, rarely imperfect and plants dioecious. Calyx synsepalous, adnate to the ovary only by 5 longitudinal septa opposite the sepals, leaving 5 antepetalous nectariferous pits; lobes 5, imbricate. Corolla sympetalous or rarely choripetalous, radially symmetric; lobes (or petals) (4)5, valvate. Stamens (4)5, epipetalous or epigynous in choripetalous species; filaments distinct; anthers tetrasporangiate, dithecal, basifixed, distinct. Gynoecium syncarpous, 2(3)-locular; ovary inferior; ovules numerous; placentation axile; style solitary; stigma capitate. Fruit a berry, crowned by the persistent perianth. Seeds minute, numerous; endosperm copious, starchy.

The family comprises only one genus of c. 30 species, and is endemic to south-eastern Asia, the Malay archipelago and New Guinea.

Vegetative Morphology and Anatomy. Species of *Pentaphragma* are perennial herbs, generally rather coarse and often quite fleshy or succulent. Latex is not produced. Branched trichomes occur frequently. In the stem, xylem and phloem typically form a continuous cylinder traversed by parenchymatous medullary rays 1–2 cells wide, surrounding a broad pith. A distinct endodermis is present. Vessel elements have scalariform perforation plates and bordered pits; helical thickenings are absent. The xylem of the root is pentarch, surrounded by both an endodermis and exodermis. Leaves are dorsiventral, large relative to plant size, estipulate and petiolate; the base of the lamina is quite asymmetric, resembling *Begonia*. Stomata are anomocytic and chiefly abaxial. The mesophyll has a single palisade layer or else is not clearly differentiated. Vascular bundles in the veins are not associated with sclerenchyma (Cronquist 1981).

Floral Structure and Anatomy. Some species are dioecious, producing staminate and carpellate flowers on separate plants. The proterandry and specialized mechanisms for secondary pollen presentation typical of Campanulaceae are lacking. The hypanthium is unique in that the calyx tube is adnate to the ovary only by 5 narrow longitudinal septa opposite the stamens. This creates five intervening pits or lacunae in which nectar is produced. The corolla is typically fleshy or cartilaginous, rarely delicate. Venation of the petals includes both a midvein and a pair of marginal veins, which anastamose distally. Though the petals are connate in most species, they are distinct in a few (e.g. *P. decurrens*). In the former, the stamens are inserted on the corolla tube just below the lobes, due to adnation of the basal portions of the filaments. In the latter, they are inserted at the rim of the top of the ovary. At least one species (*P. tetrapetalum*) is characterized by a tetramerous corolla and androecium. The style is short and thick, lacking pollen-collecting hairs. The stigma is large relative to the style.

Embryology. Anther wall development follows the Basic pattern, forming a double middle layer. Fibrous thickenings are found in the endothecium. The tapetum is glandular (secretory), and tapetal cells are binucleate. Pollen grains are binucleate when shed.

Ovules are anatropous, unitegmic and tenuinucellar. Embryo sac formation is monosporic and of the Polygonum type, and the sac protrudes from the micropyle. Upon coming in contact with the embryo sac, the inner layer of the integument develops as an endothelium (integumentary tapetum). Embryogenesis follows the Solanad pattern. Endosperm formation is cellular ab initio; the endosperm typically is copious and starchy. A haustorium forms only at the micropylar end and is single-celled. No hypostase forms (Kapil and Vijayaraghavan 1965).

Pollen Morphology. The grains are trilobate in outline and tricolporate or tricolpate. The surface is smooth and the exine nearly solid (Dunbar 1978).

Pollination, Reproductive Systems, Dispersal. Nothing is known of the reproductive biology of this family, aside from its clear lack of any mechanism of secondary pollen presentation.

Phytochemistry. Nothing is known of the secondary chemistry of the family, aside from its lack of alkaloids.

Affinities. Almost all authors have recognized a relationship between *Pentaphragma* and Campanulaceae. The genus was included among Campanuloideae by Bentham (1876) and Hutchinson (1973). Schönland (1894) treated the genus as a tribe within Campanulaceae (Pentaphragmateae) whereas Takhtajan (1980) treated it as a subfamily ("Pentaphragmatoideae", nom. invalid. sub Art. 41.1). However, the genus differs from Campanulaceae as circumscribed here in its lack of articulated lactifers, wood anatomy (Carlquist 1997), asymmetric leaf bases, sympodial helicoid cymes, absence of a specialized mechanism for proterandrous secondary pollen presentation, trilobate binucleate pollen (Dunbar 1978), basic pattern of anther wall development and endosperm with micropylar haustorium only (Kapil and Vijayaraghavan 1965), ovary adnate to hypanthium only by 5 narrow longitudinal septa, style without pollen-collecting hairs, and capitate stigma. For these reasons, most modern authors (Wagenitz 1964; Cronquist 1981; Dahlgren 1989; Lammers 1992; Thorne 1992; Gustafsson and Bremer 1995; Takhtajan 1997) have assigned the genus to a distinct family.

Among those who have accorded *Pentaphragma* familial rank, the majority still considered it to be allied at some level to Campanulaceae. Only Airy Shaw (1942, 1954, 1973) questioned this relationship, suggesting instead (largely on the basis of its asymmetric leaf base) that the family is allied to Begoniaceae. However, that family (which belongs to Malpighiales) differs from Pentaphragmataceae not only in numerous floral features but also in its bitegmic crassinucellar ovules, Onagrad embryogeny, and nuclear endosperm formation (Kapil and Vijayaraghavan 1965).

A close relationship between Pentaphragmataceae and Campanulaceae is supported by recent molecular data. Although an analysis based on *rbc*L sequences (Cosner et al. 1994) suggested that Pentaphragmataceae are sister to a clade comprising Asteraceae, Calyceraceae, Goodeniaceae, Menyanthaceae and Argophyllaceae, subsequent analyses using two genes (Kårehed et al. 1999) and three genes plus phenotypic data (Lundberg and Bremer 2003) have placed Pentaphragmataceae as the sister group of Campanulaceae as circumscribed here. At the very least, Pentaphragmataceae are clearly a member of Asterales s.l.

Distribution and Habitat. The family is distributed in wet forest habitats from Myanmar, southern China and Indochina, south through

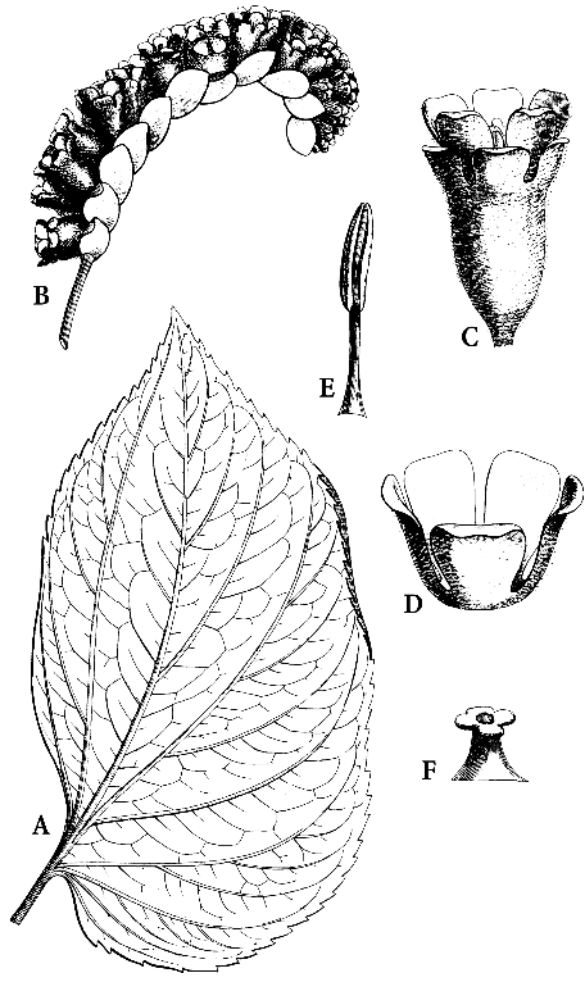

Fig. 128. Pentaphragmataceae. *Pentaphragma begonifolium*. **A** Leaf. **B** Inflorescence. **C** Flower. **D** Corolla. **E** Stamen. **F** Top of ovary with style. (Schönland 1894)

most of the Malay archipelago (excluding Java and Nusa Tenggara) to New Guinea.

Only one genus:

1. *Pentaphragma* Fig. 128

Pentaphragma Wallich ex G. Don, Gen. Hist. 3: 731 (1834); Airy Shaw, Fl. Malesiana I, 4: 517–528 (1954), part. rev.

See family description. Thirty species, southeastern Asia to New Guinea.

Selected Bibliography

Airy Shaw, H.K. 1942. Additions to the flora of Borneo and other Malay islands: XIX. The Pentaphragmataceae of the Oxford University expedition to Sarawak, 1932. Bull. Misc. Inform. 1941: 233–236.

Airy Shaw, H.K. 1954. Pentaphragmataceae. In: van Steenis, C.G.G.J. (ed.) Flora Malesiana I, 4. Djakarta: Noordhoff-Kolff, pp. 517–528.

Airy Shaw, H.K. 1973. A dictionary of the flowering plants and ferns, ed. 8. Cambridge: Cambridge University Press.

Bentham, G. 1876. Campanulaceae. In: Bentham, G., Hooker, J.D., Genera Plantarum, vol. II. London: Reeve, pp. 541–564.

Carlquist, S. 1997. *Pentaphragma*: a unique wood and its significance. IAWA J. 18: 3–12.

Cosner, M.E., Jansen, R.K., Lammers, T.G. 1994. Phylogenetic relationships in the Campanulales based on *rbc*L sequences. Pl. Syst. Evol. 190: 79–95.

Cronquist, A. 1981. An integrated system of classification of flowering plants. New York: Columbia University Press.

Dahlgren, G. 1989. The last Dahlrenogram. System of classification of the dicotyledons. In: Tan, K. (ed.) Plant taxonomy, phytogeography, and related subjects. The Davis and Hedge Festschrift. Edinburgh: Edinburgh University Press, pp. 249–260.

Dunbar, A. 1978. Pollen morphology and taxonomic position of the genus *Pentaphragm* Wall. (Pentaphragmataceae). Grana 17: 141–147.

Gustafsson, M.H.G., Bremer, K. 1995. Morphology and phylogenetic interrelationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and related families (Asterales). Amer. J. Bot. 82: 250–265.

Hutchinson, J. 1973. The families of flowering plants, ed. 3. Oxford: Clarendon Press.

Kapil, R.N., Vijayaraghavan, M.R. 1965. Embryology of *Pentaphragma horsfieldii* (Miq.) Airy Shaw with a discussion on the systematic position of the genus. Phytomorphology 15: 93–102.

Kårehed, J., Lundberg, J., Bremer, B., Bremer, K. 1999. Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae. Syst. Bot. 24: 660–682.

Lammers, T.G. 1992. Circumscription and phylogeny of the Campanulales. Ann. Missouri Bot. Gard. 79: 388–413.

Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–578.

Schönland, S. 1894. Campanulaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, IV, 5. Leipzig: W. Engelmann, pp. 40–70.

Takhtajan, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46: 225–359.

Takhtajan, A. 1997. Diversity and classification of flowering plants. New York: Columbia University Press.

Thorne, R.F. 1992. An updated phylogenetic classification of the flowering plants. Aliso 13: 365–389.

Wagenitz, G. 1964. Reihe Campanulales. In: Melchior, H. (ed.) A. Engler's Syllabus der Pflanzenfamilien, ed. 12, Band 2. Berlin: Bornträger, pp. 478–497.

Phellinaceae

Phellinaceae (Loes.) Takht., Sist. Filogen. Cvetk. Rast.: 374 (1967).

G. Barriera, V. Savolainen and R. Spichiger

Small trees or shrubs, evergreen, dioecious. Leaves alternate, spirally arranged or in pseudo-whorls, clustered at the top of the branches, estipulate; blades simple, usually papyraceous, rarely coriaceous or membranaceous, obovate, oblong, glabrous; margin entire or crenate. Flowers small, unisexual, regular, hypogynous, 4–5(6)-merous, arranged in axillary or subterminal racemes or panicles. Sepals small, connate at the base. Petals valvate, free. Stamens isomerous, alternating with the petals. Carpels isomerous, united into a plurilocular superior ovary. Fruit a polyspermous drupe, lobed or not, greenish or black, containing 1–5 pyrenes. Seeds small with copious endosperm.

One genus comprising 11 species, all endemic to New Caledonia.

Vegetative Morphology. Phellinaceae contain small trees or shrubs which are poorly branched and 1–8 m high. Branches are hollow in *Phelline comosa*. The cortex is thick, smooth or furrowed, rugose or rugose-cracked in *P. confertifolia*, generally ochre but rarely greyish. Large petiolary scars are present on the branches. They are triangulate or trilobed, and concave in *P. comosa*. The younger branches are dark brown (*P. macrophylla*) or blackish (*P. lucida*). The leaves are simple, evergreen, alternate or subopposite, and clustered in loose spirals or in pseudo-whorls at the top of the branches. They are generally papyraceous, coriaceous in *P. lucida* or membranous in *P. macrophylla*, and obovate, oblong, or sometimes elliptic or spathulate in shape. The apex of the lamina is rounded to trilobed, rarely shortly acuminate (less than 1 cm), and the margin is entire or more or less crenate-sinuate. The base can be cuneate, decurrent or not.

Vegetative Anatomy. Wood anatomy has been extensively studied by Baas (1975). The wood is fairly light and soft, and of yellowish colour. Growth rings are indistinct, and the texture of the wood is coarse through very conspicuous broad rays. Growth rings are very faint to absent. Vessels are mainly solitary, occasionally in radial pairs, angular to rounded. Perforations are scalariform in almost vertical end-walls, resulting in strong overlap of adjacent vessel-members. Inter-vessel pits are in a single vertical row, they are oval and variously flattened. Vessel-parenchyma pits are similar but half-bordered. Vessel-ray pits are transitional to scalariform, half-bordered, occasionally unilaterally compound. The ground tissue is composed of fairly thick-walled fibre-tracheids with numerous bordered pits on the radial and tangential walls, the pits with slit-like apertures extending to the pit border margins. Parenchyma is diffused and often touching on the vessels. There are four uniseriate rays per mm, the broad rays are extremely large, occupying about 40% of the volume of the wood, up to 14 cells wide and often over 2 cm high. They are composed of large cells with numerous sheath cells. No heartwood is differentiated. Baas (1975) concluded that the wood anatomy of *Phelline* is one of the most primitive among dicotyledons with vessels. Tufts of short reddish-brown hairs, hiding the axillary buds, are usually present.

Inflorescence Structure. Inflorescences are axillary racemes or simple or compound panicles. Pedicels are generally alternate, but often opposite in *P. lucida*. Bracts and prophylls are triangular or rarely linear, deciduous or persistent, and coriaceous or papyraceous. Short, reddish-brown hairs (long and stiff in *P. comosa*) are generally present at the base of the bracts.

Flower Morphology. Sepals are small and more or less persistent in fruit. The corolla is often white, red in *P. lucida*, with valvate petals which are 2–4.5 mm long. Petals are mostly fleshy and mucronate or acuminate. The acumen is often reflexed and up to 2 mm long (*P. dumbeensis*). The stamens are isomerous, alternipetalous and free.

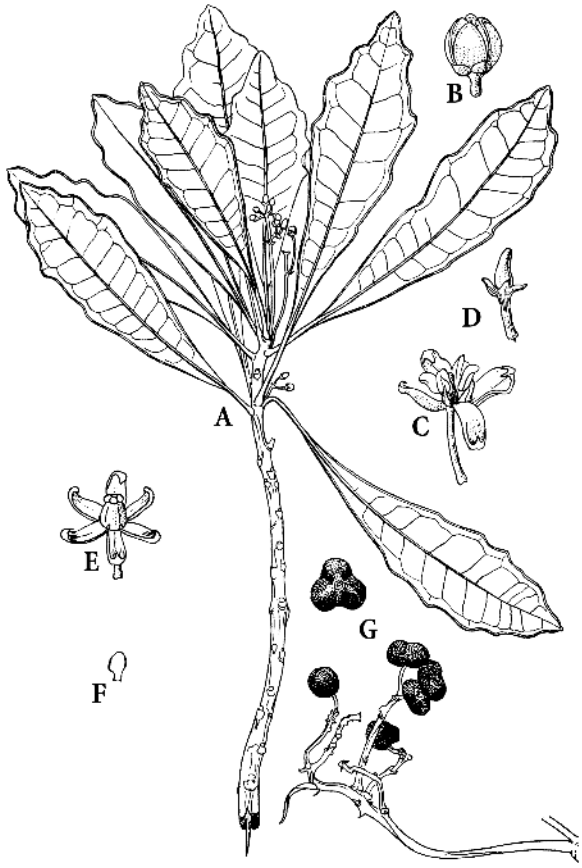

Fig. 129. Phellinaceae **A** Branch of *Phelline lucida*. **B–G** *Phelline erubescens*. **B** Flower bud. **C** Male flower. **D** Male flower (stamens and petals removed) showing calyx and pistillode. **E** Female flower. **F** Scale-shaped staminode. **G** Fruiting branch and top view of fruit. (after Loesener 1942)

Anthers are basidorsifixed, oblong and introrse. They usually are shorter than the filament and show longitudinal dehiscence. In pistillate flowers, the staminodes are similar to the stamens of the male flowers (Loesener 1942) or are reduced to small scales which are sometimes persistent in fruit. The syncarpous ovary is globose and composed of isomerous carpels with as many locules as carpels. The short style is terminal and has distinct multilobed to multipartite stigma. There is one axile, pendulous, hemitropous or slightly campylotropous, unitegmic ovule per locule (Baas 1975). In staminate flowers, the pistillode is cone- or bottle-shaped, and sometimes toothed at the apex.

Pollen Morphology. Erdtman (1952) described the pollen of *P. comosa*, and Lobreau-Callen (1977) examined nine species. The pollen grains are between 17–23 × 17–24 µm. They are isopolar and tricolporate. The ecto-apertures are long and narrower in the equatorial region. The membrane is granular and the endo-aperture is usually horizontally 8-shaped. The exine is echinulate or slightly rugulate and the foot layer is thick. The endexine s. str. is very thin in the intercolpium and very thick near the apertures. Two pollen types can be distinguished, based on the ornamentation and the location of the endexine (s.l.) thickening: a microechinulate type in *P. billardierei*, *P. brachyphylla*, *P. comosa*, *P. dumbeensis*, *P. erubescens*, *P. indivisa* and *P. macrophylla*, and a microrugulate type in *P. confertifolia* and *P. lucida*.

Fruit and Seed, Dispersal. The fruits, being polyspermous drupes, are probably adapted to dispersal by birds belonging to Turdidea. The only species of this family present in New Caledonia is *Turdus poliocephalus*.

Phytochemistry. The leaves and wood of *Phelline* are rich in alkaloids. Four species have been particularly well studied, *P. billardierei* (Seguineau and Langlois 1980), *P. brachyphylla*, *P. comosa* (Debourges and Langlois 1982) and *P.* aff. *lucida* (Langlois and Razafimbelo 1988). Alkaloids such as homoerythrin, homoerythroidin, homoazaerythrin and holidin have been isolated.

Distribution and Habitat. *Phelline* is endemic to New Caledonia where it is found from c. 20 to 1,550 m elevation in mesophile to hygrophile forests on schisteous, siliceous or serpentinous soils (Hürlimann 1964).

Affinities. Ideas about the systematic position of *Phelline* have changed several times, although it mostly was included in rosids. In 1824, Labillardière considered *Phelline* as closely related to *Pouteria* (Ebenales). Later, Bentham and Hooker (1862) included *Phelline* in Rutaceae. Loesener (1901, 1942) included it in Aquifoliaceae, but as a distinct tribe characterized by valvate and apiculate petals. Takhtajan (1966) accommodated the genus in its own family, Phellinaceae, which he considered to be related to Aquifoliaceae (within Icacinineae) "from which it differs by having valvate petals, by the character of the inflorescence, the hemitropous or campylotropous ovules, the wood anatomy, the quite different sporoderm morphology, and the leaf venation". Considered as close to Aquifoliaceae, Phellinaceae

were placed next to this family in other systems within Cornales (Dahlgren 1983), Theales (Thorne 1992) or Celastrales (Takhtajan 1980). Cronquist (1981) did not accept family status for *Phelline* and kept it within Aquifoliaceae (Celastrales). Phylogenetic analyses based on molecular data undoubtedly place Phellinaceae within Asterales (Savolainen et al. 2000; Soltis et al. 2000; APG II 2003), with their most likely sister families being Alseuosmiaceae and Argophyllaceae (Kårehed et al. 1999; Lundberg and Bremer 2003).

Only one genus:

1. *Phelline* Labill. Fig. 129

Phelline Labill., Sert. Austro-Caledon.: 35 (1824); Baillon, Bull. Mens. Soc. Linn. Paris 1: 937–939 (1891), rev.; Loesener, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 78: 504–516 (1901), rev.

Characters as for the family. Eleven species in New Caledonia.

Selected Bibliography

APG II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399-436.

Baas, P. 1975. Vegetative anatomy and affinities of Aquifoliaceae, *Sphenostemon*, *Phelline* and *Oncotheca*. Blumea 22: 311–407.

Baillon, H.E. 1891. Les *Phelline* de la Nouvelle-Calédonie. Bull. Mens. Soc. Linn. Paris 1: 937–939.

Bentham, G., Hooker, J.D. 1862. Rutaceae. Genera Plantarum, vol. I. London: Reeve, Williams & Norgate, pp. 302–303.

Cronquist, A. 1981. An integrated system of classification of flowering plants. New York: Columbia University Press.

Dahlgren, R. 1983. General aspects of angiosperm evolution and macrosystematics. Nordic J. Bot. 3: 119–149.

Debourges, D., Langlois, N. 1982. Nouveaux alcaloïdes du groupe de l'homoérythrinane isolés de *Phelline brachyphylla*. J. Nat. Prod. 45: 163–167.

Erdtman, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. Stockholm: Almquist & Wiksell.

Hürlimann, H. 1964. Phelline. In: Guillaumin, A. (ed.) Résultats scientifiques de la mission franco-suisse de botanique en Nouvelle-Calédonie (1950–1952) III. Mém. Mus. Natl Hist. Nat., B, Bot. 15: 63–65.

Kårehed, J., Lundberg, J., Bremer, B., Bremer, K. 1999. Evolution of the Australasian families Alseuosmiaceae, Argophyllaceae, and Phellinaceae. Syst. Bot. 24: 660–682.

Labillardière, J.J.H. de 1824. *Phelline*. Sertum Austro-Caledonicum. Paris: Huzard, pp. 35–36.

Langlois, N., Razafimbelo, J. 1988. Alcaloïdes de *Phelline* sp. aff. *Phelline lucida:* origine de l'holidine et du phellinamide; configuration de la comosidine, de la lucidinine, et de leurs dérivés. J. Nat. Prod. 51: 499–503.

Lobreau-Callen, D. 1977. Famille des Phellinaceae. Les pollens des Célastrales. Montpellier: Ecole Pratique des Hautes Etudes, Institut de Montpellier, pp. 42–43.

Loesener, T. 1901. Monographia Aquifoliacearum. Pars I. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 78: 504–516.

Loesener, T. 1942. Aquifoliaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, ed. 2, 20b. Leipzig: W. Engelmann, pp. 36–86.

Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–578.

Savolainen, V., Fay, M.F., Albach, D.C., Backlund, A., van der Bank, M., Cameron, K.M., Johnson, S.A., Lledó, M.D., Pintaud, J.-C., Powell, M., Sheahan, M.C., Soltis, D.E., Soltis, P.S., Weston, P., Whitten, M.W., Wurdack, K.J., Chase, M.W. 2000. Phylogeny of the eudicots: a nearly complete familial analysis based on *rbc*L gene sequences. Kew Bull. 55: 257–309.

Seguineau, M.-F., Langlois, N. 1980. Phellibilidine, nouvel alcaloïde de *Phelline billiardieri*. Phytochemistry 19: 1279–1281.

Soltis, D.E., Soltis, P.S., Chase, M.W., Mort, M.E., Albach, D.C., Zanis, M., Savolainen, V., Hahn, W.H., Hoot, S.B., Fay, M.F., Axtell, M., Swenson, S.M., Prince, L.M., Kress, W.J., Nixon, K.C., Farris, J.A. 2000. Angiosperm phylogeny inferred from 18S rDN, *rbc*L and *atp*B sequences. Ann. Missouri Bot. Gard. 84: 1–49.

Takhtajan, A.L. 1966 [1967]. Phellinaceae. Sistema i Filogenija Cvetkovyh Rastenij. Moskva: Nauka, pp. 374.

Takhtajan, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. (Lancaster) 46: 225–359.

Thorne, R.F. 1992. Classification and geography of the flowering plants. Bot. Rev. (Lancaster) 58: 225–348.

Rousseaceae

Rousseaceae A.P. de Candolle, Prodr. 7: 521 (1839).

J.A. Koontz, J. Lundberg and D.E. Soltis

Climbing shrub, up to 4 m in height. Leaves opposite, simple, obovate-lanceolate, glandular serrate, without stipules. Flowers solitary to few, axillary, nodding, bisexual, actinomorphic, hypogynous. Sepals 4–6, reflexed, connate at base, persistent in fruit. Petals 4–5, valvate in bud, thick and fleshy, connate into a lobed tube, lobes valvate, revolute at apex, persistent. Stamens 4–5, inserted on a nectary disk, anthers oblong-sagittate, extrorse. Ovary superior, 5–7-locular with numerous unitegmic, tenuinucellate ovules. Placentation axile. Style thick and persistent, stigma globose with 5–7 lobes. Fruit a 4–7-angled berry. Seeds numerous, with small embryo and copious endosperm.

The family is monotypic. *Roussea simplex* is endemic to the island of Mauritius.

Vegetative Morphology and Anatomy. The wood contains vessels with very oblique end walls and scalariform perforation plates with an average of 20 (up to 49) bars, lateral scalariform pitting, and lacks spiral thickenings. Tracheids and fibre-tracheids are imperforate with bordered pits and lack septa. Wood-rays are tri- to multiseriate and heterogeneous. The axial parenchyma are scanty paratracheal. Nodes are trilacunar.

Leaves are opposite, but sometimes are arranged in pseudo-whorls. They have peltate glandular hairs on the abaxial surface as well as on the petioles. Leaf venation is craspedodromous, and the petiole and lamina often have radially elongated, schizogynous resin canals. Stomata are anomocytic.

Inflorescence, Floral Structure and Flower Anatomy. The flowers are borne singly (sometimes 3–4) in the leaf axils, and the pedicels have peltate glandular hairs. The floral tube is 4–10 mm long, with lobes 10–20 mm long, and villous outside. The calyx lobes are light green and thick, have peltate glandular hairs but become glabrous with age. The petals are valvate in bud, and yellow to orange in colour. The stamens alternate with the petals and the anthers dehisce by longitudinal slits. The style is glabrous, thick, unbranched and persistent. The 4–5-lobed stigma is capitate and revolute at the margins. The 4–7-locular ovary has distinctly two-ranked ovules on thick, axile placentas.

Embryology. *Roussea* is similar to most other members of Asterales in its embryological features (H. Tobe, J. Lundberg and P. Raven, unpubl. data). The anthers are tetrasporangiate, with a persistent epidermis, a glandular and binucleate tapetum, but with an unspecialized endothecium and persistent middle layers. The ovules are anatropous, unitegmic and tenuinucellate, with 1-celled archesporium and Polygonum-type embryo sac development. Antipodal cells are ephemeral, and no hypostase is formed. Fertilization is porous, and endosperm development is ab initio cellular. Micropylar haustoria and a filamentous suspensor are developed. The seed coat is exotestal, and the exotesta is thick-walled and cuboidal. Mesotesta and endotesta are crushed.

Pollen Morphology. The pollen has been described in some detail by Straka and Friedrich (1988). The pollen grains are isopolar, more or less spheroidal with a diameter up to 36.5 µm, and dispersed as monads. They are penta- to hexapanporate or -panbrachycolpate, with irregular aperture border. The nexine is one-layered. The sexine has a smooth or foveolate and complete tectum, and is of about the same thickness as the nexine; the exine is c. 2 µm thick.

Pollination and Reproductive System. Copious amounts of nectar with low sugar concentration have been reported to be produced in flowers of *Roussea* (Dennis Hansen, pers. comm.). Hansen (pers. comm.) also reports visits of the passerine Mauritius Grey White-eye (*Zosterops borbonicus*

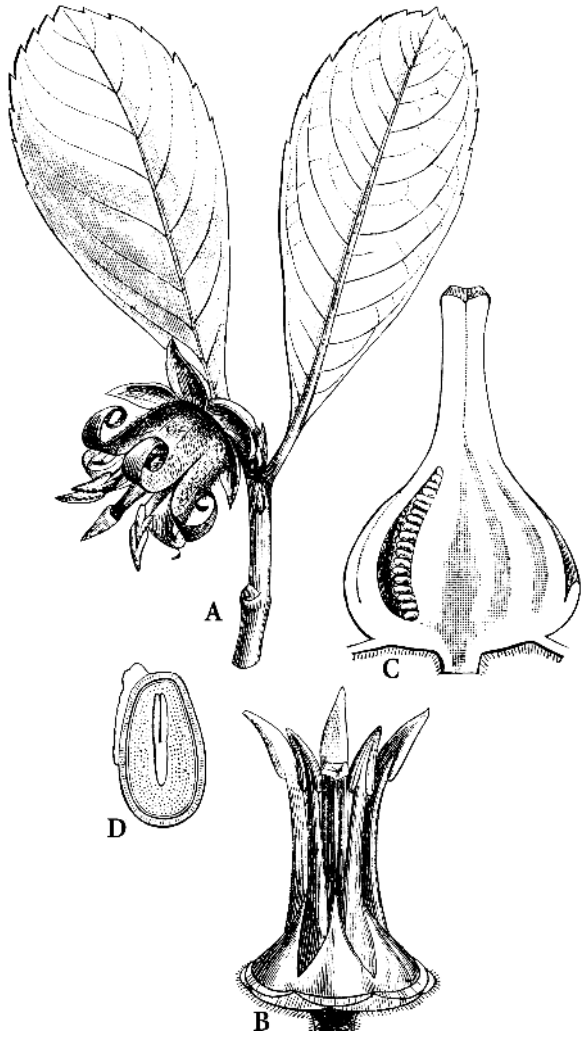

Fig. 130. Rousseaceae. *Roussea simplex*. **A** Flowering branch. **B** Flower (perianth removed) showing the lobed disc. **C** Ovary, longitudinal section. **D** Seed, longitudinal section. (Engler 1891)

mauritianus) to *Roussea*, feeding on its nectar but apparently not pollinating it.

Fruit and Seed. The fruit is a pale green angular berry with a dilated base. Seeds are numerous, ovoid and flattened.

Phytochemistry. Very little is known about the phytochemical constituents of *Roussea*. Tannins are reported as being absent (Ramamonjiarisoa 1980).

Distribution and Habitats. Endemic to the mountain forests of Mauritius, once locally abundant but now becoming increasingly rare.

Affinities. Historically, *Roussea* has often been associated with the superficially similar genera *Brexia* (East Africa, including Madagascar) and *Ixerba* (New Zealand). Engler (1930), for example, placed *Roussea* together with *Brexia* and *Ixerba* in subfamily Brexioideae of Saxifragaceae, while Dahlgren (1983), following basically the same approach, placed the three genera in Brexiaceae of Saxifragales, as did Takhtajan (1997) who treated the three genera as three monogeneric families in Brexiales. A somewhat different treatment was given by Cronquist (1981), placing *Roussea* (together with *Ixerba* and *Brexia*) in Grossulariaceae, and by Thorne (1992) who, although recognizing Brexiaceae with *Roussea*, *Ixerba* and *Brexia*, placed them not in Saxifragales but in Hydrangeales. By contrast, various anatomical data (e.g. trichomes and nodal vasculature) suggested *Roussea* to be close to *Quintinia* (Paracryphiaceae), Pittosporaceae or *Forgesia* (Escalloniaceae) (Al-Shammary and Gornall 1994). However, phylogenetic analyses of DNA sequence data strongly suggest that *Roussea* is part of the well-supported Asteridae s.s. (Savolainen et al. 1997; Soltis and Soltis 1997; Koontz and Soltis 1999; Soltis et al. 2000). *Roussea* is thus only distantly related to *Brexia* and *Ixerba*, which both appear as part of a large rosid clade. Using *ndhF* and *rbcL* data, Lundberg (2001) reanalysed the relationships of *Roussea*, and found Carpodetaceae s.s. in Asterales to be sister group to *Roussea*, thus confirming the result of Savolainen et al. (2000). This was later confirmed in an expanded analysis, using *atpB*, *ndhF*, *rbcL* and morphological data, by Lundberg and Bremer (2003). Based on the strong support for the sister-group relationship between Rousseaceae and Carpodetaceae, Lundberg (2001) suggested that the two families should be treated as subfamilies (Rousseoideae and Carpodetoideae) in an expanded Rousseaceae s.l. However, the monophyly of each subfamily is likewise well supported, and they are therefore kept separate in this treatment (see Carpodetaceae treatment in this volume). A suggested synapomorphy for the expanded Rousseaceae s.l. is the increased number of carpels and ovary locules (Lundberg and Bremer 2003). However, the basal relationships in Asterales, including the possible sister relationship between Rousseaceae s.l. and Campanulaceae, is uncertain and any unequivocal synapomorphies for Rousseaceae s.l. are still lacking.

Only one genus:

1. *Roussea* Smith. Fig. 130

Roussea Smith, Pl. Icon. Ined. 1: 6 (1789).

Characters as for the family. The genus includes one species, *Roussea simplex* Smith, on Mauritius.

Selected Bibliography

Al-Shammary, K.I.A., Gornall, R.J. 1994. Trichome anatomy of the Saxifragaceae s. l. from the southern hemisphere. Bot. J. Linn. Soc. 114: 99–131.

Cronquist, A.J. 1981. An integrated system of classification of flowering plants. New York: Columbia University Press.

Dahlgren, R. 1983. General aspects of angiosperm evolution and macrosystematics. Nordic J. Bot. 3: 119–149.

Engler, A. 1891. Saxifragaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, III, 2a. Leipzig: W. Engelmann, pp. 41–93.

Engler, A. 1930. Brexioideae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, ed. 2, 18a. Leipzig: W. Engelmann, pp. 185–187.

Koontz, J.A., Soltis, D.E. 1999. DNA sequence data reveal polyphyly of Brexioideae (Brexiaceae; Saxifragaceae sensu lato). Pl. Syst. Evol. 219: 199–208.

Lundberg, J. 2001. The asteralean affinity of the Mauritian *Roussea* (Rousseaceae). Bot. J. Linn. Soc. 137: 267–276.

Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–578.

Ramamonjiarisoa, B.A. 1980. Comparative anatomy and systematics of African and Malagasy woody Saxifragaceae sensu lato. Ph.D. Thesis, University of Massachusetts.

Savolainen, V., Spichiger, R., Manen, J.-F. 1997. Polyphyletism of Celastrales deduced from a chloroplast noncoding DNA region. Mol. Phylog. Evol. 3: 27–37.

Savolainen, V., Fay, M.F., Albach, D.C., Backlund, A., van der Bank, M., Cameron, K.M., Johnson, S.A., Lledó, M.D., Pintaud, J.-C., Powell, M., Sheahan, M.C., Soltis, D.E., Soltis, P.S., Weston, P. Whitten, W.M., Wurdack, K.J., Chase, M.W. 2000. Phylogeny of the eudicots: a nearly complete familial analysis based on *rbc*L gene sequences. Kew Bull. 55: 257–309.

Soltis, D.E., Soltis, P.S. 1997. Phylogenetic relationships in Saxifragaceae sensu lato: a comparison of topologies based on 18S rDNA and *rbc*L sequences. Amer. J. Bot. 84: 504–522.

Soltis, D.E., Soltis, P.S., Chase, M.W., Mort, M.E., Albach, D.C., Zanis, M., Savolainen, V., Hahn, W.H., Hoot, S.B., Fay, M.F., Axtell, M., Swensen, S.M., Prince, L.M., Kress, W.J., Nixon, K.C., Farris, J.S. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbc*L, and *atp*B sequences. Bot. J. Linn. Soc. 133: 381–461.

Straka, H., Friedrich, B. 1988. Palynologica Madagassica et Mascarenica Familien 65 bis 97. Trop. subtrop. Pflanzenwelt 61: 1–117.

Takhtajan, A. 1997. Diversity and classification of flowering plants. New York: Columbia University Press.

Thorne, R.F. 1992. Classification and geography of the flowering plants. Bot. Rev. 58: 225–348.

Stylidiaceae[1]

Stylidiaceae R. Br., Prodr.: 565 (1810), nom. cons.
Donatiaceae B. Chandler (1911).

R.C. Carolin

Herbs or sometimes subshrubs or cushion plants. Leaves simple, spirally arranged, without stipules, often in rosettes which may be basal, arranged along a stem or on stolons. Aerial roots sometimes present. Flowers in racemes or cymes, unisexual or bisexual, actinomorphic or zygomorphic. Sepals 5 (rarely 3–7), connate. Petals 5(–10), free (*Donatia*) or connate into a tube, abaxial lobe often differentiated into a small labellum. Stamens rarely 3 (*Donatia* p.p.), mostly 2, epigynous, free (*Donatia*) or adnate to the style to form a gynostemium. Ovary inferior, 2–3-locular, sometimes 1-locular by abortion of one locule or through reduction of the septum; style simple or (*Donatia*) 2–3 stylodia, stigmas 2–3; placentation axile or free central. Fruit a capsule. Seeds small, with endosperm.

Six genera and about 245 species, mostly Australia and New Zealand, few species in south-eastern Asia and South America.

Vegetative Morphology. The cushion plant genera *Donatia* and *Phyllachne* have a characteristic growth pattern. They are much-branched, each branch is held closely against its neighbours, and the older parts of the plant decay and new roots are produced at the upper nodes. Carlquist (1969) postulated that the habit of Stylidiaceae is determined by the fact that none have any significant secondary thickening except, for example, the relatively weak, anomalous type found in *Stylidium laricifolium.* A large number of species produce rosettes (e.g. *S. graminifolium*) with scapose inflorescences but no other stems. Some of these, as they age, bear the rosettes on substantial, thick stocks. In some *Stylidium* spp., the rosettes are scattered along the stems or the leaves appear to be whorled (e.g. *S. striatum*). *Levenhookia* spp. and some *Stylidium* spp. (e.g. *S. alsinoides*, *S. laricifolium*) bear the leaves scattered along short aerial stems. A number of species produce small bulbs at the base of the stem (e.g. *S. asteroideum*, *S. petiolare*) which may enable them to resist very dry summer conditions. Some, e.g. *S. bulbiferum*, have a branched creeping habit where aerial 'stilt' roots hold the plants above the soil surface. Yet others may be held ± erect by aerial stilt roots which apparently survive for only a few seasons and are replaced by others on the branches of the original stem. This results in vegetative fragmentation.

Carlquist (1969) suggested that the leaves are basically linear with the broader leaves showing flabellate or striate venation, indicating an expansion of a single mid-vein.

Vegetative Anatomy. The family shows anomalous secondary thickening where the cambium is formed outside the vascular bundles and where cambial activity is essentially unilateral and tissue is produced only towards the inside. Three different types of cambial activity are found. In *Stylidium* subg. *Nitrangium* sect. *Rhynchangium*, a cambium forms beneath the endodermis and produces a determinate amount of fibres and vessels with some intraxylary phloem strands towards the inside but nothing towards the outside. In lignotubers of the same section, a similar xylem with intraxylary phloem strands is formed inside a cambium inside the endodermis but the xylem elements are distorted, and outside phellem is formed. In some species, e.g. *S. laricifolium*, a cambium is formed inside the endodermis and an indeterminate xylary system with intraxylary phloem is produced inside but nothing outside. This weak, anomalous cambial activity may indicate that the family is basically herbaceous (Carlquist 1981). Rays are always absent (Carlquist 1992). The stomata are anomocytic, except in *Donatia* where they are paracytic. Sieve tubes have S-type plastids.

Inflorescence Structure. The inflorescence is basically a thyrse which in many species is re-

[1] Updated by J.W. Kadereit and J. Lundberg.

duced to a raceme or spike and, in *Donatia*, *Phyllachne* and *Oreostylidium*, to solitary terminal flowers (Carolin 1967).

Flower Structure. The flowers of Stylidiaceae are unusual in the order for having imbricate petal aestivation and extrorse anthers with divergent thecae. They often are semi-resupinate and split monosymmetrically. The floral construction of *Donatia* differs strongly from the remainder of the family. The petals, stamens and stylodia in this genus are free from each other. *Donatia fascicularis* has three stamens and three stylodia but, in the other species of this genus, there are only two stamens and stylodia. In all other genera, the two stamens are fused with the style. Erbar (1992) presented ontogenetic evidence that the stamens are fused into a tube, and the tube is fused to the style to form the gynostemium or column. The ovary basically has a lower 2-locular region, an upper 1-locular region and sometimes a small, uppermost 2-locular region. In most species, the 1-locular region has the ovules attached on a free central placenta, although in *Donatia* the ovules are attached on axile placentas in the 2-locular region. Two sterile strands of parenchyma connect the free central placentas with the top of the loculus in *Phyllachne* and some *Stylidium* spp. whilst in most *Stylidium* spp. these two parenchymatous strands project from the placenta but do not connect with the top of the loculus (Mildbraed 1908; Carolin 1960). *Donatia* has a disc-like nectary but in the other genera it is 2-lobed, one lobe being adaxial and one abaxial, or sometimes just a single lobe on one side only is present (Carolin 1960; Erbar 1992). The nectary is extrastaminal. In *Stylidium*, there are various outgrowths at the top of the corolla tube which may function as pollinator guides or to prevent access to non-pollinating insects. These outgrowths are united into an erect sheath in *Levenhookia* spp. (see below).

In *Stylidium*, the column is sensitive to touch and executes a very fast movement. This explains the vernacular name for these plants, i.e. 'trigger plants'. The movement, through an angle of 2–5 radians, occurs at the main bend in the column in a time span of 10–30 ms, probably the fastest movement known in plants (Findlay and Findlay 1975). The column at the bend consists of an epidermis, with layers of parenchyma on either side with thick-walled cells inside referred to as the anterior layer on the abaxial side and the posterior layer on the adaxial side. Both these layers are rich in starch grains and have conspicuous vacuoles and mitochondria, and both layers have cell walls which are rich in pectin and have almost no longitudinal cellulose fibrils but only circumferential ones. There is also a central layer of cells (Findlay and Findlay 1989). In the firing position, the anterior layer has high turgor and high concentrations of KCl. Findlay (1982) considered that this turgor is balanced by the stretched cells of the posterior layer. Stimulation causes the cell walls to buckle trans-

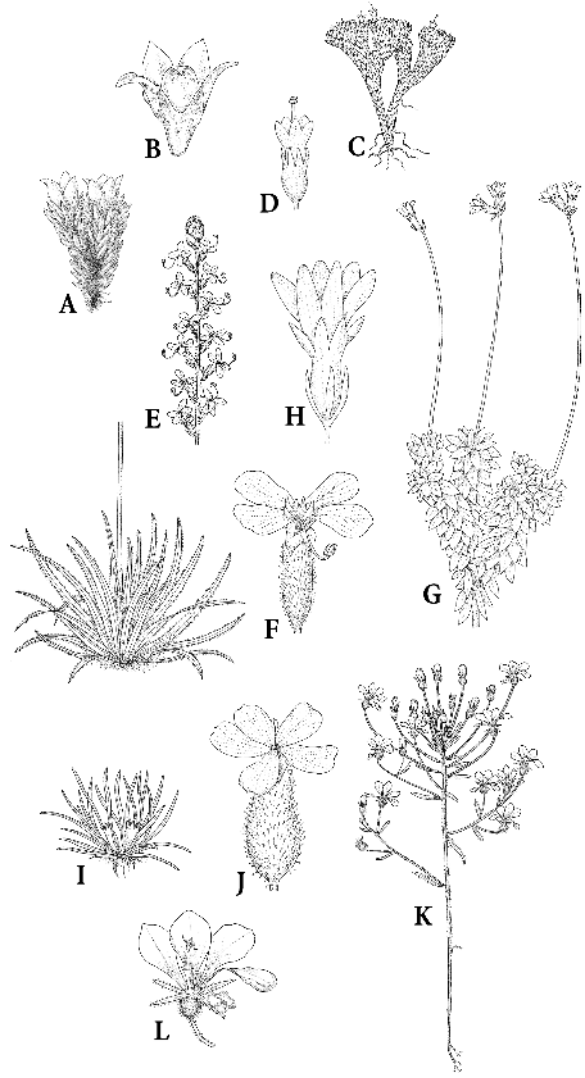

Fig. 131. Stylidiaceae. **A**, **B** *Donatia novae-zelandiae*. **A** Habit. **B** Flower. **C**, **D** *Phyllachne colensoi*. **C** Habit. **D** Flower. **E**, **F** *Stylidium graminifolium*. **E** Habit. **F** Flower. **G**, **H** *Forstera bidwillii*. **G** Habit. **H** Flower. **I**, **J** *Oreostylidium subulatum*. **I** Habit. **J** Flower. **K**, **L** *Levenhookia stipitata*. **K** Habit. **L** Flower. (Illustrations adapted from Mildbraed 1908 by Rebecca Wagstaff; **C–J** from Wagstaff and Wege 2002)

versely (presumably, the lack of longitudinal fibrils is critical in this respect), thus unbalancing the system and initiating the movement. Immediately after firing, KCl moves into the posterior layer and gradually returns to the anterior layer as the firing position is resumed. It seems that the column has to lie against the labellum to attain firing potential. Recovery takes 200–700 s. Those species which do not show movement do not show the characteristic anatomy of the bend anywhere in the column (Findlay and Findlay 1989). In *Levenhookia*, the labellum is sensitive to touch when mature.

Embryology. The ovule is anatropous, unitegmic, tenuinucellate and endotheliate. The development of the endosperm is ab initio cellular and, at the 8-tier stage, each tier consists of two cells. The upper and lower tiers remain two-celled and form intrusive haustoria at each end of the embryo sac (Subramanyam 1952; Philipson and Philipson 1973). Embryo sac formation follows the Polygonum type, and the embryo develops according to the Solanad type. Anther wall formation is dicotyledonous, the tapetum is glandular, and pollen grains are 2- or 3-celled when shed (Tobe and Morin 1996).

Fruit and Seed, Dispersal. Fruits are capsular, although those of *Donatia* do not appear to dehisce. Seeds are very small but little is known about their dispersal. Carlquist (1969) suggested that they could easily be carried in mud on the feet of birds.

Pollen Morphology. Pollen grains are fairly uniform in the family. They are spherical and colpate. The number of colpi varies in the range of 2–8, *Phyllachne* and *Forstera* having 3–4 (very rarely 5) and *Stylidium* and *Levenhookia* 2–8 colpi (Bronkers and Stainer 1972).

Karyology. Haploid chromosome numbers of $n = 5$–16, 18, 24, 26, 28 and 30 have been reported (Lammers 1992). James (1979) considered that the base number of *Stylidium* is $x = 15$. *Donatia fascicularis* has a haploid number of $n = 24$ (Moore 1983). From this, Lammers (1992) speculated that the base number of the family is $x = 6$ or 8.

Reproductive Biology. The flowers of *Stylidium* and *Levenhookia* have very precise pollination mechanisms which often appear to make use of specific pollinators (Erickson 1958). In both genera, one of the petals is modified into a small labellum. This has a different function in the two genera but, in both, the effect is that the flowers appear to be tetramerous. In *Stylidium* the column is bent over the labellum, obscuring it in most species. Mildbraed (1908) suggested that the labellum holds the column in position. Carlquist (1969) believed that the glossy swelling on the labellum of many *Stylidium* spp. is a false nectary. Except in two species, *S. insensitivum* and *S. beaugleholei*, the column is sensitive to the touch of the pollinator seeking nectar at the base of the corolla tube. The column moves very rapidly, articulating at the bend of the column (see above), and strikes the pollinator either on the back or on the undersurface, thus depositing pollen there, brushing pollen onto the stigmas, or both. Many species are protandrous, thereby excluding self-pollination within an individual flower. By contrast, the ephemeral species do not appear to be protandrous. The stigmas here, however, seem to touch the insect before pollen from the same flower is deposited (Erickson 1958). Both Erickson (1958) and Carlquist (1969) note that in some species, e.g. *S. sacculatum*, the stigmas and anthers are closely appressed to an expansion of part of the column before it is triggered. Carlquist considered this to be a mechanism to ensure self-pollination when no triggering occurs. Nothing is recorded about self-incompatibility in the family. In *Levenhoookia*, the column is tightly enclosed by the labellum. It is released only when mature, either by the pressure of the growing column or by the pollinator touching a sensitive region on the labellum. At release, the labellum springs downwards and the column moves away from the labellum across the flower and touches a sheathing outgrowth of the top of the corolla tube. The jerk brought about by this contact sprays pollen over the pollinator. The column recovers, and the labellum returns to the erect position but does not enclose the column any more. Subsequent visits by pollinators deposit pollen on the mature stigmas (Erickson 1958).

Phytochemistry. The storage carbohydrate of the family is inulin. Members of the family produce a carbocyclic iridoid similar to monotropein. No alkaloids have been recorded from the family but caffeic acid may be present (Lammers 1992).

Subdivision of and Relationships Within the Family. It is yet not finally settled whether *Donatia* is closest relative to the remainder of the family and should be included in it. This approach,

first taken by Mildbraed (1908), is supported by a morphological study by Gustafsson and Bremer (1995) and the most recent, combined molecular-morphological analysis of the order by Lundberg and Bremer (2003), but not by some other molecular analyses where Stylidiaceae and *Donatia* occupy quite separate positions in the order (Albach et al. 2001; Bremer et al. 2002; see below). Taken as one family, *Donatia* is sister to the remainder (Laurent et al. 1998), as also suggested by Mildbraed (1908). Among the remaining genera, *Forstera*/*Phyllachne* are sister to *Levenhookia*/*Stylidium*, and *Oreostylidium* appears to be nested within *Stylidium* and should perhaps be included in that genus (Laurent et al. 1998; Wagstaff and Wege 2002). *Oreostylidium*, with almost actinomorphic flowers, has been interpreted as a case of extreme paedomorphic reduction (Laurent et. 1998). The exact relationship between *Phyllachne* and *Forstera* is still uncertain but it is likely that they are nested within each other, and it has recently been suggested that *Phyllachne* should be merged with *Forstera* (Wagstaff and Wege 2002).

Affinities. Although sometimes classified outside Asterales (for discussion, see Lammers 1992; Lundberg and Bremer 2003), there is broad consensus that the family (incl. *Donatia*) is part of this order (APG II 2003). A sister-group relationship of Stylidiaceae to the Menyanthaceae/Goodeniaceae/Calyceraceae/Compositae clade (MGCA clade) of Asterales was resolved by Lundberg and Bremer (2003), although with low support. Transition from woody to herbaceous habits, and from scalariform to simple vessel perforation plates were identified as characters in support of such relationships by these authors. By contrast, Stylidiaceae (excl. *Donatia*) were sister to Campanulaceae in the analyses by Albach et al. (2001) and Bremer et al. (2002), again with low support in the former study. In these two analyses, *Donatia* was found to be closest relative, with low support, of either Alseuosmiaceae/Argophyllaceae/Phellinaceae (Bremer et al. 2002), or to all families of Asterales except Stylidiaceae/Campanulaceae (Albach et. al. 2001). Considering the lack of sufficiently good support for many nodes in all these analyses, the exact relationships of Stylidiaceae should be regarded as unclear, although the evidence presented by Lundberg and Bremer (2003) makes a relationship of the family to Campanulaceae a little less likely.

Size, Distribution and Habitats. The family contains six genera and about 170 species, of which most belong to *Stylidium*. Stylidiaceae are almost entirely a southern hemisphere family, most species being confined to Australia. One species of *Stylidium* extends into south-eastern Asia as far as Sri Lanka. With the exception of *Stylidium* and *Levenhookia*, all genera occur in New Zealand. *Phyllachne* and *Donatia* are also found in southern South America. The species occur in a variety of habitats, from seasonally wet areas in the tropics where they may be ephemerals, to the sclerophyll communities of southern Australia and the exposed alpine habitats of the higher latitudes of the southern continents. *Donatia* is the major component of the very peculiar, hard-cushion bogs in South America and New Zealand.

Palaeobotany. The fossil record of Stylidiaceae is scanty, but fossil pollen (*Tricolpites stylidioides*) similar to pollen from *Forstera* has been reported from the south-eastern Australian Oligocene (Macphail 1997).

Key to the Genera

1. Petals free; stamens free from the stylodia **1. *Donatia***
– Petals connate; stamens adnate to the style into a column **2**
2. One corolla lobe (the labellum) smaller than the others, usually lying beneath the bent column or enclosing the erect or slightly bent column **3**
– Corolla lobes ± equal **4**
3. Column usually bent, rarely almost straight and then never enclosed at top by labellum **6. *Stylidium***
– Column straight or slightly bent, top enclosed by labellum before triggering **5. *Levenhookia***
4. Peduncles longer than leaves **3. *Forstera***
– Peduncles, if present, shorter than leaves **5**
5. Flowers almost sessile; glabrous cushion plant **2. *Phyllachne***
– Flowers shortly pedicellate; stoloniferous herb with glandular hairs on the calyx **4. *Oreostylidium***

Genera of Stylidiaceae

1. *Donatia* J.R. Forst. Fig. 131A, B

Donatia J.R. Forst., Char. Gen.: 9, t. 5 (1776).

Much-branched short herbs, forming dense, often large, cushion-like expanses. Leaves small, linear, hard, crowded on the stem. Flowers solitary, terminal, sessile, regular, bi- or unisexual. Sepals 3–7. Petals 5–10, free. Stamens 2–3, epigynous inside a disc, extrorse. Ovary inferior, 2–3-locular

with axile placentation towards the top of the loculi. Fruit an indehiscent capsule. $2n$ =24. Two species, Australia, New Zealand, South America.

2. *Phyllachne* J.R. Forst. Fig. 131C, D

Phyllachne J.R. Forst., Char. Gen.: 115, t. 58 (1776).

Much-branched short herbs, forming dense, often large, cushion-like expanses. Leaves small, lanceolate-subulate, hard, crowded on the stems. Flowers solitary, terminal, sessile, regular, bi- or unisexual. Sepals 2–9, usually 5, subequal. Petals 3–9, usually 5, united into a short tube. Stamens 2, united with the style into a short erect column. Nectaries 2, reniform. Ovary incompletely 2-locular. Fruit an indehiscent capsule. Four species, New Zealand (3 spp.), Tasmania, South America.

3. *Forstera* L. f. Fig. 131G, H

Forstera L. f., Nov. Act. Upsal., 3: 184, t. 9 (1780).

Erect to decumbent herbs. Leaves scattered along the stems. Flowers almost regular, solitary on long peduncles, bisexual. Sepals 5–6, subequal. Petals 5–9, united into a short tube, sometimes with appendages in the throat. Stamens 2, united with the style into a short erect column. Ovary imperfectly 2-locular. Nectaries 2, reniform. Fruit a capsule. Five species, New Zealand, Tasmania.

4. *Oreostylidium* Berggren Fig. 131I, J

Oreostylidium Berggren, Minnesskr. Fysiogr. Sällsk. Lund. 8: 1, t. 1 (1878).

Small herbs. Leaves basal, narrow. Flowers almost sessile in the basal leaf axils, regular, bisexual, with glandular hairs. Sepals 5, subequal. Petals 5, united into a tube with short lobes. Stamens 2, united with the style into a short erect column which is exserted from the corolla tube. Nectaries 2, subglobose. Fruit a capsule. Seeds small. $2n$ = 30. One species, *O. subulatum* Berggren, New Zealand.

The genus has been included in *Stylidium* Swartz ex Willd. by Laurent et al. (1998).

5. *Levenhookia* R. Br. Fig. 131K, L

Levenhookia R. Br., Prodr. 572 (1810).

Small erect herbs, often ephemeral. Leaves spirally arranged along the stem. Flowers arranged in racemes, irregular, bisexual. Sepals 5, free. Petals 5, connate into a tube, with outgrowths usually forming a sheath at the throat; abaxial petal (labellum) erect, sensitive and enclosing the column until triggered. Stamens 2, united with the style into a ± bent, slightly sensitive column. Ovary 1-locular with a free-central placentation. Nectary on top of the ovary. Fruit a capsule. Seeds small. Ten species, Australia.

6. *Stylidium* Swartz ex Willd. Fig. 131E, F

Stylidium Swartz ex Willd., Sp. Pl. 4: 7, 146 (1805). nom. cons., non *Stylidium* Lour.

Herbs, sometimes ephemerals, or undershrubs, sometimes with bulbs. Leaves spirally arranged along the stems or in a basal rosette or in rosettes along the stems or stolons. Stems erect, sometimes very short and thick as a basal stock or creeping, often raised above the soil surface by aerial roots. Flowers arranged in thyrses, cymes or racemes, irregular, bisexual. Sepals 5, free or variously connate. Petals 5, connate into a tube, with various outgrowths in the throat; abaxial petal smaller (labellum). Stamens 2, united with the style into a bent, usually sensitive column. Ovary 2-locular with axile placentation or 1-locular with free-central placentation or 1-locular (by abortion of the other loculus) with apparently one parietal placenta. Nectaries 1–2, hemispherical or reniform. Fruit a capsule. Seeds numerous, usually small. $2n$ = 10–32, 36, 52, 56, 60. About 220 species, mostly Australia, a few species in south-eastern Asia, reaching as far as Sri Lanka (1 sp.)

The following subgenera are usually recognised. Subg. *Centridium*: column short, bent just below the anthers with an elongated stigma, or not bent and not sensitive; subg. *Forsteriopsis*: leaves short, almost scale-like, tightly overlapping; subg. *Andersonia*: capsule linear, septum of ovary almost complete; subg. *Alsinoides*: capsule linear, septum of ovary narrow; subg. *Stylidium* (*Tolypongium*): capsule ovoid-oblong, rarely linear, septum of ovary usually incomplete or absent; subg. *Nitrangium*: capsule linear, rarely ovate, septum of ovary very reduced, throat usually without appendages.

Selected Bibliography

Albach, D.C., Soltis, P.S., Soltis, D.E., Olmstead, R.G. 2001. Phylogenetic analysis of asterids based on sequences of four genes. Ann. Missouri Bot. Gard. 88: 163–212.

APG II. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436.

Bremer, B., Bremer, K., Heidari, N., Erixon, P., Olmstead, R.G., Anderberg, A.A., Källersjö, M., Barkhordarian, E. 2002. Phylogenetics of asterids based on 3 coding and 3 non-coding chloroplast DNA markers and the utility of non-coding DNA at higher taxonomic levels. Mol. Phylog. Evol. 24: 274–301.

Bronckers, F., Stainer, F. 1972. A l'étude morphologique du pollen de la famille des Stylidiaceae. Grana 12: 1–22.

Carlquist, S. 1969. Studies in Stylidiaceae: new taxa, field observations, evolutionary tendencies. Aliso 7: 13–64.

Carlquist, S. 1981. Types of cambial activity and wood anatomy of *Stylidium* (Stylidiaceae). Amer. J. Bot. 68: 778–785.

Carlquist, S. 1992. Wood anatomy of sympetalous dicotyledon families: a summary, with comments on the systematic relationships and evolution of the woody habit. Ann. Missouri Bot. Gard. 79: 303–332.

Carolin, R.C. 1960. Floral structure and anatomy in the family Stylidiaceae Swartz. Proc. Linn. Soc. New South Wales 85: 189–196.

Carolin, R.C. 1967. The concept of the inflorescence in the order Campanulales. Proc. Linn. Soc. New South Wales 92: 7–26.

Erbar, C. 1992. Floral development of two species of *Stylidium* (Stylidiaceae) and some remarks on the systematic position of the family Stylidiaceae. Canad. J. Bot. 70: 258–271.

Erickson, R. 1958. Triggerplants. Perth: Paterson Brokensha.

Findlay, G.P. 1982. Generation of torque by the column of *Stylidium*. Austral. J. Pl. Physiol. 9: 271–286.

Findlay, G.P., Findlay, N. 1975. Anatomy and movement of the column in *Stylidium.* Austral. J. Pl. Physiol. 2: 597–621.

Findlay, G.P., Findlay, N. 1989. The structure of the column in *Stylidium*. Austral. J. Bot. 37: 81–101.

Gustafsson, M.H.G., Bremer, K. 1995. Morphology and phylogenetic interrelationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and related families (Asterales). Amer. J. Bot. 82: 250–265.

James, S.H. 1979. Chromosome numbers and genetic systems in the trigger plants of Western Australia (*Stylidium*; Stylidiaceae). Austral. J. Bot. 27: 17–25.

Lammers, T.G. 1992. Circumscription and phylogeny of the Campanulales. Ann. Missouri Bot. Gard. 79: 388–413.

Laurent, N., Bremer, B., Bremer, K. 1998. Phylogeny and generic interrelationships of the Stylidiaceae (Asterales), with a possible extreme case of floral paedomorphosis. Syst. Bot. 23: 289–304.

Lundberg, J., Bremer, K. 2003. A phylogenetic study of the order Asterales using one morphological and three molecular data sets. Intl J. Pl. Sci. 164: 553–558.

Macphail, M.K. 1997. Comment on M. Pole (1994): 'The New Zealand flora – entirely long-dispersal?' J. Biogeogr. 22: 625–635.

Mildbraed, J. 1908. Stylidiaceae. In: Pflanzenreich IV: 278. Leipzig: W. Engelmann.

Moore, D.M. 1983. Flora of Tierra del Fuego. Oswestry: Anthony Nelson.

Philipson, W.R., Philipson, M.N. 1973. A comparison of the embryology of *Forstera* L. and *Donatia* Forst. et f. N. Z. J. Bot. 11: 449–460.

Subramanyam, K. 1952. The nutritional mechanism of embryo sac and embryo in the families Campanulaceae, Lobeliaceae and Stylidiaceae. J. Mysore Univ. sect. B 13: 1.

Tobe, H., Morin, N.R. 1996. Embryology and circumscription of Campanulaceae and Campanulales: a review of literature. J. Pl. Res. 109: 425–435.

Wagstaff, S.J., Wege, J. 2002. Patterns of diversification in New Zealand Stylidiaceae. Amer. J. Bot. 89: 865–874.

Index to Scientific Names

References to main entries in **bold-faced** print, to illustrations in *italics*.

Aaronsohnia **368**
Abrophyllaceae 57
Abrophyllum **59**
A. ornans 59
Abrotanella **214**
A. linearis 215
Acamptopappus **321**
Acanthocephalus **184**
Acanthocladium **252**
Acanthodesmos **152**
Acantholepis **128**
Acanthospermum **488**
Acanthostyles **546**
Acanthotheca 245
Acasma 132
Achaetogeron 340
Achillea **364**
A. group **364**
Achnophora **295**
Achnopogon **98**
Achyrachaena **499**
Achyrocline **252**
Achyrocome 263
Achyropappus **435**
Achyroseris 198
Achyrothalamus 121
Acicarpha **23**
Acilepidopsis **166**
Acilepis **166**
Acmella **471**
Acomis **252**
Acosta 146
Acourtia **103**
Acrisione **223**
Acritopappus **522**
A. connatifolius 522
Acroclinium 279
Acroptilon 143
Actinoseris 117
Actionbole **252**
A. oldfieldiana 254
Actites 191
Adelostigma **387**
Adenachaena 356
Adenanthellum **350**
Adenanthemum 350
Adenocaulon **108**
Adenocritonia **562**
Adenocyclus 159
Adenoglossa **354**
Adenoon **171**
Adenopappus 429
Adenophora **43**
Adenophyllum **424**
Adenostemma **518**
A. viscosum 519
Adenostemmatinae **518**
Adenostyles **240**
Adenothamnus **499**
Aedesia **171**
Aegialophila 145
Aegopordon 137
Aequatorium **223**
A. jamesonii 223
A. subg. *Praegynoxys* 223
Aetheolaena **234**
Aetheopappus 140
Aetheorhiza **190**
Ageratella **555**
Ageratina 167, **514**
Ageratinae **520**
Ageratinastrum **167**
Ageratum **522**
Agiabampoa 466
Agnorhiza 464
Agoseris **191**
Agrianthus **542**
A. group **542**
Ainsliaea **123**
Ajania **357**
A. group **357**
Ajaniopsis **357**
Akeassia **304**
Akylopsis 368
Alatoseta **253**
Albertinia **154**
Alcantara 163
Alciope **225**
Aldama **465**
Alepidocline **484**
Alfredia **134**
Alibum 180
Aliella **253**
Allagopappus **379**
Allardia **360**
Allendea 178
Allittia **341**
Alloispermum **484**
Allopterigeron **390**
Almutaster **334**
Alomia **556**
Alomiella **551**
Alomiinae **552**
Alseuosmia **10**
A. banksii 9
A. macrophylla 9
Alseuosmiaceae *3*, **7**
Alvordia **466**
Amauria **509**
Amauriinae 509
Amauriopsis **435**
Ambassa **167**
Amberboa **142**
Amblyocarpum **383**
Amblyolepis **404**
Amblyopappus **495**
Amblysperma **115**
Amboroa **571**
Ambrosia **444**
A. canescens 444
A. polystachya 444
Ambrosiaceae 443
Ambrosieae 443
Ambrosiinae *441*, **443**
Ameghinoa **106**
Amellus **291**
A. asteroides 291
Ammanthus 365
Ammobium **253**
A. craspedioides 254
Amolinia **572**
Ampelaster **334**
Ampherephis 160
Amphiachyris **321**
Amphidoxa 266
Amphiglossa **253**
Amphipappus **321**
Amphoricarpos **132**
Anacantha 137
Anacyclus **364**
Anaglypha 275
Anaphalioides **253**
A. bellidioides 252
Anaphalis **253**
A. margaritacea 252
Anaxeton **254**, 281
Ancathia **134**
Ancistrocarphus **254**
Anderbergia **255**
Andromachia 178

A. sect. *Chrysactinium* 179
A. sect. *Oligactis* 178
Andryala **194**
Anemocarpa **255**
A. saxatilis 254
Angelianthus 178
Angelphytum 450
Angianthus **255**
Anisocarpus **499**
Anisochaeta **255**
Anisocoma **193**
Anisopappinae **397**
Anisopappus **397**
A. chinensis 397
Anisothrix **255**
Annaea 42
Antennaria **255**
A. pulchella 256
Anteremanthus **161**
Antheidosorus 265
Anthemideae **342**
Anthemis **365**
A. group **365**
Antheropeas 495
Anthocerastes 282
Anthotium **594**
Antillanthus **227**
Antillia **562**
Antiphiona **384**
Antithrixia **256**
Antunesia 173
Anura 136
Anvillea **381**
A. garcinii 381
Anvilleina 381
Apalochlamys **256**
Apargidium 191
Apetahia **52**
Aphanactis **484**
Aphanostephus **339**
Aphylloclados **111**
Aplopappus 321, 338
A. sect. *Acamptopappus* 321
A. sect. *Leucopsis* 338
Apopyros **340**
Aposeris **196**
Apostates **435**
Arbelaezaster **234**
Archibaccharis **311**
Arctanthemum **357**
Arctium **136**
A. group **135**
A. lappa 136
Arctogeron **317**
Arctotheca **203**
Arctotideae **200**
Arctotidinae **202**
Arctotis **203**
A. stoechadifolia 203
Arcyna 132
Argentipallium **256**
Argophyllaceae *3*, **13**
Argophyllum **16**
A. ellipticum 14
Argyranthemum **369**
A. foeniculaceum 369
A. group **369**
Argyrocalymma 59
Argyroglottis **256**
Argyrophanes 260
Argyrotegium **284**
Argyrovernonia 160
Argyroxiphium **500**
A. sandwicense 500
Arida **329**
Aristeguietia **567**
Arnaldoa **90**
Arnica **494**
A. dealbata 494
A. mollis 494
Arnicastrum **430**
Arnicinae **493**
Arnoglossum **220**
Arnoseris **196**
Arrhenechthites **228**
Arrojadocharis **542**
Arrowsmithia **257**
Artanacetum 358
Artemisia **358**
A. absinthium 358
A. group **358**
Artemisiella **360**
Artemisiopsis **257**
Arthrolepis 364
Asaemia 351
Asanthus **555**
Ascaricida 172
Ascidiogyne **524**
Aspilia 459
Asplundianthus **568**
Astephania 397
Aster **317**
A. subg. *Eurybia* 287
A. subg. *Galatea* 318
A. subg. *Kalimeris* 318
A. sect. *Oritrophium* 300
Asteraceae **61**
Astereae **284**
Asteridea **257**
Asterinae **316**
Asteriscus **382**
Asteroideae **78**
Asteropsis **313**
Asterothamnus **317**
Astradelphus 340
Astranthiinae **336**
Astranthium **336**
Astrocodon 42
Asyneuma **44**
Asyneumopsis 44
Atalanthus 191
Athanasia **350**
A. dentata 351
A. group **350**
Athrixia **257**
Athroisma **398**
A. boranense 399
Athroismeae *392*, **395**
Athroisminae **398**
Atractylis **127**
Atractylodes **127**
Atrichantha **257**
Atrichoseris **193**
Aucklandia 137
Austrobrickellia **557**
Austrocritonia **568**
A. angulicaulis 568
Austroeupatorium **529**
A. inulifolium 529
Austroliabum 178
Austrosynotis **240**
Avellara 198
Axiniphyllum **489**
Ayapana **549**
A. amygdalina 549
Ayapaninae **548**
Ayapanopsis **550**
Aylacophora **295**
Aynia **154**
Azorina **41**
Aztecaster **295**

Babcockia 191
Bacasia 89
Baccharidastrum 311
Baccharidinae **310**
Baccharidiopsis 311
Baccharidoideae 310
Baccharis **311**
Baccharoides **172**
Badilloa **568**
Baeria 496
Baeriinae **494**
Baeriopsis **495**
Bafutia **238**
Bahia **435**
B. absinthifolia 435
Bahianthus **543**
B. viscosus 543
Bahieae *392*, **433**
Bahiopsis **466**
Baileya **404**
B. multiradiata 405
Bajacalia **425**
Balduina **401**
Balsamita 366
Balsamorhiza 464
Baltimora **449**
Barkleyanthus **221**
Barnadesia **89**
B. odorata 89
Barnadesieae **87**
Barnadesioideae **77**
Barroetea **554**
Barrosoa **537**
Bartlettia **436**
Bartlettina **573**
Basedowia **257**
Batopilasia **327**
Bebbia **480**
Bechium **167**
Bedfordia **224**

Behen 157
Bejaranoa **539**
Bellida **258**
B. graminea 254
Bellideae 303
Bellidiastrum 317
Bellidinae **303**
Bellieae 303
Bellis **303**
Bellium **303**
Belloa **258**
Bembycodium 350
Benitoa **329**
Berardia **130**
Berenice **39**
Berkheya **205**
B. horrida 205
Berkheyopsis 206
Berlandiera **462**
B. lyrata 462
Berroa **258**
Berthelotia 387
Berylsimpsonia **100**
Bethencourtia 229
Bidens **411**
Bidentideae 406
Bielzia 141
Bigelowia **322**
Bipontia 160
Bishopalea **163**
Bishopanthus **177**
Bishopiella **545**
Bishovia **565**
Blainvillea **449**
Blakeanthus **523**
Blakiella **295**
Blanchetia **158**
B. heterotricha 150
Blaxium 245
Blennosperma **215**
Blennospora **258**
Blepharipappus **500**
Blepharispermum **398**
Blepharizonia **501**
Blumea **377**
Blumeopsis **389**
Boeberastrum **425**
Boeberoides **425**
Bojeria 382
Bolandia **229**
Bolanosa **152**
Bolocephalus 138
Boltonia **328**
Boltoniinae **327**
Bombycilaena **258**
Boopis **24**
B. bupleuroides 24
Borkonstia 319
Borrichia **462**
Bothriocline **167**
Brachanthemum **357**
Brachionostylum **225**
Brachyactis 335
Brachychaeta 325
Brachyclados **110**
Brachycodon 42
Brachycodonia 42
Brachycome 302
Brachyglottis **223**
Brachylaena **119**
Brachymeris 356
Brachyris 321
B. sect. *Amphiachyris* 321
Brachyscome **302**
Brachyscominae **302**
Brachythrix **167**
Bracteantha 283
Brasilia 419
Breea 132
Brenandendron **173**
Brickellia **553**
Brickelliastrum **554**
Brighamia **52**
Brintonia 325
Brocchia 367
Broteroa 127
Brunonia **594**
B. australis 590, 594
Brunoniaceae 589
Bryomorphe **258**
B. aretioides 246
Bubonium 382
Buphthalmum **382**
Burkartia **103**
Burmeistera **51**
B. virescens 52

Caatinganthus **164**
Cabereriella **235**
Cabobanthus **167**
Cacalia 240
Cacaliopsis **222**
C. nardosmia 208
Cacosmia **177**
Cadiscus **237**
Caesulia **377**
Calanticaria **466**
Calcaratolobelia 47
Calcitrapa 146
Calea **419**
C. crocinervosa 419
Calendula **243**
C. arvensis 242
C. maderensis 242
Calenduleae **241**
Callicephalus **143**
Callilepis **259**
Callistemma 318
Callistephus **318**
Calocephalus **259**
Calomeria **259**
Calopappus 101
Calostephane **384**
Calotesta **259**
Calotis **303**
Calycadenia **501**
Calycera **23**
Calyceraceae *3*, **19**
Calycocorsus 186
Calycoseris **193**
Calyptocarpus **449**
Camchaya **172**
Campanula **41**
C. edulis 42
Campanulaceae *3*, **26**
Campanulastrum 42
Campanuloideae **37**
Campovassouria **547**
Camptacra **313**
Campuloclinium **540**
Canadanthus **334**
Canarina **38**
Canariothamnus 229
Cancrinia **360**
C. group **360**
Cancriniella **360**
Candidea 172
Capelio **225**
Cardopatiinae **127**
Cardopatium **127**
C. corymbosum 128
Cardueae **123**
Carduinae **129**
Carduncellus **145**
Carduoideae **78**
Carduus **132**
C. group **132**
Carelia 522
Carlina **126**
C. acaulis 126
Carlininae **126**
Carlinoides 205
Carlquistia **501**
Carminatia **557**
Carpesium **383**
Carphephorus **531**
Carphobolus 159
Carphochaete **527**
Carpodetaceae *3*, **57**
Carpodetus **59**
C. serratus 59
Carramboa **482**
Carterothamnus 513
Cartesia 165
Carthamus **144**
C. group **144**
Cassinia **259**
Castalis 245
Castanedia **569**
Castrilanthemum **367**
Castroviejoa **284**
Catamixis **119**
C. group **119**
Catananche **183**
Catananchinae **182**
Catatia **259**
Catolesia **542**
Caucasalia **241**
Cavalcantia **524**
Cavea **146**
Caxamarca **234**
Celmisia 225, **296**

Cenia 351
Cenocline 368
Centaurea 141, **146**
C. benedicta 146
C. group **146**
C. prolongi 124
Centaureinae **138**
Centaurodendron **141**
Centauropsis **173**
Centaurothamnus **143**
Centipeda **399**
C. cunninghamii 400
C. elatinoides 400
C. minima 400
C. nidiformis 400
C. thespidioides 400
Centipedinae **399**
Centrapalinae **171**
Centrapalus **172**
Centratherinae **160**
Centratherum **160**
Centromadia **502**
Centropappus **224**
Centropogon **51**
Cephalanophlos 132
Cephalipterum **259**
Cephalobembix 438
Cephalopappus **107**
C. sonchifolius 107
Cephalorrhynchus **187**
Cephalosorus **260**
Cephalostigma 38
Ceratogyne **303**
Ceruana **305**
Chacoa **566**
Chaenactideae *392*, **431**
Chaenactis **432**
C. douglasii 432
Chaetadelpha **192**
Chaetanthera **110**
Chaetopappa **335**
Chaetopappinae **335**
Chaetoseris **187**
Chaetymenia **436**
Chamaechaenactis **436**
Chamaegeron **291**
Chamaeleon 126
Chamaemelum **370**
C. group **370**
Chamaepus **260**
Chamartemisia 360
Chamomilla 368
Chaptalia **114**
C. chapadensis 114
Charadranaetes **235**
Chardinia ***131***
Chartolepis 146
Cheirolepis 146
Cheirolophus **140**
C. sempervirens 124
Chersodoma **216**
Chevreulia **260**
Chihuahuana **322**
Chiliadenus **379**
Chiliocephalum **260**
Chiliophyllum **296**
Chiliotrichiopsis **296**
C. peruviana 296
Chiliotrichum **297**
Chimantea **99**
Chionolaena **260**
Chionopappus ***177***
Chlamydophora **372**
Chlamysperma 508
Chloracantha **328**
Chondrilla **184**
Chondropyxis **260**
Chorisis 185
Chorisiva 445
Chresta **160**
Chrestinae **160**
Chromolaena **533**
C. morii 533
Chromolepidinae *441*, **446**
Chromolepis **446**
Chronopappus ***161***
Chrysactinia **425**
Chrysactinium ***179***
C. acaule 175
C. wurdackii 179
Chrysanthellinae **407**
Chrysanthellum **408**
C. filiforme 408
Chrysanthemoides **244**
Chrysanthemum **357**, 369
Chrysanthoglossum **372**
Chrysocephalum **260**
C. semicalvum 254
Chrysocoma **291**
Chrysocoryne 266
Chrysogonum **463**
Chrysolaena **154**
Chrysoma **322**
Chrysopappus 146
Chrysophthalmum **383**
Chrysopsidinae **337**
Chrysopsis **337**
Chrysothamnus **322**
Chthonocephalus **261**
Chucoa **113**
Chuquiraga **90**
C. "anomale" 88
C. erinaceae 89
C. sect. *Erinesa* 90
C. sect. *Gymnophoranta* 88
Cicerbita **187**
Ciceronia **563**
Cichorieae **180**
Cichoriinae **182**
Cichorioideae **78**
Cichorium **182**
C. intybus 182
Cineraria **229**
Cirsium **132**
C. eriophorum 133
Cissampelopsis **240**
Cladanthus **370**
Cladochaeta **261**
Clairvillea 177
Clappia **422**
Clappiinae **421**
Clermontia **53**
Clibadiinae 446
Clibadium **449**
Cloiselia 121
Cnicothamnus **111**
Cnicus 146
Codonocephalum 382
Codonopsis **37**
Coespeletia 483
Coleocoma **388**
Coleostephus **372**
Colobanthera **305**
Cololobus **154**
Columbiadoria **322**
Columellea 273
Colymbada 146
Comaclinium **425**
Comborhiza **261**
Commidendrum **286**
Complaya 457
Compositae *3*, **61**
Comptonanthus 268
Condylidium **551**
Condylopodium **559**
Conocliniopsis **539**
C. prasiifolia 538
Conoclinium **541**
Constancea **495**
Conyza **340**
Conyzella 340
Conyzinae **339**
Coopernookia **595**
Corellia 510
Coreocarpus **411**
Coreopsidaceae 406
Coreopsideae *392*, **406**
Coreopsidinae **409**
Coreopsis **411**
C. petrophiloides 411
Corethamnium **569**
Corethrogyne **330**
Corokia **16**
Corokiaceae 13
Corymbieae **207**
Corymbium **207**
C. villosum 207
Cosmos **412**
Cota **366**
Cotula **351**
Cotuleae 342
Cotulina 368
Coulterella **422**
Coulterellinae **422**
Cousinia **136**
Cousiniopsis **128**
Crantzia 160
Craspedia **261**
Crassina 476
Crassocephalum **232**
Craterocapsa **39**
Cratystylis **385**

Cremanthodium **218**
Cremnothamnus **261**
Crepidiastrum **184**
Crepidinae **183**
Crepis **184**
C. biennis 185
Crinitaria **318**
Criscia **106**
Crispiloba **10**
C. disperma 9
Critonia **562**
Critoniadelphus **562**
Critoniella **567**
Critoniinae **559**
Critoniopsis **158**
Crocidium **215**
Crociseris 231
Crockeria 496
Crocodylium **145**
C. group **145**
C. syriacum 145
Cronquistia **527**
Cronquistianthus **570**
Croptilon **338**
Crossolepis 266
Crossostephium **359**
Crossothamnus **559**
Crupina **139**
Cryptocodon 44
Cryptogyne 352
Crystallopollen 170
Ctenosperma 351
Cuatrecasanthus **159**
Cuatrecasasiella **261**
Cuchumatanea 484
Culcitium **235**
Cullumia **205**
Cuniculotinus **342**
Curio 231
Cuspidia **205**
Cuttsia **59**
C. viburnea 59
Cyananthus **37**
Cyanea **53**
Cyanopsis 141, 167
Cyanthillium **167**
Cyanus 146
Cyathocline **305**
Cyathomone **412**
Cyathopappus 266
Cyclachaena 445
Cyclocodon **38**
Cyclolepis **112**
Cylindrocarpa **45**
Cylindrocline **385**
Cymbolaena **262**
Cymbonotus **204**
Cymbopappus **354**
Cymophora **481**
Cynara **132**
Cynareae 123
Cyphia **54**
C. erecta 54
Cyphioideae **53**
Cyphocarpoideae **53**
Cyphocarpus **53**
C. psammophilus 54
Cyrtocymura **155**
C. scorpioides 155
Cyrtolepis 364

Dacryotrichia **305**
Dahlia **412**
Damnamenia **297**
Damnxanthodium **449**
Dampiera **595**
D. sp. *591*
Darwiniothamnus **340**
Dasyandantha **159**
Dasyanthina **155**
Dasycondylus **538**
Dasyphyllum **90**
Dauresia **240**
Daveaua **371**
Decachaeta **573**
Decaneurum 170, 173, 363
Decastylocarpus **168**
Decazesia **262**
Deinandra **502**
Delairea **240**
Delamerea **388**
Delilia **450**
Delissea **53**
Dendranthema 357
Dendrocacalia **217**
Dendrophorbium **233**
Dendrosenecio **236**
D. keniensis 208
Dendroseris **190**
Denekia **262**
Desmanthodiinae **479**
Desmanthodium **480**
D. fruticosum 480
Detris 292
Dewildemania **168**
Diacantha 89
Diacranthera **538**
Dialesta 159
Dialypetalum **47**
Dianthoseris **184**
Diaphractanthus **168**
Diaspananthus 123
Diaspasis **595**
Diastatea **49**
Dibothrospermum 367
Dicercoclados **217**
Dichaetophora **336**
Dichrocephala **305**
Dichromochlamys **313**
Dicoma **121**
D. group **120**
Dicomeae 120
Dicoria **444**
Dicranocarpus **413**
Didelta **206**
Dielitzia **262**
Dielsantha **48**
Dieteria **330**
Digitacalia **220**
Dillandia **177**
D. perfoliata 175
Dimeresia **432**
Dimerostemma **450**
Dimorphocoma **313**
Dimorpholepis 283, 548
Dimorphotheca **245**
D. caulescens 245
D. cuneata 245
D. dregei 245
D. ecklonis 245
D. fruticosa 245
D. jucunda 245
D. montana 245
D. nudicaulis 245
D. polyptera 245
D. scabra 245
D. walliana 245
D. zeyheri 245
Dinoseris 96
Diodontium **408**
Diosphaera 42
Diotis 365
Diplopappus 337
Diplostephium **297**
Dipterocome **147**
Dipterocypsela **155**
Disparago **262**
Dissothrix **557**
Distasis 335
Distephanus **173**
Distreptus 164
Disynaphia **547**
D. praeficta 547
Disynaphiinae **546**
Dithyrostegia **262**
Dittrichia **380**
Doellia **390**
Doellingeria **286**
Dolichoglottis **225**
Dolichorrhiza **241**
Dolichothrix **262**
Doliclasium **105**
Dolomiaea **138**
Dominella 50
Donatia **617**
D. novae-zelandiae 615
Donatiaceae 614
Doniophyton **87**
D. anomalum 88
Dorobaea **230**
Doronicum **215**
Downingia **50**
Dracopis 471
Dresslerothamnus **234**
Dubautia **502**
Dubyaea **185**
Dugesia **446**
Dugesiinae *441*, **446**
Duhaldea **377**
Duidaea **97**
Duseniella **88**
D. patagonica 88

Dymondia **204**
Dyscritogyne **556**
Dyscritothamninae **480**
Dyscritothamnus **481**
Dyssodia **426**
D. sect. *Acyphyllaea* 429
D. sect. *Aurantiacae* 429
D. sect. *Boeberastrum* 425
D. sect. *Boeberoides* 425
D. papposa 426
Dyssodiopsis **426**

Eastwoodia **323**
Eatonella **497**
Echinacea **475**
Echinocodon **38**, 42
Echinocodonia 42
Echinocoryne **155**
Echinops **128**
E. ritro 129
Echinopsinae **128**
Eclipta **450**
E. prostrata 450
Ecliptinae *441*, **446**
Edmondia **263**
Edraianthus **41**
Eenia 397
Egletes **306**
Eirmocephala **155**
Eitenia **534**
Ekmania **159**
Ekmaniopappus **226**
Elachanthemum **357**
Elachanthus **313**
Elachopappus 273
Elaphandra **451**
Elcisimia 296
Elekmania **227**
Elephantopinae **163**
Elephantopus **164**
Elephantosis 164
Eleutheranthera **451**
Ellenbergia **524**
Elvira 450
Elytropappus **263**
Embergeria 191
Emilia **238**
Emiliella **238**
Encelia **460**
Enceliinae *441*, **460**
Enceliopsis **460**
Endocellion **216**
Endopappus **371**
Engelmannia **463**
Engelmanniinae *441*, **461**
Engleria **292**
Enydra **418**
Enydrinae **418**
Epallage 397
Epaltes **386**
Epilasia **198**
Episcothamnus 162
Epitriche **263**
Erato **179**
Erechtites **232**
Eremanthus **161**
E. sect. *Pycnocephalum* 160
Eremiastrum 336
Eremohylema 387
Eremosis **158**
Eremothamnus **202**
Eriachaenium **108**
E. magellanicum 104
Ericameria **287**
Ericentrodea **413**
Ericopsis 594
Erigeron **340**
Eriocarpum 333
Eriocephalus **352**
Eriochlamys **263**
Eriophyllum **495**
Eriotrix **239**
Erlangea **168**
E. sect. *Platylepis* 168
Erlangeinae **165**
Erodiophyllum **306**
Eroeda 274
Erymophyllum **263**
Eryngiophyllum **408**
Erythradenia **573**
Erythrocephalum **121**
Espejoa **436**
Espeletia **483**
Espeletiinae **482**
Espeletiopsis 483
Ethulia **168**
Ethuliopsis 386
Eucephalus **287**
Euchiton **263**
Eumorphia **355**
Eupatoriadelphus 528
Eupatoriastrum **564**
Eupatorieae *392*, *441*, **510**
Eupatoriinae **528**
Eupatorina **563**
Eupatoriopsis **534**
Eupatorium **528**
E. sect. *Austrobrickellia* 557
E. sect. *Austroeupatorium* 529
E. sect. *Campovassouria* 547
E. sect. *Campuloclinium* 540
E. sect. *Chromolaena* 533
E. sect. *Cylindrocephala* 533
E. sect. *Dimorpholepis* 548
E. sect. *Dysinaphia* 547
E. sect. *Gyptis* 530, 537, 569, 571
E. sect. *Hebeclinium* 572
E. sect. *Heterocondylus* 550, 571
E. sect. *Laevia* 564, 566
E. sect. *Macropodina* 540, 541
E. sect. *Microstemon* 520
E. sect. *Osmia* 533
E. sect. *Praxelis* 533
E. sect. *Raulinoreitzia* 546
E. sect. *Sphaereupatorium* 565
E. sect. *Steyermarkina* 570
E. sect. *Symphyopappus* 548
E. sect. *Urolepis* 537
Euphrosyne **445**
Eurybia **287**
Eurydochus **98**
Euryops **236**
Eutetras **509**
Euthamia **323**
Evacidium **264**
Evacopsis 265
Evax 265
E. sect. *Hesperevax* 267
Ewartia **264**
E. catipes 252
Ewartiothamnus **264**
Exomiocarpon **451**
Eyrea 387

Fabera 196
Faberia 189
Faberiopsis 188
Facelis **264**
Farfugium **216**
Faujasia **239**
Faujasiopsis **239**
Fauria 603
Favratia **42**
Faxonia **485**
Feddea **390**
Fedorovia 43
Feeria **41**
Feldstonia **264**
Felicia **292**
Feliciinae 290
Femeniasia **145**
Fenixia **451**
Ferreyranthus **177**
Ferreyrella **525**
Filaginella 266
Filaginopsis 265
Filago **264**
Filifolium **359**
Fitchia **413**
Fitchiinae 409
Fitzwillia **265**
Flaveria **422**
Flaveriinae **422**
Fleischmannia **520**
Fleischmanniinae **520**
Fleischmanniopsis **563**
Florestina **436**
Floscaldasia **297**
Flosmutisia **297**
Flotovia 90
Flotowia 90
Flourensia **461**
Flustula 156
Flyriella **554**
Fontquera 379
Forstera **618**
F. bidwillii 615
Foveolina **354**
Fradinia 370
Francoeuria 379
Franseria 444
Freya 485

Frolovia 138
Fulcaldea **88**

Gadellia 42
Gaillardia **401**
Gaillardiinae **401**
Galactites **133**
Galatella **318**
Galeana **508**
G. pratensis 508
Galeaninae **508**
Galeatella 47
Galeomma **265**
Galinsoga **485**
Galinsoginae **483**
Gamocarpha **23**
Gamochaeta **265**
Gamochaetopsis **265**
Gamolepis 236, 238
Garberia **530**
Garcibarrigoa **234**
Gardnerina **524**
Garhadiolus **196**
Garuleum **245**
G. bipinnatum 242
Gastrosulum 367
Gazania **206**
Geigeria **384**
Geissolepis **337**
Gelasia 198
Geraea **461**
Gerbera **116**
Gerberinae **113**
Geropogon **198**
Gibbaria **244**
G. scabra 242
Gifola 265
Gilberta **265**
G. tenuifolia 254
Gilruthia **265**
Githopsis **44**
Gladiopappus **122**
Glaziovianthus 160
Glebionis **369**
Glossanthis 361
Glossarion **97**
Glossocardia **409**
Glossopappus **372**
Glyptopleura **194**
Gnaphalieae **246**
Gnaphaliothamnus **266**
Gnaphalium **266**
G. subg. *Achyrocline* 252
G. sect. *Eu-Gnaphalium* 266
G. sect. *Euchiton* 263
G. sect. *Gamochaeta* 265
G. supinum 246
G. uliginosum 256
Gnaphalodes 252
Gnaphalon 276
Gnephosis **266**
G. eriocarpa 254
G. uniflora 271
Gnomophalium **266**
Gochnatia **117**
G. floribunda 117
G. subg. *Nardophyllum* 299
Gochnatiinae **116**
Goldmanella **413**
Goldmania 413
Golionema 332
Gongrostylus **550**
Gongrothamnus 173
Gongylolepis **98**
Goniocaulon **141**
Gonospermum **366**
Goodenia **595**
G. macroplecta 596
Goodeniaceae *3*, **589**
Goodenovieae 589
Gorceixia **152**
Gorteria **206**
Gorteriinae **204**
Gossweilera 170
Goyazianthus **558**
Graciela 429
Grammatotheca **48**
Grangea **306**
Grangeinae **304**
Grangeopsis **306**
Grantia 380
Graphistylis **233**
Gratwickia **266**
Grauanthus **306**
Grazielia **548**
Greenella 323
Greenmaniella **419**
Grindelia **330**
Grisebachianthus **565**
Grossheimia 146
Grosvenoria **569**
Guaicaia 97
Guardiola **486**
G. mexicana 487
G. tulocarpus 487
Guardiolinae **486**
Guayania **573**
Guevaria **525**
Guizotia **489**
Gundelia **200**
Gundelieae **199**
Gundlachia **323**
Gunillaea **40**
Gutenbergia **168**
Gutierrezia **323**
Guynesomia **298**
Gymnantheminae **173**
Gymnanthemum **173**
Gymnarrhena **147**
Gymnarrheneae **147**
Gymnaster 319
Gymnocline 366
Gymnocondylus **551**
Gymnocoronis **519**
Gymnodiscus **237**
Gymnogyne 351
Gymnolaena **426**
Gymnolomia **451**
Gymnopentzia **355**
Gymnosperma **324**
Gymnostephium **292**
Gymnostyles 352
Gynoxys **223**
G. sect. *Praegynoxys 223*
Gynura **232**
Gypothamnium **112**
Gyptidinae **535**
Gyptidium **537**
Gyptis **537**
G. group **537**
Gyrodoma **307**
Gyrostephium 280

Haarera 168
Haastia **224**
Haeckeria **267**
Haegiela **267**
Halacsyella 41
Hanabusaya **43**
Handelia **361**
H. group **361**
Haplocarpha **204**
Haploësthes **422**
Haplopappus **330**
H. sect. *Inulopsis* 314
H. sect. *Leucopsis* 338
Haplostephium 162
Haptotrichion **267**
H. conicum 254
Harleya **156**
Harmonia **503**
Harnackia **427**
Harthamnus 111
Hartwrightia **532**
Hasteola **230**
Hatschbachiella **530**
Hazardia **331**
Hebecliniinae **572**
Hebeclinium **572**
Hecastocleideae 118
Hecastocleis **118**
H. group **118**
Hedosyne **445**
Hedypnois **196**
Helenieae *392*, **400**
Heleniinae 401
Helenium **402**
H. mexicanum 402
Heliantheae *392*, **440**
Helianthella **461**
Helianthinae *441*, **464**
Helianthopsis 467
Helianthus **466**
H. laciniatus 466
Helichrysopsis **267**
Helichrysum **267**
H. adenophorum 254
H. aureum 254
H. calvertianum 254
H. depressum 252
H. lanceolatum 252
H. sect. *Lawrencella* 269

H. sect. Leontopodioides 270
H. miconiifolium 254
H. milforidiae 254
H. sect. *Ozothamnus* 275
H. subg. *Ozothamnus* 275
H. sect. *Rhodanthe* 279
Heliocauta **365**
Heliomeris **467**
Heliopsis **475**
Helipterum 281
H. sect. *Leucochrysum* 270
H. sect. *Pachypterum* 268
Helminthotheca **196**
Helogyne **559**
Hemibaccharis 311
Hemipappus 366
Hemisphaera 42
Hemistepta 137
Hemizonella **503**
Hemizonia **503**
H. subg. *Blepharizonia* 501
H. [unranked] *Hemizonella* 503
Henricksonia **413**
Heptanthinae **418**
Heptanthus **418**
Herderia **168**
Herodotia **226**
Herreranthus **227**
Herrickia 287, **342**
Hertia **237**
Hesperastrum 331
Hesperevax **267**
Hesperodoria **324**
Hesperomannia **174**
Heteracia **185**
Heteractis 292
Heteranthemis **370**
Heterochaenia **39**
Heterocodon **44**
Heterocoma **163**
Heterocondylus **550**
Heterocypsela **156**
Heteroderis **185**
Heterolepis **202**
Heteromera **371**
Heteromma **307**
Heteropappus **318**
Heteroplexis **287**
Heterorhachis **206**
Heterosperma **414**
H. pinnatum 414
Heterothalaminae 310
Heterothalamus **311**
Heterotheca **338**
Heterotoma **50**
H. lobelioides 51
Hexinia 190
Hidalgoa **414**
Hieraciinae **194**
Hieracium **194**
H. umbellatum 195
Hilliardia **352**
Hilliardiella **168**
Himalaiella 137
Hinterhubera **298**
Hinterhuberinae **294**
Hippia **353**
Hippobroma **50**
Hippolytia **362**
Hirpicium **206**
Hirschia 380
Hirtellina 130
Hispidella **194**
Hochstetteria 121
Hoehnelia 168
Hoehneophytum **232**
Hoffmanniella **452**
Hofmeisteria **513**
Hofmeisteriinae **513**
Holocarpha **504**
Holocheilus **106**
Hololeion **195**
Hololepis **163**
Holophyllum 350
Holoschkuhria **437**
Holozonia **504**
Homochaete 272
Homochroma 293
Homochrominae **290**
Homocodon **44**
Homognaphalium 266, 266
Homogyne **216**
Homopappus 332
Hoplophyllum **202**
Howellia **50**
Huarpea **89**
Huberopappus **159**
Hubertia **239**
Hughesia **570**
Hullsia **342**
Hulsea **497**
Hulseinae **497**
Hulteniella **358**
Humbertacalia **239**
Humea 259
H. sect. *Haeckeria* 267
Humeocline **268**
Hyalaea 146
Hyalis **113**
Hyalochaete 137
Hyalochlamys **268**
Hyalolepis 273
Hyaloseris **96**
Hyalosperma **268**
H. cotula 254
Hybridella **474**
Hydrodyssodia 427
Hydroidea **268**
Hydropectis **427**
Hymenocephalus 140
Hymenoclea 444
Hymenolepis **351**
Hymenonema **183**
Hymenopappus **437**
Hymenostemma **367**
Hymenostephium **467**
Hymenothrix **437**
Hymenoxys **404**
Hyoseris **196**
Hypacanthium **136**
Hypericophyllum **437**
Hypochaeridinae **195**
Hypochaeris **196**
Hypsela 47
Hyssaria 42
Hysterionica **341**
Hystrichophora **169**

Ianthopappus **112**
Ichthyothere **490**
Idiopappus **452**
Idiothamnus **566**
Ifloga **268**
Ighermia **382**
Ignurbia **228**
Iltisia **528**
Imeria **569**
Inezia ***353***
Inula **382**
I. sect. *Cappa* 377
I. sect. *Chrysopsis* 337
Inulanthera **353**
Inuleae **374**
Inuloides **244**
I. tomentosa 242
Inulopsis **314**
Io **232**
I. ambondrombeensis 208
Iocaste 356
Iocenes **232**
Iodocephalis **169**
Iogeton **452**
Ionactis **288**
Iostephane **467**
Iotasperma **314**
Iphiona **380**
I. anthemidifolia 380
Iphionopsis **385**
Iranecio **241**
Irwinia **159**
Ischnea **215**
Ismelia **370**
Isocarpha **552**
Isocoma **331**
Isoetopsis **314**
Isonema 167
Isopappus 338
Isostigma **409**
Isotoma **49**
Iva **445**
Ixeridium **185**
Ixeris **185**
Ixiochlamys **314**
Ixiolaena **268**
Ixodia **268**

Jacea 146
Jacmaia **228**
J. incana 208
Jacobaea 231
Jacobaeastrum 236
Jaegeria **487**

Jaegeriinae **487**
Jalcophila **269**
Jaliscoa **515**
Jamesianthus **430**
Jaramilloa **516**
Jasione **41**
Jasionella 41
Jasonia **379**
Jaumea **423**
Jaumeinae **423**
Jefea **452**
Jeffreya **292**
Jensia **504**
Jessea **228**
Joannea 90
Joannesia 90
Johannia 90
Joseanthus **159**
Jungia **104**
J. woodii 104
Jurinea **137**
J. pjatajeviae 137
Jurinella 137

Kalimeris **318**
Kanimia 517
Karelinia **387**
Karvandarina **142**
Kaschgaria **362**
Kastnera 180
Kaunia **516**
Kemulariella **319**
Kentrophyllum 144
Keumkangsania 43
Keysseria **308**
Kinghamia **169**
Kingianthus **452**
Kippistia **314**
Kirkianella 191
Klasea **144**
Kleinia **231**
K. longiflora 208
Klenzea 257
Koanophyllon **564**
K. adamantium 564
Koehneola **416**
Koelpinia **198**
Koyamacalia 217
Koyamasia **169**
Kremeria 372
Krigia **191**
Krylovia 319
Kuhniinae 552
Kyhosia **504**
Kyrsteniopsis **556**

Lachanodes **225**
Lachnophyllum **292**
Lachnorhiza **172**
Lachnospermum ***269***
Lactuca **188**
L. saligna 188
Lactuceae 180
Lactucella 188
Lactucinae **187**
Lactucosonchus 191
Laennecia **315**
Laestadia **298**
Lagascea **467**
Lagasceinae 464
Lagedium 188
Lagenifera 308
Lagenithrix 309
Lagenocypsela **309**
Lagenopappus 309
Lagenophora **308**
Lagenophorinae **307**
Laggera **389**
Lagophylla **505**
Lagoseriopsis **186**
Lamprachaenium 170
Lamprocephalus **236**
Lampropappus **174**
Lamyra 133
Lamyropappus **135**
Lamyropsis **134**
Lancisia 351
Landtia 204
Langebergia **269**
Lantanopsis **453**
Lapsana **186**
Lapsanastrum **186**
Lasianthaea **453**
Lasiocephalus **234**, 234
Lasiocoma 236
Lasiolaena **543**
L. morii 544
Lasiopogon **269**
Lasiospermum **353**
Lasiospora 198
Lasthenia **496**
Latouria 594
Launaea **190**
Lawrencella **269**
L. davenportii 254, 271
Layia **505**
Lechenaultia **594**
L. sp. *591*
Lecocarpus **488**
Legenere **50**
Legousia **44**
Leibnitzia **115**
Leiboldia **152**
Leiboldiinae **152**
Leiocarpa **284**
Lembertia 496
Lemooria **269**
Leonis **226**
Leontodon **197**
Leontonyx 267
Leontopodium **269**
L. alpinum 256
Lepia 476
Lepidanthus 368
Lepidaploa **156**
L. salzmannii 150
Lepidella 171
Lepidesmia **552**
Lepidolopha **363**
Lepidolopsis **361**
Lepidonia **153**
Lepidophorum **372**
Lepidophyllum **298**
Lepidospartum **222**
Lepidostephium **270**
Lepidotheca 368
Leptilon 340
Leptinella **352**
Leptocarpha **453**
Leptoclinium **558**
Leptophytus 271
Leptorhynchos **270**
Leptostelma **341**
Leptotriche **270**
Lescaillea **427**
Lessingia **331**
Lessingianthus **156**
Leucactinia **427**
Leucanthemella **363**
Leucanthemopsis **367**
L. group **367**
Leucanthemum **373**
L. group **372**
Leucheria **104**
Leuciva 445
Leucoblepharis **399**
Leucochrysum **270**
L. albicans 246
L. stipitatum 254
Leucocyclus **365**
Leucogenes **270**
L. grandiceps 246
Leucoglossum 373
Leucomeris **119**
Leucophyta **270**
Leucopsis 338
Leucoptera **354**
Leunisia **106**
Leuzea 143
Levenhookia **618**
L. stipitata 615
Leysera **271**
Liabeae **175**
Liabellum **178**
Liabinae **177**
Liabum **178**
L. subg. *Chrysastrum* 180
L. sect. *Paranephelius* 179
Liatrinae **530**
Liatris **531**
Libanothamnus 483
Lidbeckia **353**
Lifago **381**
Lightfootia 38
Ligularia **218**
Ligulariopsis **218**
Limbarda **381**
Limnanthemum 603
Lindheimera **463**
Linosyris 318
Linzia **172**
Liparophyllum **602**

Lipochaeta **453**
Lipschitziella 137
Lipskyella 136
Litogyne **386**
Litothamnus **545**
L. group **545**
Litrisa **532**
Llerasia **298**
Lobelia **47**
L. welwitschii 48
Lobelioideae **47**
Logfia **271**
L. gallica 256
Lomatozona **534**
Lonas **373**
Lopholaena **237**
Lophopappus **101**
Lorandersonia **342**
Lordhowea **228**
L. insularis 208
Lorentzianthus **566**
Loricaria **271**
L. leptothamna 271
L. thuyoides 271
Lourteigia **541**
Loxothysanus **437**
Lucilia **272**
L. acutifolia 254
Luciliocline **272**
Luciliopsis 110
Lugoa 366
Luina **222**
Lulia **113**
Lundellianthus **453**
Lundinia **227**
Luteidiscus 316
Lycapsinae **509**
Lycapsus **509**
Lychnocephalus 162
Lychnophora **162**
Lychnophorinae **161**
Lychnophoriopsis **162**
Lycoseris **111**
Lygodesmia **192**
Lyonnetia 365
Lysichlamys 236
Lysipomia **50**
Lysistemma 166

Machaeranthera **331**
M. sect. *Arida* 329
M. subg. *Dieteria* 330
M. subg. *Sideranthus* 333
Machaerantherinae **328**
Machlis 351
Macledium 121
Macowania **272**
M. hamata 254
Macrachaenium **102**
Macroclinidium **123**
Macropodina **541**
Macvaughiella **528**
Madagaster **299**
Madaractis 231
Madia **505**
Madieae *392*, *441*, **492**
Madiinae **497**
Mairia **299**
Malacothricinae **193**
Malacothrix **194**
Mallotopus 494
Malmeanthus **569**
Malperia **555**
Mandonia 481
Mantisalca **141**
Manyonia **156**
Marasmodes **354**
Marcelia 370
Marshallia **402**
Marshalliinae **402**
Marshalljohnstonia **192**
Marticorenia **106**
Maruta 365
Matamoria 164
Matricaria **368**
Mattfeldanthus **156**
Mattfeldia **226**
Matudina **574**
Mauranthemum **373**
Mausolea **359**
Mecomischus **370**
Medranoa **324**
Megaliabum 178
Megalodonta **414**
Melampodiinae **487**
Melampodium **488**
M. dicoelocarpum 488
M. divaricatum 488
M. nutans 488
M. perfoliatum 488
M. sericeum 488
Melanodendron **288**
Melanoloma 146
Melanthera **454**
Memecylanthus 11
Menyanthaceae *3*, **599**
Menyanthes **602**
M. trifoliata 603
Merciera **40**
Merrittia **378**
Mesadenia 220
Mesanthophora **169**
Mesogramma **229**
Metalasia **272**
Metastevia **527**
Mexerion **272**
Mexianthus **566**
Michauxia 46
Micractis **490**
Microcephala **363**
Microchaete 233
Microcodon **40**
Microglossa **288**
Microgyne 315
Microgynella **315**
Microliabum **178**
M. humile 175
Microlonchus 142
Micropsis **272**
Micropus **273**
M. sect. *Bombycilaena* 258
Microseridinae **191**
Microseris **191**
Microspermum **528**
Mikania **517**
M. grazielae 517
Mikaniinae **516**
Mikaniopsis **240**
Millefolium 364
Milleria **490**
M. quinqueflora 490
Millerieae *392*, *441*, **477**
Milleriinae 488
Millotia **273**
Minasia **162**
Minuria **315**
Miricacalia **217**
Misbrookea **235**
Miyamayomena **319**
Mniodes **273**
M. pulvinulata 246
Modestia 137
Molina 311
Mollera 384
Monactis **454**
Monanthemum 159
Monarrhenus **388**
Monenteles 385
Monochlaena 352
Monoculus **243**
M. monstrosus 242
Monogereion **551**
Monolopia **496**
Monopsis **49**
Monoptera 369
Monoptilon **336**
Monosis 173
M. sect. *Eremosis* 158
Montanoa **470**
Montanoinae *441*, **469**
Monticalia **233**
Moonia **415**
Moquinia **148**
M. racemosa 149
Moquinieae **148**
Morithamnus **546**
Morysia 350
Moscharia **107**
Msuata **169**
Mtonia **307**
Muehlbergella **43**
Mulgedium 188
Munnozia **180**
M. subg. *Erato* 179
M. subg. *Kastnera* 180
M. tenera 175
Munnoziinae **179**
Munzothamnus **193**
Muschleria **169**
Musschia **41**
Mutisia **108**
M. subspinosa 109

Mutisieae **90**
Mutisiinae **108**
Mutisioideae **77**
Myanmaria **174**
Mycelis 188
Myconella 372
Myconia 372
Myopordon **143**
Myriactis **309**
Myriocephalus **273**
Myriogyne 399
Myripnois **123**
Myxopappus **355**
Mzymtella 42

Nabalus **188**
Nablonium 253
Namacodon **39**
Nananthea **366**
Nannoglottis **288**
Nannoseris 184
Nanothamnus **390**
Nardophyllum **299**
Nardosmia 216
Narvalina **415**
Nassauvia **101**
N. dentata 101
Nassauviinae **100**
Nauplius 382
Neblinaea **98**
Neesia 365
Neja **341**
Nelsonianthus **221**
Nemacladoideae **46**
Nemacladus **46**
N. rigidus 46
Nemosenecio **218**
N. yunnanensis 219
Neocabreria **571**
Neocodon 42
Neocuatrecasia **540**
Neogoodenia 595
Neohintonia **567**
Neojeffreya **388**
Neomirandea **574**
Neomirandeinae **574**
Neomolina 311
Neonesomia **324**
Neopallasia **359**
Neothymopsis 439
Neotysonia **273**
Neowimmeria 47
Nephrophyllidium **603**
Nephrotheca **245**
N. ilicifolia 242
Nesampelos **226**
Nesocodon **38**
Nesomia **525**
Nestlera **273**
Nestotus **342**
Neurolaena **420**
Neurolaeneae *392*, **417**
Neurolaeninae **419**
Neurolakis **172**
Newtonia 173
Niclouxia 381
Nicolasia **389**
Nicolletia **428**
Nidorella **307**
Nigromnia 595
Nikitinia **144**
Nipponanthemum **363**
Nivellea **374**
Nolletia **293**
Nordenstamia **223**
Norlindhia **243**
N. amplectens 242
N. aptera 242
N. breviradiata 242
Nothobaccharis **565**
Nothocalais 191
Noticastrum **338**
Notobasis **134**
Notonia 231
Notoniopsis 231
Notoseris **188**
Nouelia **119**
N. group **118**
Novaguinea **342**
Novenia **299**
Nymphoides **603**

Oaxacania **513**
Oaxacaniinae 513
Oblivia **454**
Ochrocephala **143**
Oclemena **288**
Odixia **274**
O. achlaena 274
Odontocline **227**
O. tercentenariae 208
Odontoloma 159
Odontospermum 382
Odontotrichum 219
Oedera **274**
O. genistifolia 274
Oglifa 271
Oiospermum **161**
Oldenburgia **120**
Oldfeltia **227**
Olearia **299**
Olgaea **134**
Oligactis **178**, 325
Oligandra 272
Oliganthes **174**
Oligocarpus **243**
O. calendulaceus 242
Oligochaeta **143**
Oligodora 351
Oligonema 332
Oligoneuron **324**
Oligosporus 358
Oligothrix **238**
Olivaea **332**
Omalanthus 366
Omalotes 366
Omalotheca 266
Omphalopappus **170**
Oncosiphon **355**
Ondetia **385**
Onopordum **134**
O. group **134**
Onoseris **112**
Oocephala **170**
Oonopsis **332**
Oparanthus **415**
Ophryosporus **570**
Opisthopappus **363**
Orbivestus **170**
Oreastrum 289
Oreochrysum **325**
Oreoleysera **274**
Oreostemma **289**
Oreostylidium **618**
O. subulatum 615
Oresbia **236**
Orithrophium **300**
Ormenis 370
Orochaenactis **433**
Orthopappus **164**
Osbertia **338**
Osmadenia **506**
Osmiopsis **535**
Osmitopsis **353**
Osteospermum **244**
O. sect. *Blaxium* 245
O. burttianum 244
O. ciliatum 242
O. grandidentatum 242
O. herbaceum 242
Ostrowskia **38**
Otanthus **365**
Oteiza **485**
Othonna **237**
O. brandbergensis 208
Othonnopsis 237
Otocarpum 374
Otochlamys 351
Otopappus **454**
Otospermum **374**
Outreya 137
Oxycarpha **472**
Oxylaena **275**
Oxylobinae **513**
Oxylobus **514**
Oxypappus **430**
Oxyphyllum **102**
Oxytenia **445**
Oyedaea **455**
Ozothamnus **275**
O. bidwillii 254
O. lepidophyllus 254
O. leptophyllus 252

Pachydiscus 11
Pachylaena **109**
P. atriplicifolia 110
Pachystegia **300**
Pachythamnus **515**
Pacifigeron **300**
Packera **230**
Pacourina **165**

Pacourininae **165**
Palafoxia **438**
Paleaepappus **300**
Paleocyanus 140
Pallenis **382**
Palmerella **49**
Pamphalea **107**
Panaetia 276
Pappobolus **467**
Pappochroma **309**
Pappothrix 510
Papuacalia **225**
Paracalia **222**
Parachionolaena 260
Parafaujasia **239**
Paragynoxys **222**
Paraixeris 184
Paralychnophora 161
Paramicrorhynchus 190
Paramiflos 483
Paranepheliinae **178**
Paranephelius **179**
Parantennaria **275**
Parapiqueria **552**
Paraprenanthes **188**
Parasenecio **217**
Parastrephia **301**
Parishella **47**
Parthenice **445**
Parthenium **445**
Pasaccardoa **120**
Pascalia **455**
Paurolepis **170**
Pechuel-loeschea **386**
Pectidinae **423**
Pectis **428**
P. decemcarinata 428
Pegolettia **384**
Pelucha **403**
Pembertonia **342**
Pentacalia **233**
Pentachaeta **327**
Pentachaetinae **326**
Pentalepis **455**
Pentanema **383**
Pentaphorus **117**
Pentaphragma **607**
P. begonifolium 606
Pentaphragmataceae *3*, **605**
Pentaptilon **596**
Pentatrichia **275**
Penthea 89
Pentzia **355**
P. group **354**
Peracarpa **42**
Perdicium **116**
Perezia **103**
Pericalia 220
Pericallis **229**
Pericome **510**
Perideraea 370
Periomphale **11**
P. balansae 9
Peripleura **315**
Perityle **510**
P. feddemae 510
Perityleae *392*, *441*, **507**
Peritylinae **509**
Perplexia 137
Perralderia **379**
Perralderiopsis 380
Pertya **122**
P. group **122**
Pertyeae 122
Perymeniopsis **455**
Perymenium **456**
Petalacte **275**
P. sect. *Ampilasia* 269
Petasites **216**
Peteravenia **567**
Petradoria **325**
Petrobiinae 409
Petrobium **415**
Petromarula **45**
Peucephyllum **438**
Peyrousea 356
Phaenocoma **275**
P. prolifera 274
Phaeocephalus 351
Phaeopappus 140, 146
Phaeostigma **358**
Phagnalon **276**
Phalacrachena 140
Phalacraea **523**
Phalacrocarpum **368**
Phalacrodiscus 373
Phalacroseris **192**
Phaneroglossa **236**
Phanerostylis **554**
Phania **523**
Phellinaceae *3*, **608**
Phelline **610**
P. erubescens 609
P. lucida 609
Philactis **476**
Philoglossa **180**
Philyrophyllum **276**
Phitosia **186**
Phoebanthus **468**
Phonus **145**
Phyllachne **618**
P. colensoi 615
Phyllocalymma 255
Phyllocephalum **170**
P. scabridum 150
Phyllocharis 49
Phymaspermum **356**
P. group **355**
Physoplexis **45**
Phyteuma **45**
P. comosa 45
Picnomon **132**
Picris **197**
P. hieracoides 197
Picrosia **192**
Picrothamnus **359**
Pietrosia 194
Pilosella **195**
Piloselloides 116
Pilostemon 137
Pinardia 370
Pinaropappus **194**
Pingraea 311
Pinillosia **416**
Pinillosiinae **416**
Piora **309**
Pippenalia **220**
Piptocarpha 90, **159**
Piptocarphinae **158**
Piptocoma **159**
Piptolepis **162**
Piptostemma 260
Piptothrix **515**
Piqueria **526**
Piqueriella **525**
Piqueriinae 520
Piqueriopsis **525**
Pithecoseris **160**
Pithocarpa **276**
Pithosillum 238
Pittocaulon **221**
Pityopsis **339**
Pladaroxylon **225**
Plagiobasis **142**
Plagiocheilus **307**
Plagiolophus **456**
Plagius **373**
Planaltoa **558**
Planea **276**
Plateilema **403**
Plateileminae **403**
Platycarpha **202**
Platychaete 379
Platycodon **37**
Platypodanthera **540**
Platyschkuhria **438**
Platyspermatiaceae 7
Platyspermation **11**
Plazia **111**
Plectocephalus **140**
Plectostachys **276**
Plectreca 173
Pleiacanthus **193**
Pleiogyne 351
Pleiotaxis **122**
Pleocarphus **105**
Pleurocarpaea **172**
Pleurocoronis **555**
Pleuropappus **276**
Pleurophyllum **301**
Pluchea **387**
P. microcephala 387
Plucheeae 374
Podachaenium **473**
Podanthus **456**
Podocoma **315**
Podocominae **312**
Podolepis **276**
Podopappus 315
Podosperma 277
Podospermum 198
Podotheca **277**

Poecilolepis **293**
Pogonolepis **277**
Pojarkovia **240**
Poljakovia 366
Pollalesta 159
Polyacantha 134
Polyachyrus **102**
Polyactis 340
Polyanthina **550**
Polyarrhena **293**
Polycalymma **277**
Polychaetia 279
Polychrysum **362**
Polydora **170**
Polygyne 307
Polymnia **440**
Polymniastrum 440
Polymnieae *392*, **439**
Polymniinae 439
Polytaxis **138**
Popoviocodonia 42
Porophyllum **428**
Porphyrostemma **390**
Porterella **49**
Postia 378
Pratia 47
Praxeliinae **532**
Praxeliopsis **534**
Praxelis **533**
Preauxia 369
Prenanthella 192
Prenanthes s.str. **189**
Prestelia **162**
Printzia **301**
Prionolepis 180
Prionopsis 330
Prismatocarpus **40**
Pristocarpha 350
Prolobus **539**
Prolongoa **368**
Proteopsis **162**
Protoedraianthus 41
Proustia **100**
Psacaliopsis **219**
Psacalium **219**
Psanacetum 366
Psathyrotes **403**
Psathyrotinae **403**
Psathyrotopsis **438**
Psednotrichia **238**
P. xyridopsis 208
Psephellus **140**
Pseudactis 238
Pseudelephantopus **164**
Pseudobahia **496**
Pseudobartlettia 438
Pseudoblepharispermum **389**
Pseudobrickellia **557**
P. brasiliensis 558
Pseudocadiscus 237
Pseudocampanula 42
Pseudoclappia **431**
Pseudoconyza **389**
Pseudognaphalium **277**
P. luteoalbum 252, 254
Pseudogynoxys **234**
Pseudohandelia **362**
Pseudokyrsteniopsis 556
Pseudoligandra 260
Pseudolinosyris 318
Pseudonemacladus **46**
Pseudonoseris **179**
Pseudopiptocarpha **156**
Pseudostifftia **149**
P. kingii 148
Pseudostifftiinae 148
Psiadia **289**
Psiadiella **289**
Psilactis **335**
Psilocarphus **277**
Psilostrophe **405**
Psilostrophinae 404
Psilothonna 238
Psychrogeton **319**
Psychrophyton 279
Ptarmica 364
Pterachaenia **198**
Pterigeron 390
Pterocaulon **385**
P. virgatum 386
Pterochaeta **277**
Pterocypsela **189**
Pteronia **301**
Pteropogon 279
P. sect. *Pteropogonopsis* 263
Pterothrix **278**
Pterygopappus **278**
Ptilostemon **133**
Ptilostephium 481
Ptosimopappus 146
Pulicaria **379**
Punduana 174
Pycnocephalum 160
Pycnosorus **278**
Pyrethrum 366
Pyrrhopappus **192**
Pyrrocoma **332**
Pytinicarpa **309**

Quechualia **157**
Quelchia **99**
Quinetia **278**
Quinqueremulus **278**

Rachelia **278**
Radlkoferotoma **522**
Rafinesquia **193**
Raillardella **506**
Raillardellinae 497
Raillardia 502
Raillardiopsis 499
Railliarda 502
Railliardia 502
R. [unranked] *Raillardella* 506
Rainiera **221**
Raoulia **278**
R. eximia 246
Raouliopsis **279**
Rastrophyllum **170**
Ratibida **470**
Raulinoreitzia **546**
Rayjacksonia **332**
Reichardia **190**
Relhania **279**
R. fruticosa 254
Remya **302**
Rennera **355**
Rensonia **456**
Revealia **527**
Rhagadiolus **197**
Rhamphogyne **309**
Rhanteriopsis **378**
Rhanterium **378**
Rhaponticum **143**
R. group **142**
Rhaponticoides **140**
Rhetinodendron 230
Rhetinolepis **371**
Rhigiophyllum **41**
Rhinactina 319
Rhinactinidia **319**
Rhizocephalum 50
Rhodanthe **279**
R. anthemoides 254
R. frenchii 254
R. moschata 254
Rhodanthemum **373**
Rhodogeron **385**
Rhynchocarpus 279
Rhynchopsidium **279**
Rhynchospermum **310**
Rhynea 282
Rhysolepis **468**
Rhytidanthe 270
Rhytidospermum 367
Richea 261
Richterago **117**
R. discoidea 118
Richteria **361**
Riddelliinae 404
Riencourtia **456**
Rigiopappus **327**
Robinsonecio **220**
Robinsonia **230**
Roccardia 279, 281
Rochonia **302**
Roella **40**
Rojasianthe **470**
Rojasianthinae *441*, **470**
Rolandra **164**
Rolandrinae **164**
Roldana **220**
Roodebergia **293**
Rosenia **279**
Rothmaleria **183**
Roucela 42
Roussea **613**
R. simplex 612
Rousseaceae *3*, **611**
Ruckeria 236
Rudbeckia **471**
Rudbeckiinae *441*, **470**

Rugelia **220**
Ruilopezia 483
Rumfordia **491**
Russowia **142**
Ruthiella **49**
Rutidosis **280**
R. leptorrhynchoides 254

Sabazia **485**
Sachokiella **42**
Sachsia **385**
Saintmorysia 350
Salcedoa **100**
Salmea **472**
Santolina **371**
Santosia **565**
Sanvitalia **476**
Sarcanthemum **289**
Sartorina **520**
Sartwellia **423**
Saussurea **137**
S. group **137**
Scabrethia 464
Scaevola **595**
Scalesia **468**
Scariola 188
Scherya **523**
Schischkinia **141**
Schistocarpha **486**
Schistostephium **356**
Schizogyne **378**
Schizoptera **457**
Schizotrichia **429**
Schkuhria **438**, 491
S. pinnata 439
Schlechtendalia **87**
S. luzulifolia 88
Schmalhausenia **136**
Schoenia **280**
Schumeria 144
Sciadocephala **519**
Sclerocarpus **468**
Sclerolepis **518**
Sclerorhachis **362**
Sclerostephane 379
Sclerotheca **52**
Scolyminae **182**
Scolymus **182**
Scorzonera **198**
Scorzonerinae **198**
Scrobicaria **226**
Scyphocoronis **280**
Scyphopappus 369
Selleophytum **415**
Selliera **596**
S. radicans 590
Selloa 324, **486**
Semiria **543**
S. viscosa 544
Senecio **230**
S. sect. *Bethencourtii* 229
S. sect. Dendrophorbium 233
S. eligulatus 208
S. sect. *Nemosenecio* 218
S. sect. *Praegynoxys* 223
S. vernalis 231
Seneciodes 167
Senecioneae **208**
Sergia **45**
Sergilus 311
Sericocarpus **325**
Seridia 146
Seriphidium 358
Seriphium 281
Seris 117
Serratula **144**
S. group **144**
Shafera **226**
Sheareria **310**
Shinnersia **518**
Shinnersoseris **193**
Siapaea **551**
Sideranthus 333
Siebera **131**
Sigesbeckia **491**
Siloxerus **280**
Silphium **463**
Silybum **133**
Simsia **468**
Sinacalia **217**
Sinclairia **178**
Sinclairiopsis 178
Sinoleotopodium **280**
Sinosenecio **218**
Siphocampylus **51**
Siphocodon **41**
Sipolisia **163**
Sipolisiinae **162**
Skirrhophorus 255
S. sect. *Pogonolepis* 277
Smallanthus **491**
Soaresia **160**
Solanecio **231**
Solenogyne **310**
Solenopsis **48**
Solidagininae **320**
Solidago **325**
Soliva **352**
Sommerfeltia **316**
Sonchinae **189**
Sonchus **190**
S. arvensis 190
Sondottia **280**
Soroseris **186**
Spadonia 148
Spaniopappus **515**
Sparganophoros **157**
Spathipappus 366
Specularia 44
Sphacophyllum 397
Sphaeranthus **389**
Sphaereupatorium **564**
Sphaeroclinium 351
Sphaeromeria **360**
Sphaeromorphaea 386
Sphaerophora 161
Sphagneticola **457**
Sphenogyne 356
Spilanthes **472**
Spilanthinae *441*, **471**
Spiracantha **164**
Spirochaeta 164
Spiroseris **186**
Squamopappus **473**
Stachyanthus 160
Stachycephalum **491**
Staehelina **130**
Standleyanthus **516**
Starkea 178
Staurochlamys **417**
Stebbinsia 186
Stebbinsoseris 191
Steetzia 299
Steiractinia **457**
Steirodiscus **238**
Stemmacantha 143
Stenachaenium **384**
Stengelia 172
Stenocarpha 485
Stenocephalum **157**
Stenocline **281**
Stenopadus **99**
S. group **97**
S. subg. *Stomatochaeta* 99
Stenophalium **281**
Stenops **237**
Stenoseris **189**
Stenotheca 194
Stenotus **325**
S. sect. *Oonopsis* 332
Stephanochilus 146
Stephanodoria **333**
Stephanolepis 168
Stephanomeria **193**
Stephanomeriinae **192**
Stephanopappus 273
Steptorhamphus ***189***
Stera 385
Stereosanthus 288
Stevia **526**
S. morii 526
Steviopsis **556**
Steyermarkina **570**
Stifftia ***96***
S. group **96**
Stifftieae 96
Stigmatotheca 369
Stilpnogyne **229**
Stilpnolepis **364**
Stilpnopappus **157**
Stilpnophyton 350
Stizolophus **140**
Stoebe **281**
Stokesia **165**
Stokesiinae **165**
Stomatanthes **529**
Stomatochaeta **99**
Stramentopappus **153**
Streptoglossa **390**
Strobocalyx 174
Strongylosperma 351
Strophopappus 157

Strotheria **429**
Struchium 157
Stuartina **281**
Stuckertiella **281**
Stuessya **469**
Stylidiaceae *3*, **614**
Stylidium **618**
S. graminifolium 615
Stylocline **281**
Stylolepis 276
Styloncerus 280
Stylotrichium **544**
S. rotundifolium 545
Sventenia 191
Symblomeria 154
Symphyandra 42
Symphyllocarpus **574**
Symphyochaeta 230
Symphyomera 352
Symphyopappus **548**
S. decussatus 548
Symphyotrichinae **334**
Symphyotrichum **335**
Syncalathium **189**
Syncarpha **281**
Syncephalum **282**
Syncretocarpus **469**
Synedrella **457**
Synedrellopsis **457**
Syneilesis **217**
Synosma 230
Synotis **239**
Synotoma 45
Syntrichopappus **496**
Synurus **135**
Syreitschikovia **135**

Taeckholmia 191
Tageteae *392*, **420**
Tagetes **429**
Takeikadzuchia **135**
Takhtajaniantha 198
Talamancalia **233**
Tamananthus **483**
Tamania 483
Tamaulipa **541**
Tanacetopsis **364**
Tanacetum **366**
Taplinia **282**
Taraxacum **186**
Tarchonanthinae **119**
Tarchonanthus **120**
Tecmarsis 387
Tehuana **476**
Teixeiranthus **524**
Telanthophora **221**
Telekia **383**
Telmatophila **171**
Temnolepis 397
Tenrhynea **282**
Tephroseris **219**
Tephrothamnus 158
Tessaria **388**
Tetrachyron **473**
Tetradymia **222**
Tetragonotheca **481**
Tetramolopium **316**
Tetraneuriinae **404**
Tetraneuris **405**
Tetranthus **472**
Tetraperone **417**
Thaminophyllum **356**
Thamnoseris **191**
Theilera **39**
Thelechitonia 457
Thelesperma **416**
Theodorovia **43**
Thespidium **388**
Thespis **310**
Thevenotia **127**
Thiseltonia **282**
Thodaya 236
Thorelia 172
Thoreliella 172
Thurovia **326**
Thymophylla **429**
Thymopsis **439**
Tiarocarpus 136
Tietkensia **282**
Tilesia **458**
Tisserantia 389
Tithonia **469**
Toiyabea **342**
Tolpis **195**
Tomanthea 146
Tomentaurum **339**
Tonestus **289**
Tostimontia 104
Tourneuxia **199**
Townsendia **337**
Toxanthes **282**
Tracheliopsis 42
Trachelium **46**
Tracyina **327**
Tragoceros 476
Tragopogon **199**
T. pratensis 199
Tragopogonoides 197
Trallesia 367
Traversia **224**
Treichelia **40**
Trematolobelia **52**
Trepadonia **157**
Trianthaea 174
Tricarpha 485
Trichanthemis **361**
Trichanthodium **282**
Trichapium 449
Trichocline **114**
Trichocoroninae **517**
Trichocoronis **517**
Trichocoryne **476**
Trichogonia **539**
Trichogoniopsis **540**
Trichogyne **283**
T. sect. *Ifloga* 268
Tricholepis **142**
Trichoptilium **403**
Trichospira **174**
Trichospirinae **174**
Tridactylina **358**
Tridax **481**
T. mexicana 482
Trigonopterum **458**
Trigonospermum **492**
Trilisa **531**
Trimeris 47
Trimorpha 340
Triniteurybia **342**
Triodanis **44**
Trioncinia **409**
Tripleurospermum **367**
Triplocephalum **389**
Triplotaxis 167
Tripolium **319**
T. subg. *Astropolium* 335
T. sect. *Oxytripolium* 335
Tripteris **244**
T. nervosa 242
Triptilion **102**
Triptilodiscus **283**
T. pygmaeus 254
Trixis **105**
T. vauthieri 105
Troglophyton **283**
Trommsdorffia 196
Tuberculocarpus **458**
Tuberostylis **571**
Tugarinovia **127**
Turaniphytum **364**
Turpinia 158
Tursenia 311
Tussilago **216**
Tuxtla **458**
Tyleropappus 419
Tyrimnus **133**
Tysonia 273

Uechtritzia **115**
Ugamia **361**
Uleophytum **571**
Unamia 324
Unigenes **49**
Unxia **492**
Urbananthus **562**
Urbinella **430**
Urmenetia **109**
Urolepis **537**
Uropappus 191
Urospermum **197**
Urostemon **224**
Ursinia **356**
Ursiniopsis 356
Ursinieae 342

Vanclevea **326**
Vanillosmopsis 161
Varilla **430**
Varillinae **430**
Varthemia **384**
Vasquezia 509
Velleia **596**