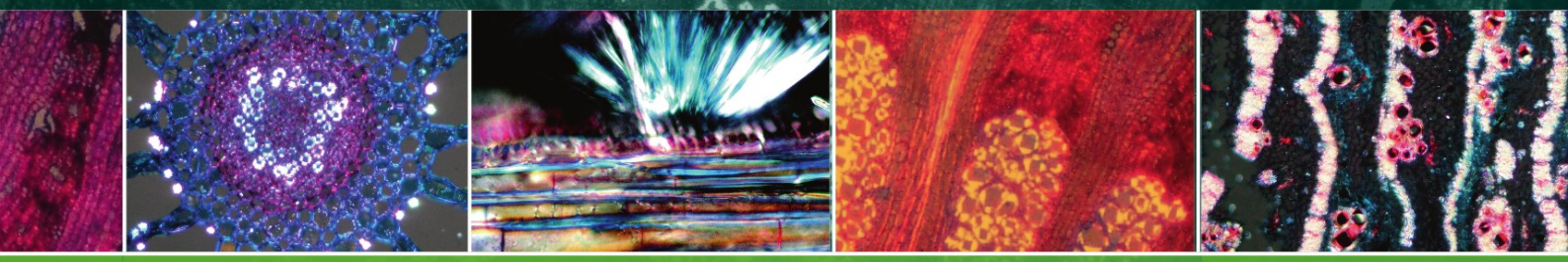
Volume 1



Fritz Hans Schweingruber · Annett Börner
Ernst-Detlef Schulze

1

# Atlas of Stem Anatomy in Herbs, Shrubs and Trees

Springer

F. H. Schweingruber A. Börner E.-D. Schulze

# Atlas of Stem Anatomy in Herbs, Shrubs and Trees

Volume I

F. H. Schweingruber
A. Börner
E.-D. Schulze

# Atlas of Stem Anatomy in Herbs, Shrubs and Trees

## Volume I

With over 2000 colour illustrations

Springer

Prof. Dr. Fritz Schweingruber
Institute for Forest, Snow and Landscape Research WSL
Zürcherstrasse 111
8903 Birmensdorf, Switzerland

Annett Börner
Prof. Dr. Ernst-Detlef Schulze
Max Planck Institute for Biogeochemistry
PO Box 100164
07701 Jena, Germany

ISBN 978-3-642-11637-7 e-ISBN 978-3-642-11638-4
DOI 10.1007/978-3-642-11638-4
Springer Heidelberg Dordrecht London New York

© Springer-Verlag Berlin Heidelberg 2011
The photos on the following pages are published with the kind permission of the respective authors, whose names are indicated in the figure legends:

Klaus-Dieter Zinnert - pp. 39, 49, 61, 67, 73, 88, 93, 104, 135, 152, 193, 210, 217, 222, 228, 232, 237, 246, 250, 254, 264, 268, 275, 304, 305, 311, 328, 333, 344, 345, 376, 395, 401, 415, 419, 439, 450, 459, 465, 474
Elias Landolt - pp. 80, 104, 113, 126, 135, 149, 157, 177, 214, 237, 305, 323, 344, 345, 353, 385, 439
Marianne Lauerer - pp. 67, 73, 134, 156, 222, 232, 254, 272, 275, 278, 282, 401
Thomas Stützel - pp. 118, 130, 205, 323, 415, 447, 470
Gregor Aas - pp. 49, 67, 126, 407
Simon S. Cohen - p. 261
Harmen Hendriksma - p. 372
Ottmar Holdenrieder - p. 120
Tara Massad - p. 465
Gary A. Monroe @ USDA-NRCS PLANTS Database - p. 225
Angela Nüske - p. 352
Birgit Schulze - p. 175
Waltraud Schulze - p. 38
Horst Thor - p. 372
Scott Zona - p. 47

All rights reserved.

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 permission for use must always be obtained from Springer. Violations are liable to prosecution under the German Copyright Law.

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 illustrations (from right):*
Cross-section of a dwarf shrub stem with successive cambia. Vessels and fibers are stained red, parenchyma cells are stained blue. *Chenopodium frutescens*, Amaranthaceae, grows in the Mongolian steppes.
Cross-section of an old rhizome of an herb. The large red stained rays separate yellow stained radial vessel/fiber zones. *Peucedanum venetum*, Apiaceae, grows in the dry meadows of the Southern Alps.
Radial section of a liana stem. Radially arranged crystals in the vessel of a vine. *Vitis vinifera*, Vitaceae, grows in Mediterranean riparian zones.
Cross-section of a water plant stem. Vessels in the center of the stems are surrounded by the phloem and an air-conducting tissue. The white dots represent calcium oxalate crystals. *Myriophyllum alternifolium*, Haloragaceae, grows in ponds.
The picture to the left is part of *Peucedanum venetum*.
All slides were stained with safranin and astra blue and photographed in polarized light.

*Cover design:* deblik Berlin, Germany

*Camera-ready* by Annett Börner, Jena, Germany

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

# Acknowledgements

by Fritz Schweingruber

Without the patience of my wife Elisabeth at home and on countless fieldtrips the present work would not have been possible.

I have to thank many colleagues and institutions:
The Federal Research Institute provided me at Birmensdorf a scientific infrastructure. Many colleagues in the mechanical workshop (Arthur Kölliker), the carpenter shop (Sigi Witzemann, Albert Buchwalder), the IT-Departement (Bert Höwecke), the library (Christine Matter, Claudia Grütter-Berger) and friends supported the study. Silvia Dingwall and Melissa Dawes spent much time to correct my English texts. Margrith Wiederkehr edited the list of references. My friend Willy Neuhaus was always willing to explain me mechanisms of the Excel-Format.

Many Botanical Gardens provided Material: Basel, Switzerland (Bruno Erni), Bern, Switzerland (Christian Bühler), Ekaterinburg, Russia (Sergei Shavnin), München, Germany (Susanne Renner), Regensburg, Germany (Peter Poschlod), Zürich, Switzerland (Bernhard Hirzel and Peter Enz), Viera y Clavijo, Jardin Canario, Gran Canaria, Spain (David Bramwell), Jardim Botanico Lisboa, Portugal, Gärtnerei Ernst Rieger, Blaubeuren, Germany. The xylarium of the Rijksherbarium Leiden provided some material. Pieter Baas (Leiden, Netherlands), Helmut Freitag (Kassel, Germany), Rudolf Häsler (Zürich, Switzerland), Heike Heklau (Halle, Germany), Christian Körner (Basel, Switzerland) and Simcha Lev-Yadun (Haifa, Israel) made many substantial critical remarks and suggestions to improve the scientific content.

My friends Stephan Shiyatov (Yekaterinburg, Russia), Eugene Vaganov and Vera Benkova (Krasnoyarsk, Russia) collected material on many expeditions in Siberia and helped with the identification of plants. Victor Voronin (Irkutsk, Russia) provided an excellent collection of the cold steppes of the Lake Baikal.

Marina Mosulishvili introduced me to the Flora of Georgia and identified all species from the Caucasus region.

Fidel Roig jun. (Mendoza, Argentina) accompanied me on an excursion to the Andes and his father Fidel Roig sen. identified many plants from Argentina and Chile. Davoud Parsa Pajouh, Karadj, Iran, accompanied me on excursions in Iran. Martin Fisher, Muscat, Oman, identified many species from Oman.

Vera Markgraf (Flagstaff, USA) and Hal and Miriam Fritts (Tucson, USA) supported me with the collection and identification of plants from Colorado and Arizona. Hansjorg Diez (Zürich, Switzerland) provided many species from the Great Plains in USA and Germany and John Banks (Canberra, Australia) from Australia.

We also thank the following people for providing photos: Klaus-Dieter Zinnert, Elias Landolt, Marianne Lauerer, Thomas Stützel, Gregor Aas, Simon S. Cohen, Harmen Hendriksma, Ottmar Holdenrieder, Tara Massad, Gary A. Monroe, Angela Nüske, Birgit Schulze, Waltraud Schulze, Horst Thor and Scott Zona.

# Table of Contents


Acknowledgements ..... V

Abbreviations ..... VIII

1. Introduction ..... 1

2. Material and Methods ..... 5

3. Vegetation and Plant Parameters ..... 9

4. Definition of Anatomical Features ..... 13

5. Monographic Descriptions ..... 33

- Aizoaceae ..... 35
- Amaranthaceae ..... 38
- Amborellaceae ..... 47
- Anacardiaceae ..... 49
- Apocyanaceae and Asclepiadaceae ..... 54
- Aristolochiaceae ..... 61
- Berberidaceae ..... 67
- Betulaceae ..... 73
- Brassicaceae ..... 79
- Buxaceae ..... 88
- Cannabaceae ..... 93
- Capparaceae ..... 98
- Caryophyllaceae ..... 103
- Celastraceae ..... 113
- Ceratophyllaceae ..... 118
- Cercidiphyllaceae ..... 120
- Cistaceae ..... 122
- Clusiaceae ..... 126
- Cneoraceae ..... 130
- Crassulaceae ..... 134
- Cucurbitaceae ..... 141
- Droseraceae ..... 149
- Elaeagnaceae ..... 152
- Ericaceae ..... 156
- Euphorbiaceae ..... 164
- Fabaceae ..... 175
- Fagaceae ..... 193
- Gentianaceae ..... 199
- Geraniaceae ..... 205
- Grossulariaceae ..... 210
- Haloragaceae ..... 214
- Hamamelidaceae and Altingiaceae ..... 217
- Juglandaceae ..... 222
- Krameriaceae ..... 225
- Lardizabalaceae ..... 228
- Lauraceae ..... 232
- Linaceae ..... 237
- Loranthaceae and Viscaceae ..... 241
- Lythraceae ..... 246
- Magnoliaceae ..... 250
- Malvaceae ..... 254
- Menispermaceae ..... 261
- Menyanthaceae ..... 264
- Moraceae ..... 268
- Myricaceae ..... 272
- Myrtaceae ..... 275
- Nepenthaceae ..... 278
- Nyctaginaceae ..... 282
- Nymphaeaceae ..... 286
- Onagraceae ..... 290
- Oxalidaceae ..... 296
- Paeoniaceae ..... 300
- Papaveraceae ..... 304
- Phytolaccaceae ..... 311
- Piperaceae ..... 314
- Platanaceae ..... 319
- Plumbaginaceae ..... 323
- Polygalaceae ..... 328
- Polygonaceae ..... 332
- Portulacaceae ..... 341
- Primulaceae ..... 344
- Ranunculaceae ..... 352
- Resedaceae ..... 372
- Rhamnaceae ..... 376
- Rosaceae ..... 383
- Rubiaceae ..... 395
- Rutaceae ..... 401
- Salicaceae ..... 406
- Salvadoraceae ..... 413
- Santalaceae ..... 415
- Sapindaceae ..... 419
- Saxifragaceae ..... 423
- Simmondsiaceae ..... 429
- Staphyleaceae ..... 431
- Tamaricaceae ..... 434
- Thymelaeaceae ..... 439
- Tiliaceae ..... 444
- Trochodendraceae ..... 447
- Ulmaceae ..... 450
- Urticaceae ..... 454
- Violaceae ..... 459
- Vitaceae ..... 465
- Winteraceae ..... 470
- Zygophyllaceae ..... 474

References ..... 479

Alphabetic List of Species ..... 485

# Abbreviations

| | |
|---|---|
| ae | aerenchym |
| bpit | bordered pit |
| ca | cambium |
| cal | callus, parenchymatic cells |
| clu | cell lumen, cell lumina |
| co | cortex |
| cork | |
| ct | conjunctive tissue |
| cry | crystal |
| csi | collapsed sieve tubes |
| cu | cuticula |
| di | (ray) dilatation |
| ds | dark-stained substances |
| duct | |
| ep | epidermis |
| en | endodermis |
| ew | earlywood |
| ewv | earlywood vessel |
| ewt | earlywood tracheid |
| ft | fiber tracheid |
| f | fiber |
| ge | gelatinous fibers |
| gr | growth ring |
| grb | growth ring boundary |
| he | helical thickenings |
| ivp | intervessel pit |
| la | laticifers |
| lf | libriform fiber |
| lcw | lignified cell wall |
| lw | latewood |
| lwv | latewood vessel |
| lwt | latewood tracheid |
| mu | mucilage |
| nu | nucleus |
| p | perforation |
| pa | parenchyma |
| ph | phloem |
| phe | phellem |
| phg | phellogen |
| pit | |
| pith | |
| r | ray |
| rd | resin duct |
| sc | sclereid |
| sf | septate fibers |
| shc | sheet cell |
| si | sieve tube, sieve element |
| spit | simple pit |
| ta | tannins |
| te | tension wood |
| tr | tracheid |
| ty | tylosis |
| ulcw | unlignified cell wall |
| v | vessel |
| vab | vascular bundle |
| vat | vascular tracheid |
| vrp | vessel-ray pits |
| xy | xylem |

# 1. Introduction

Xylem and phloem are the "highways" for transport and communication in all higher plant species. The transport system is substantially important for plant functioning to an extent that as plants germinate, a protophloem and a protoxylem is being formed at the very beginning. However, as soon as a cambium develops, xylem cells are formed for water transport, which is the structure, generally known as wood. Phloem cells are formed outside of the cambium for transport of assimilates. After loosing their function, phloem cells and a secondary cambium contribute to the formation of bark.

Wood structure has been investigated since the days of early anatomy, and most woody species have been described anatomically (Wheeler et al. 2007). Nevertheless, despite of the long history of wood investigations, the term "wood" remains not well defined. Generally, the term "wood" designates an intensively lignified xylem which excludes a partial lignification that is characteristic for most species. Obviously, there is a continuum from intensively lignified to partially lignified stems, and this gradient of stem anatomy has neither been studied adequately nor has the expression of stems with differently lignified stems been studied in relation to climate and habitats where these plants grow. It is this shortcoming which prompted us to investigate the products of secondary growth of plant stems in a large variety of families and species representing the full range of life forms and plant sizes, ranging from herbaceous to truly woody species in a broad range of climatic conditions. Thus, we can make the attempt to investigate the anatomy of plant stems not only in a taxonomic and morphological but also in a climatic context. Many of the anatomical features are genetically fixed and characteristics of the respective species. It remains unclear how these features relate to the evolution and taxonomy of these species. Some anatomical features are plastic. The environment may modulate them, but it is not understood, if specific environmental conditions just cause the replacement of species or genotypes having additional features, or if single species can respond with their stem anatomy to the environment. Obviously, our understanding of why plant stems are that different can only be advanced if we place the anatomy in the context of the environmental conditions in which these species grow. Thus, the main focus of the present taxonomic, morphological and anatomical features to the environmental conditions of dicotyledonous plant form the new and old world in which these species live, even though, it was not possible to study the plasticity of anatomical features within a species.

In contrast to the extended literature on woody xylem, anatomical studies of the phloem and bark are rare (Esau 1969, Roth 1981, Trockenbrodt 1990, Junikka 1994). In this book we try to close this gap with a description of the bark, where possible.

## Sampling Design of the Present Study

A major aim of this study is to create a collection of slides containing transverse, tangential and radial sections from a large number of species according to a uniform and standardized methodology of collection, preparation, and the location where the stem was cut. The establishment of this collection has been a major task for Fritz Schweingruber for the last 40 years.

Most of the material (96%) was collected from natural sites, harvesting one or few individuals of average size. An examination of replicated individuals shows that anatomical variation exists, but this could not be followed up in a systematic manner.

Fresh material is the basis for the preparation of all cross-, tangential- and radial sections. Only 5 out of 1658 species were taken from xylothecs because the habitats were not accessible.

The investigations are carried out on the basis of cutting the stem in the zone of the hypocotyls (root collar). Rhizomes were cut at the oldest stage.

Most sections were stained with Safranin, which makes lignin visible and with Astrablue which stains cellulose. All slides were embedded in Canada Balsam.

Plant samples were collected in the course of field tours and expeditions of Fritz Schweingruber. Species were identified according to local identification keys and confirmed, if needed, by comparison with herbarium specimens. The collection encompasses most but not all families of the Angiosperms including the Magnoiliid complex, Eudicots, the Rosoid clade, the Eurosides and a few families of the Asterid clade. The phylogeny follows Judd et al. (2002) and Strassburger et al. (2008), which are based on the APG III system. The figure opposite shows for which families representatives were described.

Emphasis was put on smaller plant statures (5-150 cm) because these had mostly been neglected in the past. Thus, the collection contains 1292 species of small stature and only 366 species of tall stature. According to the biodiversity of the floral regions, more Mediterranean than arctic species were collected.

The collection focuses on the European region, ranging from the arctic to the Sahara, and including the Canary Islands. Some material was collected in North America (Rocky Mountains), South America (Andes) and in Siberia.

Plant height and the environmental conditions of the growing habitat were recorded for each specimen. Climatic conditions were classified according to biomes (Walter and Breckle 1991). Most anatomical features were recorded as presence or absence of a trait, except for morphological features such as plant age and annual ring width, which were recorded on a continuous scale. Vessel size, vessel number as well as fiber-wall thickness and ray width were classified in groups.

For all species the anatomy of xylem, phloem, cortex and, in some cases, the pith was described. Plant age was determined based on annual rings.

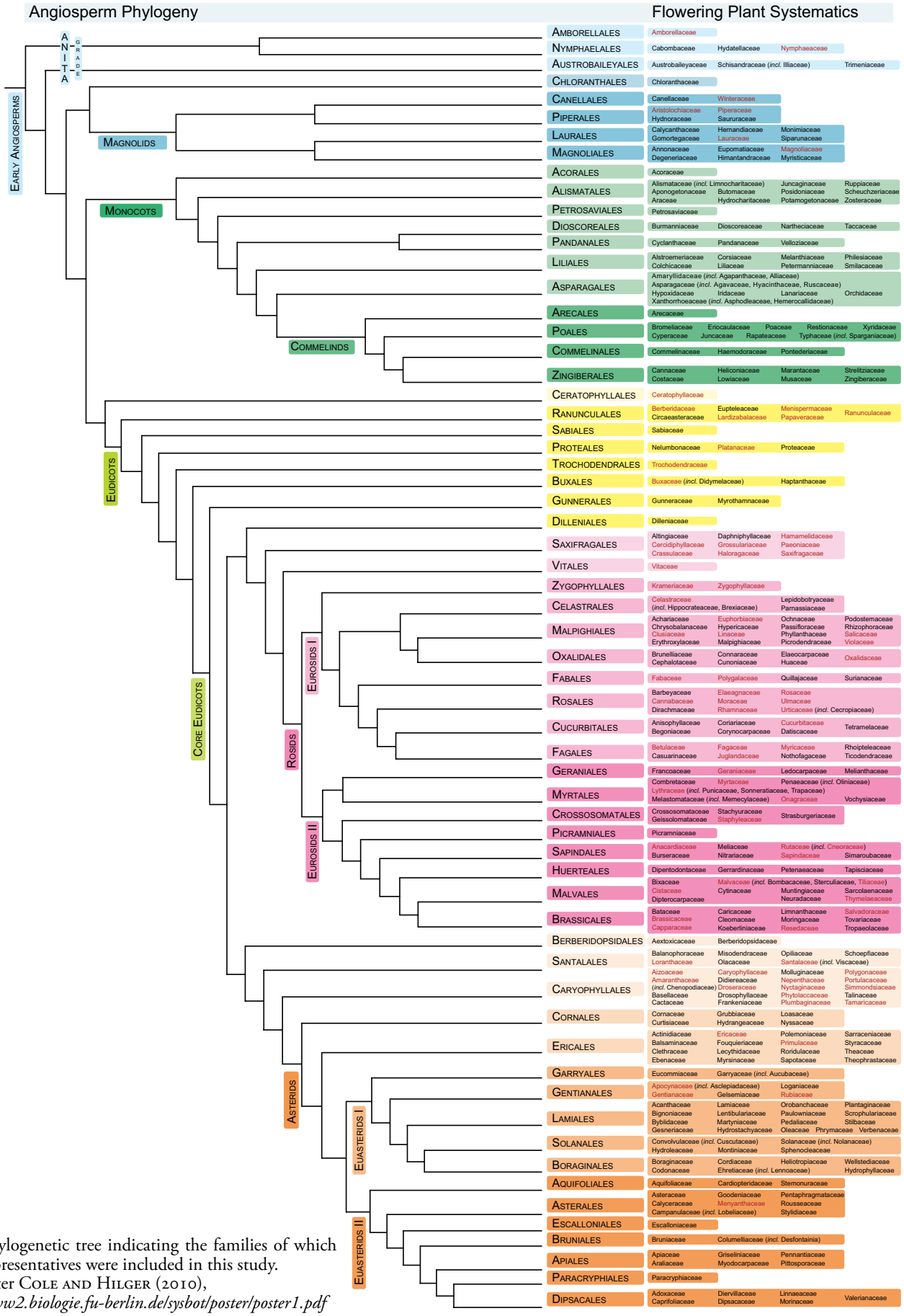
## Limitations of the Study

The study started with a focus on woody species, but over time the emphasis changed from woody towards herbaceous species. Thus, at each sampling location not all species were collected quantitatively, but it was the aim to get at least one sample per species. Not described are Monocots, Proteaceae and Cactaceae, and other families which are not represented in the European flora. However, the main objective was to obtain a representative collection of species for each family. It was not possible to collect all taxa within a family.

For comparison, the number of known taxa and species occurring worldwide and in Europe is indicted at the beginning of each family described.

The age of stems was determined using polar roots of annuals (therophytes), perennial herbs (hemicryptophytes), and dwarf shrubs. The data do not represent the full range of ages, and not the maximum possible ages, because the sampling was not conducted to find the oldest specimen of a given species. Nevertheless, the range of ages gives a first insight into the longevity of species in the European non-woody flora. Ages were not determined for shrubs and trees.

The collection is based on healthy individuals growing on "typical" sites. We avoided crippled individuals. Also, extreme habitats in terms of nutrition (extremely poor habitats as well as fertilized habitats) were avoided.




Phylogenetic tree indicating the families of which representatives were included in this study. After Cole and Hilger (2010), *www2.biologie.fu-berlin.de/sysbot/poster/poster1.pdf*

## Comparison with Other Studies

Following references served as guidelines throughout this study:

Gregory (1994) and the updated Kew Bibliography (http://kbd.kew.org/kbd/login.do) give an excellent overview on xylem anatomy, which served as basis for the present analysis.

Metcalf and Chalk (1957) summarized the basic anatomical features of plant families.

Most studies (e.g. Carlquist and Hoekman 1985, Carlquist 2001, Baas and Schweingruber 1987) focused on woody species (trees and shrubs) only, while Schweingruber and Poschlod (2005) and Krumbiegel and Kästner (1993) gave a summary of the herbaceous species based on cross section photography. Here we extend these studies with features seen in longitudinal sections. An extended bibliography concerning dwarf shrubs and herbs is given by Schweingruber and Poschlod (2005).

The INSIDE WOOD database characterizes thousands of woody species with micro-photographs and IAWA-code numbers (see *http://insidewood.lib.ncsu.edu/search*). This database especially served as comparison for the present study. It remains a problem that the IAWA code (Wheeler et al. 1989) focuses mainly on trees and not on dwarf shrubs and herbs. Comparisons are possible for families where most species belong to woody species (trees and shrubs) such as Ericaceae, Cistaceae and others. The comparisons fail wherever the IAWA database is centered around woody species for a given family, but this study is focused on all existing life forms. This study includes many families containing mainly therophytes and hemicryptophytes e.g. Amaranthaceae, Brassicaceae, Cucurbitaceae. It emerges that comparisons are only useful if the material originated from the same biome.

Holdheide (1951) is the main bark monograph for European species. However, many of the species, which are described in this collection, are not included in the Holdheide monograph.

The collection, which is primarily focused on a representation of different families and the range of taxa, does not include the anatomical variability within species growing in the full range of habitats. It was beyond the scope of this study to comprehensively investigate this plasticity of traits within species in relation to the range of habitat conditions in which these species grow. We are aware that such plasticity exists.

# 2. Material and Methods



## Geographic Origin of the Material

Plant material was collected during numerous field tours and expeditions. The geographic origin of the investigated specimens and the species nomenclature are summarized in **Table 1**. Details are given at *http://www.wsl.ch/dendro/xylemdb/index.php.*

Clearly, the largest fraction of plants (about 80%) originated from Europe. Species from outside Europe served mainly to enlarge the taxonomic range and to demonstrate anatomical similarities between tectonically early separated regions.

**Table 1.** Geographic origin of the sampled species.

| Continent | Region | Country | No. of species | Nomenclature |
|---|---|---|---|---|
| Europe | Scandinavia and Svalbard | Sweden, Finland, Norway, Russia | 3 | Tutin et al. 1964 |
| | Western Siberia | Russia | 81 | Tutin et al. 1964 |
| | Central | Austria, France, Germany, Hungary, Poland, Romania, Slovakia, Slovenia, Switzerland | 812 | Aeschimann et al. 2004<br>Lauber and Wagner 2001<br>Eggenberg and Möhl 2007<br>Rothmaler, 2005 |
| | West | England | 13 | Tutin et al. 1964 |
| | South | Greece, Italy, Portugal, Spain, Ex-Yugoslavia | 242 | Tutin et al. 1964 |
| | Macaronesia | Canary Islands, Madeira | 160 | Bramwell and Bramwell 2000<br>Hohenester and Wels 1993<br>Schönfelder and Schönfelder 1997 |
| Africa | North | Algeria, Egypt, Etiopia, Libya, Marocco, Tunesia | 49 | Ozenda 1983 |
| | Arabian Peninsula | Oman | 38 | Miller and Morris 1988<br>Jagiella and Kürschner 1987 |
| Asia | Central | Mongolia | 3 | determined by H. Heklau, Halle, Germany |
| | Near East | Georgia, Iran, Israel | 52 | Flora of Georgia |
| | South East | wood collection various countries | 5 | |
| America | North | USA, Canada | 184 | Weber 1976<br>Epple 1995 |
| | South | Argentina, Chile | 13 | determined by Prof. F. Roig sen. |
| Oceania | Australia and New Zealand | Australia (New South Wales) and New Zealand (South Island) | 2 | Costerman 1989<br>NZ species determined by H. Ullmann, Würzburg, Germany |
| **Total** | | | **1657** | |

## Families and Number of Species Treated in this Volume

Aizoaceae ..... 5
Amaranthaceae ..... 62
Amborellaceae ..... 1
Anacardiaceae ..... 10
Apocyanaceae ..... 10
Asclepiadaceae ..... 11
Aristolochiaceae ..... 6
Berberidaceae ..... 16
Betulaceae ..... 25
Brassicaceae ..... 161
Buxaceae ..... 6
Cannabaceae ..... 2
Capparaceae ..... 8
Caryophyllaceae ..... 100
Celastraceae ..... 10
Ceratophyllaceae ..... 1
Cercidiphyllaceae ..... 1
Cistaceae ..... 35
Clusiaceae ..... 18
Cneoraceae ..... 2
Crassulaceae ..... 31
Cucurbitaceae ..... 7
Droseraceae ..... 4
Eleagnaceae ..... 4
Ericaceae ..... 59
Euphorbiaceae ..... 48
Fabaceae ..... 211
Fagaceae ..... 22
Gentianaceae ..... 26
Geraniaceae ..... 20
Grossulariaceae ..... 15
Haloragaceae ..... 2
Hamamelidaceae ..... 8
Juglandaceae ..... 1
Krameriaceae ..... 1
Lardazibalaceae ..... 6
Lauraceae ..... 6
Linaceae ..... 10
Loranthaceae ..... 8
Lythraceae ..... 5
Magnoliaceae ..... 6
Malvaceae ..... 25
Menispermaceae ..... 1
Menyanthaceae ..... 2
Moraceae ..... 8
Myricaceae ..... 3
Myrtaceae ..... 1
Nepenthaceae ..... 2
Nyctaginaceae ..... 5
Nymphaeaceae ..... 3
Onagraceae ..... 14
Oxalidaceae ..... 4
Paeoniaceae ..... 3
Papaveraecae ..... 23
Phytolaccaceae ..... 1
Piperaceae ..... 3
Platanaceae ..... 3
Plumbaginaceae ..... 10
Polygalaceae ..... 7
Polygonaceae ..... 41
Portulacaceae ..... 3
Primulaceae .....
Ranunculaceae ..... 63
Resedaceae ..... 9
Rhamnaceae ..... 28
Rosaceae ..... 158
Rubiaceae ..... 33
Rutaceae ..... 8
Salicaceae ..... 39
Salvadoraceae ..... 1
Santalaceae ..... 9
Sapindaceae ..... 15
Saxifragaceae ..... 27
Simmondsiaceae ..... 1
Staphyleaceae ..... 2
Tamaricaceae ..... 9
Thymelaceae ..... 15
Tiliaceae ..... 5
Trochodendraceae ..... 2
Ulmaceae ..... 6
Urticaceae ..... 10
Violaceae ..... 17
Vitaceae ..... 5
Winteraceae ..... 6
Zygophyllaceae ..... 7

Total ..... 1627

## Families Treated in Vol. 2

Actinidiaceae
Adoxaceae
Apiaceae
Aquifoliaceae
Araliaceae
Asteraceae
Balsaminaceae
Boraginaceae
Campanulaceae
Caprifoliaceae
Convolvulaceae
Cornaceae
Diapensiaceae
Diervilleaceae
Dipsacaceae
Ebenaceae
Frankeniaceae
Garryaceae
Hydrangeaceae
Lamiaceae
Lentibulariaceae
Linnaeaceae
Myrsinaceae
Oleacea
Orobanchacea
Phrymacea
Pittosporaceae
Plantaginaceae
Polemoniaceae
Sapotaceae
Sarraceniaceae
Scrophulariaceae
Solanaceae
Styracaceae
Valerianaceae
Verbenaceae

## Internet Data

Tables and pictures are an integral part of the present volume.

Microscopic pictures and the occurrence of anatomical features of all species analyzed with ecological characteristics (modified feature code of the IAWA-list (Wheeler et al. 1989) can be viewed in the internet.

In addition, a special table with all recorded anatomical taxonomic, morphological, environmental parameters is listed here.

- *http://www.wsl.ch/dendro/xylemdb/index.php*

## Preparation of the Plant Material

For wood anatomical studies and for age determinations the most important plant part is the transition zone between root and stem, (root collar). For rhizomes the oldest end of the rhizome system has been used. For collection the plant was usually excavated.

Plant material was conserved in the field in 40% ethanol or any commercial alcohol, and stored and transported in thick-walled plastic bags which were collectively stored in plastic boxes.

Each sample was labeled with a sticker inscribed with a soft pencil (not alcohol soluble) containing the Latin plant name, the identification of the plant part (root, rhizome etc.), the plant life form according to Raunikiaer, plant height, phenology and obvious stem deformations, site conditions, altitude, location and sampling date.

The sample preparation was described in detail by Chaffey (2002) and Schweingruber et al. (2006).

All stems were cut as fresh material (not embedded in paraffin) into 1 $cm^3$ sections. Large stems were sectioned in pieces near the pith (juvenile wood) and near the cambium (adult wood). Thin stems were clamped in cork (*Quercus suber*). Sections were cut with a Reichert microtome or with the GSL-sliding microtom. The knives of the Reichert microtome were sharpened with the Leica knife sharpening machine. The GSL-microtome uses disposable paper knife blades.

The thin sections are placed on a glass object holder (slide) and covered with glycerol. Staining liquids are dropped in excess to run off into a container. The sections were stained with Astrablue (0.3 g in 100ml aqua dest. with 2 ml acetic or tartaric acid) and Safranin (0.4 g in 100 ml aqua dest.) mixed in a 1:1 ratio. A drop of the solution is placed on the section every 3 minutes.

The stained sample is washed with 95% alcohol and dehydrated with absolute alcohol. The absolute alcohol is replaced again by 95% alcohol mixed with 2,2-Dimethoxypropanaceton-dimethyacetat (Fluka). Finally, a drop of xylol tests for the presence of any water. Dehydration is incomplete, and requires more washing with absolute alcohol, if the xylol turns milky. A drop of Canada Balsam is placed on the dehydrated section with a cover glass pressed on top. To avoid buckling of the sample, two PVC-plastic stripes are placed above and below the slide and pressed together using two small magnets while drying in an oven at 60°C for 12 hours.

Specimens containing slimes (mucilage), starch or dark-staining-substances (phenols) were initially soaked in a drop of calcium hypochloride (Bleach, Javelle water) for 5-10 minutes. The section is then rinsed with water until any chloride smell disappears.

Sections were microscopically inspected using magnifications of 20-1000 (Olympus BX51 with camera Olympus C5050).

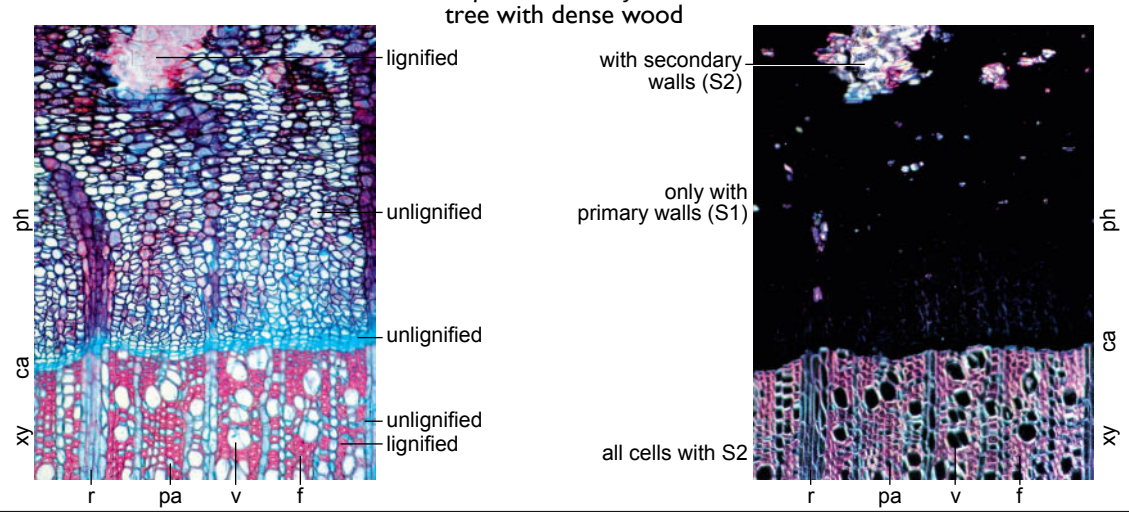
Polarized light is an extremely useful technique for the differentiation of the cell wall construction. Cell walls with a net-like, unordered fibril orientation disappear in polarized light. Cells with more ordered fibrils exhibit birefringency when illuminated with polarized light. Birefringence, or double refraction, is the decomposition of a ray of light into two rays when it passes through certain types of material. Therefore primary and tertiary walls (S1 and S3) and parenchyma cells with a non-crystalline fibril construction appear black and all cells with secondary walls (S2) and with parallel ordered fibrils appear lighter. The practical value of Astrablue/Safranin staining and the use of polarized light is demonstrated in the figure on the next page.

stained with Astrablue / Safranin

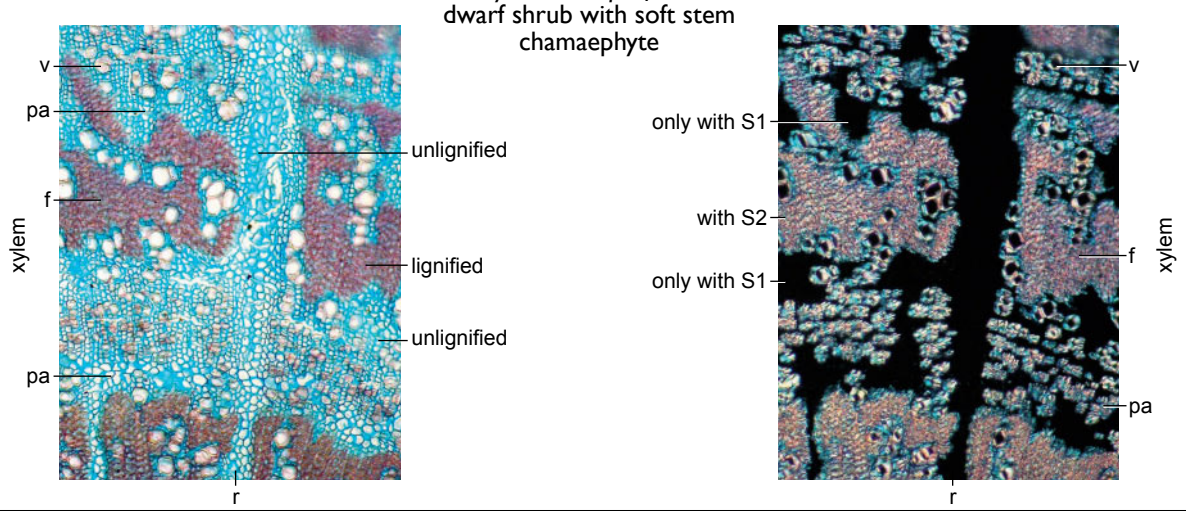
unpolarized light

polarized light

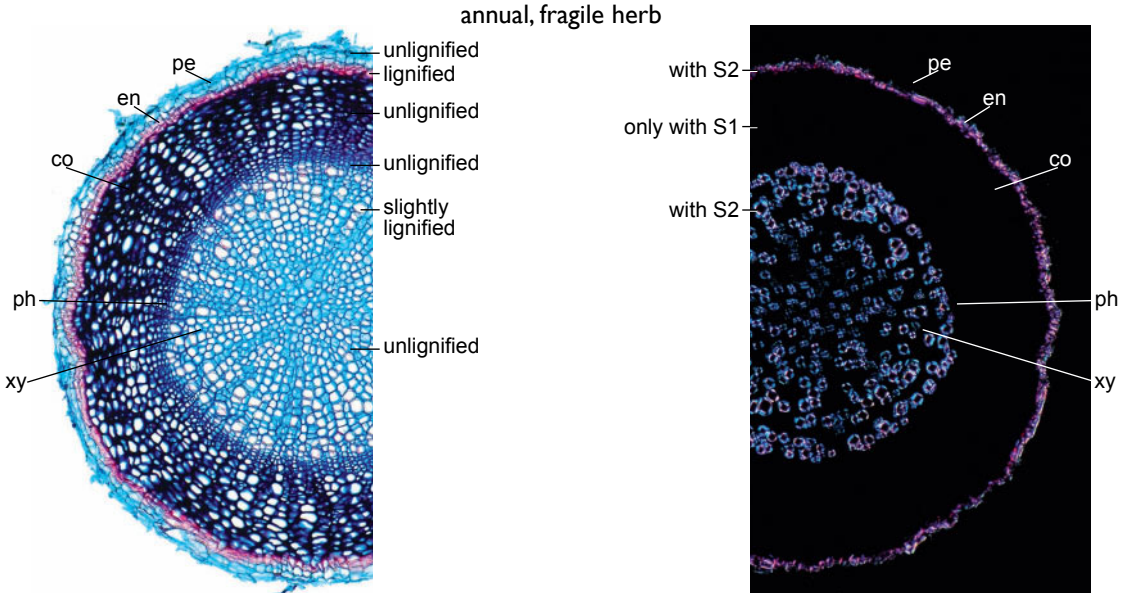
*Apollonias barbujana*
tree with dense wood




*Erysimum crepidifolium*
dwarf shrub with soft stem
chamaephyte




*Cerastium semidecandrum*
annual, fragile herb



# 3. Vegetation and Plant Parameters



## Definition of Vegetation/Climate Types

We relate each analyzed species to vegetation/climate types, (Walther and Lieth 1967 and Walther and Breckle 1991). The following plant growth relevant parameters are presented in **Table 2** below.

- Mean January temperatures and precipitations indicate the severity of winter frosts and the water availability at the beginning of the growing season.
- Mean July temperatures and precipitations indicate the growing conditions in summer.
- Total annual precipitations indicate the general hydrological conditions.
- The number of arid months is an indicator for potential growth limitations.
- The number of winter month indicates the period without radial growth.

**Table 2.** Climatic values in relation to vegetation/climate types climatic data after Walter and Lieth (1967). The selection of climatic stations is in accordance with collected samples.

| Classified vegetation types | Vegetation | Meteorological station | Elevation (m a.s.l.) | Jan temperature (°C) | Jan precipitation (mm) | July temperature °C) | July precipitation (mm) | Ann. precipitation (mm) | No. of arid months | No. of winter onths |
|---|---|---|---|---|---|---|---|---|---|---|
| **arid** subtropical desert | desert | Tucson, USA | 739 | 10 | 22 | 30 | 60 | 293 | 10 | - |
| | | Tobruk, Libya | 46 | 13 | 35 | 26 | 0 | 146 | 10 | - |
| | | Gat, Libya | 561 | 15 | 0 | 33 | 1 | 10 | 12 | - |
| | coastal desert below summer rain forest | Salalah, Oman | 18 | 23 | 5 | 28 | 20 | 90 | 12 | - |
| **subtropical** subtropical evergreen forest | laurel forest | La Laguna, Canary Islands, Spain | 547 | 13 | 95 | 21 | 5 | 594 | 4 | - |
| **Mediterranean** thermomediterranean | evergreen oak forest | Santa Barbara, USA | 37 | 12 | 100 | 25 | 0 | 371 | 7 | 2-3 |
| | | Tripolis, Libya | 18 | 13 | 25 | 25 | 5 | 625 | 5 | 2-3 |
| | | Faro, Portugal | 153 | 12 | 50 | 25 | 0 | 363 | 6 | 2-3 |
| | | Athens, Greece | 105 | 10 | 29 | 25 | 0 | 383 | 6 | 2-3 |
| | succulent bush | St. Cruz de Tenerife, Canary Islands, Spain | 50 | 18 | 35 | 22 | 0 | 290 | 8 | - |
| | | Las Palmas, Canary Islands, Spain | 12 | 18 | 40 | 20 | 2 | 543 | 9 | - |
| submediterranean | dry deciduous forest | Valence, France | 126 | 5 | 40 | 21 | 45 | 904 | 1 | 3-4 |
| | | Turin, Italy | 260 | 2 | 45 | 23 | 40 | 679 | 1 | 3-4 |
| | | Mostar, Croatia | 70 | 6 | 100 | 25 | 40 | 1343 | 1 | 3-4 |
| **temperate hill zone** warm temperate, humid | conifer forest | Astoria, USA | 70 | 5 | 120 | 15 | 25 | 1935 | - | 5 |
| | oak forest | Cardiff, U.K. | 62 | 5 | 105 | 16 | 60 | 1043 | - | 5 |
| | chestnut forest | Lugano, Switzerland | 276 | 2 | 70 | 21 | 110 | 1725 | - | 5 |
| **temperate hill zone and temperate hill and mountain zone** temperate hill zone | humid deciduous forest | Basel, Switzerland | 343 | 1 | 45 | 18 | 95 | 815 | - | 4 |
| | dry pine forest | Sion, Switzerland | 549 | -1 | 55 | 20 | 50 | 590 | - | 4 |
| | | St. Foy, France | 430 | 4 | 80 | 20 | 60 | 938 | - | 4 |
| | pine forest | Vienna, Austria | 203 | 0 | 45 | 19 | 80 | 685 | - | 4 |
| **temperate mountain zone** temperate mountain zone | pine forest | Barcelonette, France | 1134 | -1 | 45 | 17 | 40 | 731 | - | 5-6 |
| | spruce forest | La Brévine, Switzerland | 1077 | -3 | 105 | 12 | 105 | 1446 | - | 5-6 |
| | beech forest | Bachtel, Switzerland | 1131 | -1 | 100 | 12 | 110 | 1635 | - | 5-6 |
| | spruce forest | Mittenwald, Austria | 910 | -2 | 70 | 14 | 105 | 1337 | - | 5-6 |
| **temperate alpine zone** temperate subalpine zone | meadow, fir forest | Mt. Ventoux, France | 1912 | -4 | 80 | 10 | 60 | 1228 | - | 7 |
| | *Rhododendron* bush | Grimsel Hospiz, Switzerland | 1962 | -7 | 105 | 9 | 105 | 2070 | - | 7 |
| | larch, stone pine forest | St. Moritz, Switzerland | 1853 | -7 | 50 | 10 | 100 | 935 | - | 7 |
| | spruce forest | Wolf Creek Pass, Colorado, USA | 3100 | -7 | 15 | 14 | 10 | 100 | - | 7 |
| alpine zone | rocks, meadow | Säntis, Switzerland | 2500 | -8 | 110 | 5 | 115 | 2785 | - | 8 |
| | | Zugspitze, Austria | 2962 | -11 | 70 | 2 | 105 | 1350 | - | 8 |
| **boreal zone** | pine forest | Irkutsk, Russia | 467 | -19 | 10 | 16 | 95 | 369 | - | 8 |
| | | Sljud, Russia | 401 | -18 | 5 | 14 | 105 | 474 | - | 8 |
| | larch forest | Ochotsk, Russia | 6 | -23 | 3 | 11 | 60 | 238 | - | 8 |
| | spruce forest | Fort Yukon, Canada | 127 | -30 | 5 | 15 | 30 | 172 | 1 | 8 |

The classification used for each species corresponds with the following descriptions.

***Arid.*** Subtropical arid zone (desert), with 10-12 arid months, occasionally with night frosts. Rainfall is below 300 mm. The present dataset includes species from the following regions:

- Regions with two rain periods (Sonora desert, Southwest N-America), see **Tab. 3.1** Tucson. Land cover 20-40%. Shrubs and small trees, e.g. *Larrea divaricata* and many succulent species.

- Regions with one winter rain period (Northern Sahara, Marocco), see **Tab. 3.1** Tobruk. Land cover 20-30%. Shrubs and small trees, e.g. *Acacia* sp.

- Regions with one summer rain period (Dhofar, Oman), see **Tab. 3.1** Salalah. Land cover 10-40%. Shrubs and small trees, e.g. *Ficus salicifolia*, *Dodonea viscosa*.

- Regions without periodic rainfall (central Sahara), see **Tab. 3.1** Gat. Land cover <5%. Shrubs, e.g. *Leptadenia pyrotechnica*.

***Subtropical.*** This zone has generally an arid season of 3 to 6 months, but no frost. The present dataset includes the following regions:

- Canary Islands: Warm, frost-free climate with minor seasonal temperature differences and without a distinct dry summer period. Permanent clouds on northern facing slopes of the Islands create fairly dense forest (Laurel forest). See **Tab. 3.1** La Laguna.

- Southern coast of Oman: Temperatures like on the Canary island but with high precipitation from July to September.

***Mediterranean.*** Mediterranean climate has winter rains, and an arid summer period, but occasional cyclonal rains are possible all year long.

***- Thermomediterranean (Macchia and chaparral).*** Winter frosts are not below -5°C. Distribution along coasts mainly on south-facing slopes up to approximately 200 m a.s.l. The vegetation in Europe is characterized by *Quercus ilex*, *Quercus suber* and macchia shrubs. See **Tab. 3.1** Santa Barbara, Tripolis, Faro and Athens.
The subtropical succulent bush zone at lower altitudes on the Canary Islands (Macaronesia) is included here because a long arid summer period mainly influences the composition of the vegetation. The zone is characterized by high winter temperatures and long summer droughts in the lowland on the Canary Islands (Macaronesia). See **Tab. 3.1** St. Cruz de Tenerife and Las Palmas. Land cover 10-40%. Shrubs, succulents e.g *Kleinia* sp. and many introduced European species.

***- Submediterranean.*** Mediterranean climate with winter rains and a short dry summer period, without a distinct cold winter but occasionally with winter frosts but not below -10°C. See **Tab. 3.1** Valence, Turin, Mostar.
Wide region of southern Europe and the Black Sea at north facing slopes at low altitudes and on south-facing slopes at higher altitudes. The vegetation is characterized by *Quercus pubescens*.

***Temperate Zone.***
The temperate Zone has summer and winter rains, and a distinct growing season of 6 to 10 months. Frost may reach -30°.

***Temperate hill zone.*** Warm temperate regions without drought periods. Distinct temperature- seasonality with a few frosts. Coastal and hill zone in Europe and North America. See **Tab. 3.1** Astoria, Cardiff and Lugano. Forests are dominated by:

- Tall conifers, e.g. *Sequoia sempervirens*, *Abies grandis* and *Pseudotsuga menziesii* along the Pacific coast in the USA.

- Oak (*Quercus robur*) in Great Britain.

- Chestnut (*Castanea sativa*) in the Southern Alps.

***Temperate hill and mountain zone.*** Cold temperate zone without drought periods. Distinct temperature-seasonality with some frosts. Vegetation period lasts 6-8 month. January temperatures are around freezing point. July temperatures vary between 17-20°C and annual precipitations between 600-1000 mm. See **Tab. 3.1** St. Foy, Basel, Sion and Vienna. Forests are normally dominated by various species of summer green trees, e.g. *Fagus sylvatica* and *Quercus robur*, but on south-facing slopes by pines (*Pinus sylvestris*). The hill zone extends in the Alps from 200-1000 m a.s.l.

***Temperate mountain zone.*** January temperatures are a few degrees below the freezing point. July temperatures vary between 12-16°C and annual precipitations between 1000-2000 mm. The duration of vegetation periods varies between 5-6 months. See **Tab. 3.1** Barcelonette, La Brévine, Bachtel and Mittenwald.
Forests are normally dominated by various species of summer green trees e.g. *Fagus sylvatica* and *Abies alba* but south facing slopes by pines (*Pinus sylvestris*). The hill zone extends in the Alps from 800-1600 m a.s.l.

***Temperate alpine zone.*** The present classification includes the subalpine and alpine zone.

***- Subalpine zone.*** Mean January temperatures vary between 5-9°C below freezing point and July temperatures between 9-12°C. Annual precipitation is mostly more than 1500-2000 mm. Growing seasons vary between 3-4 months. See **Tab. 3.1** Mt. Ventoux, Grimsel Hospiz, St. Moritz, Wolf Creek Pass.
Forests in humid regions are dominated by spruce (*Picea abies*), those in more continental regions by larch and stone pine and mountain pine (*Larix decidua*, *Pinus cembra*, *Pinus mugo*). Deforested areas are dominated by meadows and dwarf shrubs, e.g. *Rhododendron ferrugineum* and *Calluna vulgaris*. The subalpine zone extends in the Alps from 1600-2300 m a.s.l.

***- Alpine zone.*** Mean January temperatures vary between 8-11°C below freezing point. July temperatures rarely reach 10°C and annual precipitation is mostly more than 2000 mm. The duration of growing season varies between 1-2.5 months. See **Tab. 3.1** Säntis and Zugspitze. Open meadows and rock fields are characteristic of the zone.

***Boreal zone, Taiga.***
The boreal zone has a growing season of 3-6 months with an average summer temperature of >10°C. Winter temperatures reach <30°C. See **Tab. 3.1** Irkutsk, Sljud, Ochotsk, Fort Yukon. Forests are dominated by spruce (*Picea obovata*, *P. mariana*, *P. glauca*) and various *Larix* species.

***Arctic Zone, Tundra.***
The arctic reagion has July temperatures <10°C, and a growing season of up to 3 months. Open meadows and rock fields are characteristic of the zone.

## Definition of Life Forms (after Ellenberg et al. 1992)

***P: Phanerophytes.*** Woody plants that grow taller than 4 m high (trees).

***N: Nanophanerophytes.*** Woody, shrub-like 0.5-4 m high plants.

***C: Chamaephytes.*** Herbaceous to semi-woody perennials. Dwarf shrub-like plants whose mature branch or shoot system remains perennially 25-50 cm above ground surface.

***Z: Woody chamaephytes.*** Dwarf shrubs with less than 50 cm height.

***H: Hemicryptophytes.*** Perennial herbaceous (including biennials) plants. With periodic shoot reduction to a remnant shoot system that grows relatively flat on the ground. Here we include most of the *geophytes (G)* whose surviving shoot system normally remains below surface. Also included are winter-annuals, which perform their life cycle between fall to late spring. These winter annual plants form two rings.

***T: Therophytes.*** Annuals. Plants whose shoot and root system dies after seed production and which complete their life cycle within one growing season (spring, summer, fall). Included are only specimens with one tree ring.

***Liana:*** Mostly perennials, plants with extremely long shoots, which need normally structural support by other species.

## Definition of Plant Height (after Aeschimann et al. 2004)

Plant height is principally genetically fixed but ecological conditions can modify height in a certain range. Since we did not record the height of all plants analyzed in detail we classified each species in the following height classes:

| Height variability | Height class |
|---|---|
| 2-10 cm | 5 cm |
| 10-25 cm | 20 cm |
| 25-50 cm | 40 cm |
| 50-100 cm | 80 cm |
| 100-150 cm | 150 cm |
| 150-300 cm | 300 cm |
| 300->1000 cm | 1000 cm |

# 4. Definition of Anatomical Features

Precondition for a valuable comparison of anatomical structures is the definition and coding of features. Here, we separately define ring distinctness and microscopic features.

## Classification of Ring Distinctness after Schweingruber and Poschlod 2005

**Type a:** Growth-ring numbers can be exactly determined: All ring boundaries are clearly demarcated (**Figs. 1-3**). In this case the number of observed growth rings corresponds to the true age of the plant tissue. Growth rings in the collar of primary taproots yield the ontogenetic age; growth rings in rhizomes provide the age of the preserved tissue.

**Type b:** There is some uncertainty in the determination of the age: Clearly demarcated rings are only visible along some radii and some rings may be ill-defined due to tangential intra-annual bands or wedging rings. In such cases, it is important to examine the complete cross section. **Fig. 4**

**Type c:** Age determination is uncertain. Ring numbers indicate a rough estimation. Growth zones may either look like annual rings, or be weakly expressed, or only visible in small areas of the cross section. **Figs. 5** and **6**

**Type d:** Age cannot be determined: Growth rings are invisible or growth-ring formation is insignificant. **Figs. 7** and **8**

**Type e:** The growth zone of annual plants (therophytes) cannot be classified because only one zone is present. When therophytes germinate in autumn and flower in the next growing season they form two rings. In this case they may be classified as belonging to any one of the types a, b or c.

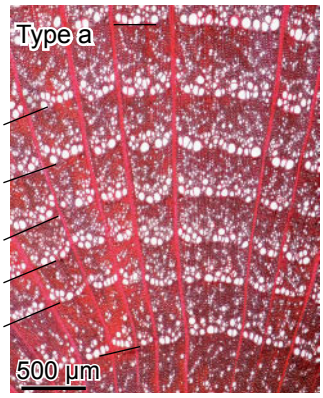



**Fig. 1.** *Berberis aetnensis*, Berberidaceae.

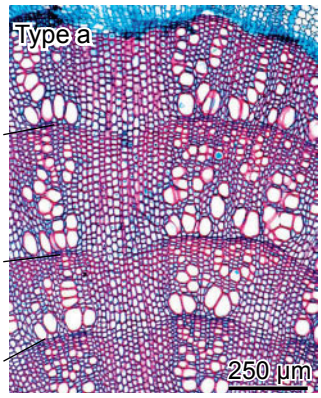



**Fig. 2.** *Helleborus viridis*, Ranunculaceae.

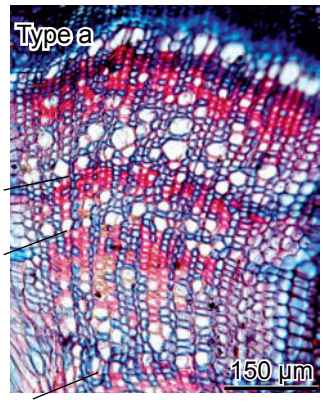



**Fig. 3.** *Viola odorata*, Violaceae.

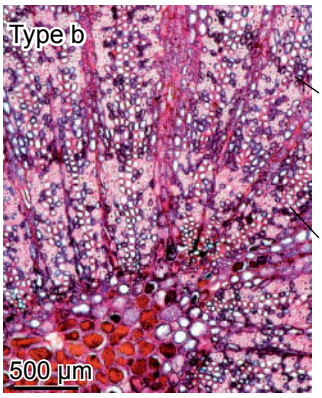



**Fig. 4.** Boundary marked by thick-walled fibers in the latewood and their absence in the earlywood. *Loranthus aphyllus*, Loranthaceae, dwarf shrub.

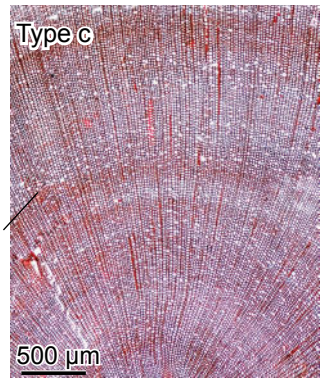



**Fig. 5.** Radial growth variations marked by zones with fibers of variable cell wall thickness. *Ixanthus viscosus*, Gentianaceae, dwarf shrub.

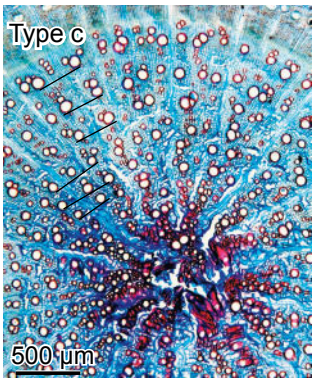



**Fig. 6.** Annual rings partially indicated by the difference in vessel size between latewood and earlywood. *Laserpitium gallicum*, Apiaceae, herb.

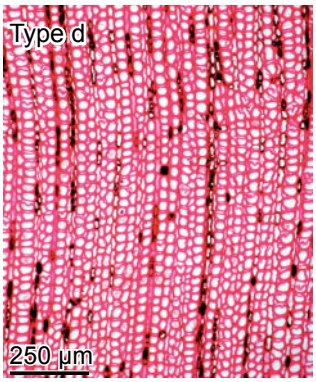



**Fig. 7.** Growth zones absent. *Amborella trichopoda*, Amborellaceae, small tree.

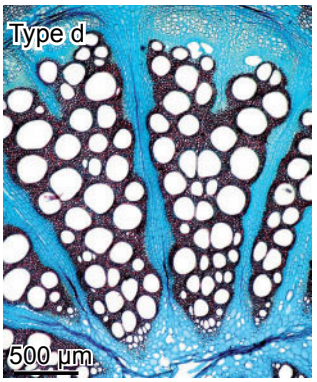



**Fig. 8.** Growth zones absent. *Aristolochia gigantea*, Aristolochiaceae, shrub.

## Definition of Features According to the IAWA List (Wheeler et al. 1989), and Complements

**2.1** Only one ring. Annual plants = therophytes.

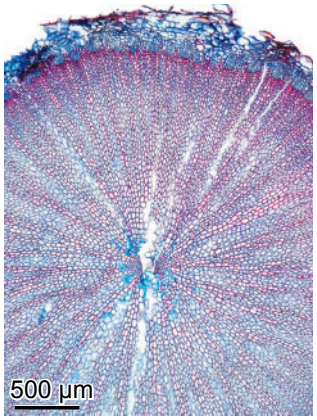



**Fig. 9.** Root collar, without pith. Very small vessels. *Adonis flammea*, Ranunculaceae.

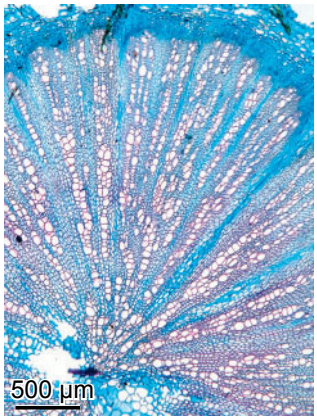



**Fig. 10.** Root collar, without pith. Vessels in radial multiples *Fumaria officinalis*, Papaveraceae.

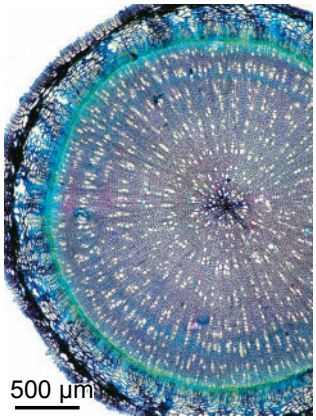



**Fig. 11.** Root collar, without pith. Vessels in tangential bands. *Capsella bursa-pastoris*, Brassicaceae.

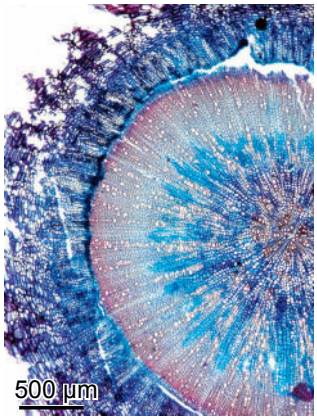



**Fig. 12.** Root collar, without pith. With pervasive parenchyma in the center. *Echium bonnettii*, Boraginaceae.

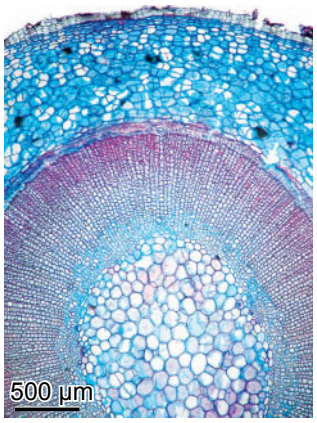



**Fig. 13.** Root collar, with pith. Vessels are absent in the latewood. *Umbilicus horizontalis*, Crassulaceae.

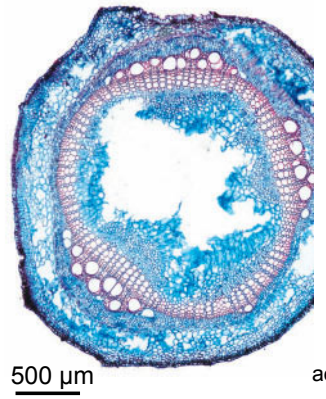



**Fig. 14.** Root collar, with pith. Vessel dimorphism. Large vessels in the second part. *Calystegia sepium*, Convolvulaceae.

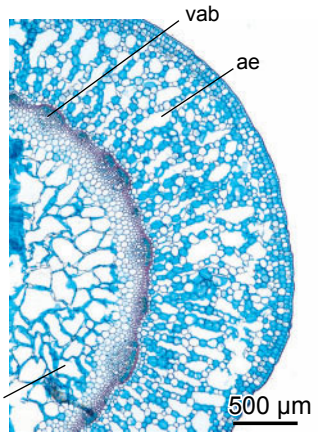



**Fig. 15.** Vascular bundles are connected by inter-vascular fiber zones. *Lysimachia thyrsiflora*, Primulaceae.

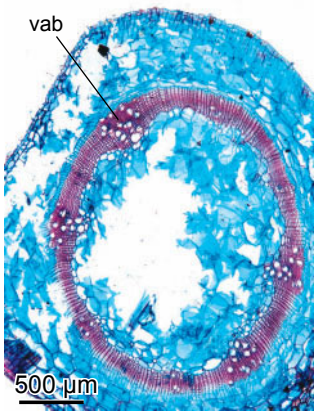



**Fig. 16.** Vascular bundles are connected by inter-vascular fiber zones. *Impatiens parviflora*, Balsaminaceae.

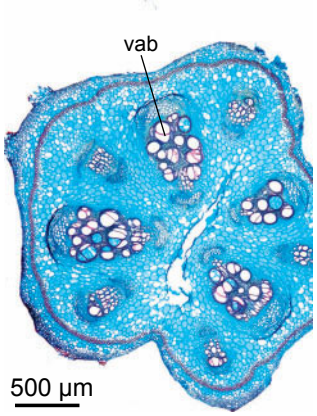



**Fig. 17.** Vascular bundles are connected by large inter-parenchyma zones. *Cucumis sativus*, Cucurbitaceae.

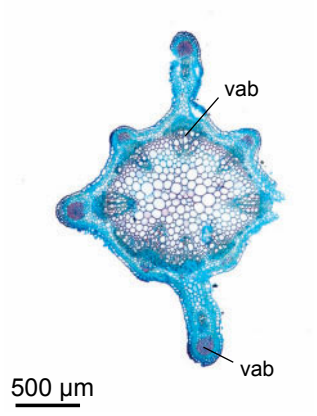



**Fig. 18.** Vascular bundles are connected by small inter-parenchyma zones. *Vicia hirsuta*, Fabaceae.

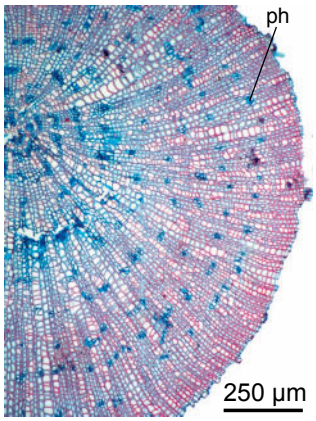



**Fig. 19.** Root collar without pith. Groups of inter-xylary phloem in tangential rows. *Plantago aschersonii*. Plantaginaceae.

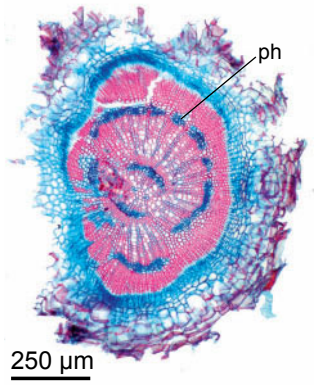



**Fig. 20.** Root collar without pith. Bands of inter-xylary phloem. *Sagina maritima*, Caryophyllaceae.

**2.2** Without secondary growth.

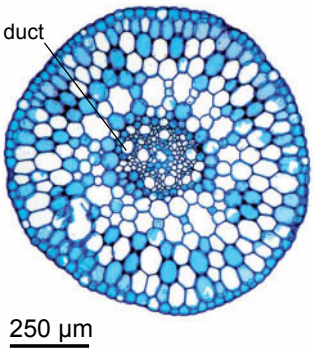



**Fig. 21.** Central vascular bundle with air ducts. Hydrophyte, *Ceratophyllum demersum*, Ceratophyllaceae.

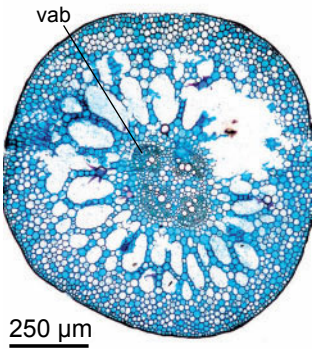



**Fig. 22.** Four centrally arranged vascular bundles. Helophyte, *Nymphoides peltata*, Menyanthaceae.

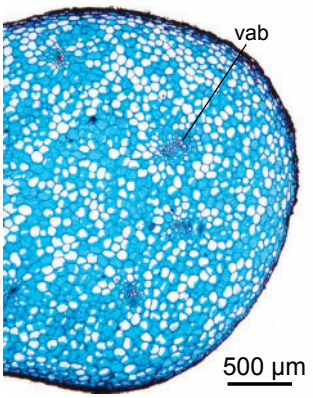



**Fig. 23.** Isolated vascular bundles in a parenchymatic tissue. Rhizome. *Anemone ranunculoides*, Ranunculaceae.

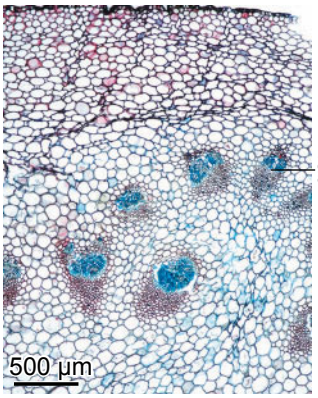



**Fig. 24.** Isolated vascular bundles in a parenchymatic tissue. Annual shoot. *Cistanche tinctoria*, Orobanchaceae.

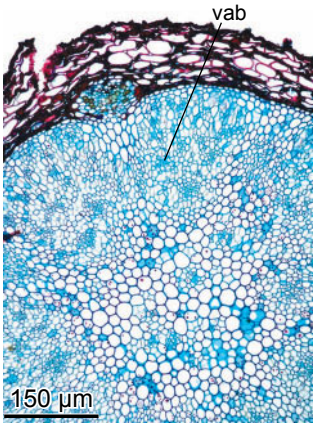



**Fig. 25.** Isolated vascular bundles in a parenchymatic tissue. Perennial shoot. *Drosera capensis*, Droseraceae.

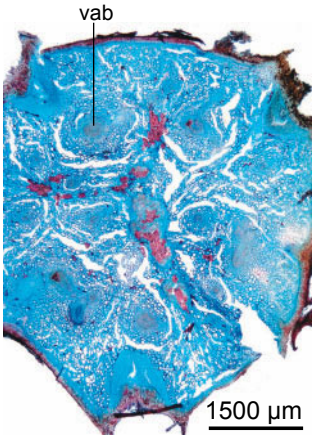



**Fig. 26.** Concentric vascular bundles within a parenchymatic tissue. *Primula hirsuta*, Primulaceae.

**3** Ring-porous. Vessels in earlywood are 6 to >10x larger in diameter than those in the latewood.

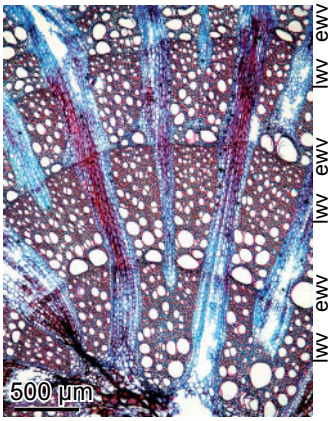



**Fig. 27.** *Aristolochia macrophylla*, Aristolochiaceae, liana.

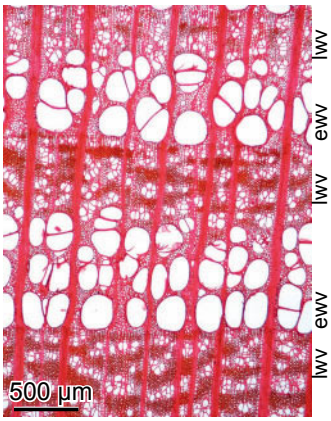



**Fig. 28.** *Morus alba*, Moraceae, tree.

**4** Semi-ring-porous. Vessels in earlywood are 3 to 5x larger in diameter than those in the latewood. Transitions between semi-ring-porous and diffuse-porous may occur even within an individual.

**Fig. 29.** *Aethionema thomasiana*, Brassicaceae, herb.

**Fig. 30.** *Sedum album*, Crassulaceae, herb.

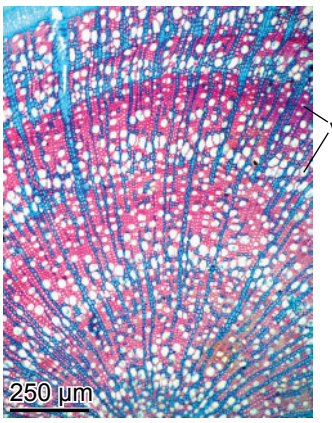



**Fig. 31.** *Adenolinum lewisii*, Linaceae, herb.

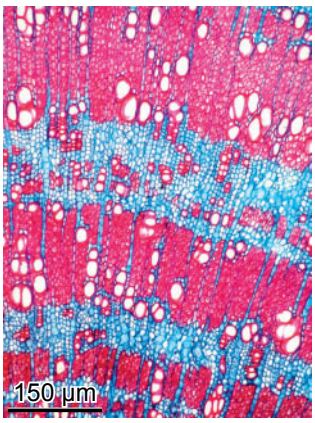



**Fig. 32.** *Euphorbia seguieriana*, Euphorbiaceae, dwarf shrub.

**5** Diffuse-porous. Vessels diameter is constant throughout the growth ring.

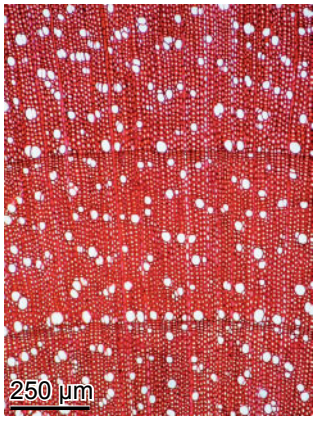



**Fig. 33.** *Ribes alpinum*, Grossulariaceae, small shrub.

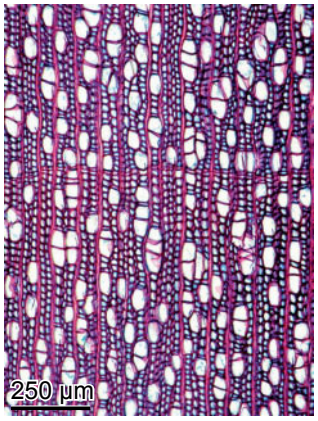



**Fig. 34.** *Aesculus hippocastaneum*, Sapindaceae, tree.

**6** Vessels in intra-annual tangential rows. See also **Figs. 11**, **95** and **152**.

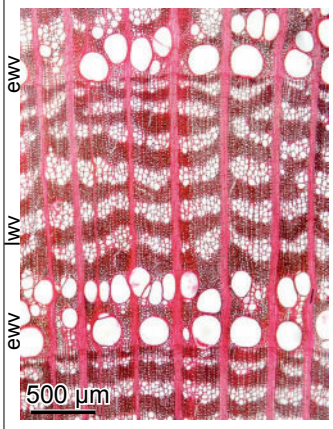



**Fig. 35.** *Ulmus laevis*, Ulmaceae, tree.

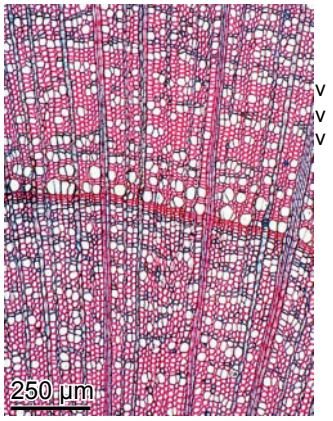



**Fig. 36.** *Enkianthus campanulatus*, Ericaceae, shrub.

**7** Vessels in diagonal and/or radial patterns. Transitions between diagonal and dendritic distribution exist within an individual.

**Fig. 37.** *Mahonia bealei*, Berberidaceae, shrub.

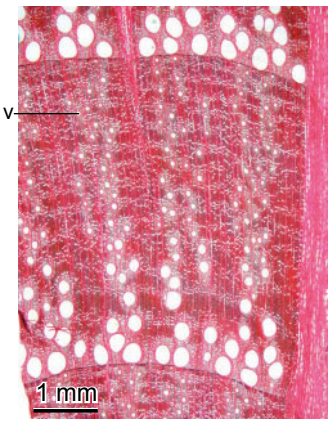



**Fig. 38.** *Quercus cerris*, Fagaceae, tree.

**8** Vessels in dendritic patterns. Transitions between diagonal vessel distribution and semi-ring-porosity exist within an individual.

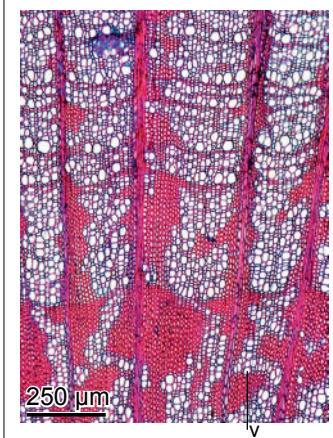



**Fig. 39.** *Berberis julianae*, Berberidaceae, herb.

**Fig. 40.** *Genista radiata*, Fabaceae, shrub.

**9** Vessels predominantly solitary. See also **Figs. 101** and **120**.

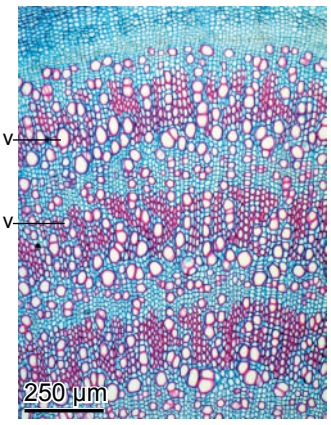



**Fig. 41.** *Silene maritima*, Caryophyllaceae, herb.

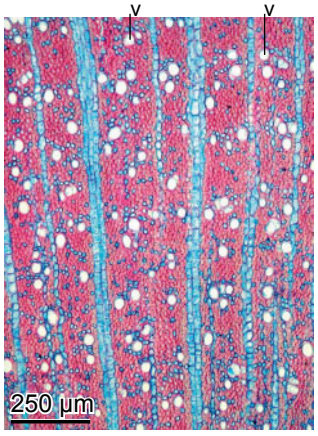



**Fig. 42.** *Zygophyllum fontanesii*, Zygophyllaceae, succulent chamaephyte.

**9.1** Vessels in radial multiples of 2 to 4 common. See also **Figs. 95** and **117**.

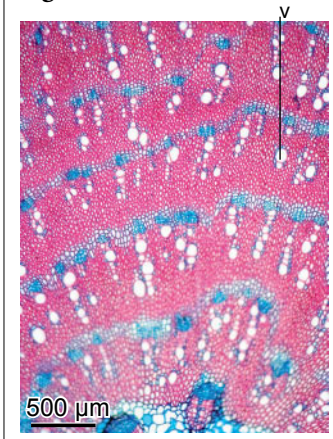



**Fig. 43.** *Atriplex patula*, Amaranthaceae, annual herb.

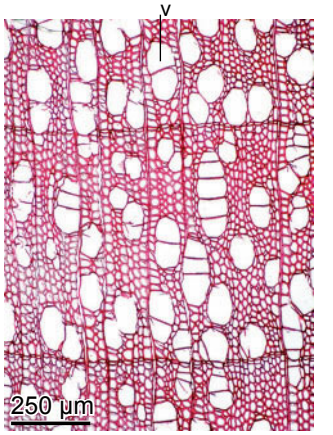



**Fig. 44.** *Populus suaveolens*, Salicaceae, tree.

**10** Vessels in radial multiples of 4 or more common. See also **Fig. 10.**

**Fig. 45.** *Erodium ciconium*, Geraniaceae, annual herb.

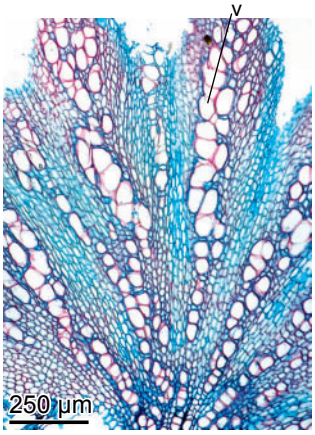



**Fig. 46.** *Asperugo procumbens*, Boraginaceae, annual herb.

**11** Vessels predominantly in clusters. Groups of 3 or more vessels having both radial and tangential contacts.

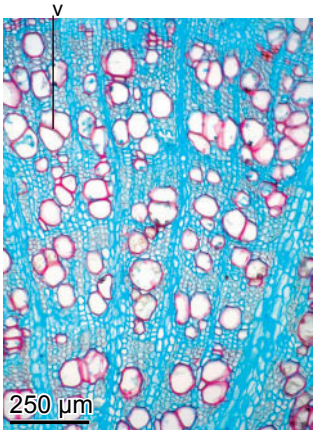



**Fig. 47.** *Euphorbia nicaeensis*, Euphorbiaceae, herb.

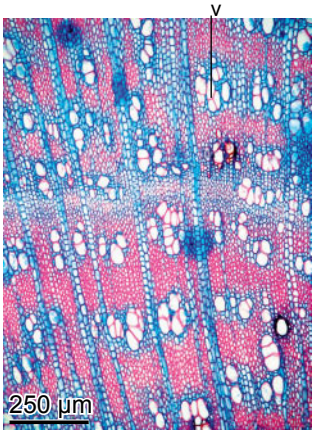



**Fig. 48.** *Malva moschata*, Malvaceae, herb.

**13** Vessels with simple perforation plates. Perforation plate with a single circular or elliptical opening.

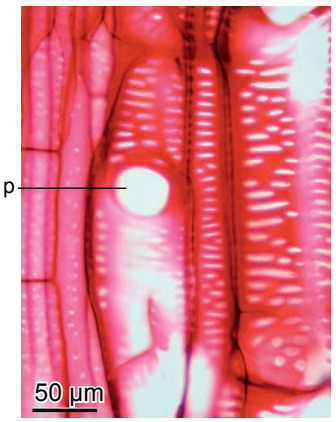



**Fig. 49.** *Euphorbia piscatoria*, Euphorbiaceae, shrub.

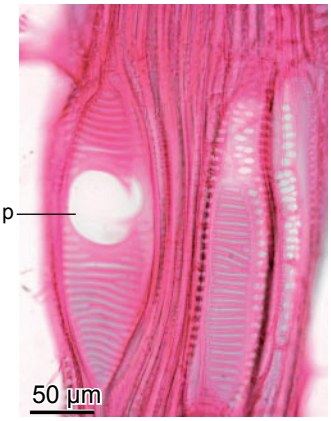



**Fig. 50.** *Parthenocissus inserta*, Vitaceae, herb.

**14** Vessels with scalariform perforation plates. Numbers of bars are of some taxonomic value. Transitions to scalariform intervessel pits occur. See also **Fig. 92**.

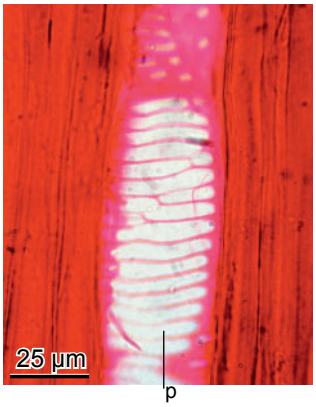



**Fig. 51.** Perforation plate with >10 bars. *Ribes alpinum*, Grossulariaceae, shrub.

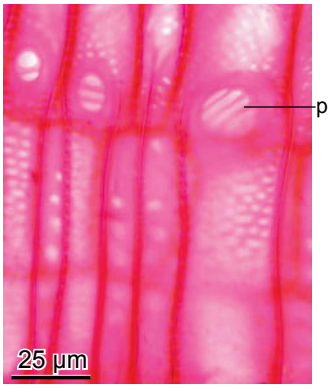



**Fig. 52.** Scalariform perforation plates with 1-3 bars. *Tolpis fruticosa*, Asteraceae, dwarf shrub.

**20** Intervessel pits scalariform. Pits with horizontally elongated apertures. See also **Fig. 92**.

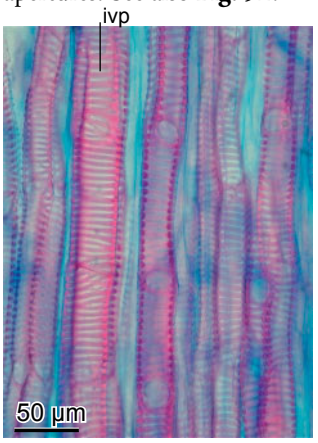



**Fig. 53.** *Viola calcarata*, Violaceae, herb.

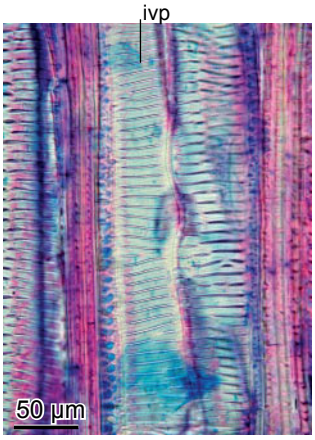



**Fig. 54.** *Parthenocissus tricuspidara*, Vitaceae, climber.

**20.1** Intervessel pits pseudoscalariform to reticulate. Pits with enlarged apertures.

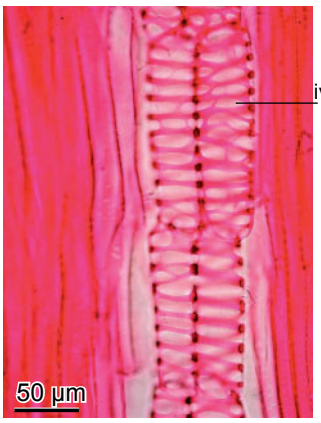



**Fig. 55.** *Aeonium urbicum*, Crassulaceae, dwarf shrub.

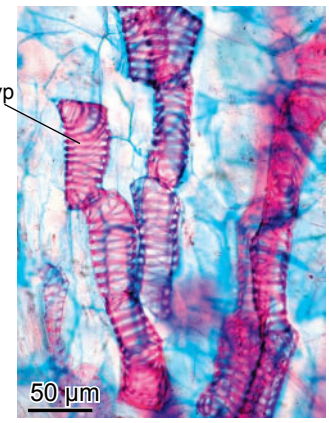



**Fig. 56.** *Orobanche canescens*, Orobanchaceae, annual herb.

**21** Intervessel pits opposite. Arranged in horizontal rows across the length of the vessel.

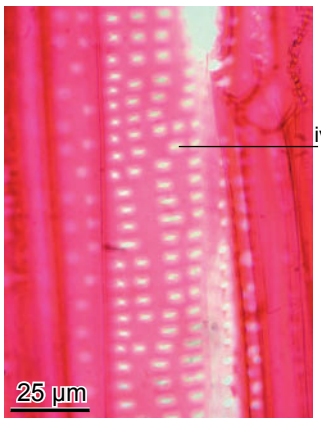



**Fig. 57.** Regular formed pits. *Platanus orientalis*, Platanaceae, tree.

**Fig. 58.** Irregular formed pits. *Impatiens noli-tangere*, Balsaminaceae, annual herb.

**22** Intervessel pits alternate. Arranged irregularly or in diagonal rows.

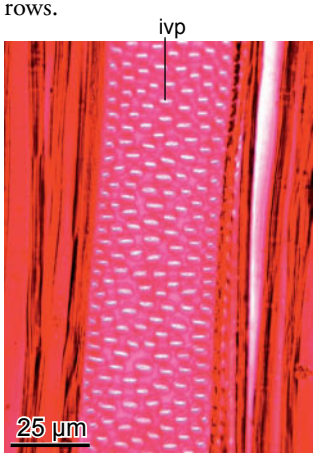



**Fig. 59.** *Reseda suffruticosa*, Resedaceae, shrub.

**Fig. 60.** *Salix planifolia*, Salicaceae, shrub.

**31** Vessel-ray pits with large round apertures, *Laurus* type. Summarized are all forms from large round to irregular and to reticulate.

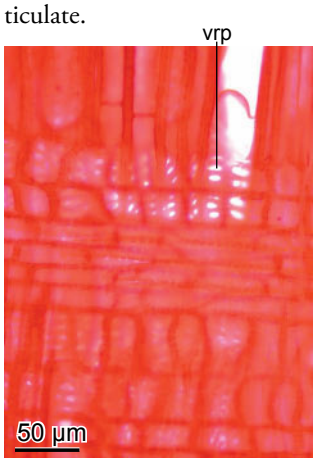



**Fig. 61.** *Olea europaea* ssp. *cuspidata*, Oleaceae, large shrub.

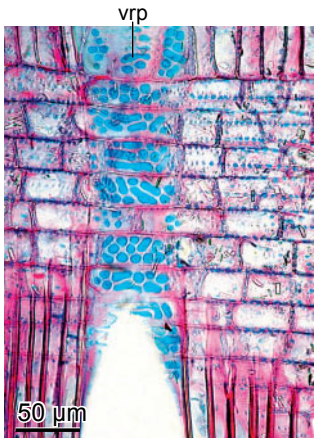



**Fig. 62.** *Laurus nobilis*, Lauraceae, tree.

**32** Vessel-ray pits with large horizontal apertures, Hamamelidaceae type. All forms with one to several pits in one vessel-ray cross-field.

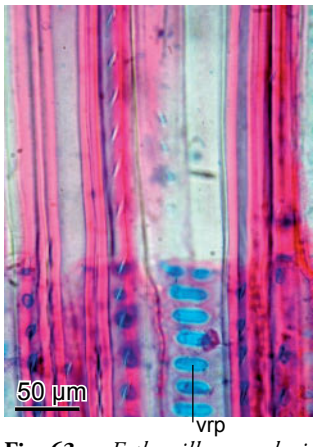



**Fig. 63.** *Fothergilla gardeni*, Hamamelidaceae, shrub.

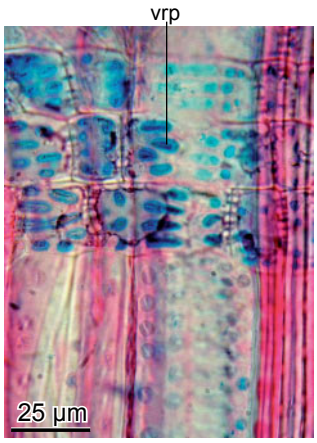



**Fig. 64.** *Fagus orientalis*, Fagaceae, tree.

**36** Helical thickenings present. All types of thickenings e.g. very thin and thick spirals in small and large vessels.

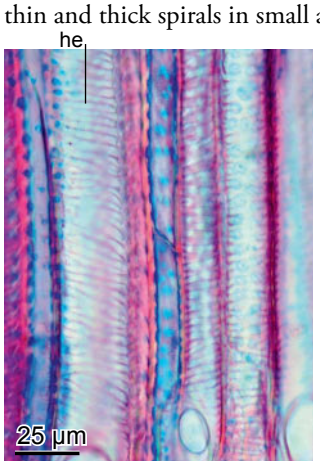



**Fig. 65.** *Nandina domestica*, Berberidaceae, shrub.

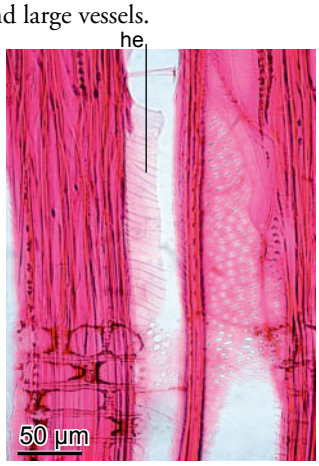



**Fig. 66.** *Corylus avellana*, Betulaceae, shrub.

**39.1** Vessel cell-wall thickness >2 µm. Cell walls are thick in relation to the surrounding tissue. See also **Fig. 113**.

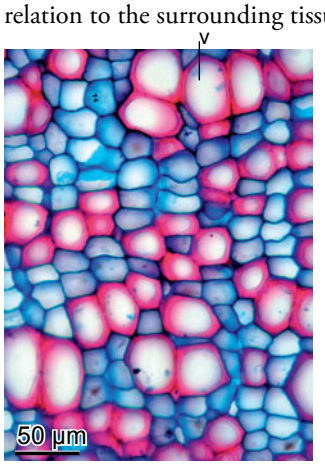



**Fig. 67.** *Pulsatilla vulgaris*, Ranunculaceae, herb.

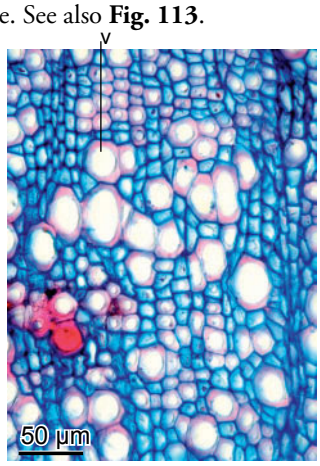



**Fig. 68.** *Armeria arenaria*, Plumbaginaceae, herb.

**40.1** Earlywood vessels: tangential diameter <20 µm. See also **Fig. 30**.

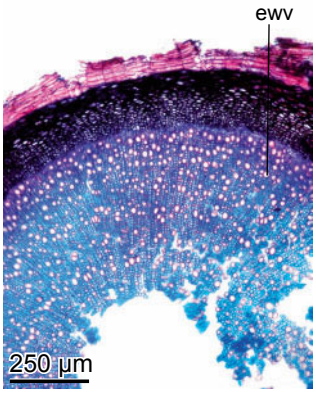



**Fig. 69.** *Arenaria ciliata*, Caryophyllaceae, herb.

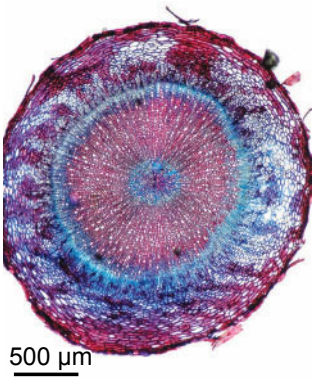



**Fig. 70.** *Neatostema apulum*, Boraginaceae, annual herb.

**40.2** Earlywood vessels: tangential diameter 20-50 µm. See also **Fig. 31**.

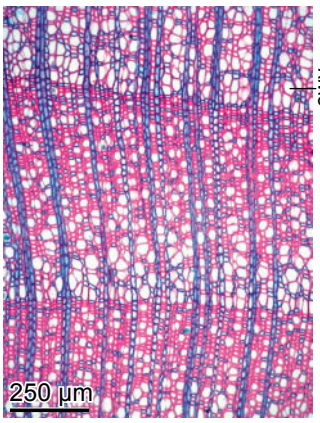



**Fig. 71.** *Paeonia suffruticosa*, Paeoniaceae, shrub.

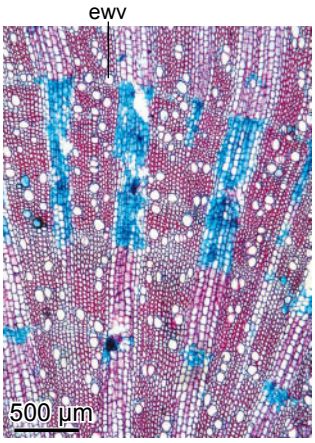



**Fig. 72.** *Kleinia neriifolia*, Asteraceae, succulent.

**41** Earlywood vessels: tangential diameter 50-100 µm. See also **Figs. 47** and **48**.

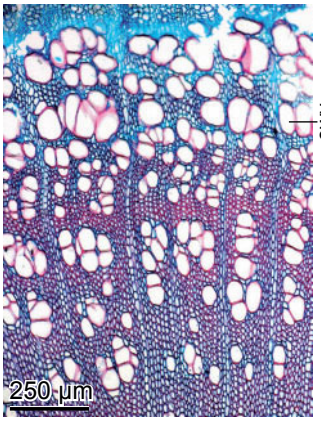



**Fig. 73.** *Cakile maritima*, Brassicaceae, herb.

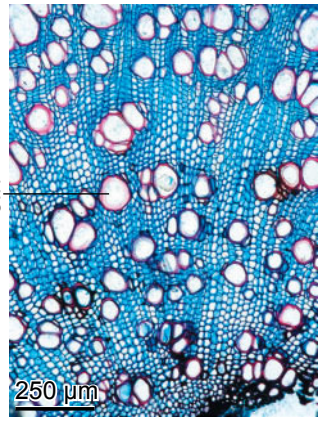



**Fig. 74.** *Nonea erecta*, Boraginaceae, herb.

**42** Earlywood vessels: tangential diameter 100-200 µm.

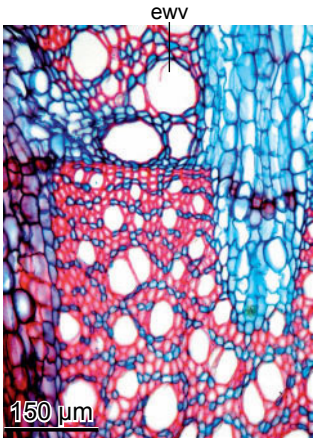



**Fig. 75.** *Aristolochia macrophylla*, Aristolochiaceae, liana.

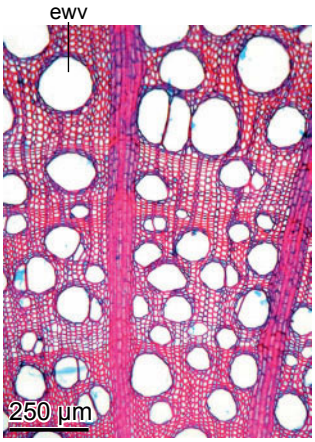



**Fig. 76.** *Sinofranchetia chinensis*, Lardizabalaceae, liana.

**50** <100 vessels per mm² in earlywood.
Vessel counting is unambiguous in structures with a more or less regular vessel distribution e.g. **Figs. 71** and **77**. Problems arise in types with isolated vascular bundles e.g. **Figs. 23** and **24**. In such cases the vessels within the vascular bundle are counted. Vessel numbers are also difficult to determine in ring porous woods (**Fig. 28**) or types with irregular vessel distribution (**Figs. 40** and **85**).

**50.1** 100-200 vessels per mm² in earlywood.
See **Figs. 95** and **96**.

**50.2** 200-1000 vessels per mm² in earlywood.
See **Figs. 30** and **41**.

**Fig. 77.** *Andromeda polifolia*, Ericaceae, dwarf shrub.

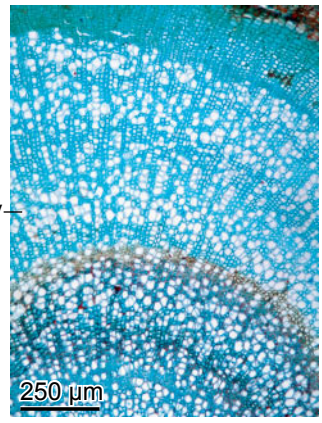



**Fig. 78.** *Castilleja arctica*, Orobanchaceae, hemicryptophyte.

**56** Tylosis with thin walls common.
They are mostly unlignified and blue-stained.

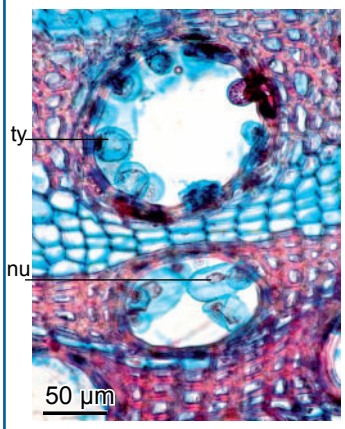



**Fig. 79.** *Cissus quadrangularis*, Vitaceae, succulent liana.

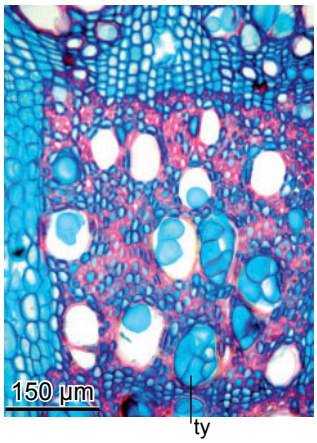



**Fig. 80.** *Aristolochia clematitis*, Aristolochiaceae, herb.

**58** Dark-stained substances in vessels and/or fibers present (gum, tannins).

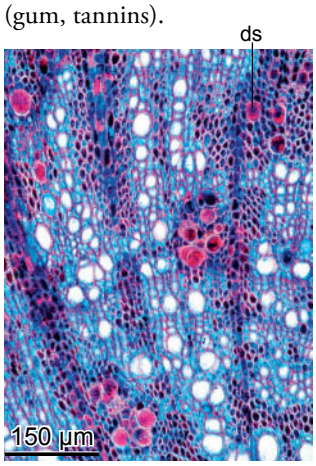



**Fig. 81.** *Eriogonum ovalifolium*, Polygonaceae, herb.

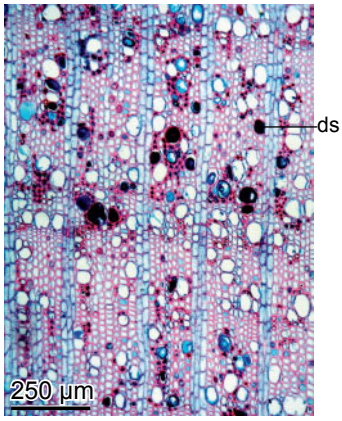



**Fig. 82.** *Arbutus canariensis*, Ericaceae, tree.

**59** Vessels absent or indistinguishable from fibers. Xylem without vessels composed of only imperforate tracheary elements (**Fig. 83**) or vessels absent in the fiber zone of the latewood (**Fig. 84**).

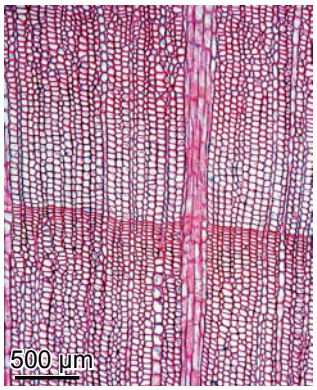



**Fig. 83.** *Trochodendron araloides*, Trochodendraceae, tree.

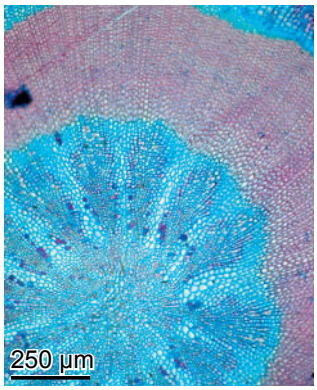



**Fig. 84.** *Jovibarba hirta*, Crassulaceae, succulent plant.

**60** Vascular/vasicentric tracheids, *Daphne* type. Vessels are surrounded by tracheids.

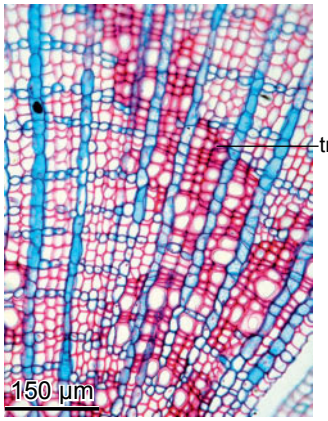



**Fig. 85.** *Daphne striata*, Thymelaeaceae, dwarf shrub.

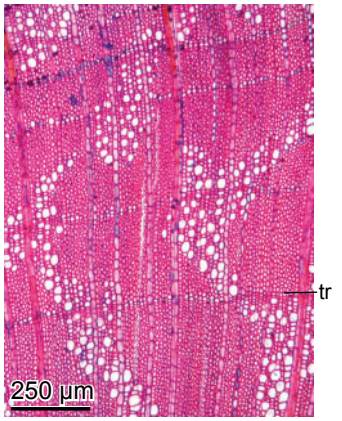



**Fig. 86.** *Osmanthus decorus*, Oleaceae, shrub.

**60.1** Fibers absent. Xylem without fibers; composed of only parenchyma and vessels. See **Figs. 67** and **68**.

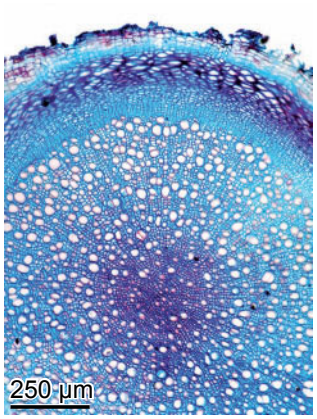



**Fig. 87.** *Cerastium arvense*, Caryophyllaceae, herb.

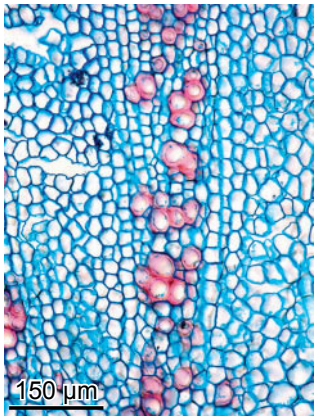



**Fig. 88.** *Campanula beckiana*, Campanulaceae, herb.

**61** Fiber pits small and simple to minutely bordered (<3 µm = libriform fibers).

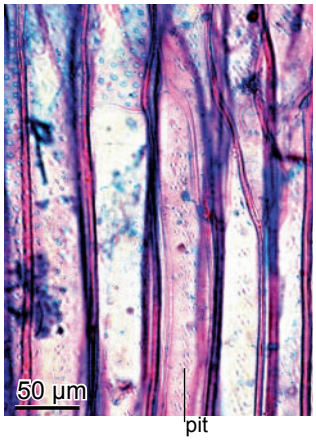



**Fig. 89.** *Fumaria officinalis*, Papaveraceae, herb.

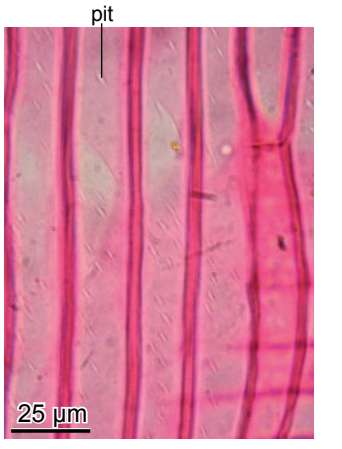



**Fig. 90.** *Betula glandulosa*, Betulaceae, shrub.

**62** Fiber pits large and distinctly bordered (>3 µm = fiber tracheids). See also **Fig. 58**.

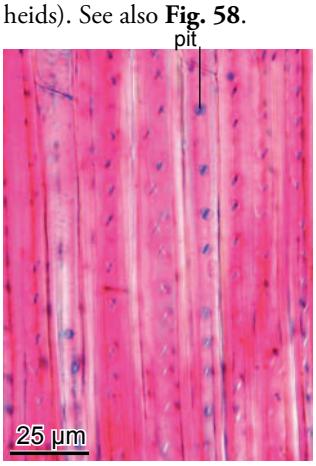



**Fig. 91.** *Sarcococca hookeriana*, Buxaceae, small shrub.

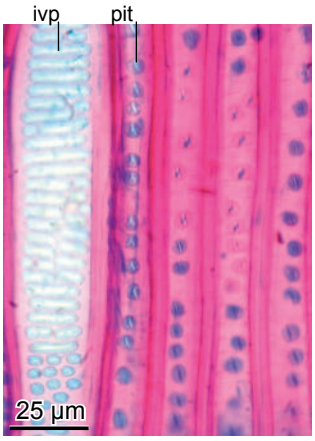



**Fig. 92.** *Gaultheria shalon*, Ericaceae, shrub.

**65** Septate fibers present. Fibers with thin, mostly unlignified, transverse walls.

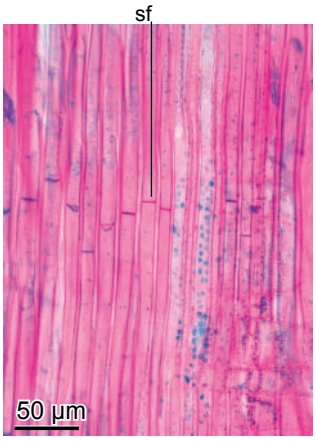



**Fig. 93.** *Hypericum inodorum*, Clusiaceae, shrub.

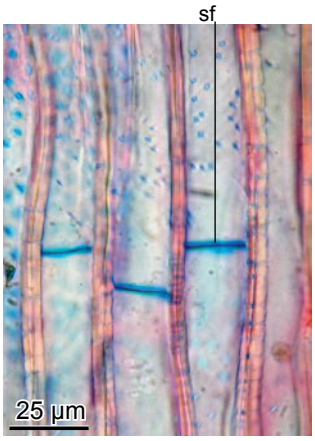



**Fig. 94.** *Berberis julianae*, Berberidaceae, shrub.

**67** Thick- and thin-walled fiber bands, *Acer* type.

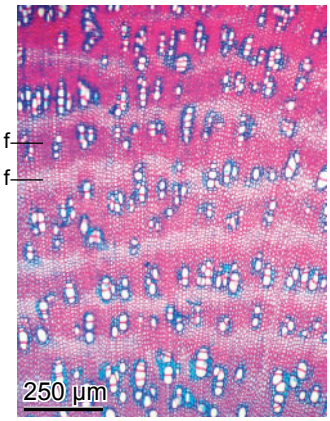



**Fig. 95.** *Lepidium campestre*, Brassicaceae, herb.

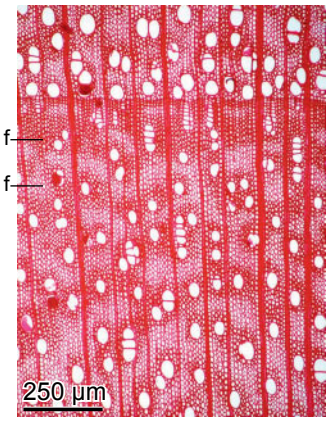



**Fig. 96.** *Acer tataricum*, Sapindaceae, tree.

**68** Fibers thin-walled. Fiber lumina 3 or more times wider than the double wall thickness.

**Fig. 97.** *Rhinanthus glacialis*, Orobanchaceae, parasite.

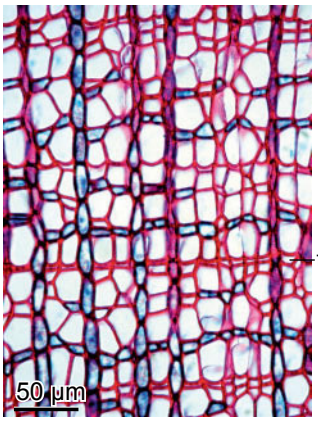



**Fig. 98.** *Ledum decumbens*, Ericaceae, dwarf shrub.

**69** Fibers thick-walled. Fiber lumina almost completely closed. See also **Figs. 4** and **119**.

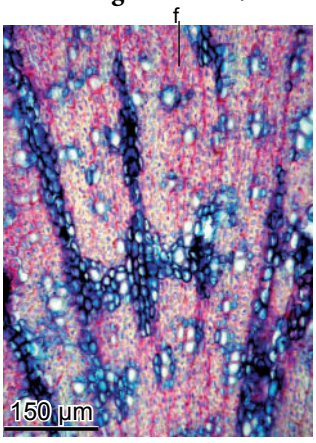



**Fig. 99.** *Limonium pectinatum*, Plumbaginaceae, herb.

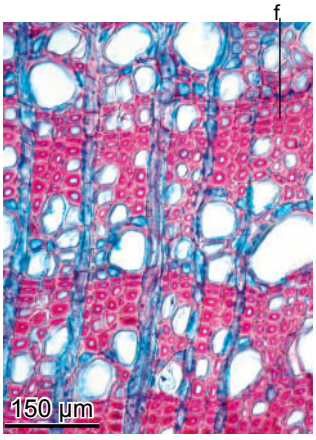



**Fig. 100.** *Syringa vulgaris*, Oleaceae, shrub.

**70** Fibers thin- to thick-walled. Fiber lumina less than 3 times the double wall thickness, distinct lumina. See **Figs. 109** and **115**.

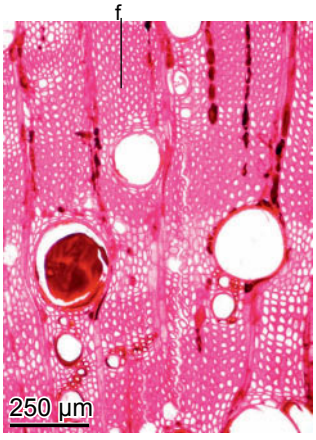



**Fig. 101.** *Calligonum comosum*, Polygonaceae, shrub.

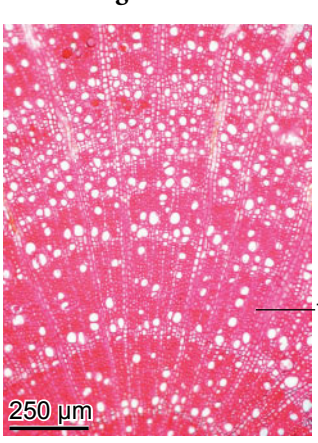



**Fig. 102.** *Thesium bavarum*, Santalaceae, herb.

**70.1** Intra-annual thick-walled tangential fiber bands. Fiber bands (red) are located between fiber-less zones (blue).

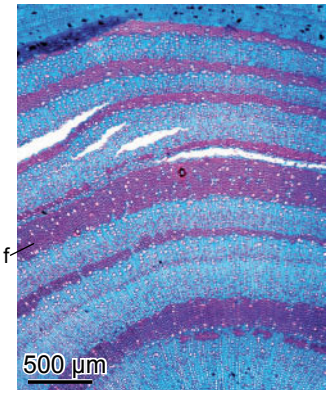



**Fig. 103.** *Dianthus seguieri*, Caryophyllaceae, herb. With continuous bands.

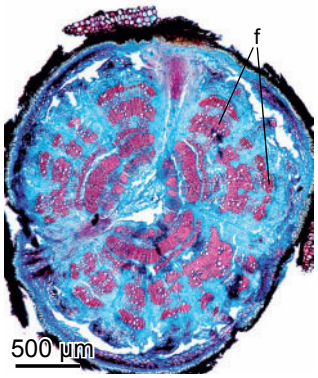



**Fig. 104.** *Matthiola fruticulosa*, Brassicaceae, herb. With lateral interrupted bands.

**70.2** Fibers contain tension wood. Gelatinous, unlignified, blue secondary walls in fibers.

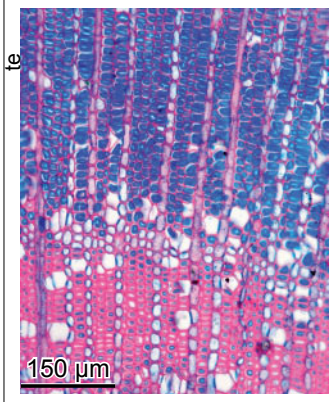



**Fig. 105.** *Sycopsis sinensis*, Hamamelidaceae, shrub.

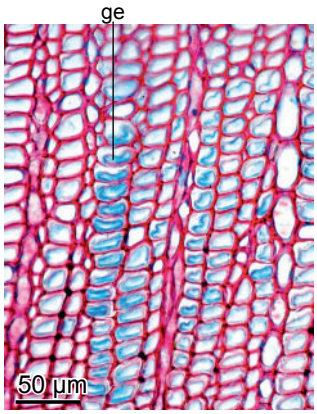



**Fig. 106.** *Trochodendron araliodes*, Trochodendraceae, small tree.

**75** Parenchyma absent or unrecognizable. Parenchyma cells unrecognizable in Safranin/Astrablue stained slides.

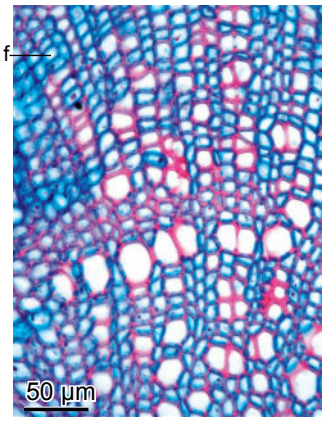



**Fig. 107.** *Viola elatior*, Violaceae, herb. Unlignified fibers.

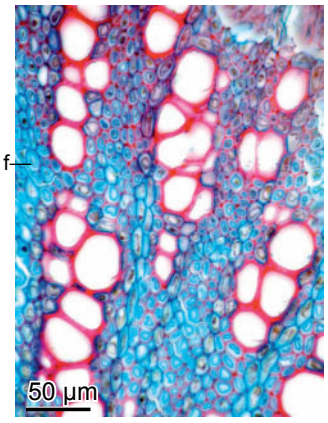



**Fig. 108.** *Euphorbia maculata*, Euphorbiaceae, herb.

**76** Parenchyma apotracheal, diffuse in aggregates. Parenchyma cells single or grouped into short discontinuous tangential or oblique lines. See also **Fig. 75**.

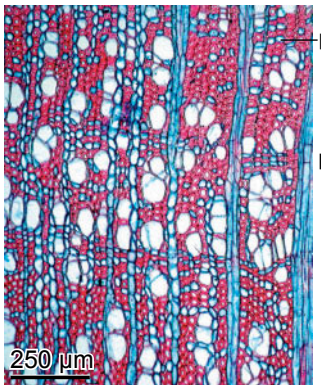



**Fig. 109.** *Apollonias barbujana*, Lauraceae, tree.

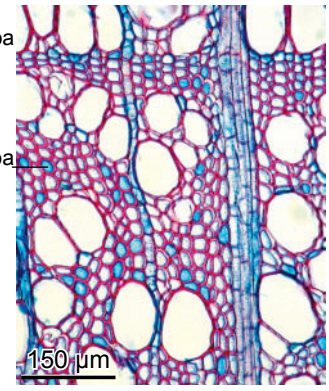



**Fig. 110.** *Hedera helix*, Araliaceae, climber.

**79** Parenchyma paratracheal. Axial parenchyma associated with vessels.

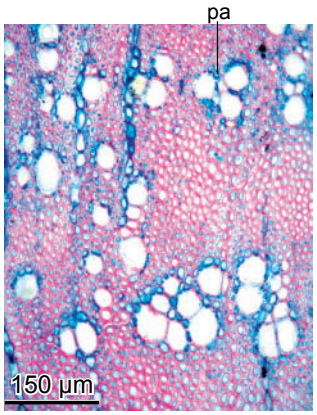



**Fig. 111.** *Eriogonum trichopes*, Polygonaceae, herb. Parenchyma vasicentric.

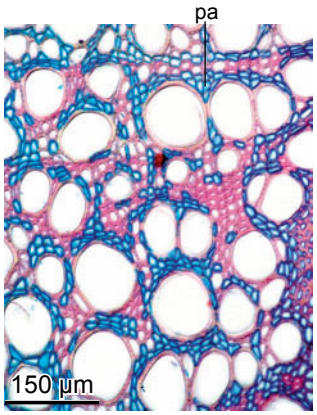



**Fig. 112.** *Clematis flammula*, Ranunculaceae, herb. Parenchyma vasicentric in groups.

**79.1** Parenchyma pervasive. The ground tissue consists exclusively of thin-walled, unlignified parenchyma. See also **Figs. 67** and **68**.

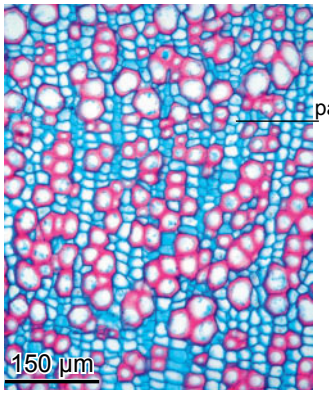



**Fig. 113.** *Pulsatilla montana*, Ranunculaceae, herb.

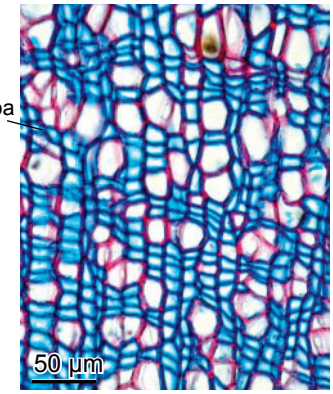



**Fig. 114.** *Polemonium coerulea*, Polemoniaceae, herb.

**79.2** Parenchyma intervascular, Crassulaceae type. Isolated groups of vessels are surrounded by parenchyma and occur in a dense fiber tissue (Carlquist 2001).

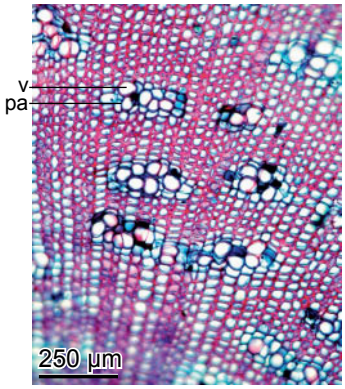



**Fig. 115.** *Aeonium viscatum*, Crassulaceae, dwarf shrub.

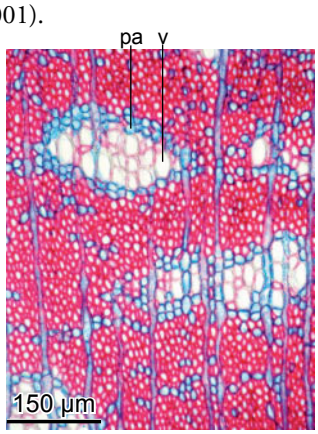



**Fig. 116.** *Thymelaea hirsuta*, Thymelaeaceae, shrub.

**85** Axial parenchyma bands more than three cells wide, *Ficus/Urtica* type.

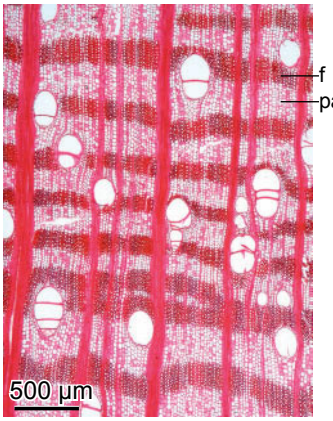



**Fig. 117.** *Ficus sycomorus*, Moraceae, tree.

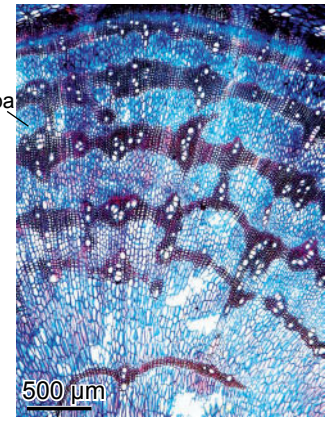



**Fig. 118.** *Urtica urens*, Urticaceae, herb.

**89** Parenchyma marginal. Parenchyma bands form continuous layer in late- or earlywood. Cell walls can be lignified or unlignified.

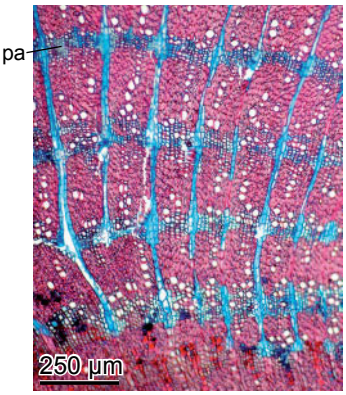



**Fig. 119.** *Vella spinosa* ssp. *lucentina*, Brassicaceae, dwarf shrub. Marginal terminal.

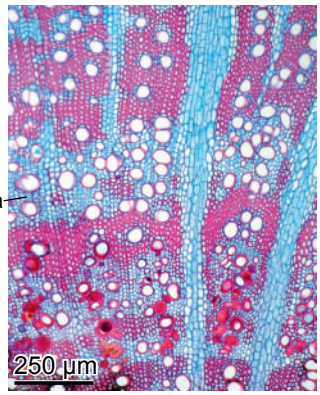



**Fig. 120.** *Diplotaxis tenuifolia*, Brassicaceae, herb. Marginal initial.

**89.1** Parenchyma marginal thin-walled; dark in polarized light. Parenchyma cells without secondary walls do not reflect polarized light and appear as dark zones.

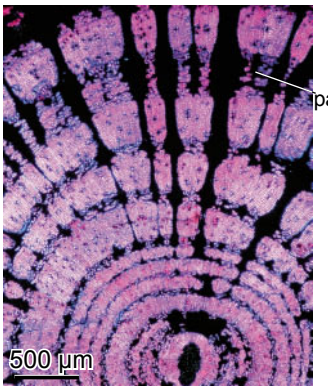



**Fig. 121.** *Alyssum argenteum*, Brassicaceae, herb.

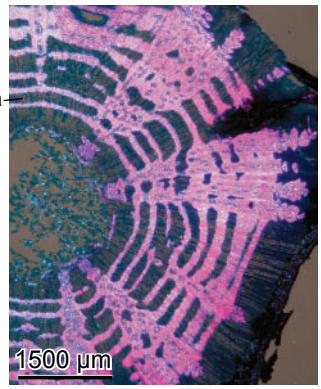



**Fig. 122.** *Urtica dioica*, Urticaceae, herb.

**89.2** Ring shake, *Saxifraga* type. During mechanical stress, drought or preparation procedure rings or compartments of rings fall apart.

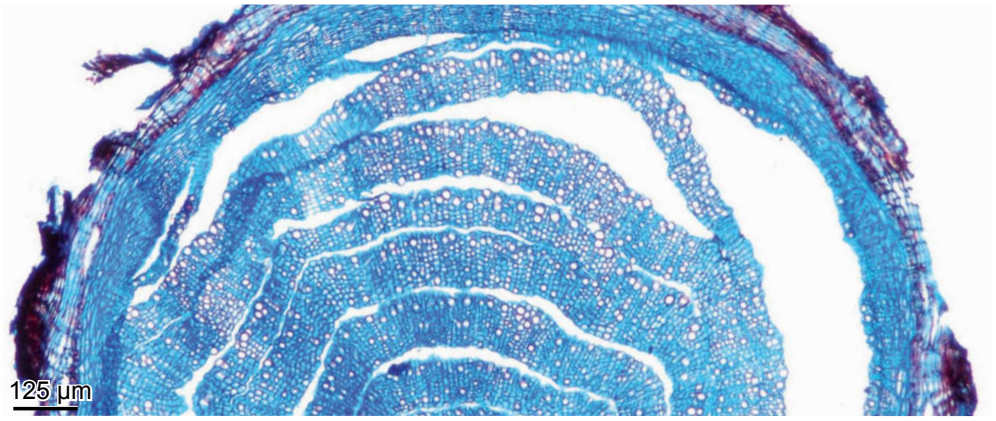



**Fig. 123.** *Saxifraga moschata*, Saxifragaceae, herb.

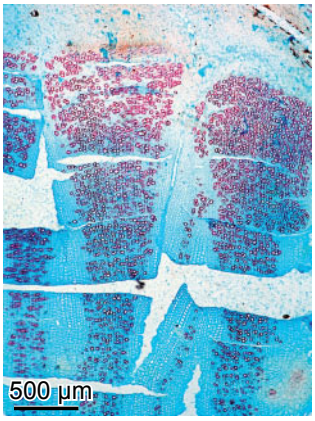



**Fig. 124.** *Geum glaciale*, Rosaceae, herb.

**96** Rays exclusively uniseriate.

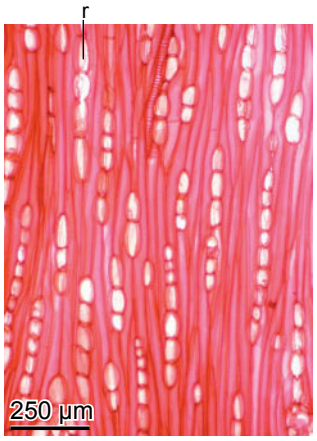



**Fig. 125.** *Euphorbia echinus*, Euphorbiaceae, shrub.

**97** Rays width 1-3 cells.

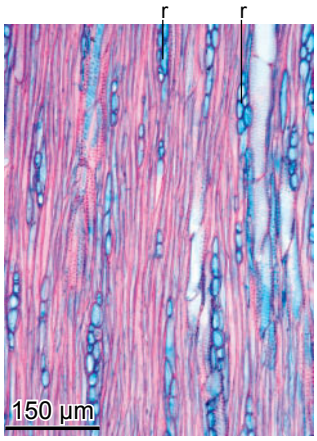



**Fig. 126.** *Eriogonum inflatum*, Polygonaceae, herb.

**98** Rays commonly 4-10-seriate.

**Fig. 127.** *Parthenocissus inserta*, Vitaceae, liana.

**99** Rays commonly >10-seriate.

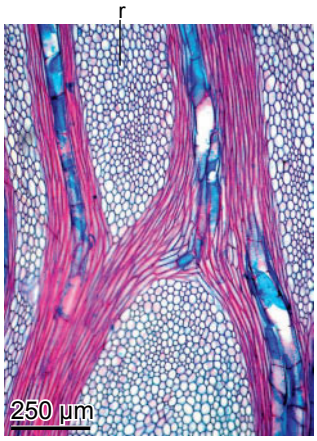



**Fig. 128.** *Brassica nigra*, Brassicaceae, herb.

**99.1** Vascular-bundle form remaining. Vascular bundles are separated by pith-like parenchyma cells. It lacks a continuous fiber/vessel zone. See also **Figs. 8** and **29**.

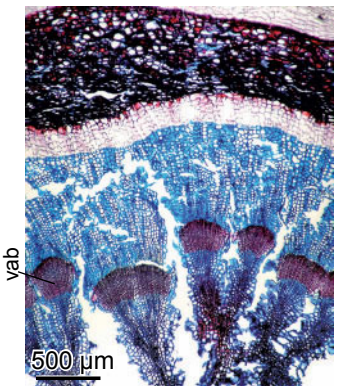



**Fig. 129.** *Sempervivum tectorum*, Crassulaceae, herb.

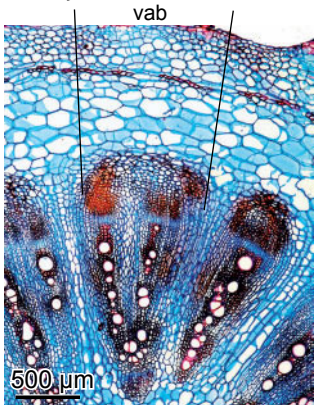



**Fig. 130.** *Ecballium elaterinum*, Cucurbitaceae, creeping liana.

**99.2** Stem fluted.

**Fig. 131.** *Eriogonum jamesii*, Polygonaceae, chamaephyte.

**Fig. 132.** *Satureja montana*, Lamiaceae, chamaephyte.

**100.1** Rays confluent with ground tissue. Lateral borders of rays merge with axial tissue.

**Fig. 133.** *Geranium columbinum*, Geraniaceae, herb.

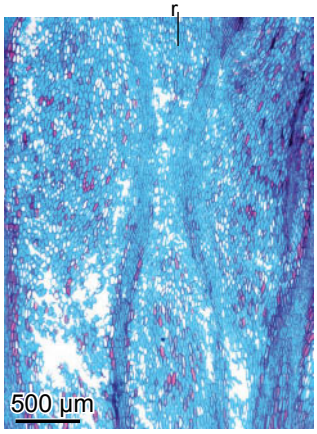



**Fig. 134.** *Sedum anopetalum*, Crassulaceae, herb.

**100.2** Rays not visible in polarized light.

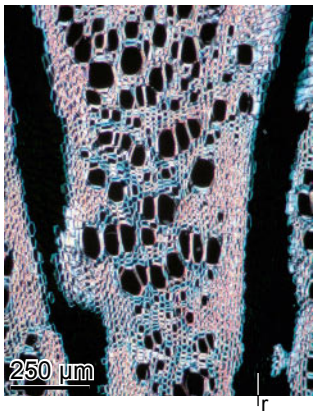



**Fig. 135.** *Clematis recta*, Ranunculaceae, herb. Dark strips represent thin-walled parenchymatic ray tissue.

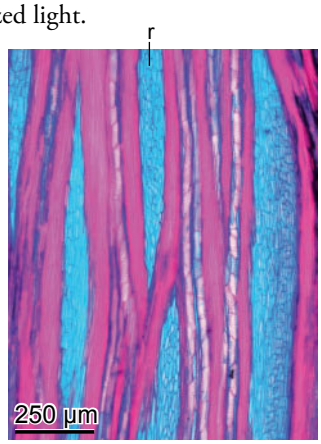



**Fig. 136.** *Sisymbrium austriacum*, Brassicaceae, herb. Thin-walled, unlignified ray cells do not reflect polarized light.

**101** Aggregate rays: vessel-free zone with many rays.

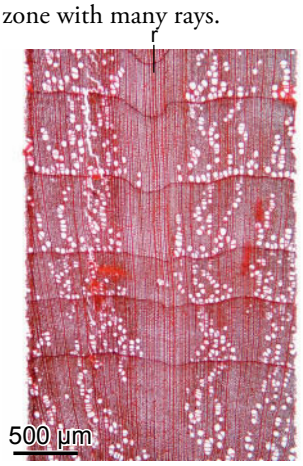



**Fig. 137.** *Corylus mandshurica*, Betulaceae, shrub.

**102** Ray height > 1 mm. Large rays normally exceed 1 mm in height. See also **Fig. 127**.

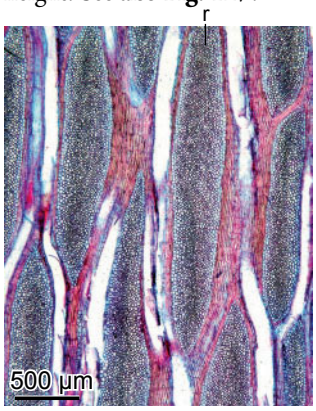



**Fig. 138.** *Tamarix articulata*, Tamaricaceae, small tree.

**103** Rays of two distinct sizes. Rays uni- and 2-seriate. See also **Fig. 126**.

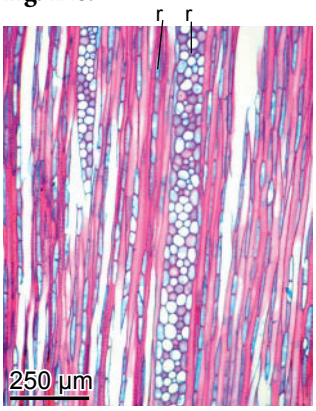



**Fig. 139.** *Gaultheria shalon*, Ericaceae, shrub.

**104** Ray homocellular, all cells procumbent (radial section).

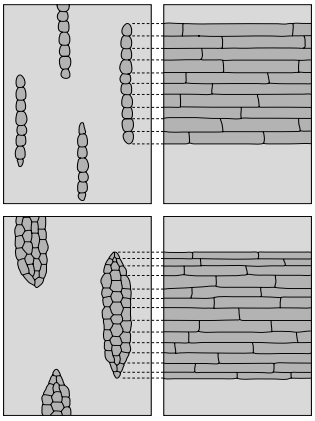


**Fig. 140.**

**105** Ray homocellular, all cells upright or square. There are frequently transitions between Feature 106, 107 and 108.

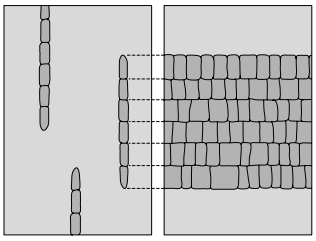


**Fig. 141.**

**106** Ray heterocellular with 1 upright cell row (radial section).

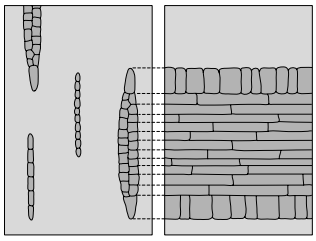


**Fig. 142.**

**107** Ray heterocellular with 2-4 upright cell rows (radial section).

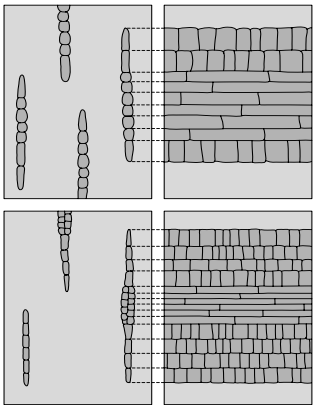


**Fig. 143.**

**108** Ray heterocellular with > 4 upright cell rows (radial section).

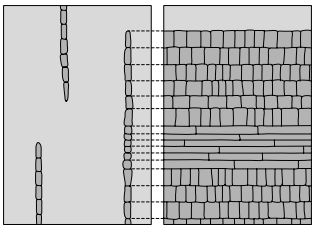


**Fig. 144.**

**110** Rays with sheet cells (tangential section). Cells located along sides of broad rays, larger than central ray cells.

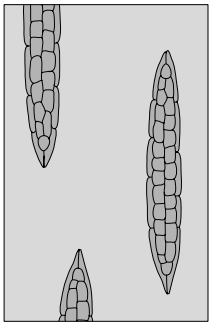


**Fig. 145.**

**117** Rayless wood only with axial elements. Identification of this feature is only possible using tangential sections. In cross-sections ray cells with the same form as fibers or parenchyma can be mistaken for ray absence.

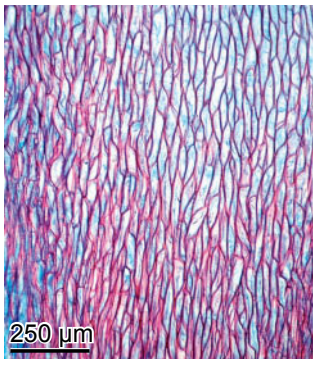



**Fig. 146.** *Umbilicus horizontalis*, Crassulaceae, herb. With short, thin-walled, lignified fibers.

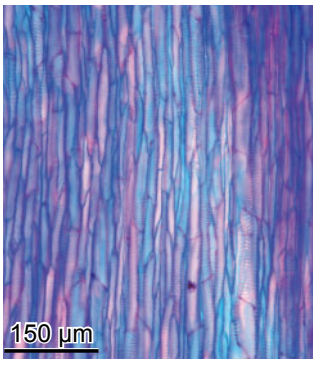



**Fig. 147.** *Silene viscaria*, Caryophyllaceae, herb. With short, thin-walled, unlignified fibers.

**Fig. 148.** *Sedum reflexum*, Crassulaceae, herb. Relatively long, thick-walled, lignified fibers.

**120** Storied axial tissue (parenchyma, fibers, vessels in tangential section). Cells oriented in horizontal series.

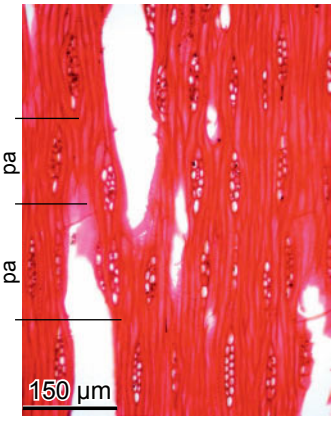



**Fig. 149.** *Hippophae rhamnoides*, Eleagnaceae, shrub.

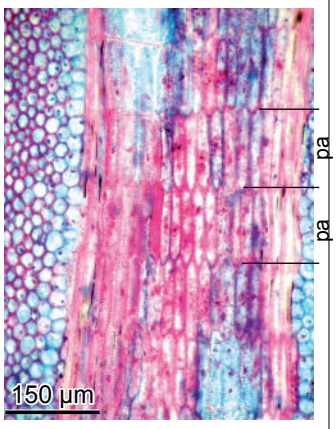



**Fig. 150.** *Tamarix articulata*, Tamaricaceae, tree.

**124** Oil and mucilage cells and canals.

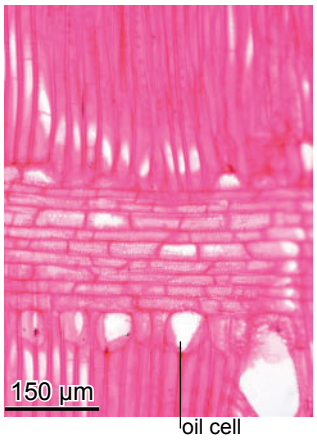



**Fig. 151.** *Laurus azorica*, Lauraceae, tree. Oil cells at the margins of rays.

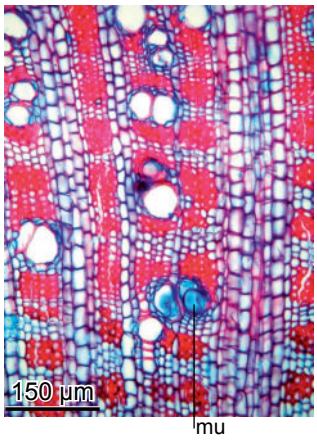



**Fig. 152.** *Lavatera assurgentiflora*, Malvaceae, shrub. Mucilage canals.

**129** Axial canals in the xylem. Tubular intercellular ducts mostly surrounded by epithelium. See **Fig. 21**.

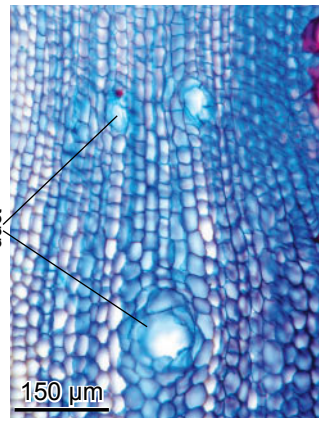



**Fig. 153.** *Cardopatium corymbosum*, Asteraceae, herb. Air duct.

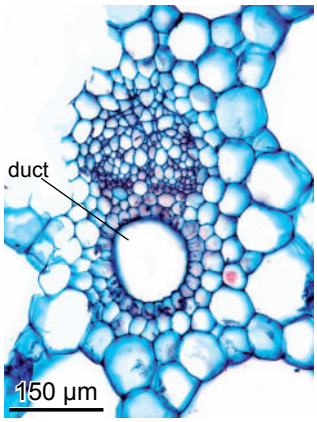



**Fig. 154.** *Nuphar lutea*, Nymphaeaceae, herb. Air duct.

**130** Radial canals in the xylem.

**Fig. 155.** *Euphorbia pulcherrima*, Euphorbiaceae, shrub.

**Fig. 156.** *Euphorbia schimperi*, Euphorbiaceae, succulent shrub.

**133** Successive cambia, Caryophyllaceae type. Large irregular bands of unlignified parenchyma and phloem cells within the stem.

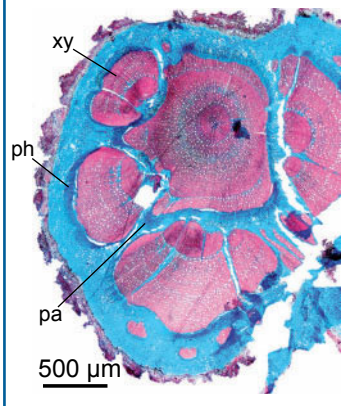



**Fig. 157.** *Polycarpaea aristata*, Caryophyllaceae, Paronychioideae, herb.

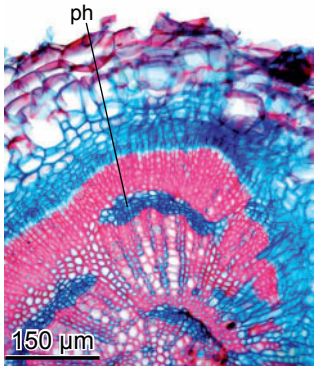



**Fig. 158.** *Sagina maritima*, Caryophyllaceae, Alsinideae, herb.

**133.1** Successive cambia: Concentrically arranged single vascular bundles. Vascular bundles, consisting of xylem and phloem, are separated by parenchyma cells.

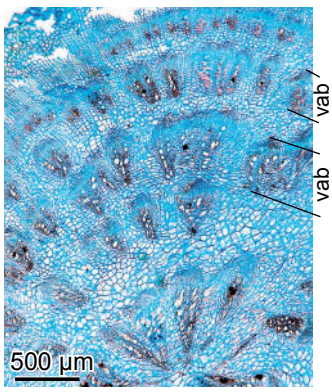



**Fig. 159.** *Chenopodium glaucum*, Amaranthaceae, herb.

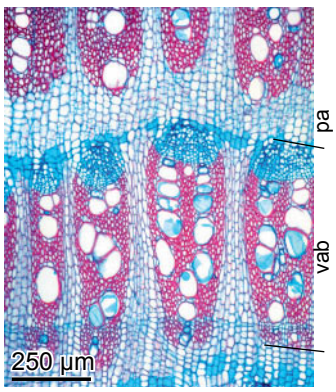



**Fig. 160.** *Bosea cypria*, Amaranthaceae, liana.

**133.2** Successive cambia: Concentric continuous. The successive cambia produce tangential bands of lignified xylem and radial strips of unlignified parenchyma and phloem. See also **Figs. 43** and **165**.

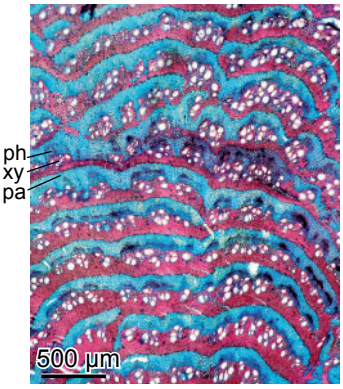



**Fig. 161.** *Atriplex semibaccata*, Amaranthaceae herb.

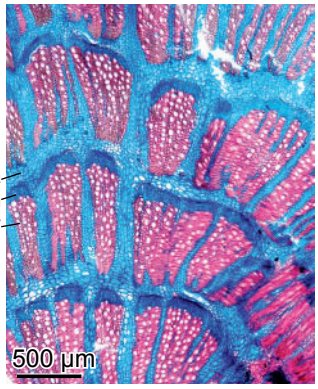



**Fig. 162.** *Aizoon canariense*, Aizoaceae, herb.

**134** Successive cambia: Diffuse = foraminate. More or less irregularly arranged vascular bundles are located in a conjunctive tissue.

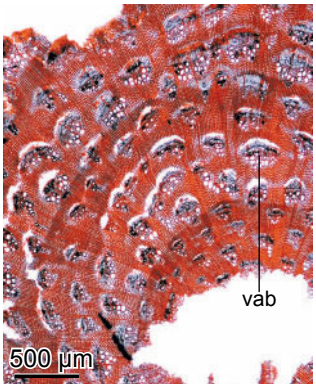



**Fig. 163.** *Noea mucronata*, Amaranthaceae, dwarf shrub.

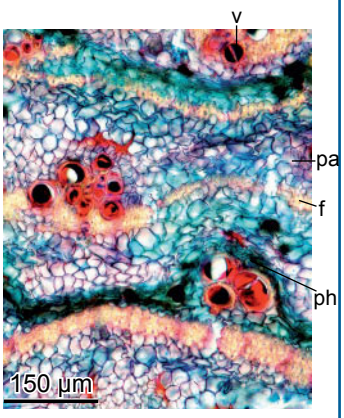



**Fig. 164.** *Chenopodium frutescens*, Amaranthaceae, dwarf shrub.

**134.1** Conjunctive tissue thin-walled. Tissue between phloem strands and fibre bands is thin-walled and unlignified.

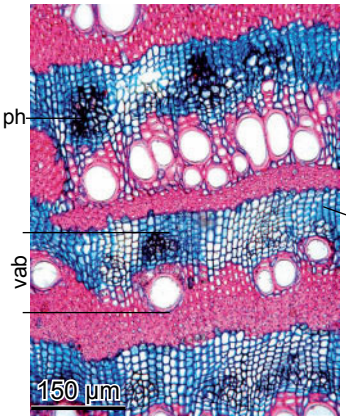



**Fig. 165.** *Einadia nutans*, Amaranthaceae, herb.

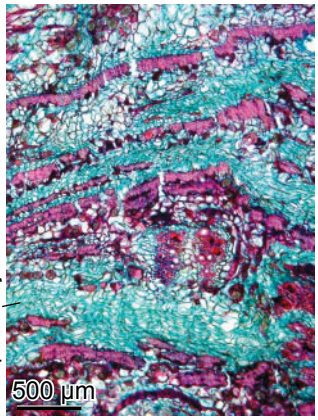



**Fig. 166.** *Anabasis brevifolia*, Amaranthaceae, annual herb.

**135** Interxylary phloem present.

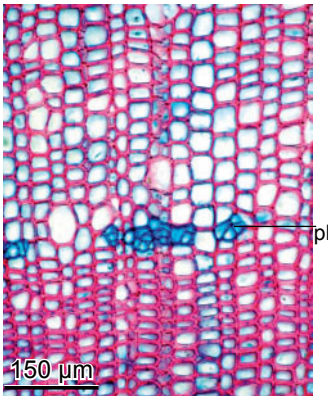



**Fig. 167.** *Ixanthus viscosus*, Gentianaceae, dwarf shrub. Small groups of sieve tubes within the xylem.

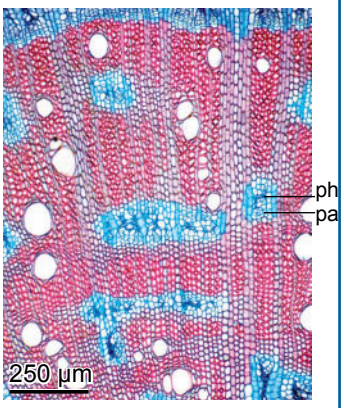



**Fig. 168.** *Leptadenia pyrotechnica*, Asclepiadaceae, shrub. Large groups of sieve tubes, surrounded by parenchyma.

**135.1** Interxylary periderm (cork band).

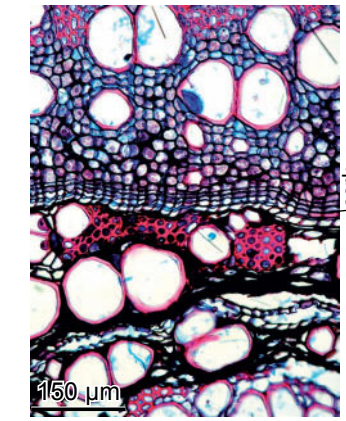



**Fig. 169.** *Epilobium angustifolium*, Onagraceae, herb. Cork band between living and dead xylem.

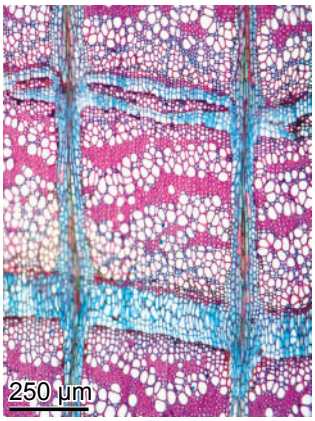



**Fig. 170.** *Artemisia tridentata*, Asteraceae, shrub.

**136** Prismatic crystals present. Solitary rhombohedral or octahedral crystals composed of calcium oxalate.

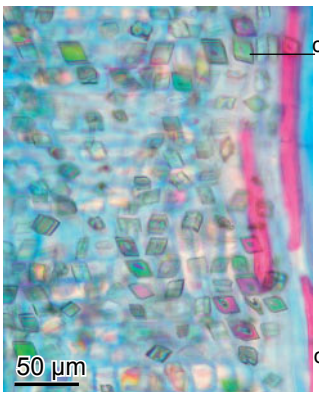



**Fig. 171.** *Berberis julianae*, Berberidaceae, shrub. Prismatic crystals in ray cells.

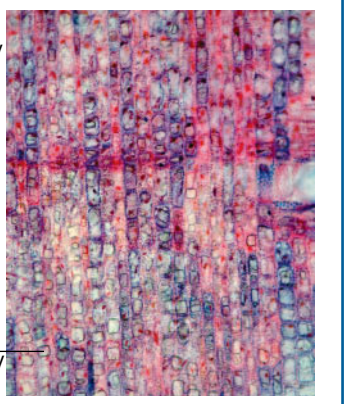


**Fig. 172.** *Proustia cuneifolia*, Asteraceae, shrub.

**142** Prismatic crystals in axial chambered cells.

**Fig. 173.** *Suaeda vermiculata*, Amaranthaceae, dwarf shrub.

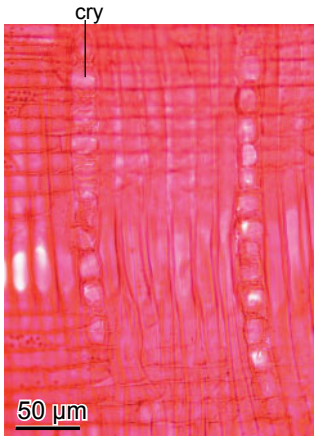



**Fig. 174.** *Acer obtusifolium*, Sapindaceae, tree

**144** Druses present. A compound, irregular, star-like crystal. See **Figs. 197**, **198** and **203**.

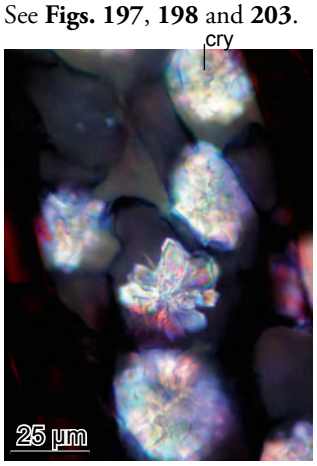



**Fig. 175.** *Euonymus* sp., Celastraceae, shrub.

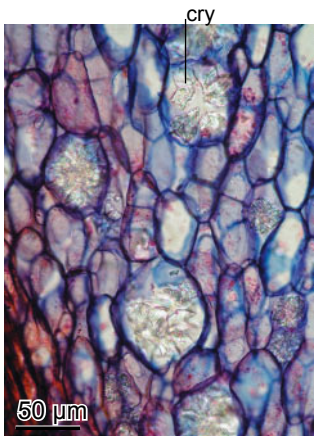



**Fig. 176.** *Astrantia major*, Apiaceae, herb.

**149** Rhaphides present. Bundles of needle-like crystals. See also **Fig. 203**.

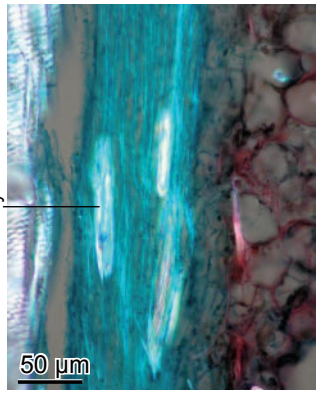



**Fig. 177.** *Asperula aristata*, Rubiaceae, herb. Raphids in idioblasts.

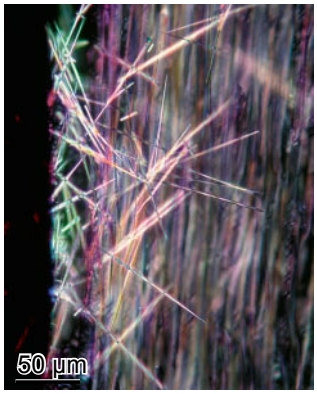



**Fig. 178.** *Bougainvillea spectabilis*, Nyctaginaceae, liana. Type with long needles.

**153** Crystal sand present. Small, irregular crystals.

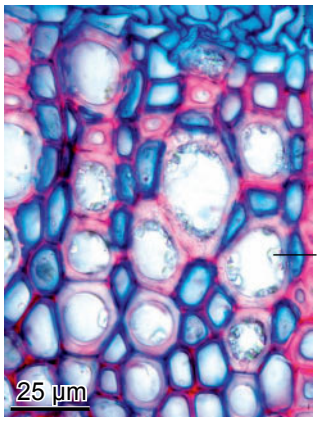



**Fig. 179.** *Traganum moquinii*, Amaranthaceae, shrub. Small crystals at the inside of vessels.

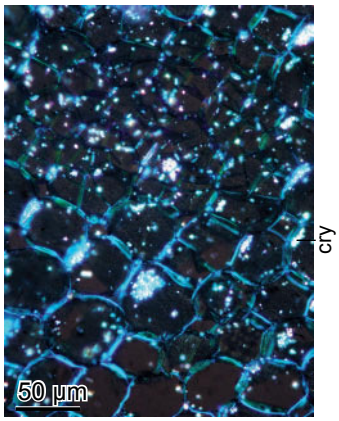



**Fig. 180.** *Piper nigrum*, Piperaceae, shrub. Many small crystals isolated and in clusters in parenchyma cells.

## Bark Features

All characteristics under **R** (*Rinde* = bark) include the phloem and the cortex but not parts outside of the active cork cambium (phellogen). For further definitions see http://www.caf.wvu.edu/Bark/whatis.htm

**R1** Groups of sieve tubes present. Irregularly arranged groups of sieve elements in the phloem.

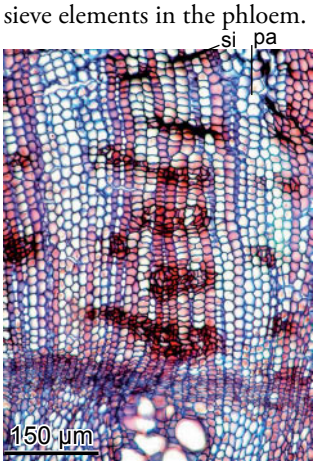



**Fig. 181.** *Thalictrum alpinum*, Ranunculaceae, herb.

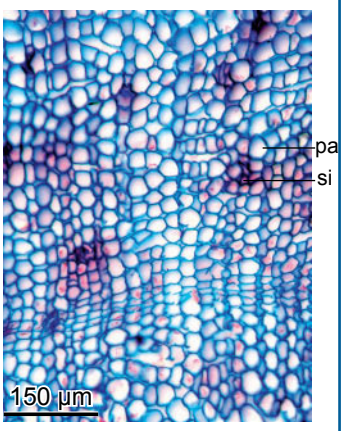



**Fig. 182.** *Aquilegia vulgaris*, Ranunculaceae, herb.

**R2** Groups of sieve tubes in tangential rows.

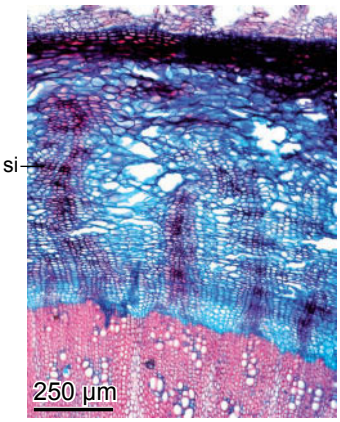



**Fig. 183.** *Erysimum asperum*, Brassicaceae, herb. Groups of sieve tubes in radial and tangential rows.

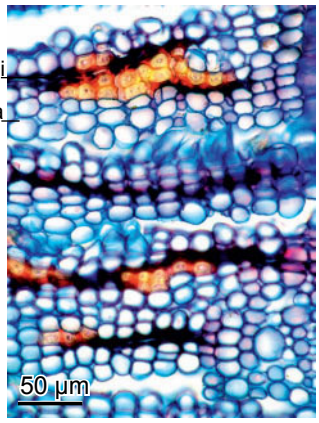



**Fig. 184.** *Berberis vulgaris*, Berberidaceae, shrub. Sieve tubes are compressed black.

**R3** Distinct ray dilatations. Wedge-like zone of parenchyma cells.

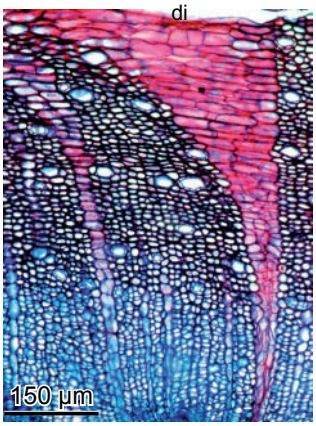



**Fig. 185.** *Hypericum reflexum*, Clusiaceae, shrub. Dilatation between a slightly structured phloem with oil ducts.

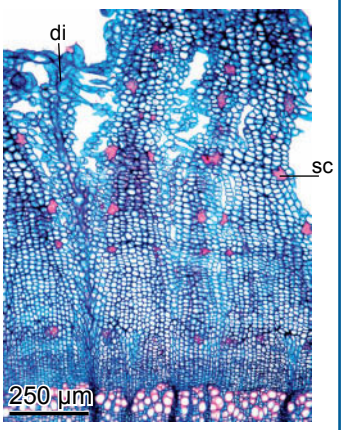



**Fig. 186.** *Armeria arenaria*, Plumbaginaceae, shrub. A dilatation in the radial continuation of a xylem ray.

**R4** Sclereids in phloem and cortex. Groups of cells with lignified, thick-walled cell walls. See also **Fig. 186**.

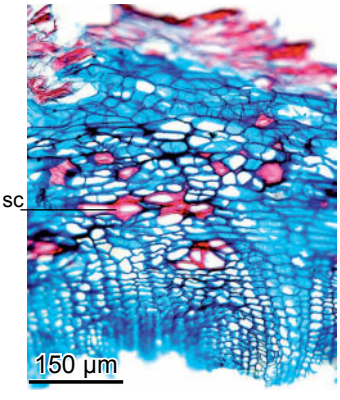



**Fig. 187.** *Carrichtera annua*, Brassicaceae, herb. Single sclereids or small groups in the cortex.

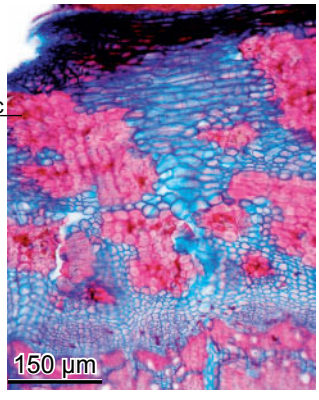



**Fig. 188.** *Alyssum lusitanicum*, Brassicaceae, herb. Large groups of sclereids in phloem and cortex.

**R6** Sclereids in radial rows.

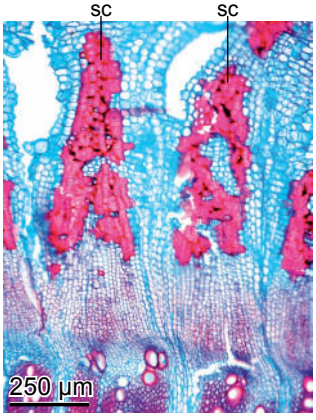



**Fig. 189.** *Diplotaxis tenuifolia*, Brassicaceae, herb. Large groups of sclereids between ray dilatations.

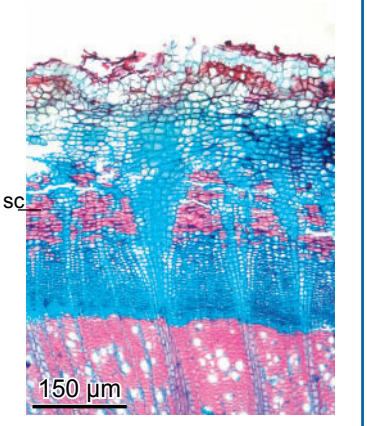



**Fig. 190.** *Marrubium vulgare*, Lamiaceae, chamaephyte. Formation of sclereids occurs in older phloem.

**R.6.1** Sclereids in tangential rows.

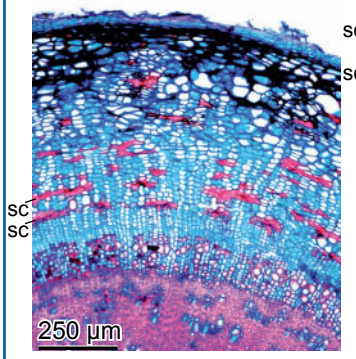



**Fig. 191.** *Arabis hirsuta*, Brassicaceae, herb. Small band-like groups.

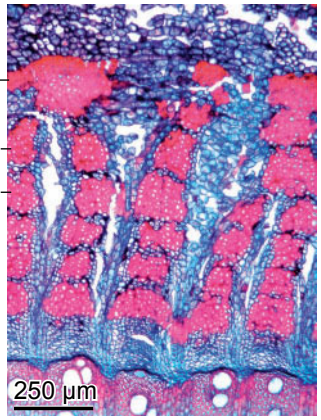



**Fig. 192.** *Myricaria germanica*, Tamaricaceae, small tree. Square groups radially and tangentially arranged.

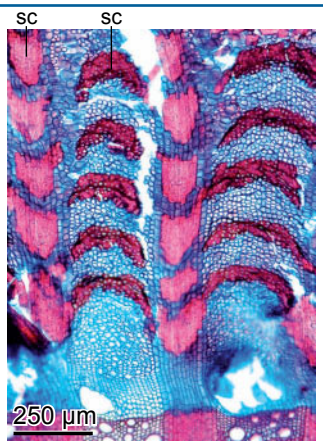



**Fig. 193.** *Tamarix balanse*, Tamaricaceae, small tree. Arc-shaped groups in the sieve-tube region and V-shaped groups in the rays.

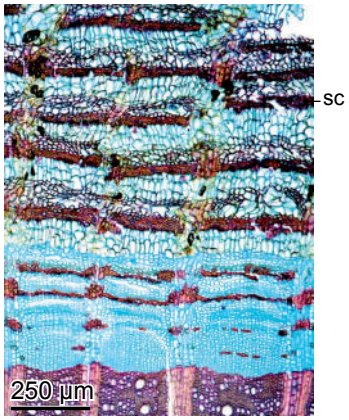



**Fig. 194.** *Mahonia fremontii*, Berberidaceae, shrub. Tangential bands of sclereids between thin-walled sieve-tube/parenchyma zones.

**R7** With prismatic crystals. Solitary rhombohedral or octahedral crystals. See **Fig. 171**.

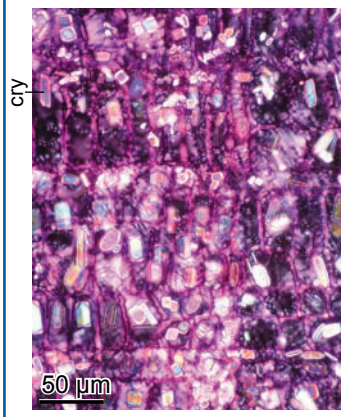



**Fig. 195.** *Marrubium alysson*, Lamiaceae, chamaephyte.

**R7.1** With acicular crystals. Small needle-like crystals which do not occur in bundles.

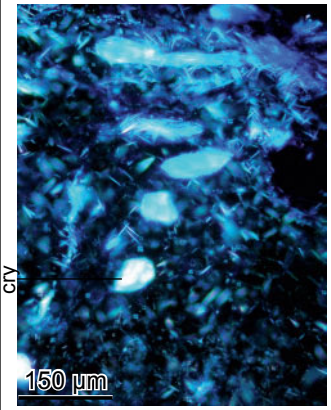



**Fig. 196.** *Phytolacca americana*, Phytolaccaceae, large herb.

**R8** With crystal druses. Compound, irregular, star-shaped crystals.

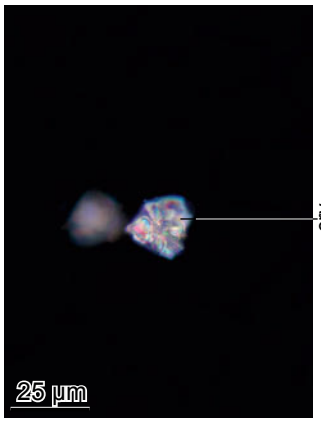



**Fig. 197.** *Buxus sempervirens*, Buxaceae, shrub. Single druse.

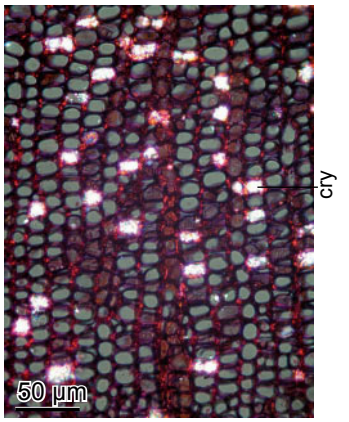



**Fig. 198.** *Buxus sempervirens*, Buxaceae, shrub. Irregular distribution of druses in the phloem.

**R9** With crystal sand. Small, irregular crystals. See also **Fig. 178**.

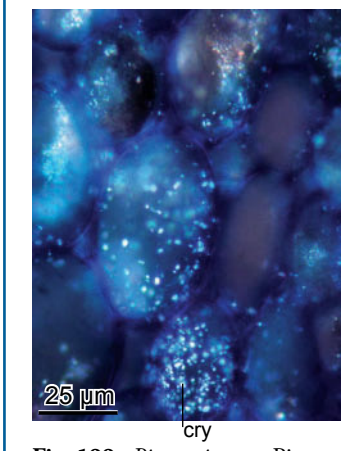



**Fig. 199.** *Piper nigrum*, Piperaceae, shrub.

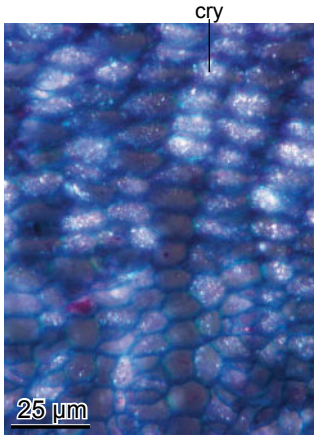



**Fig. 200.** *Teucrium luteum*, Lamiaceae, hemicryptophyte.

**R10** Phloem not well structured. Sieve tubes and parenchyma cells cannot be distinguished in the transverse section.

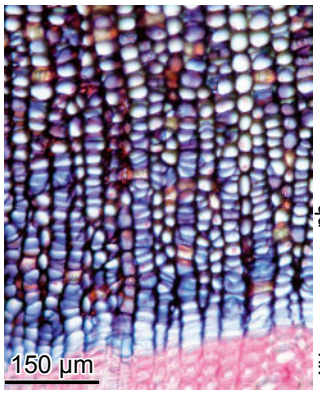



**Fig. 201.** *Buxus sempervirens*, Buxaceae, shrub.

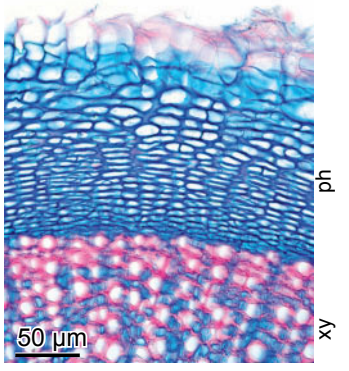



**Fig. 202.** *Arenaria serpyllifolia*, Caryophyllaceae, Alsinoideae, herb.

**R11** With rhaphides. Bundles of needle-like crystals.

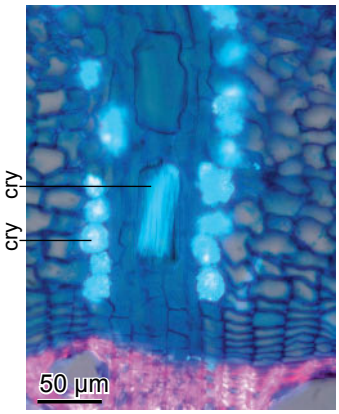



**Fig. 203.** *Parthenocissus inserta*, Vitaceae, liana. Rhaphides in the center and druses at the periphery of the ray.

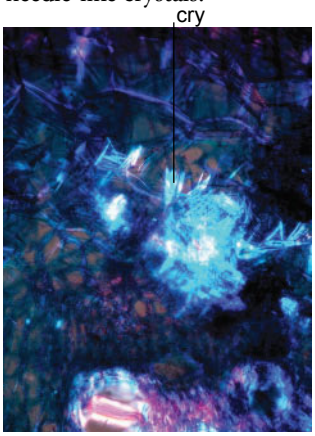



**Fig. 204.** *Impatiens balfourii*, Balsaminaceae, therophyte.

**R12** With laticifers.

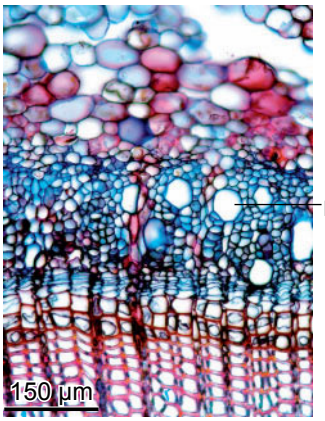



**Fig. 205.** *Drimys winteri*, Winteraceae, tree. Laticifers in the phloem.

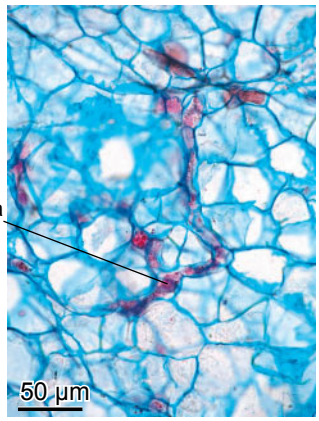



**Fig. 206.** *Sonchus pustulatus*, Asteraceae, shrub.

**R12** With ducts.

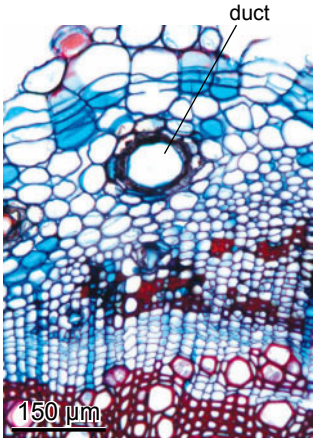



**Fig. 207.** *Artemisia dracunculus*, Asteraceae, herb.

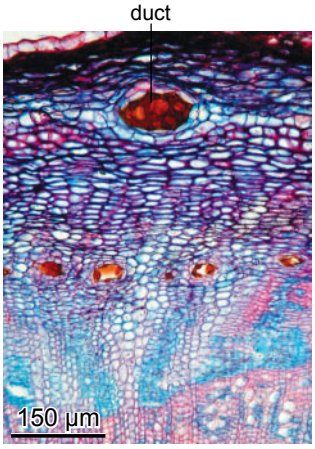



**Fig. 208.** *Centaurea solstitialis*, Asteraceae, herb.

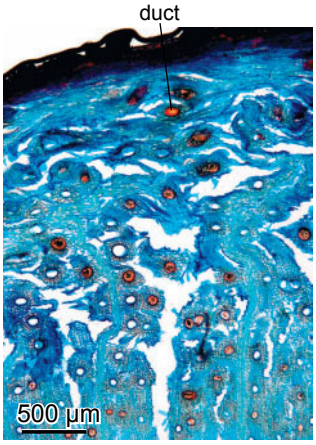



**Fig. 209.** *Pleurospermum austriacum*, Apiaceae, herb.

**R12.1** Excretions produced by cells which are anatomically not different from parenchyma cells.

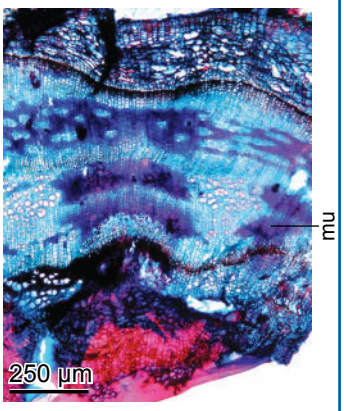



**Fig. 210.** *Mertensia ciliata*, Boraginaceae, herb.

**R14** Cortex with aerenchyma. Parenchyma tissue with large intercellular spaces.

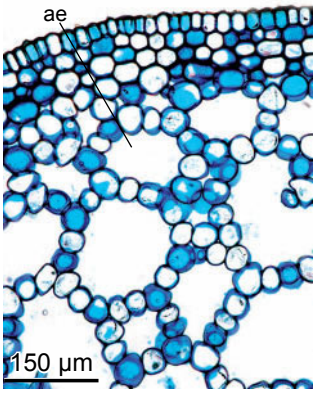



**Fig. 211.** *Menyanthes trifoliata*, Menyanthaceae, herb. Irregularly distributed spaces in the cortex.

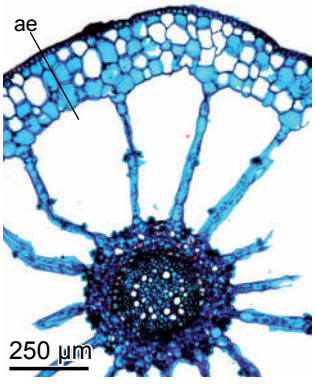



**Fig. 212.** *Myriophyllum spicatum*, Haloragaceae, herb. Large aerenchyma exists outside of the central cylinder.

**Fig. 213.** *Bidens cernua*, Asteraceae, herb.

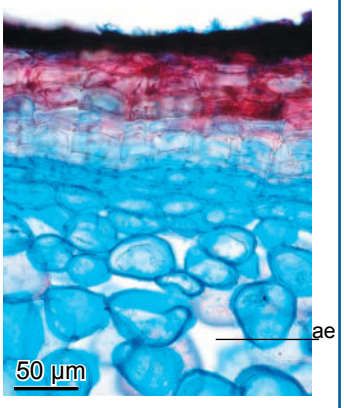



**Fig. 214.** *Primula farinosa*, Primulaceae, herb. With large intercellulars.

**R17** Phelloids. Structural variation of phellem (Evert 2007).

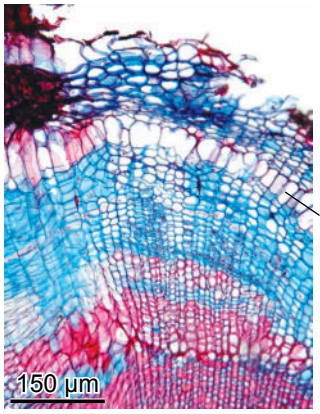



**Fig. 215.** *Antennaria canescens*, Asteraceae, herb. Uni-seriate, phellem-like layer of cells.

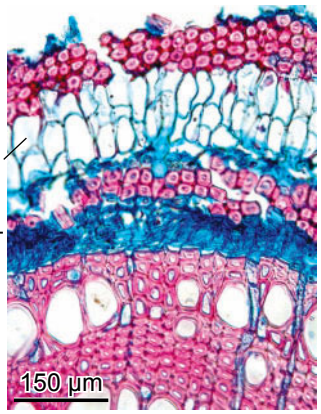



**Fig. 216.** *Sideritis hirsuta*, Lamiaceae, herb. Intra-xylary, uni-seriate, phellem-like layer of cells.

Phellem.

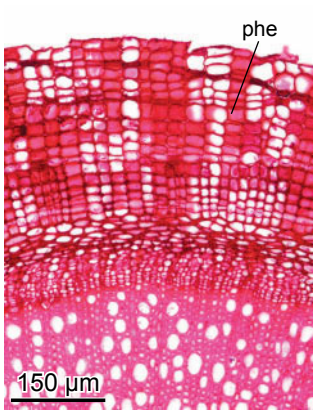



**Fig. 217.** *Alchemilla alpina*, Rosaceae, herb. Radial orientation of rectangular cork cells.

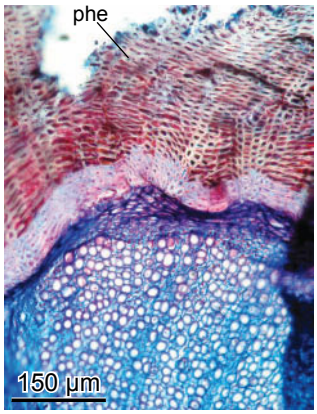



**Fig. 218.** *Saxifraga caesia*, Saxifragaceae, herb. Thick-walled cork cells.

Unknown chemical composition of excretions.

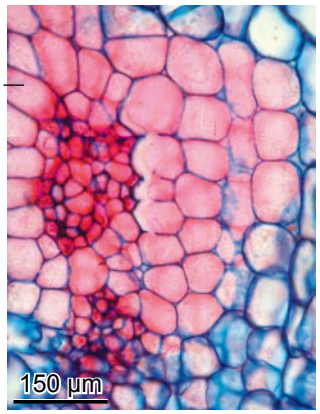



**Fig. 219.** *Cichorium intybus*, Asteraceae, herb. Normal light.

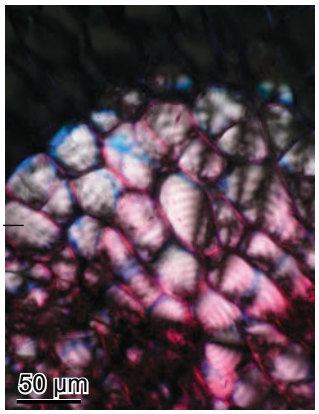



**Fig. 220.** *Cichorium intybus*, Asteraceae, herb. Polarized light.

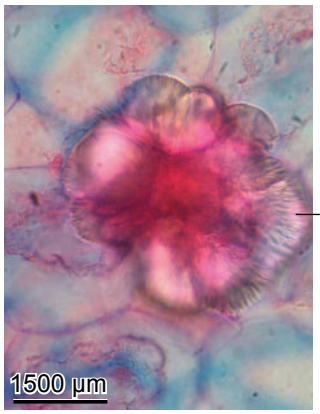



**Fig. 221.** *Peucedanum ostruthium*, Apiaceae, herb. Polarized light.

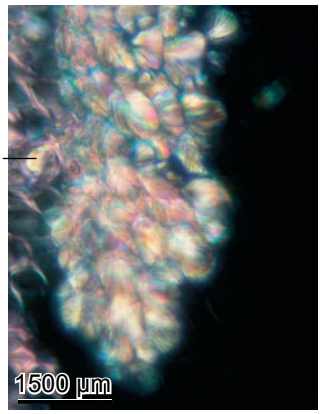



**Fig. 222.** *Acinos arvensis*, Lamiaceae, herb. Polarized light.

**P1** Pith with medullary phloem or vascular bundles.

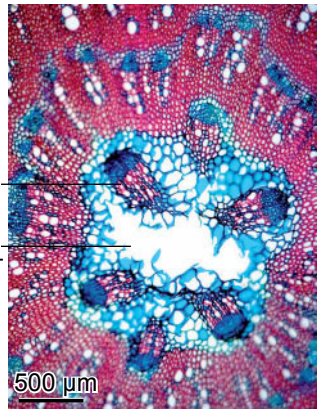



**Fig. 190.** *Atriplex patula*, Amaranthaceae, herb. Star-like arrangement of the vascular bundles in the pith.

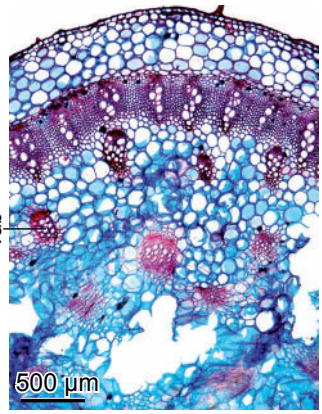



**Fig. 191.** *Abronia fragrans*, Nyctaginaceae, herb. Irregular arrangement of the vascular bundles in the pith.

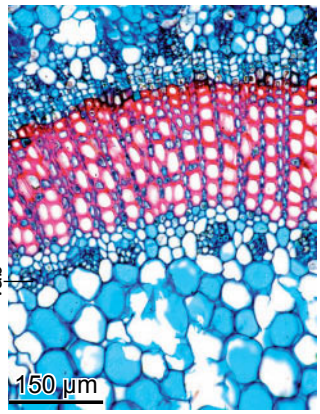



**Fig. 192.** *Vinca major*, Apocynaceae, herb. With groups of sieve tubes at the periphery of the pith.

**P2** Pith with lacitifers or intercellular canals.

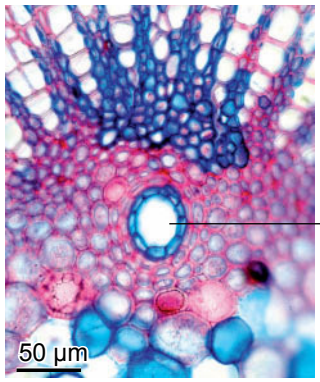
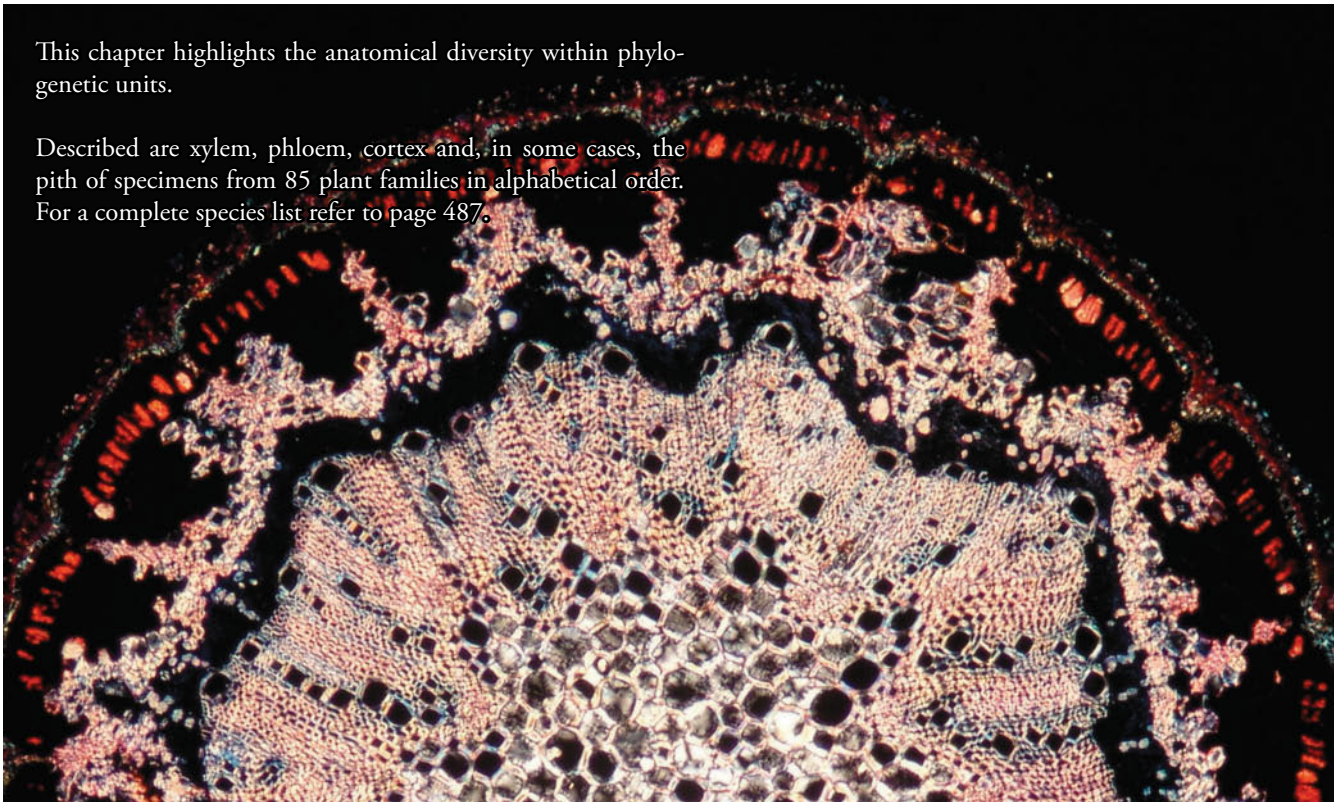



**Fig. 193.** *Liquidambar styraciflua*, Hamamelidaceae, tree. Duct surrounded by unlignified parenchyma cells.

# 5. Monographic Descriptions



This chapter highlights the anatomical diversity within phylogenetic units.

Described are xylem, phloem, cortex and, in some cases, the pith of specimens from 85 plant families in alphabetical order. For a complete species list refer to page 487.

# Aizoaceae



### Number of species, worldwide and in Europe

The Aizoaceae family includes 127 genera with 2500 species. Most of the species grow in the tropics of the southern hemisphere.
In Europe, there are 7 genera with 10 species. Only 2 species of the geneus *Mesembryanthemum* are endemic. All other taxa are naturalized in Europe and the Canary Islands.

### Analyzed material

The xylem and phloem of 5 Aizoaceae species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Semi-woody chamaephytes | 2 | 18 genera |
| Hemicryptophytes and geophytes | 1 | |
| Therophytes | 2 | |
| **Plants analyzed from different vegetation zones:** | | Studies from other authors: |
| Mediterranean | | 18 genera |
| Arid | 3 | |
| Subtropical | 2 | |

All species analyzed grow near the seashore in the Mediterranean and in subtropical climates.

**Analyzed species:**

*Aizoon canariense* L.
*Aptenia cordifolia* (L. fil.) N.E. Br.
*Carpobrotus acinaciformis* (L.) L.
*Mesembryanthemum crystallinum* L.
*Mesembryanthemum nodiflorum* L.

*Mesembryanthemum crystallinum*

*Carpobrotus edulis*

*Aptenia cordifolia*

**Characteristics of the xylem**

Annual rings are absent. Characteristic is the presence of successive cambia. The more-or-less circular arranged xylem/phloem zones are separated by parenchymatic zones (conjunctive tissue) (**Figs. 1-4**). Perforations are simple and inter-vessel pits are small and round (**Fig. 5**). Fibres are thin- to thick-walled. The axial parenchyma is absent or paratracheal (**Fig. 4**). Rays can be fairly large with often irregularly formed cells, 1-3-seriate or absent (**Figs. 2**, **4** and **6**). Ray cell walls are mostly thin and unlignified (**Fig. 1**). Short rhaphides (20 µm) are bundled in a few idioblasts in the inter-vascular bundle zone (**Fig. 3**). Crystals are absent in *Aizoon canariensis*.

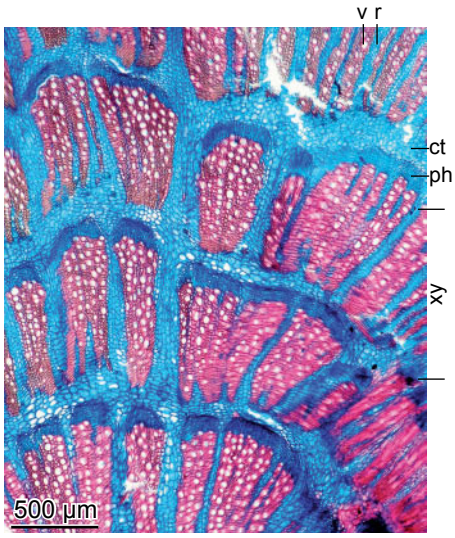



**Fig. 1.** Stem with successive cambia. Irregular bands of xylem, phloem and adjacent parenchymatic cells, connected with large rays. Root collar of a 15 cm-high plant with succulent leaves, ruderal site, thermophile zone, subtropical climate. Gran Canaria, Canary Islands. *Aizoon canariense*, transverse section.

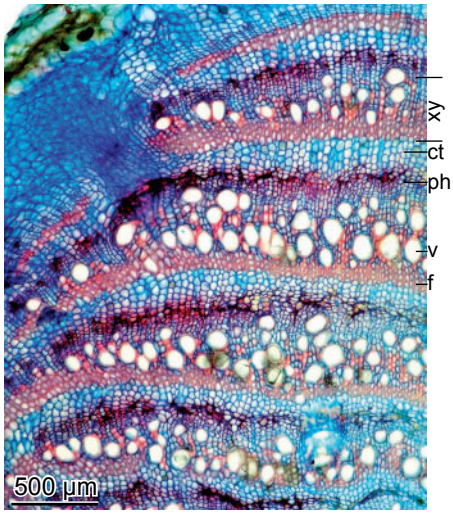



**Fig. 2.** Stem with successive cambia. Tangential bands of xylem, phloem and adjacent parenchymatic conjunctive tissue. Rays are absent. Root collar of a long hanging plant with succulent leaves, thermophile zone, subtropical climate, Gomera, Canary Islands. *Aptenia cordifolia*, transverse section.

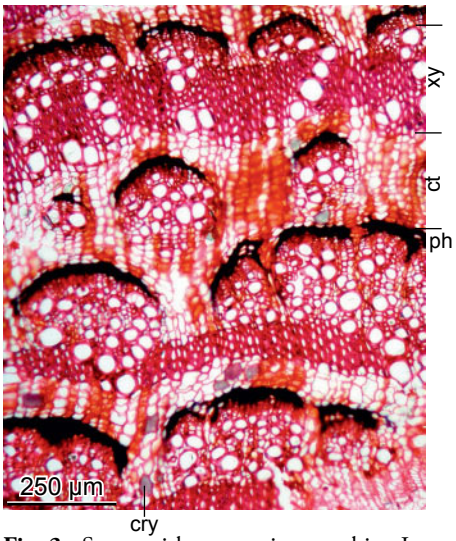



**Fig. 3.** Stem with successive cambia. Irregular bands of xylem, phloem and parenchyma bands. Grey filled cells represent idioblasts with bundles of rhaphides. Stem of a several-meter-long chamaephyte with succulent leaves, garden on the coast, Mediterranean zone, Algarve, Portugal. *Carpobrotus acinaciformis*, transverse section.

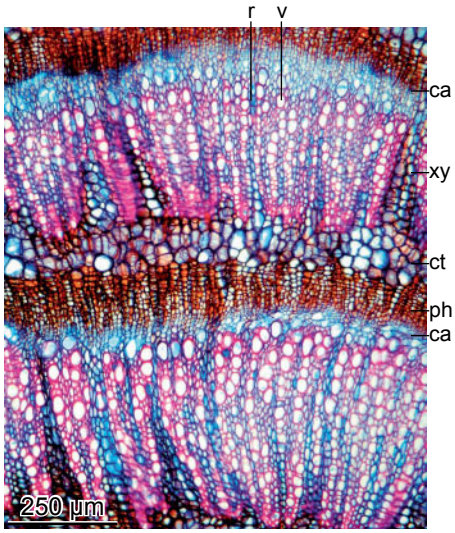



**Fig. 4.** Stem with successive cambia. Tangential bands of xylem and phloem, in formation process in mid February. Phloem with small, radially oriented cells, adjacent parenchyma with large cells. Rays mostly unlignified, 1-3-seriate. Root collar of succulent, 10 cm-high plant, ruderal site, thermophile zone, subtropical climate, Tenerife, Canary Islands. *Mesembryanthemum cristallinum*, transverse section.

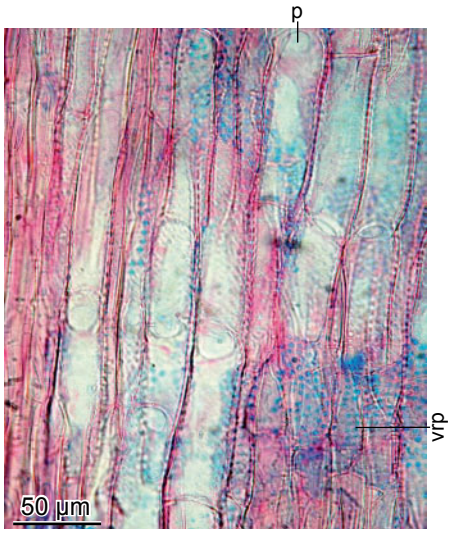



**Fig. 5.** Vessels with simple perforations and small round inter-vessel pits. Root collar of a 15 cm-high annual plant with succulent leaves, ruderal site, thermophile zone, subtropical climate, Gran Canaria, Canary Islands. *Aizoon canariense*, radial section.

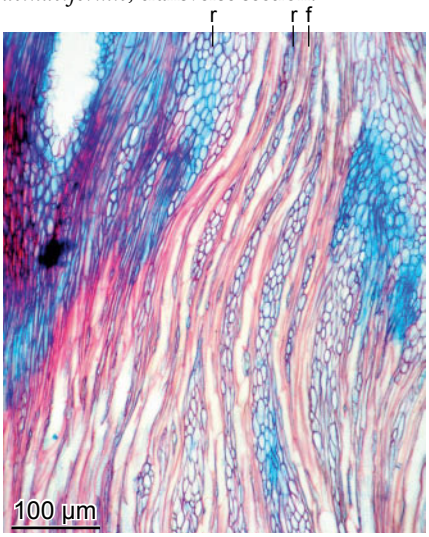



**Fig. 6.** Rays 3 to 6-seriate. Cell size and form is variable. Root collar of a 15 cm-high annual plant with succulent leaves, ruderal site, thermophile zone, subtropical climate, Gran Canaria, Canary Islands. *Aizoon canariense*, tangential section.

### Characteristics of the phloem

Outside the peripheral circle of vascular bundles is a parenchymatic zone, which is delimitated by the lateral meristem and the phellem (**Fig. 7-9**). Many idioblasts with rhaphides are in both *Mesembryanthemum* species (**Fig. 9**).

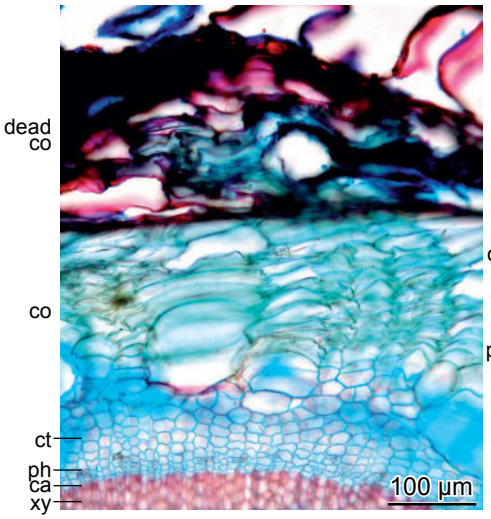



**Fig. 7.** Bark with a small phloem with small cells, large parenchyma cells and very thin-walled phellem cells (black and red). Root collar of a long hanging chamaephyte with succulent leaves, wall, thermophile zone, subtropical climate, Gomera, Canary Islands. *Aptenia cordifolia*, transverse section.

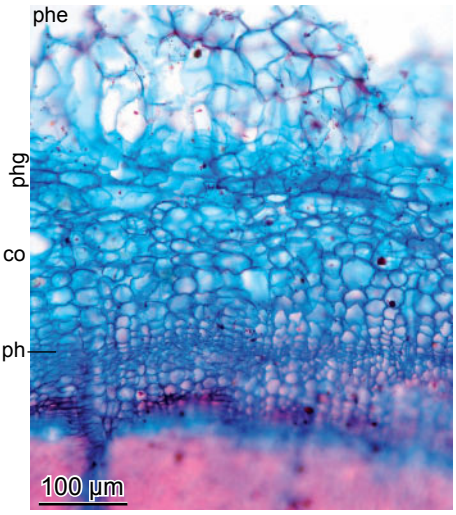



**Fig. 8.** Bark with a small phloem with small cells, a primary bark with large parenchyma cells and an irregular, very thin-walled phellem. A lateral meristem consisting of a band of small cells is outside of the phloem. Root collar of a succulent 10 cm-high plant, ruderal site, thermophile zone, subtropical climate, Gomera, Canary Islands. *Mesembryanthemum nodiflorum*, transverse section.

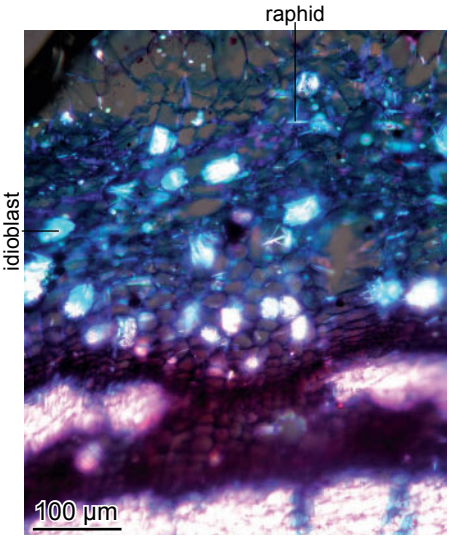



**Fig. 9.** Bundles of rhaphides in idioblasts in the parenchyma zone of the primary bark. Root collar of a succulent 10 cm-high plant, ruderal site, thermophile zone, subtropical climate, Gomera, Canary Islands. *Mesembryanthemum nodiflorum*, transverse section, polarized light.

### Characteristic features of taxa

The presence or absence of ray-like radial strips of thin-walled parenchyma, the size and distribution of earlywood vessels, as well as the presence of rhaphides can differentiate species. There is not enough material to present a definite classification neither in relation to species nor to growth forms.

### Ecological trends and relations to life forms

Since all species analyzed grow in dry regions an ecological grouping could not be recognized.

### Discussion in relation to previous studies

Carlquist 2007 analyzed much material and studied in detail the ontogeny of successive cambia of 11 perennial species of 11 genera representing a wide range of growth forms. The present study does not include the whole range of anatomical structures. Not represented are species with vascular strands (*Stayleria neilii*) or species with scalariform inter-vessel pits.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| | **Total number of analyzed species** | **5** |
| 2 | growth rings indistinct or absent | 5 |
| 5 | diffuse-porous | 5 |
| 10 | vessels in radial multiples of 4 or more common | 3 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 5 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 5 |
| 58 | dark-stained substances in vessels and/or fibers present (gum, tannins) | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 5 |
| 70 | fibers thin- to thick-walled | 5 |
| 75 | parenchyma absent or unrecognizable | 3 |
| 79 | parenchyma paratracheal | 2 |
| 96 | rays exclusively uniseriate | 1 |
| 97 | ray width predominantly 1-3 cells | 2 |
| 98 | rays commonly 4-10-seriate | 4 |
| 105 | ray: cells upright or square | 2 |
| 117 | rayless | 2 |
| 133 | successive cambia, Caryophyllacea type | 5 |
| 133.2 | successive cambia, concentric continuous | 5 |
| 134.1 | conjunctive tissue thin-walled | 5 |
| 149 | raphids present | 2 |
| R1 | groups of sieve tubes present | 1 |
| R10 | phloem not well structured | 5 |
| R11 | with rhaphides | 2 |
| P1 | with medullary phloem or vascular bundles | 1 |

# Amaranthaceae



**Number of species, worldwide and in Europe**

The Amaranthaceae family, including Chenopodiaceae, has 170 genera with 2400 species. Cosmopolitan and especially characteristic of disturbed, arid or saline habitats.

In Europe there are 38 genera with 106 species. The majority are represented by the genera *Salsola* (25 species), *Chenopodium* (23 species), *Atriplex* (19 species), and *Amaranthus* (12 species).

**Analyzed material**

The xylem and phloem of 15 genera with 62 species are analyzed here.

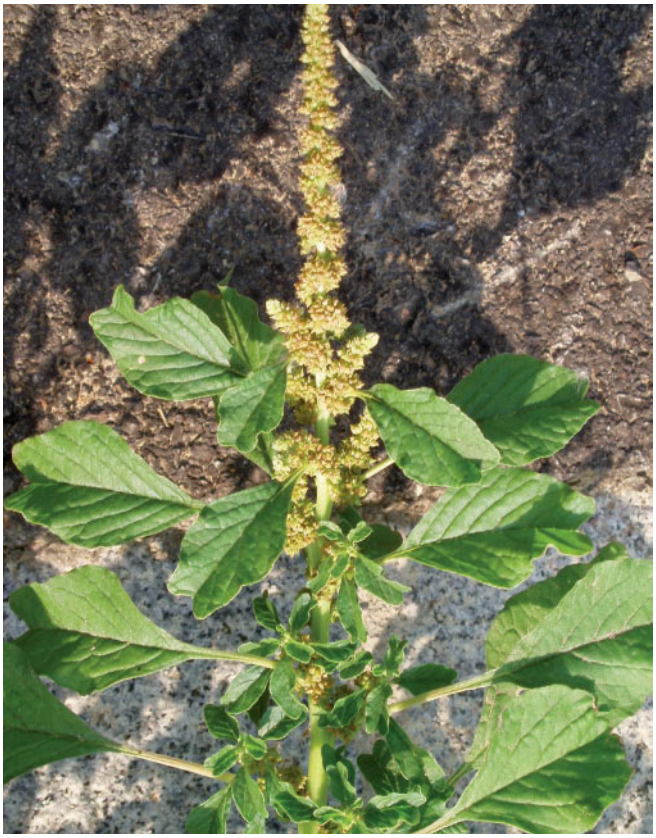
| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 15 | 30 species |
| Woody chamaephytes | 11 | |
| Semi-woody chamaephytes | 3 | 16 genera |
| Liana | 3 | 1 species |
| Hemicryptophytes and geophytes | 3 | |
| Therophytes | 27 | 1 species |
| **Plants analyzed from different vegetation zones:** | | Studies from other authors: |
| Alpine and subalpine | 1 | |
| Hill and mountain | 12 | |
| Mediterranean | 12 | 2 species |
| Arid | 22 | 23 |
| Subtropical | 10 | 2 species |
| Tropical | | 2 species |

*Haloxylon ammodendron* (photo: W. Schulze)

**Analyzed species:**

*Achyranthes aspera* L.
*Achyranthes sicula* (L.) All.
*Aerva javanica* Juss. ex Schult.
*Aerva persica* Merr.
*Agathophora alopecuroides* (Del.) Fenzl.
*Amaranthus blithum* L.
*Amaranthus cruentus* L.
*Amaranthus deflexus* L.
*Amaranthus hybridus* L.
*Amaranthus lividus* L.
*Amaranthus retroflexus* L.
*Amaranthus standleyanus* Covas
*Amaranthus viridis* L.
*Anabasis brevifolia* C.A. Mey
*Arthrocneumum fruticosum* (L.) Moq.
*Arthrocneumum glaucum* (Del.) Ung.
*Arthrocneumum macrostachya* Moris et Delponte
*Arthrocneumum perenne* (Mill) Moss.
*Atriplex canescens* (Pursh) Nutt.
*Atriplex dimorphostegia* Kareilin & Kiriloff
*Atriplex glauca* Maire
*Atriplex halimus* L.
*Atriplex patula* L.
*Atriplex portulacoides* L.
*Atriplex prostrata* DC
*Atriplex saggitata* Bork.
*Atriplex semibaccata* R.Br.
*Bosea cypria* Boiss.ex Hook
*Bosea yervamora* L.
*Cheneloides tomentosa* Botsch
*Chenopodium album* L.
*Chenopodium bonus-henricus* L.
*Chenopodium frutescens* C.A. Mey
*Chenopodium glaucum* L.
*Chenopodium hybridum* L.
*Chenopodium murale* L.
*Chenopodium polyspermum* L.
*Chenopodium strictum* Roth
*Chenopodium urbicum* L.
*Cornulaca monacantha* Del.
*Einadia nutans* Scott
*Haloxylon articulatum* (Moq.) Bunge
*Haplopeplis perfoliata* (Forsk.) Bg. ex Schweinf.
*Kochia prostrata* DC
*Krascheninnikovia ceratoides* (L.) Gueldenst.
*Krascheninnikovia lanata* (Pursh) A. Meeuse & Smit
*Mairena pyramidata* (Benth.) Paul G.Wilson
*Noea mucronata* Ascherson et Schweinf.
*Patellifolia patellaris* Scott et al.
*Patellifolia procumbens* F. L. et W.
*Polycneum arvense* L.
*Salsola foetida* Del.
*Salsola genistoides* Juss. ex Poir.
*Salsola kali* L.
*Salsola oppositifoila* Desf.
*Salsola vermiculata* L.
*Salsola verticillata* Schousboe
*Suaeda fruticosa* Forsk.
*Suaeda pruniosa* Lange
*Suaeda vera* L.F. Gmelin
*Suaeda vermiculata* Forsk.
*Traganum moquinii* Webb

*Amaranthus caudatus* (photo: Zinnert)



*Amaranthus lividus*

*Salsola kali*

*Chenopodium bonus-henricus*

**Characteristics of the xylem**

Annual rings occur in the present material in a few species of the arid, Mediterranean and subtropical climate (**Figs. 1** and **2**). Circle-like intra-annual bands with successive cambia should not be confused with annual rings (**Fig. 3**). Amaranthaceae do not get very old. The maximum age found was 21 years (*Haloxylon persicum*, 3 m-high tree). Most species with countable rings do not exceed 6 years. Ring-boundaries are defined by semi-ring porosity (**Fig. 2**) or a zone of thick-walled fibers (**Fig. 1**). Rings are indistinct or absent in 60 of the 64 species analyzed.

Vessels of most species are solitary (**Fig. 2**) or are arranged in mostly short (2-4 vessels) radial multiples (**Fig. 3**). Only 5 species have vessels in long radial multiples (**Fig. 4**). The diameter of earlywood vessels varies from 15-150 µm. Earlywood vessels are smaller than 20 µm in small plants (*Polycneum arvense*, *Cheneloides tomentosa* and *Kochia prostrata*; **Fig. 2**) as well in the dwarf shrubs *Arthrocneumum glaucum* and *Suadea pruniosa*. The diameter of earlywood vessels of the majority of species varies between 25-70 µm. The diameter in the liana *Bosea cypria* exceeds 100 µm. Vessel density varies in the majority of analyzed species between 100-200/mm$^2$. In 15 species it exceeds 200/mm$^2$. Vessels are thin- to thick-walled (**Fig. 4**) or thick-walled (39 species; **Fig. 5**). Vessels contain exclusively simple perforations mainly in a vertical position (**Fig. 6**). Inter-vessel pits are predominantly small and round (**Fig. 6**), locally slightly scalariform e.g. in *Patellifolia procumbens* and almost scalariform along the whole radial vessel wall in *Chenopodium bonus-henricus* (**Fig. 7**). Vestured pits were not clearly visible with the light microscope even on material stained only with safranin.

Dark-stained substances in the center of the stem (heartwood) are quite frequent in dwarf shrubs and shrubs (**Fig. 8**), but never in herbs. Small, thin-walled, unlignified tylosis can be found in *Amaranthus blithum*, *Amaranthus hybridus*, *A. retroflexus*, *Achyranthes aspera*, *A. sicula*, *Bosea cypria* and *B. yervamora* (**Fig. 9**).

In all species the radial walls of fibers are perforated by very small slit-like or round pits (<2 µm; **Fig. 24**). Fibers are in the majority of analyzed species thin- to thick-walled (30 species; **Figs. 4** and **29**) or thick-walled (28 species; **Fig. 10**). Fibers are missing in *Amaranthus blithum*, *A. standleyanus*, *Chenopodium bonus-henricus* and *C. glaucum*. The distribution of axial parenchyma is paratracheal (**Figs. 4**, **10** and **29**) or pervasive (*Amaranthus blithum*, *A. standleyanus*, *Chenpodium bonus-henricus* and *C. glaucum*; **Fig. 11**). Xylem components are rarely storied unlike the parenchyma cells of the stem-intern phloem, which are mostly storied (**Fig. 12**).

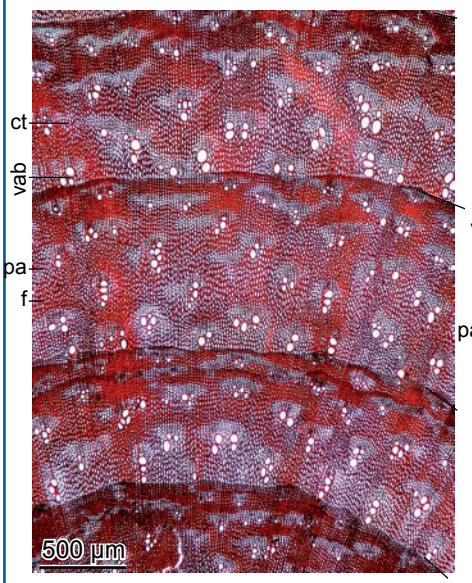



**Fig. 1.** Distinct rings in the rayless xylem of a species with diffuse (foraminate) dispersed vascular bundles. The ring boundary is characterized by thick-walled latewood and thin-walled earlywood fibres. Stem of a 50 cm-high dwarf shrub, seashore with brackish water, Mediterranean zone, Narbonne, France. *Arthrocneumum fruticosum*, transverse section.

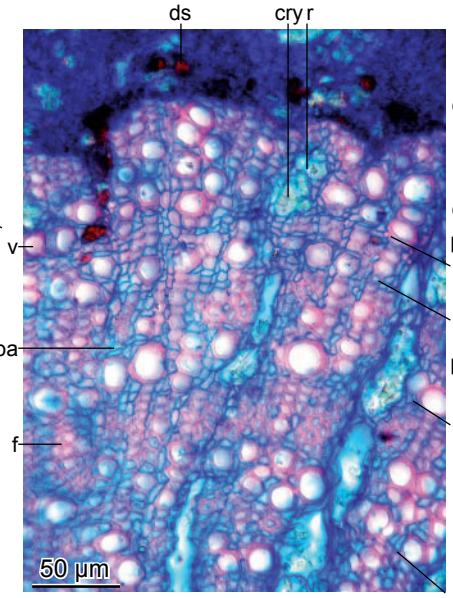



**Fig. 2.** Recognizable rings in the xylem. The ring boundary is characterized by an indistinct, semi-ring porosity. Between the thick-walled lignified vessels with a diameter < 20 µm occur thin-walled pervasive parenchyma cells. Root collar of a 10 cm-high dwarf shrub in the cold steppe, subalpine zone, Mongolia. *Kochia prostrata*, transverse section.

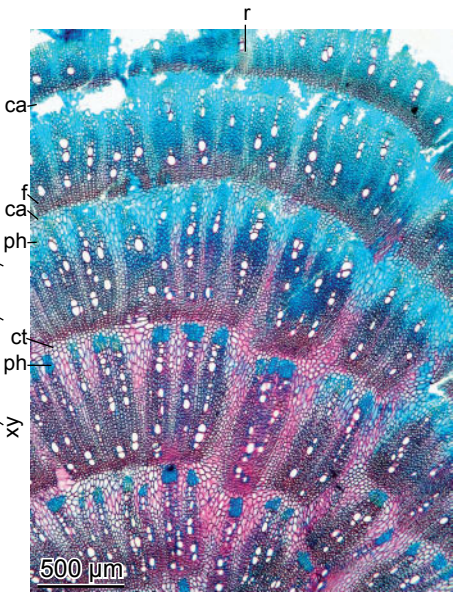



**Fig. 3.** Intra-annual growth zones produced by successive cambia. The radial dimension of the two outermost blue and green zones are complete, but unlignified. Two stem-internal cambia are active. The vessels stay solitary or in short radial multiples. 40 cm-high annual plant, ruderal site, hill zone, Jena, Germany. *Chenopodium urbicum*, transverse section.

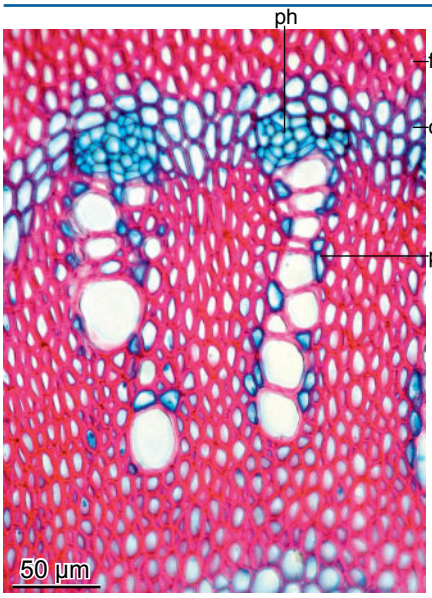



**Fig. 4.** Vessels of the xylem stay in long radial multiples which are accompanied by paratracheal parenchyma. Xylem fibres around the vessels are fairly small and intensively lignified, conjunctive parenchyma cells (at the periphery of the phloem) are larger and less lignified. 50 cm-high annual plant, ruderal site, hill zone, Birmensdorf, Switzerland. *Atriplex patula*, transverse section.

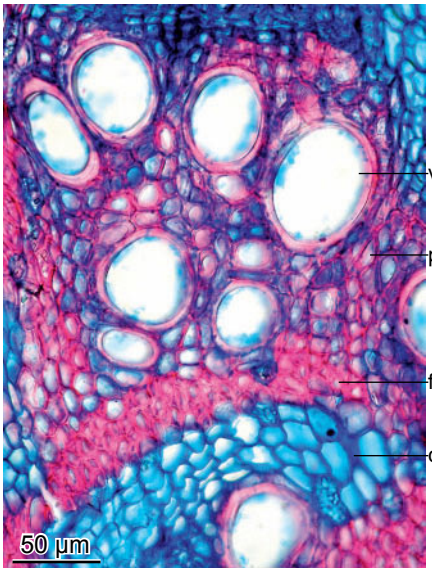



**Fig. 5.** Thick-walled vessels are surrounded by parenchyma cells. Fibres in the tangential band are fairly thick-walled. Conjunctive parenchyma cells are thin-walled and unlignified. 30 cm-high annual plant, seashore, subtropical climate, Gran Canaria, Canary Islands. *Atriplex semibaccata*, transverse section.

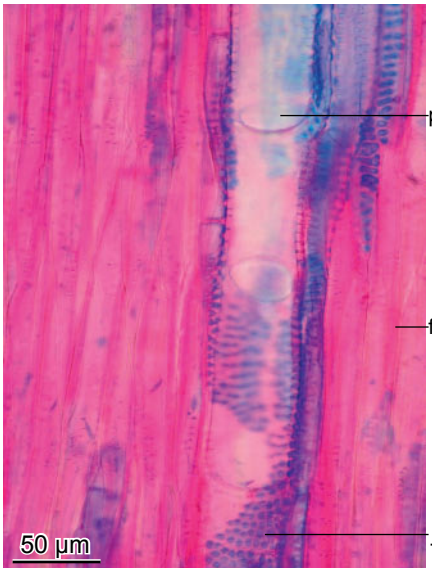



**Fig. 6.** Vessels with simple perforations and round inter-vessel pits in opposite position. 40 cm-high annual plant, Ruderal site, subtropical climate, Gomera, Canary Islands. *Achyranthes aspera*, radial section.

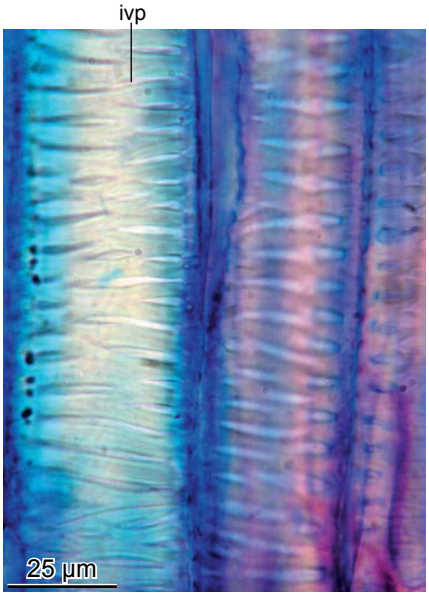



**Fig. 7.** Vessels with almost scalariform inter-vessel pits. 40 cm-high annual plant, ruderal site, subalpine zone, Davos, Switzerland. *Chenopodium bonus-henricus*, radial section.

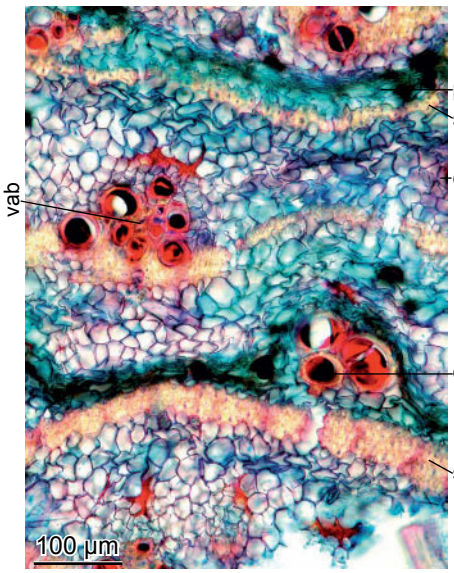



**Fig. 8.** Dark-stained substances (phenols?) in thick-walled vessels. Some conjunctive tissue is partially very thick-walled (sclerenchyma) but it is mostly thin-walled. 30 cm-high dwarf shrub, cold steppe, subalpine zone, Mongolia. *Chenopodium frutescens*, transverse section.

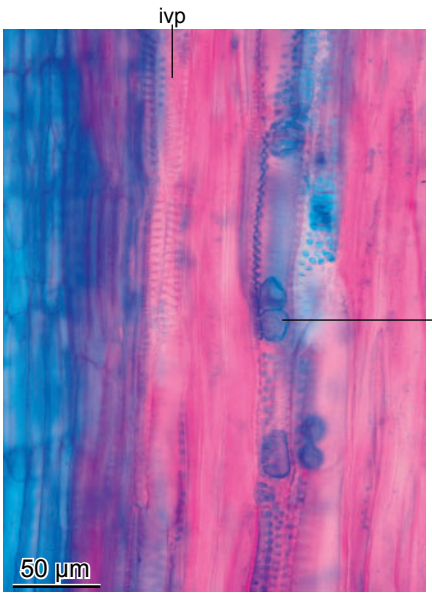



**Fig. 9.** Thin-walled, unlignified tyloses in vessels. 40 cm-high annual plant, ruderal site, subtropical climate climate, Gomera, Canary Islands. *Achyranthes aspera*, radial section.

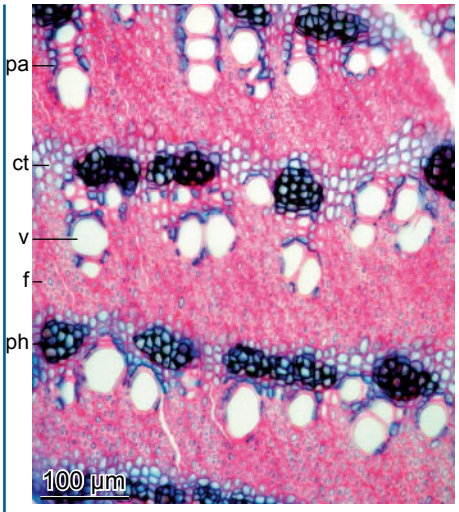



**Fig. 10.** Thick-walled fibres of the xylem surround vessels with paratracheal parenchyma. There are groups of phloem in tangential bands of conjunctive parenchyma cells. 40 cm-high dwarf shrub, seashore, subtropical climate, Gomera, Canary Islands. *Suaeda vermiculata*, transverse section.

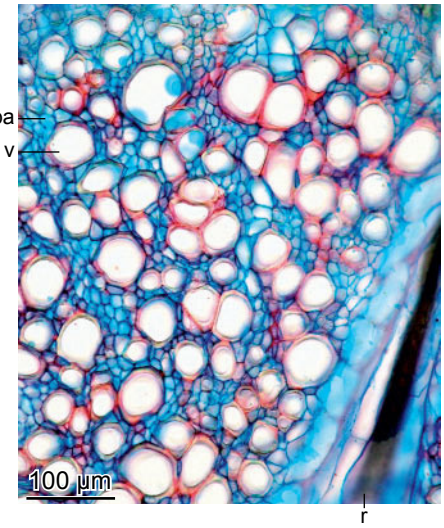



**Fig. 11.** Thick-walled vessels are surrounded by thin-walled pervasive parenchyma. 30 cm-high perennial plant, ruderal site, Mediterranean zone, Provence, France. *Amaranthus blithum*, transverse section.

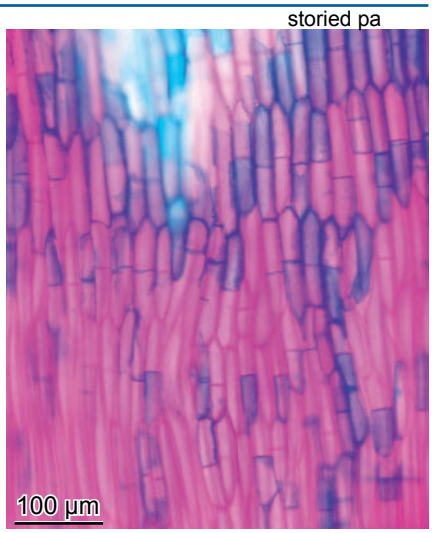



**Fig. 12.** Transition zone between thin-walled parenchymatic tissue (blue) and thick-walled xylem fibres. Parenchyma cells are divided and storied. 40 cm-high annual plant, ruderal site, subtropical climate, Gomera, Canary Islands. *Achyranthes aspera*, tangential section.

Ray diversity is high. It varies from 1-2 to >10 cells (**Figs. 13-15**). Many species contain large rays between vascular bundles, with 4-8 square and upright cells (**Fig. 16**). Ray and axial parenchyma are often confluent (**Fig. 14**). 23 of the 64 analyzed species are rayless e.g. some *Atriplex* and *Chenopodium* species, as well as *Kraschenninnikovia*, *Salsola kali* and others (**Figs. 20-23**). Ray cells are often thin-walled and unlignified (**Fig. 15**). Successive cambia are a characteristic of the majority of the Amaranthaceae but they are missing in the annual *Polycneum arvense* (**Fig. 17**). Vascular bundles are concentric and separated from each other in 19 species (**Figs. 18** and **19**), or concentric continuous in 40 species (**Figs. 20** and **21**) and arranged diffuse (foraminate) in 13 species (**Fig. 22**). The distribution of xylem and phloem varies within plants (**Fig. 23**) and between species. 45 of the 64 species have unlignified conjunctive tissue (**Figs. 20** and **21**). The other species show lignified conjunctive tissue cells with slightly thickened walls (**Fig. 23**). Prismatic crystals occur in 16 species (**Fig. 24**), partially in chambered cells (6 species, **Fig. 25**). 12 show crystal druses. Crystals are deposited in the rays (**Fig. 24**) or the interxylary parenchyma and small crystals surround the inner walls of vessels (**Fig. 26**).

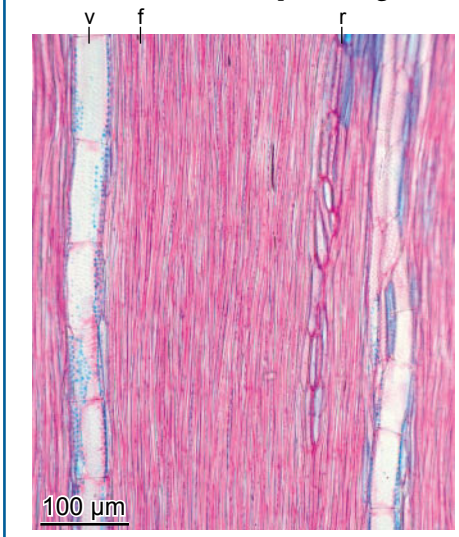



**Fig. 13.** 1-3-seriate rays embedded in a thick-walled fibre tissue. 40 cm-high dwarf shrub, windy coast, subtropical climate, Gran Canaria, Canary Islands. *Atriplex glauca*, tangential section.

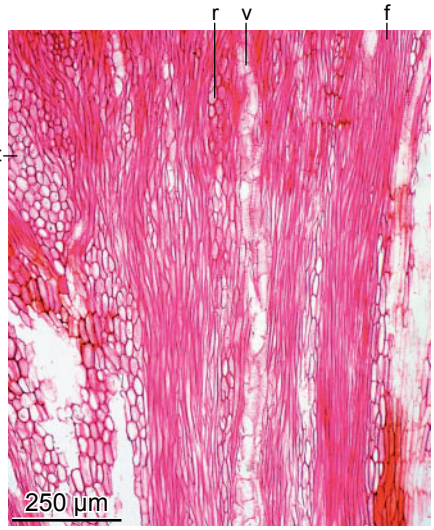



**Fig. 14.** 1-5-seriate rays. Some are confluent to the conjunctive axial tissue. 40 cm-high annual plant, ruderal site, hill zone, Grisons, Switzerland. *Amaranthus retroflexus*, tangential section.

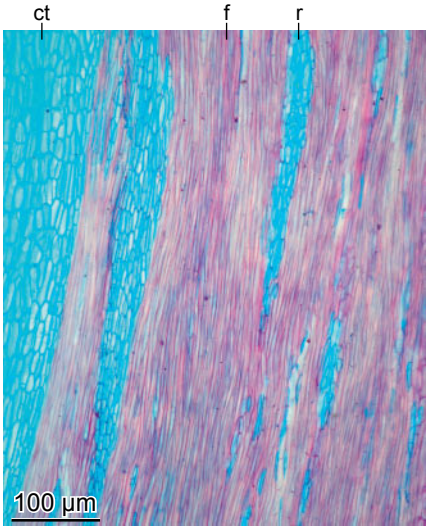



**Fig. 15.** 1- and multi-seriate rays with unlignified cell walls (blue). 40 cm-high annual plant, ruderal site, hill zone, Birmensdorf, Switzerland. *Amaranthus viridis*, tangential section.

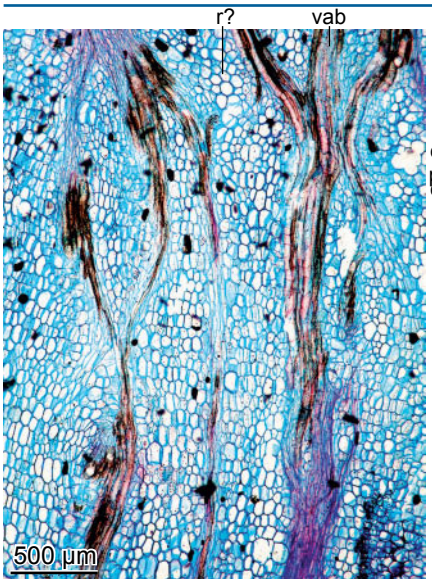



**Fig. 16.** Parenchymatic tissue between vascular bundles. The parenchymatic zones can be interpreted as large rays. 30 cm-high perennial herb, ruderal site, Mediterranean zone, Provence, France. *Amaranthus blithum*, tangential section.

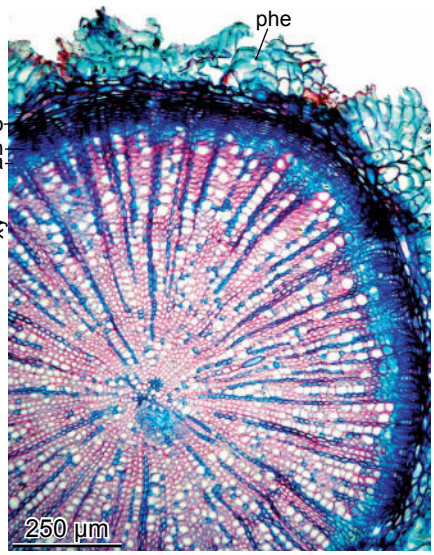



**Fig. 17.** An Amaranthaceae without successive cambia. Characteristic are radial multiple vessels with paratracheal parenchyma and 1-3-seriate rays. 15 cm-high annual plant, ruderal, Mediterranean, Provence, France. *Polycneum arvense*, transverse section.

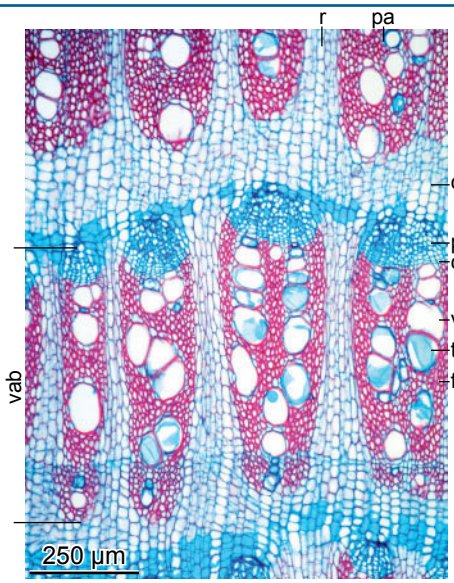



**Fig. 18.** Stem internal xylem/phloem bands consist of concentrically arranged vascular bundles, separated by unlignified rays. Ray-like between the tangential rows of vascular bundles is a thin-walled, unlignified conjunctive parenchymatic tissue. Vessels contain tylosis. Liana, hedge, Mediterranean, Paphos, Cyprus. *Bosea cypria*, transverse section.

**Fig. 19.** Stem internal xylem/phloem bands consist of concentrically arranged vascular bundles, separated from each other. The conjunctive tissue consists of large, thin-walled, unlignified parenchymatic cells. Rays in a strict sense are absent, see **Fig.16**. 50 cm-high annual plant, field, moist site, Mediterranean, Haute Provence, France. *Amaranthus hybridus*, transverse section.

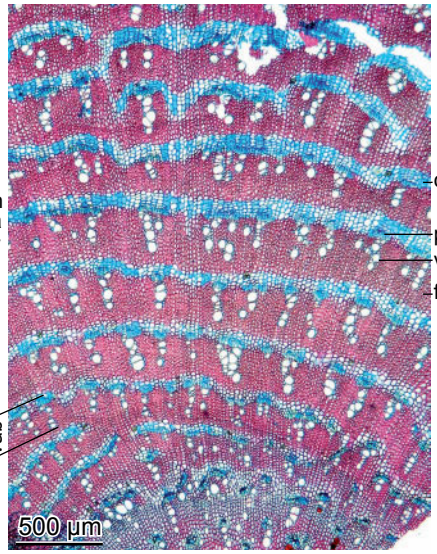



**Fig. 20.** Stem internal xylem/phloem bands consist of regularly concentrically arranged vascular bundles which are laterally connected by a band of fibres = concentric continuous. Between the tangential rows of intensively lignified xylem is a thin-walled, unlignified conjunctive parenchymatic tissue. Vascular bundles are solitary near the pith. 60 cm-high perennial dwarf shrub, dry canyon, subtropical climate, Dhofar, Oman. *Aerva javanica*, transverse section.

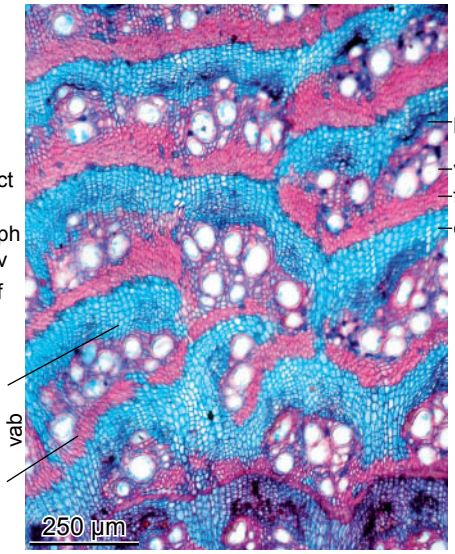



**Fig. 21.** Included phloem consisting of more-or-less concentrically arranged vascular bundles laterally connected by a band of fibres = concentric continuous. Between the tangential rows of intensively lignified xylem is a thin-walled, unlignified conjunctive parenchymatic tissue. 50 cm-high annual plant, ruderal site, coast, subtropical climate, Gran Canaria, Canary Islands. *Atriplex semibaccata*, transverse section.

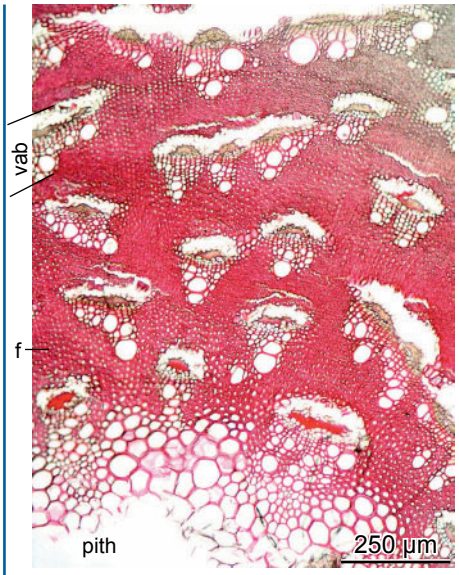



**Fig. 22.** Diffusely distributed stem internal xylem/phloem. The vascular bundles are embedded in a conjunctive tissue consisting of thick-walled fibres. Annual 1 m-high plant on sandy places in arid region, Sahara, oasis, Algeria. *Atriplex dimorphostegia*, transverse section.

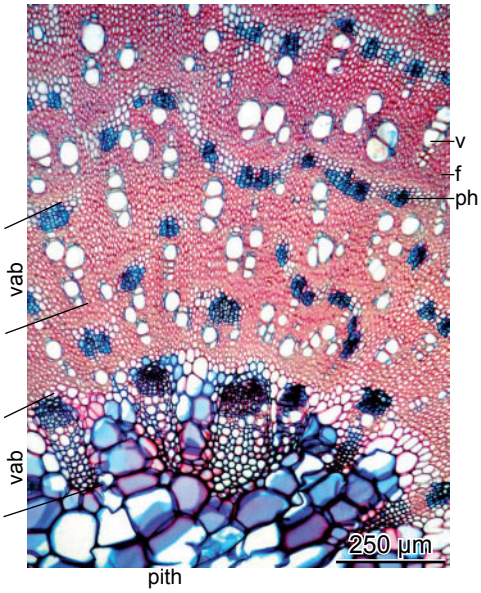



**Fig. 23.** Variable distribution of the vascular bundles. Vascular bundles surround the pith in a circle. Vessels in the xylem are always irregularly distributed. Sieve tube groups (blue) are irregularly distributed around the pith and tend to be arranged in tangential rows later on. 70 cm-high annual plant, ruderal site, hill zone, Ticino, Switzerland. *Chenopodium strictum*, transverse section.

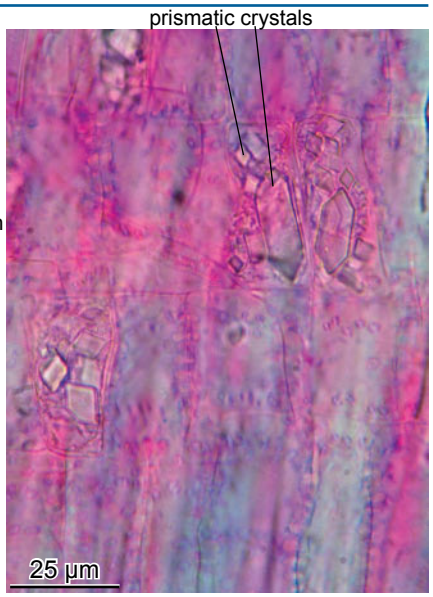



**Fig. 24.** Prismatic crystals of different sizes in upright ray cells. Root collar of an annual, prostrate plant, windy coast, subtropical climate, Gran Canaria, Canary Islands. *Cheneloides tomentosa*, radial section.

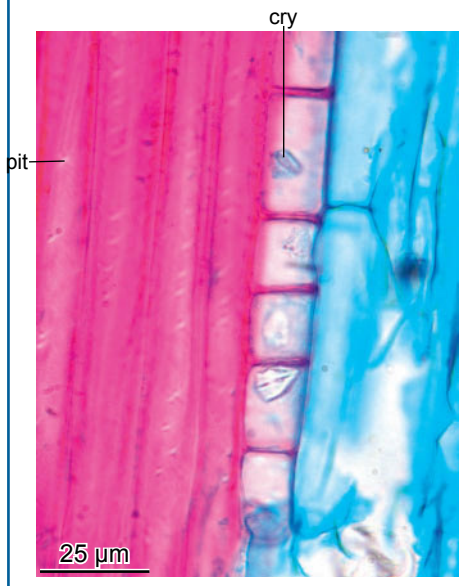



**Fig. 25.** Prismatic crystals in axially chambered square cells. The radial walls of the adjacent fibres (red) have small slit-like simple pits. 60 cm-high dwarf shrub, coast, Mediterranean, Mallorca, Spain. *Suaeda fruticosa*, radial section.

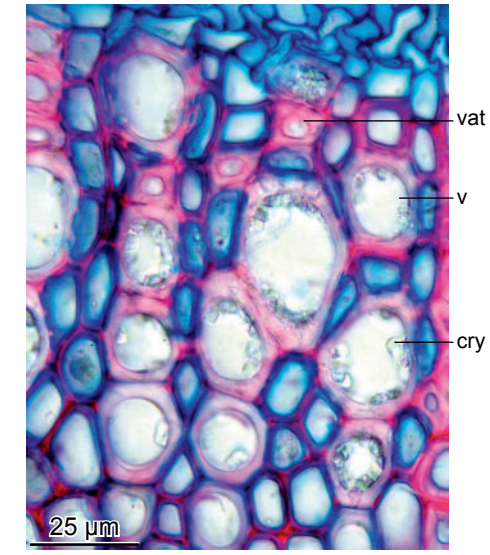



**Fig. 26.** Small prismatic crystals at the inner surface of thick-walled vessels, 1.5 m-high shrub, coastal dune, subtropical climate, Gomera, Canary Islands. *Traganum moquinii*, transverse section.

### Family characteristics of phloem, cortex and pith

The bark of all species is simply structured. Parenchyma cells are oriented in more or less radial rows (**Figs. 27** and **28**) or are enlarged in succulent species (**Fig. 28**). Sclereids occur in the cortex of 5 species but are normally very small (**Fig. 29**). Prismatic crystals occur in 5 species (3 *Atripex* species, *Traganum moquinii* and *Cheneloides tomentosa*). Crystal druses are more frequent and occur in 11 species of *Atriplex*, *Bosea*, *Chenopodium* and *Haloxylon*. Crystal sand occurs in 23 species of different genera. Medullary vascular bundles occur in 14 of the analyzed species (7 *Amaranthus*, 3 *Chenopodium*, 2 *Atriplex*, 2 *Arthrocneumum*, **Fig. 30**). All other species analyzed have no medullar vascular bundles (**Fig. 31**).

### Ecological trends in the xylem

No correlations could be found between the distinctness of growth rings and the climatic and vegetation zones in which the plants grow. The few species with distinct rings grow in dry regions of the in subtropical climate (*Suaeda fruticosa*) and Mediterranean *Salsola genistoides*) regions. Fibres are absent only in herbaceous species of the humid subtropical climate and the temperate zone. No other ecological trends in any anatomical feature of the xylem or bark could be detected.

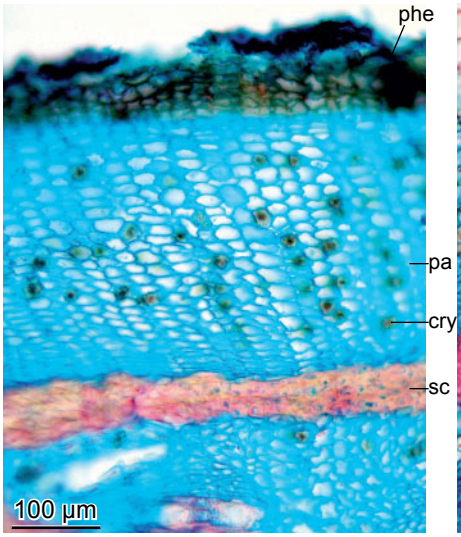



**Fig. 27.** Simple construction of the bark. Phloem and cortex consist of small, radially oriented, unlignified parenchyma cells. Some cells contain crystal druses (dark spots). Bark of the stem, 40 cm-high dwarf shrub, dry place, Mediterranean, Aragon, Spain. *Kraschenninnikovia ceratoides*, transverse section.

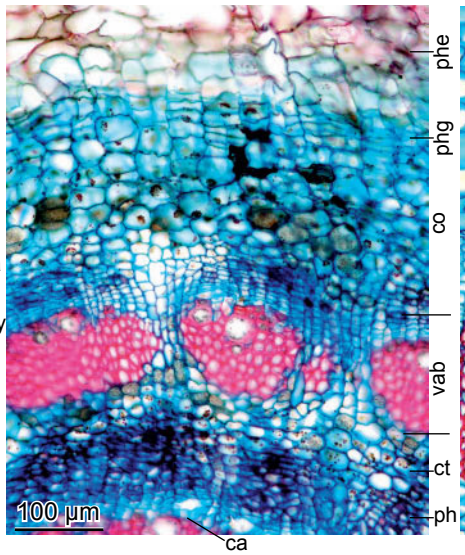



**Fig. 28.** Simple construction of the bark. Phloem and cortex consist of large, more-or-less radial orientated, succulent cells. The lignified tissue below the phloem is part of the xylem. Some cells contain crystal druses. 40 cm-high annual succulent plant, ruderal site, subtropical climate, Gomera, Canary Islands. *Patellifolia patellaris*, transverse section.

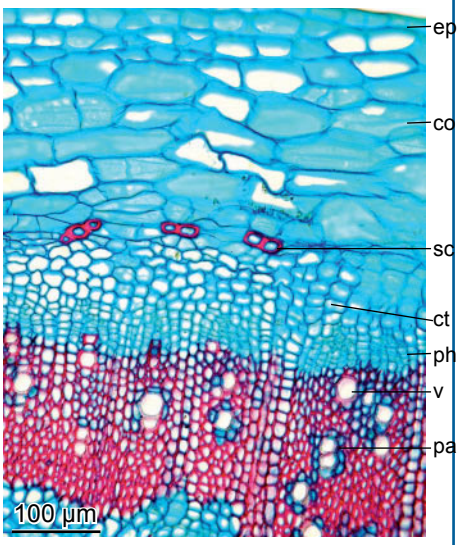
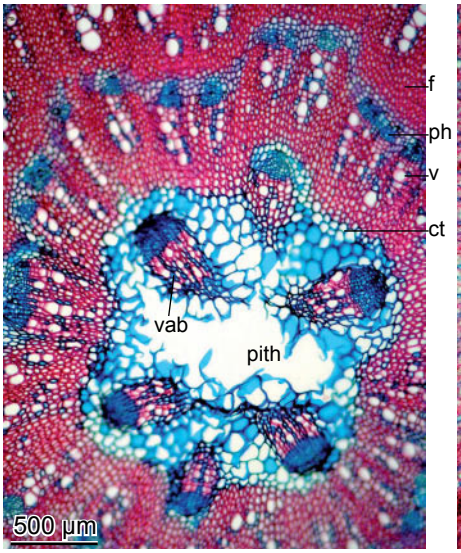
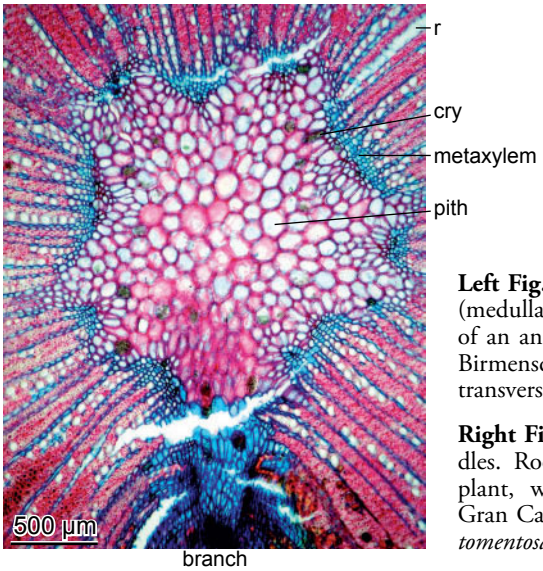



**Fig. 29.** The cambial zone consists of parenchyma and sieve tubes, the phloem itself only of parenchyma cells. Parenchyma cells of the cortex are enlarged succulent cells. Between phloem and cortex are a few lignified sclerenchyma cells. 40 cm-high, annual, succulent plant, ruderal site, subtropical climate, Gomera, Canary Islands. *Chenopodium murale*, transverse section.




branch

**Left Fig. 30.** Vascular bundles in the pith (medullary vascular bundles). Root collar of an annual plant, ruderal site, hill zone, Birmensdorf, Switzerland. *Atriplex patula*, transverse section.

**Right Fig. 31.** Pith without vascular bundles. Root collar of an annual, prostrate plant, windy coast, subtropical climate, Gran Canaria, Canary Islands. *Cheneloides tomentosa*, transverse section.

**Discussion in relation to previous studies**

Successive cambia of Amaranthaceae and Chenopodiacea have been subject to many studies. Gregory (1994) gives bibliographic overview. Many authors have studied the mechanism of xylem formation (Heklau 1992). Artschwager (1929) concentrated on the annual herbaceous *Chenopodium album*, Esau (1977) on *Beta vulgaris*, Heklau (1992) on 6 herbaceous *Atriplex* and *Chenopodium* species. Miskell (1979) studied very carefully the formation of the xylem and phloem of woody species of Amaranthaceae. Carlquist (2001) summarized the results of several studies. The wood anatomy of Amaranthaceae has been systematically studied by Pfeiffer (1926), Chalk and Chattaway (1937), Metcalfe and Chalk (1957), Butnik (1983), Fahn et al. (1986), Neumann et al. (2001) and Carlquist (2003).

Most observations could be confirmed by the present study e.g. the occurrence of successive cambia, the sporadic presence of annual rings in the xylem of a few species from dry regions and the occurrence of confluent rays except in the hyperarid zone of the Sahara (Neumann et al. 2001). The present study, however, differs from the previous studies: Most previous authors, with the exception of Heklau (1992), concentrated on the xylem of shrubs and dwarf shrubs from dry regions. This study includes many herbaceous species including those in humid regions. The absence of fibres and the presence of pervasive parenchyma is characteristic of some herbaceous species. Some species contain prismatic crystals. The pith has hardly been observed. Only Carlquist (2003) described the pith of 2 species (*Amaranthus caudatus* and *Nototrichium sandwicense*). The presence of medullar phloem is frequent but probably not a species-characteristic feature. Vessel diameter seems to be site dependent therefore it is difficult to construct keys on the basis if a few individuals per species (Fahn et al. 1986). The present study seems to be representative for the family.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of analyzed species** | | **62** |
| 1 | growth rings distinct and recognizable | 3 |
| 2 | growth rings indistinct or absent | 59 |
| 2.1 | only one ring | 1 |
| 9 | vessels predominantly solitary | 46 |
| 9.1 | vessels in radial multiples of 2-4 common | 29 |
| 10 | vessels in radial multiples of 4 or more common | 5 |
| 11 | vessels predominantly in clusters | 18 |
| 13 | vessels with simple perforation plates | 62 |
| 20 | intervessel pits scalariform | 7 |
| 39.1 | vessel cell-wall thickness >2 µm | 29 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 5 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 46 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 14 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 1 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 47 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 15 |
| 56 | tylosis with thin walls common | 7 |
| 58 | dark-stained substances in vessels and/or fibers present (gum, tannins) | 8 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 58 |
| 69 | fibers thick-walled | 28 |
| 70 | fibers thin- to thick-walled | 30 |
| 79 | parenchyma paratracheal | 58 |
| 79.1 | parenchyma pervasive | 5 |
| 97 | ray width predominantly 1-3 cells | 8 |
| 98 | rays commonly 4-10-seriate | 29 |
| 99 | rays commonly >10-seriate | 5 |
| 100.1 | rays confluent with ground tissue | 3 |
| 105 | ray: cells upright or square | 42 |
| 117 | rayless | 24 |
| 120 | storied axial tissue (parenchyma and vessels) | 1 |
| 133.1 | successive cambia, concentrically arranged single vascular bundles | 18 |
| 133.2 | successive cambia, concentric continuous | 40 |
| 134 | successive cambia, diffuse = foraminate | 13 |
| 134.1 | conjunctive tissue thin-walled | 43 |
| 136 | prismatic crystals present | 17 |
| 142 | prismatic crystals in axial chambered cells | 6 |
| 144 | druses present | 10 |
| 153 | crystal sand present | 32 |
| R3 | distinct ray dilatations | 2 |
| R4 | sclereids in phloem and cortex | 6 |
| R7 | with prismatic crystals | 5 |
| R8 | with crystal druses | 11 |
| R9 | with crystal sand | 22 |
| R10 | phloem not well structured | 47 |
| P1 | with medullary phloem or vascular bundles | 14 |

# Amborellaceae

**Number of species, worldwide and in Europe**

The Amborellaceae family includes 1 genera with 1 species. It is endemic to New Caledonia.

**Analyzed material**

The xylem and phloem of 1 Amborella tree species are analyzed here: *Amborella trichopoda* Baill. (Slide leg. by Carlquist). Carlquist (2001) analyzed the same material.

*Amborella trichopoda* (photos: Zona)

### Characteristics of the xylem

Annual rings are absent (**Fig. 1**). The conifer-like, vesselless wood has thin to thick-walled tracheids (**Fig. 2**). Radial cell walls of most tracheids are characterized of large distinctly bordered pits with oval to slit like apertures (**Fig. 3**). Round pits are arranged in one to 2 rows on radial walls. Scalariform pits occur in large tracheids (**Fig. 3**). Axial parenchyma is rare or if present apotracheal diffuse. It contains dark staining substances (**Fig. 2**).

Rays occur in two forms: Uniseriate, homocellular rays with upright cells and larger heterocellular rays (2-4 square or upright marginal cells) with 3-4 cells in width (**Fig. 4** and **5**). Bordered pits (piceoid) with slit-like apertures occur on uniseriate rays and on marginal ray cells of large rays. They are arranged in axial uniseriate rows (**Fig. 6**).

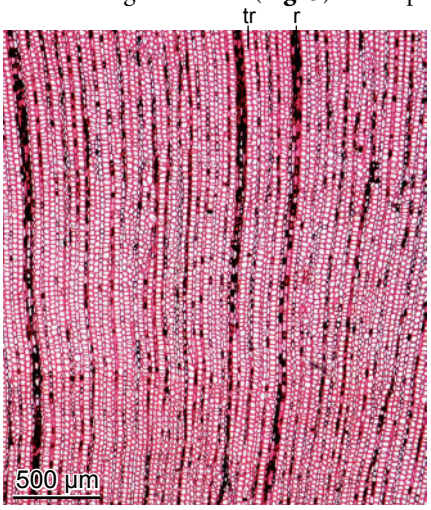



**Fig. 1.** Vessel-less xylem with indistinct growth zones. Stem of a shrub, moist forest, tropical climate, New Caledonia. *Amborella trichopoda*, transverse section.

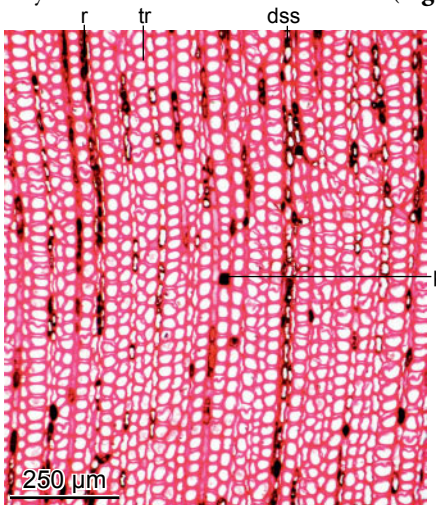



**Fig. 2.** Thin-to thick-walled tracheids. Parenchyma cells (axial and radial) are filled with dark staining substances. *Amborella trichopoda*, transverse section.

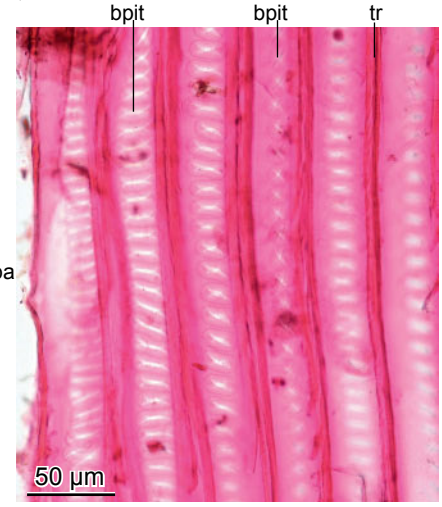



**Fig. 3.** Radial cell walls of tracheids with bordered pits with oval and scalariform apertures. *Amborella trichopoda*, radial section.

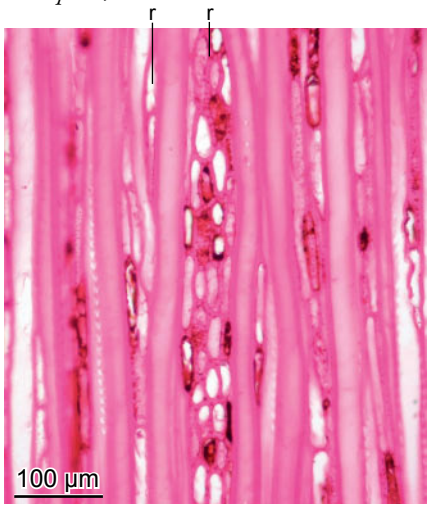



**Fig. 4.** Uniseriate and multiseriate rays, 3-4 cells wide. *Amborella trichopoda*, tangential section.

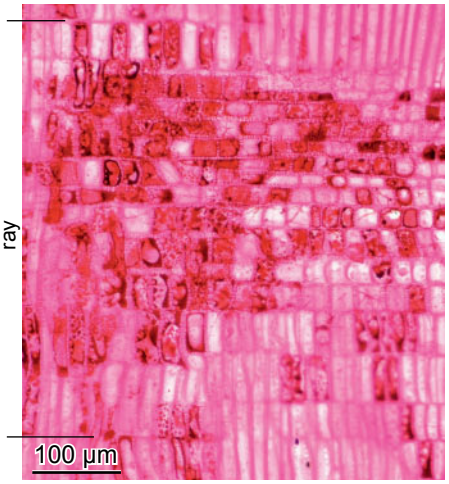



**Fig. 5.** Heterocellular ray with >4 marginal upright cells. *Amborella trichopoda*, radial section.

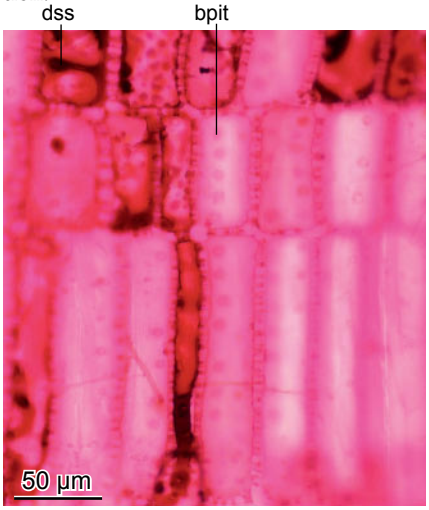



**Fig. 6.** Upright ray cells with bordered pits (piceoid) in uniseriate axial rows. *Amborella trichopoda*, radial section.

### Characteristic of the phloem and cortex

No slide available.

### Discussion in relation to previous studies

Detailed descriptions of the xylem have been made by Bailey 1957 and Carlquist (2001). All observations made by Carlquist and Schneider (2001) could be confirmed.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of analyzed species** | | **1** |
| 2 | growth rings indistinct or absent | 1 |
| 20 | intervessel pits scalariform | 1 |
| 58 | dark-stained substances in vessels and/or fibers present | 1 |
| 59 | vessels absent or indistinguishable from fibers | 1 |
| 62 | fiber pits large and distinctly bordered (>3µm = fiber tracheids) | 1 |
| 70 | fibers thin- to thick-walled | 1 |
| 76 | parenchyma apotracheal, diffuse | 1 |

# Anacardiaceae



### Number of species, worldwide and in Europe

The mainly pantropical Anacardiaceae family includes 75 genera with 600 species. In Europe, there are 3 genera with 9 species.

### Analyzed material

The xylem and phloem of 4 genera with 10 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes | 3 | numerous |
| Nanophanerophytes 0.5-4 m | 7 | a few |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 1 | |
| Mediterranean | 8 | |
| Arid | 1 | |

**Analyzed species:**
*Cotinus coggygria* Scop.
*Pistacia lentiscus* L.
*Pistacia palaestina* Boiss.
*Pistacia terebinthus* L.
*Rhus coriaria* Scop.
*Rhus glabra* L.
*Rhus trilobata* Nutt.
*Rhus tripartitus* R. Sch.
*Rhus typhina* L.
*Schinus molle* L.

*Pistacia terebinthus*

*Cotinus coggygria* (photo: Zinnert)

*Cotinus coggygria* (photo: Zinnert)

*Rhus glabra* (photo: Aas)

**Characteristics of the xylem**

All species with distinct rings are ring-porous (**Figs. 1**, **2** and **5**). Growth zones occur in *Rhus tripartituts* and *Schinus molle* (**Fig. 3**). Latewood vessels in radial multiples and occasionally arranged in diagonal patterns (**Figs. 1** and **2**). Earlywood vessel diameter varies between 80-150 µm and a vessel density between 50-90/mm$^2$ is characteristic for all species. Vessels of all species have simple perforations and helical thickenings (**Fig. 4**). Intervessel pits are round in alternating position and ray-vessels pits are enlarged (**Fig. 4**). Earlywood vessels of most species contain tylosis (**Fig. 5**) and latewood vessels are accompanied by vascular tracheids in the latewood. Fibers with small pits with slit-like apertures are thin- to thick-walled (**Fig. 4**). Septate fibers occur only in *Rhus tripartitus* (**Fig. 6**). Tension wood is almost a constant feature within the family (**Fig. 7**). Parenchyma is scanty paratracheal (**Fig. 8**).

Ray width varies between 1- to 4-seriate (**Figs. 9** and **10**). Rays are heterocellular with one to a few rows of square and upright cells (**Fig. 11**). Prismatic crystals are present in most species except *Rhus typhina* (**Figs. 11** and **12**). Particular for the family is the presence of horizontal ducts (**Fig. 9**) in rays of many species and vertical ducts in the pith (**Fig. 13** and **14**).

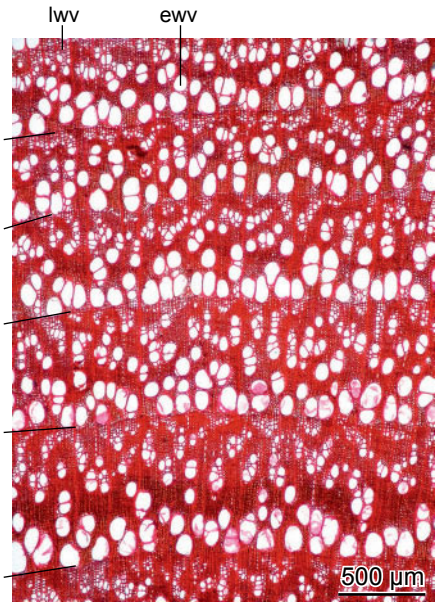



**Fig. 1.** Ring-porous xylem with distinct annual rings. Latewood vessel-groups are in diagonal patterns. Stem of a 2 m-high shrub, on limestone rock, hill zone, Trento, Italy. *Cotinus coggygria*, transverse section.

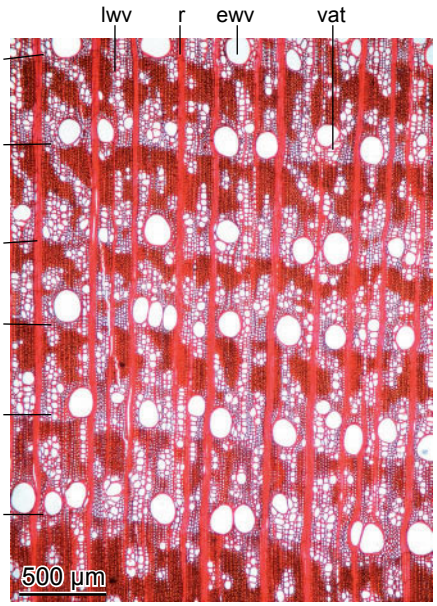



**Fig. 2.** Distinct annual rings in a ring-porous xylem with few earlywood vessels. Small vessels and vascular tracheids are mostly in radial groups. Stem of a 2 m-high shrub, maccia, Mediterranean zone, Cevennes, France. *Pistacia terebinthus*, transverse section.

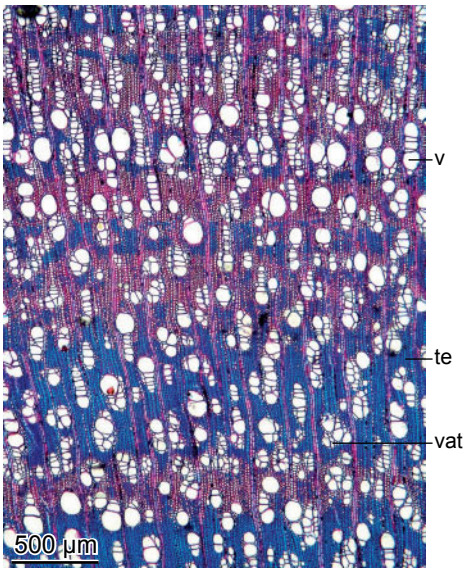
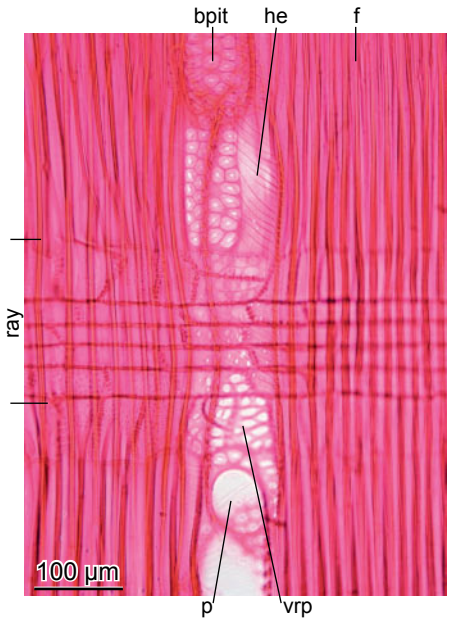
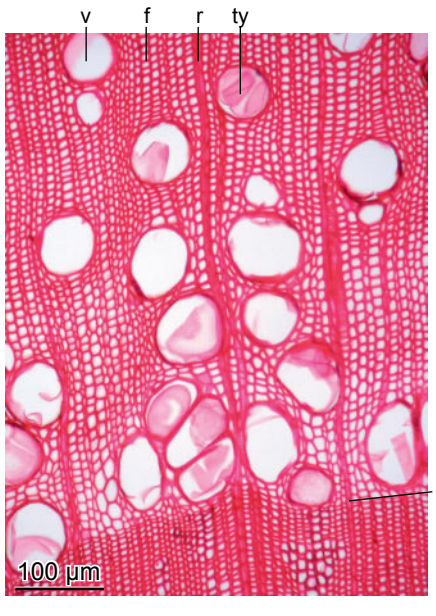



**Fig. 3.** Growth zones with large and small vessels. Small vessels are arranged in radial multiples. Stem of an 8 m-high tree, cultivated, subtropical climate, Gomera, Canary Islands. *Schinus molle*, transverse section.




**Left Fig. 4.** Vessel-ray cross-field with enlarged pits. Vessels have simple perforations, helical thickenings and large, bordered pits. The ray is heterocellular, with one row of upright, marginal cells. Stem of 4 m-high tree, ruderal, hill zone, Zürich, Switzerland. *Rhus typhina*, radial section.




**Right Fig. 5.** Tylosis in earlywood vessels. Stem of 4 m-high tree, ruderal site, hill zone, Zürich, Switzerland. *Rhus typhina*, transverse section.

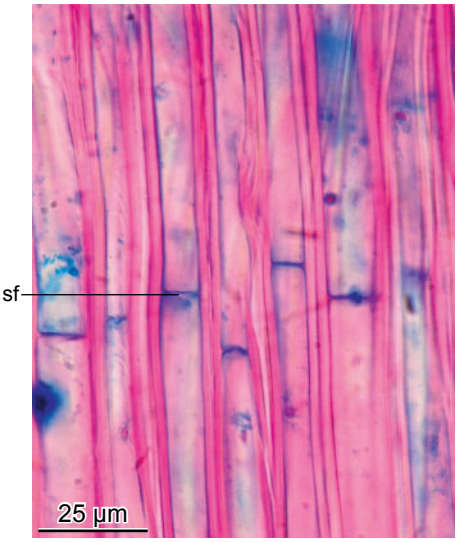



**Fig. 6.** Septate fibers with unlignified horizontal walls. Stem of a 2 m-high shrub, maccia, Mediterranean, Libya. *Rhus tripartitus*, radial section.

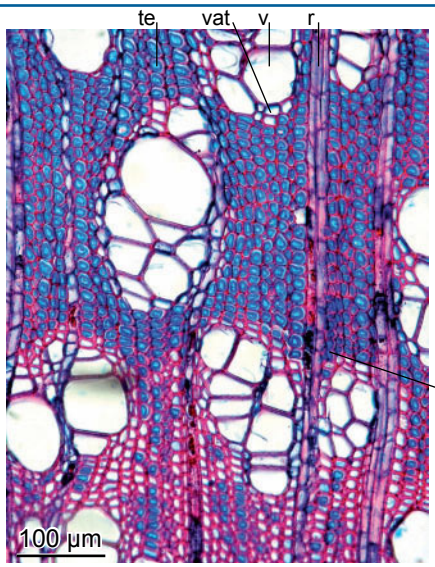



**Fig. 7.** Tension wood characterized by unlignified gelatinous fibers (blue). Stem of an 8 m-high tree, cultivated, subtropical climate, Gomera, Canary Islands. *Schinus molle*, transverse section.

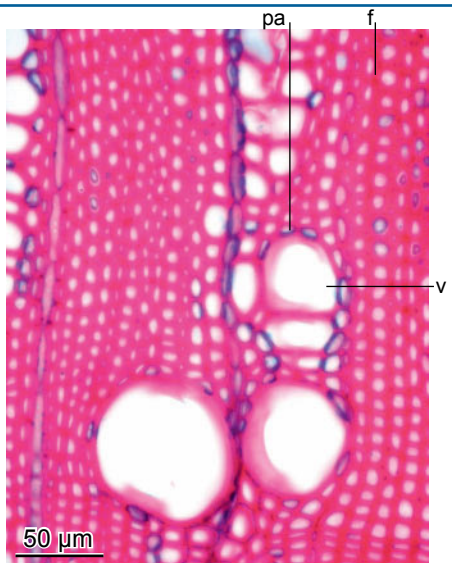
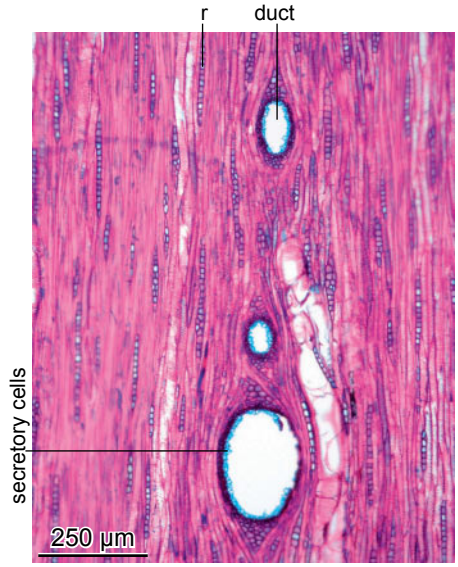
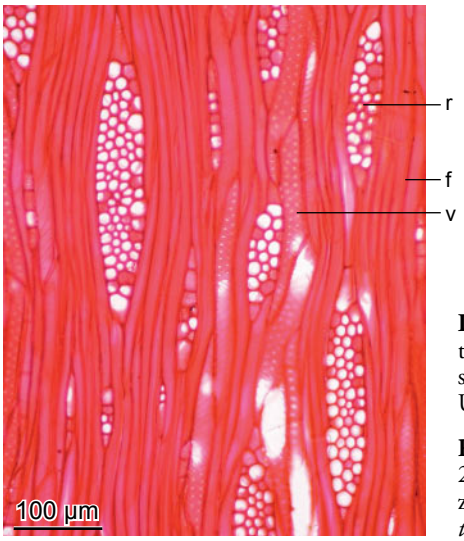


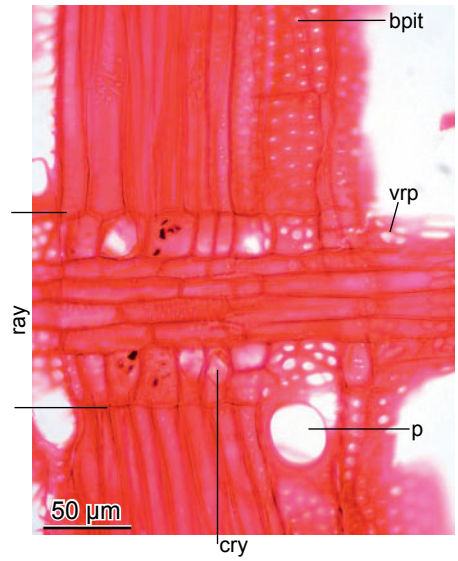

**Fig. 8.** Axial parenchyma is scanty paratracheal. Stem of a 3 m-high shrub, maccia, Mediterranean, Provence, France. *Pistacia lentiscus*, transverse section.

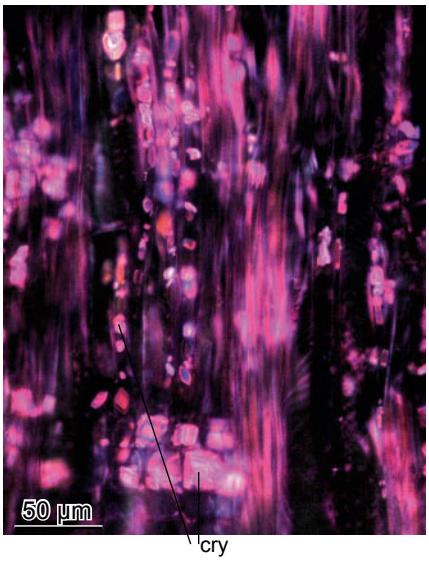



**Left Fig. 9.** 1-2-seriate rays. Three rays contain horizontal canals. Stem of a 2 m-high shrub, on rock, arid zone, Moab, Utah, USA. *Rhus glabra*, tangential section.

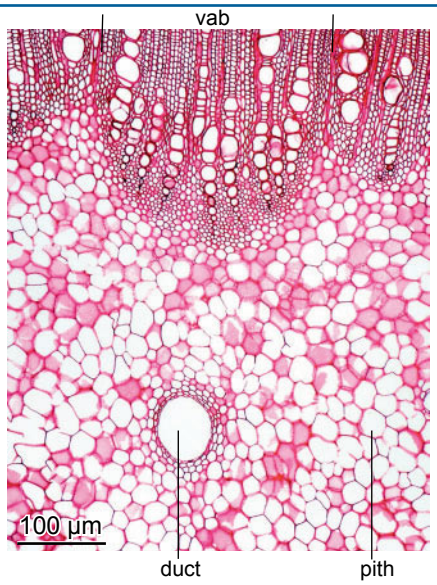
**Right Fig. 10.** 1-5-seriate rays. Stem of a 2 m-high shrub, maccia, Mediterranean zone, Cevennes, France. *Pistacia terebinthus*, tangential section.

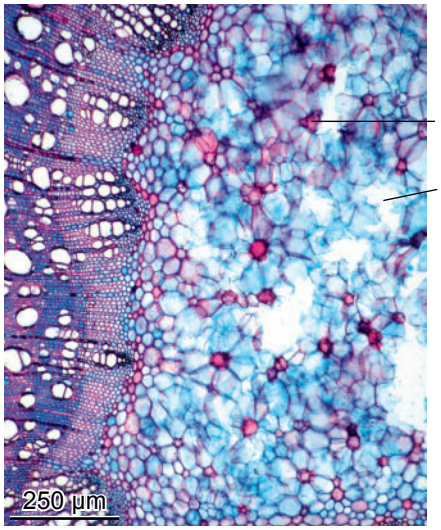



**Left Fig. 11.** Heterocellular ray with one row of upright, marginal cells. Marginal cells contain prismatic crystals. Stem of a 2 m-high shrub, maccia, Mediterranean zone, Cevennes, France. *Pistacia terebinthus*, radial section.

**Right Fig. 12.** Prismatic crystals of different forms and sizes in rays and axial elements. Stem of a 2 m-high shrub, on rock, arid zone, Moab, Utah, USA. *Rhus glabra*, radial section, polarized light.



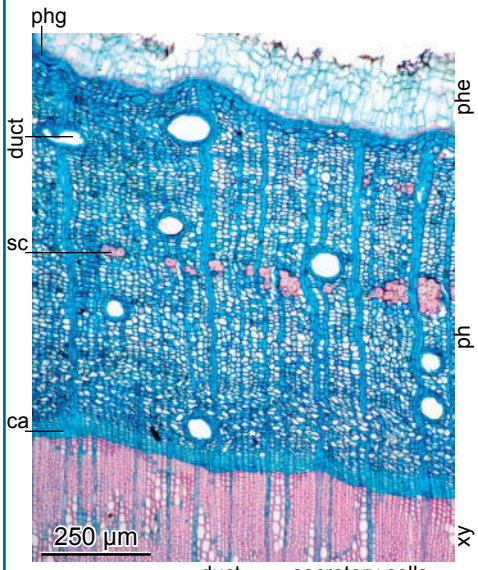



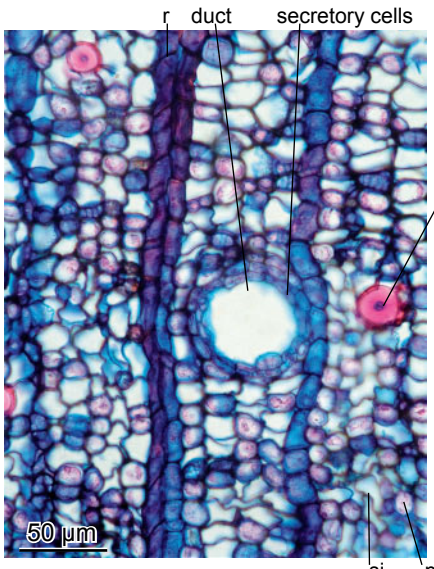

**Left Fig. 13.** Axial canal with surrounding excretion cells in the pith. Stem of 4 m-high tree, ruderal site, hill zone, Zürich, Switzerland. *Rhus typhina*, transverse section.

**Right Fig. 14.** Small, round cells in the pith contain oil (red). Stem of a 2 m-high shrub, maccia, Mediterranean, Libya. *Rhus tripartitus*, transverse section.

**Characteristics of the phloem and the cortex**

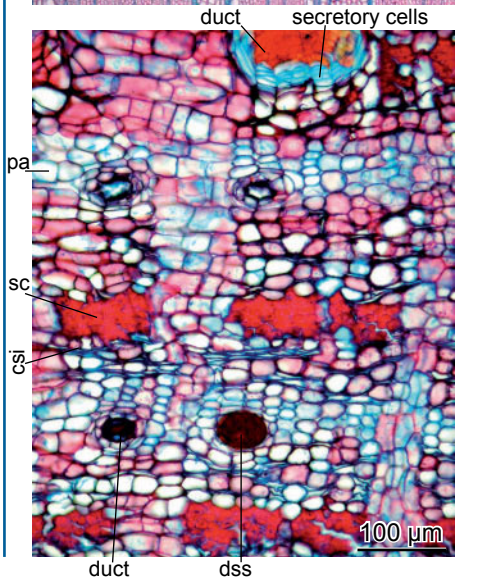
Characteristic of all species is the radial structure of sieve tubes and parenchyma cells and the presence of ducts (**Figs. 15-17**). Groups of sclerenchyma occur in most species either in groups (**Fig. 17**) or in tangential bands (**Fig. 18**). Crystals occur in prismatic and druse form.

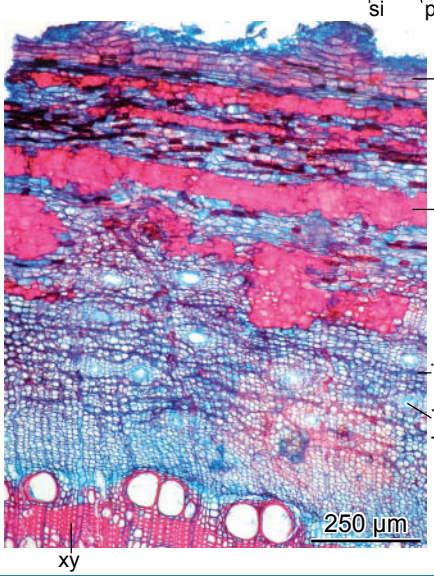



**Left Fig. 15.** Phloem with radial rows of sieve tubes and parenchyma cells and with canals and a few groups of sclerenchyma. Stem of a 2 m-high shrub, on limestone rock, hill zone, Trento, Italy. *Cotinus coggygria*, transverse section.

**Right Fig. 16.** Large duct surrounded by smaller secretory cells in the phloem. Sieve tubes and parenchyma cells have similar forms. Stem of a 2 m-high shrub, on limestone rock, hill zone, Trento, Italy. *Cotinus coggygria*, transverse section.




**Left Fig. 17.** Phloem with tangential rows of sclereid groups and with darkly stained substances in ducts. Stem of an 8 m-high tree, cultivated, subtropical climate, Gomera, Canary Islands. *Schinus molle*, transverse section.

**Right Fig. 18.** Phloem, cortex and phellem. The phloem contains ducts and the cortex has tangential bands of sclerenchyma. Stem of a 3 m-high shrub, maccia, Mediterranean, Provence, France. *Pistacia lentiscus*, transverse section.

**Discussion in relation to previous studies**

Many tropical genera have been described before. Gregory (1994) mentions 180 references. All genera (*Pistacia, Rhus*) described here have been studied e.g by Greguss (1945), Huber and Rouschal (1954), Fahn et al. (1986) and Edlmann et al. (1994). Schweingruber (1990) additionally described *Cotinus* and *Schinus molle*. All bark descriptions are new in this study.

The anatomical structure of the xylem is fairly homogeneous. Ring-porosity, vascular tracheids, helical thickenings, gelatinous fibers and prismatic crystals and for the phloem the presence of ducts are common for the genera described.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of analyzed species** | | **10** |
| 1 | growth rings distinct and recognizable | 8 |
| 2 | growth rings absent | 2 |
| 3 | ring-porous | 8 |
| 7 | vessels in diagonal and/or radial patterns | 3 |
| 8 | vessels in dendritic patterns | 1 |
| 9.1 | vessels in radial multiples of 2-4 common | 4 |
| 10 | vessels in radial multiples of 4 or more common | 4 |
| 11 | vessels predominantly in clusters | 7 |
| 13 | vessels with simple perforation plates | 10 |
| 22 | intervessel pits alternate | 10 |
| 31 | vessel-ray pits with large apertures, *Salix/Laurus* type | 5 |
| 36 | helical thickenings present | 9 |
| 39.1 | vessel cell-walls thickness >2 µm | 2 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 3 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 7 |
| 50 | <100 vessels per $mm^2$ in earlywood | 6 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 4 |
| 56 | tylosis with thin walls common | 5 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 10 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 10 |
| 65 | septate fibers present | 1 |
| 69 | fibers thick-walled | 2 |
| 70 | fibers thin- to thick-walled | 9 |
| 70.2 | tension wood present | 6 |
| 79 | parenchyma paratracheal | 10 |
| 89 | parenchyma marginal | 1 |
| 96 | rays uniseriate | 1 |
| 97 | ray width predominantly 1-3 cells | 9 |
| 98 | rays commonly 4-10-seriate | 3 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 6 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 4 |
| 130 | with radial canals | 5 |
| 136 | prismatic crystals present | 8 |
| R1 | groups of sieve tubes present | 4 |
| R2 | groups of sieve tubes in tangential rows | 4 |
| R4 | sclereids in phloem and cortex | 4 |
| R6.1 | sclereids in tangential rows | 3 |
| R7 | with prismatic crystals | 5 |
| R8 | with crystal druses | 2 |
| R12 | with laticifers, oil ducts or mucilage ducts | 7 |
| P2 | with laticifers or intercellular canals | 2 |

# Apocyanaceae and Asclepiadaceae

**Number of species, worldwide and in Europe**

The Apocyanaceae family, which includes the Asclepiadacea, consists of 355 genera with 3700 species. They occur worldwide, excluding the boreal zone. 9 genera with 27 species are found in Western Europe and one genus is endemic to the Canary Islands (*Ceropegia*).

**Analyzed material**

10 Apocyanaceae species and 11 Asclepiadaceae species have been analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 6 | 9 |
| Woody chamaephytes | 1 | |
| Liana | 3 | 1 |
| Hemicryptophytes and geophytes | 9 | |
| Succulent | 2 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 6 | |
| Mediterranean | 2 | |
| Arid | 11 | |
| Subtropical | 2 | |

**Analyzed species:**

Apocynaceae
- *Acokanthera oblongifolia* Codd.
- *Adenium obesum* Roem. Schult.
- *Apocynum androsaemifolium* L.
- *Apocynum cannabinum* L.
- *Nerium mascatense* A. Dc.
- *Nerium oleander* L.
- *Rhazya stricta* Decaisne
- *Vinca major* L.
- *Vinca minor* L.
- *Vincetoxicum officinale* Medik.

Asclepiadaceae
- *Asclepias subverticillata* (Grey) Vail
- *Asclepias syriaca* L.
- *Asclepias tuberosa* L.
- *Calotropis procera* W.T. Aiton
- *Caralluma quadrangula* N.E. Brown
- *Ceropegia fusca* Bolle
- *Gomphocarpus fruticosus* R.Br.
- *Leptadenia pyrotechnica* Decne.
- *Periploca aphylla* Decaisne
- *Periploca graeca* L.
- *Periploca laevigata* Ait.

*Nerium oleander*

*Leptadenia pyrotechnica*

*Adenium obesum*

*Vincetoxicum hirudinaria*

*Vinca minor*

*Calotropis procera*

**Characteristics of the xylem**

The characteristics of the two families are described together because no feature characterizes only one or the other family. The Apocyanaceae/Asclepiadaceae are anatomically a very heterogeneous taxonomic unit. 15 of the 21 species analyzed have distinct rings (**Figs. 1-6**). Most species are diffuse-porous (**Figs. 1** and **2**) and/or semi-ring-porous (**Figs. 1**, **3**, **5**). Only the Mediterranean liana *Periploca graeca* is ring-porous (**Fig. 6**). Vessel diameter normally ranges from 30 to 80 µm. It is less than 20 µm in the rhizome of *Vinca minor* (**Fig. 1**) and *V. major*, and larger than 100 µm in the liana *Periploca graeca* (**Fig. 6**) and the desert shrub *Calotropis procera* (**Fig. 5**). Vessel densities vary between <50/mm² (**Fig. 8**) and >200/mm² (**Fig. 1**).

Vessel cell walls are perforated by small alternating (**Fig. 7**) or rarely scalariform pits and simple perforations (**Fig. 7**). Most species have vestured pits. They seem to be absent in *Vinca minor* and *V. major*, *Vincetoxicum officinale* and *Caralluma quadrangula*. Fiber-wall thickness is extremely variable: very thin-

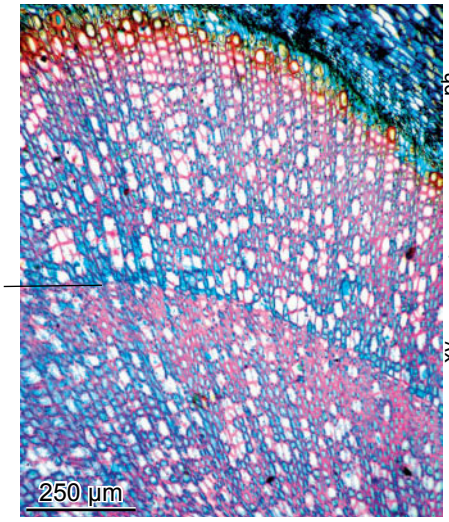



**Fig. 1.** Distinct annual boundary of a slightly semi-ring-porous xylem. Vessels are small (<20 µm) and numerous (>200/mm²). Rhizome of a perennial herb, garden, mountain subtropical climate, Gomera, Canary Islands. *Vinca major*, transverse section.

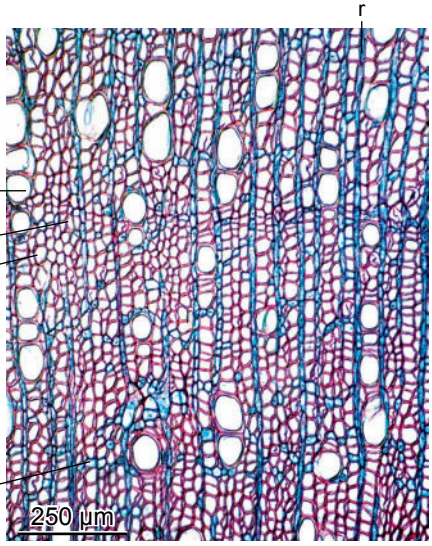



**Fig. 2.** Annual boundaries are marked by a row of radial flat fibers in the latewood. Xylem with semi-porous vessel distribution, apotracheal parenchyma and uniseriate rays. Shrub, canyon, succulent zone, subtropical climate, Gomera, Canary Islands. *Nerium oleander*, transverse section.

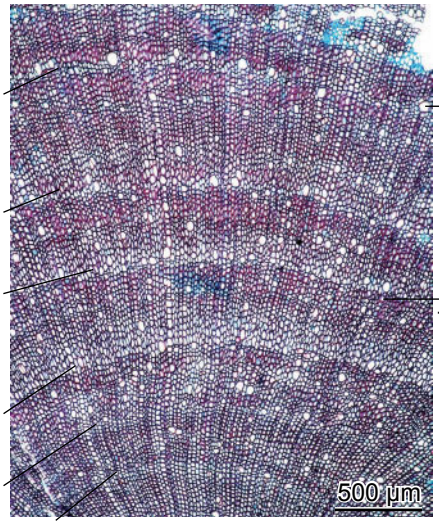



**Fig. 3.** Annual boundaries are marked by semi-ring-porous vessel distribution and thin-walled fibers in the earlywood. Root collar of succulent plant, succulent zone of the dry subtropical climate, Gomera, Canary Islands. *Ceropegia fusca*, transverse section.

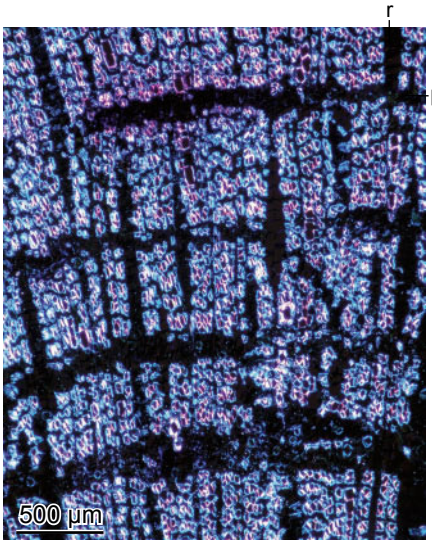



**Fig. 4.** Annual boundaries are marked by an unlignified marginal parenchyma. Stem of a succulent shrub, rock, tropical zone, Dhofar, Oman. *Adenium obesum*, transverse section, polarized light.

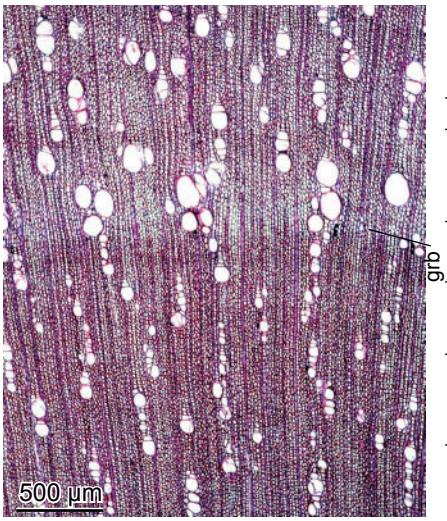



**Fig. 5.** Annual boundary of a semi-ring-porous to ring-porous wood. Fiber cell walls are slightly thicker in the latewood than in the earlywood. Stem of a shrub, arid climate, Arabian desert, Oman. *Calotropis procera*, transverse section.

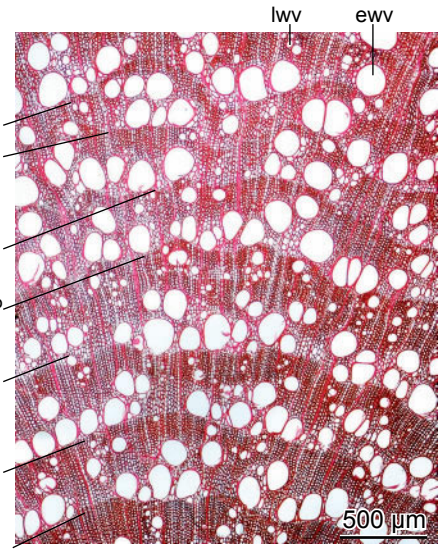



**Fig. 6.** Distinct annual ring boundaries of a ring-porous xylem. Fiber cell walls are slightly thicker in the latewood than in the earlywood. Stem of a liana, thermophile zone, subtropical climate, Tenerife, Canary Islands. *Periploca graeca*, transverse section.

walled in *Adenium obesum* (**Fig. 8**) and extremely thick-walled in *Acokanthera oblongifolia* (**Fig. 9**).

Axial parenchyma, as far as it could be observed, is apotracheal (**Figs. 2**, **8** and **9**). The hemicryptophytes *Vinca* and *Vincetoxicum* (**Fig. 10**) are rayless. Ray width varies mostly from one- to 3-seriate rays (**Figs. 11** and **12**), but *Leptadenia pyrotechnica* has large multiseriate rays (**Figs. 15** and **17**). The xylem of most stems forms a closed circle. Only the succulent *Caralluma quadrangula* remains in the form of a siphonostele (**Fig. 13**); the vascular bundles are laterally isolated and the parenchymatic tissue in-between the vascular bundles can be interpreted as primary rays (**Fig. 13**). Ray cells are mostly upright or square. A special feature is the presence of sieve-cell groups (interxylary phloem) in *Adenium obesum* (**Fig. 14**), *Leptadenia pyrotechnica* (**Fig. 15**) and *Rhazya stricta* (**Fig. 16**). Interxylary phloem is diffuse in *Leptadenia*, diffuse and concentric in *Rhazya* and concentric in *Adenium*. In addition, *Leptadenia* has lacitifers in the rays (**Fig. 17**). Septate fibers are present only in *Ceropegia fusca* (**Fig. 18**).

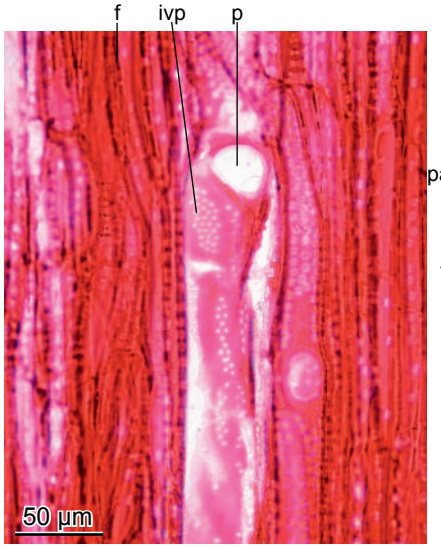



**Fig. 7.** Small, round, alternating inter-vessel pits and a simple perforation. Stem of a cultivated shrub, succulent zone, subtropical climate, Tenerife, Canary Islands. *Acokanthera oblongifolia*, radial section.

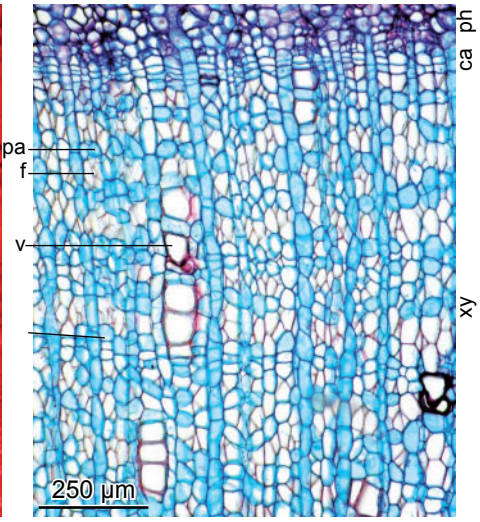



**Fig. 8.** Few radial multiple vessels (< 50/mm²) in a very thin-walled tissue. Many apotracheal parenchyma cells lie between fibers. Stem of a succulent shrub on a rock, dry, subtropical climate, Dhofar, Oman. *Adenium obesum*, transverse section.

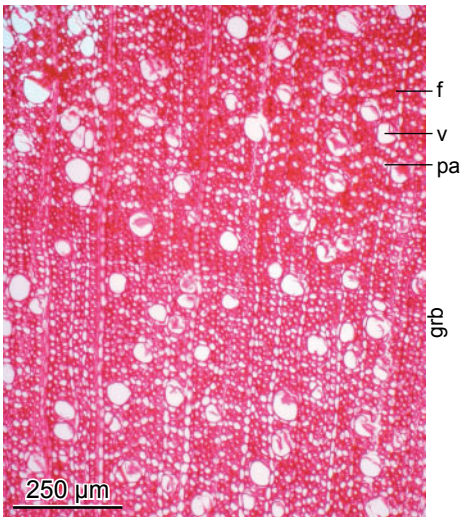



**Fig. 9.** Solitary vessels in a very thick-walled fiber tissue. Parenchyma is apotracheal. Stem of a cultivated shrub, succulent zone, subtropical climate, Tenerife, Canary Islands. *Acokanthera oblongifolia*, transverse section.

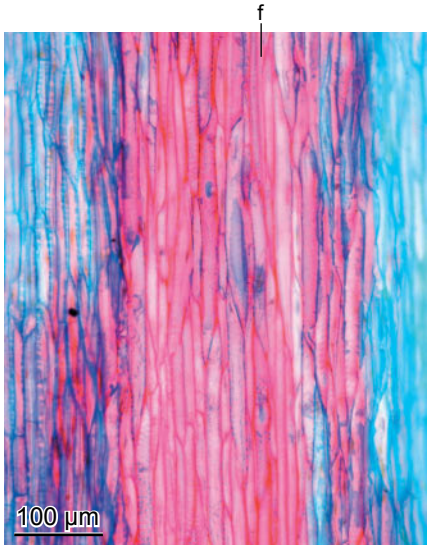



**Fig. 10.** Rayless xylem. Rhizome of a perennial herb, garden, mountain subtropical climate, Gomera, Canary Islands. *Vinca major*, tangential section.

**Fig. 11.** Uniseriate rays. Shrub in a canyon, succulent zone, subtropical climate, Gomera, Canary Islands. *Nerium oleander*, tangential section.

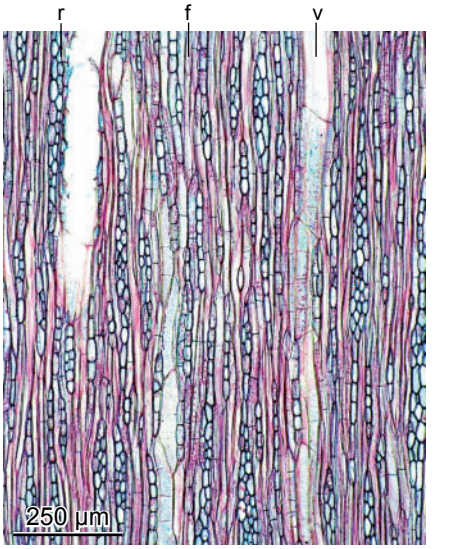



**Fig. 12.** Uniseriate to 3-seriate rays. Stem of shrub, arid climate, Arabian desert, Oman. *Calotropis procera*, tangential section.

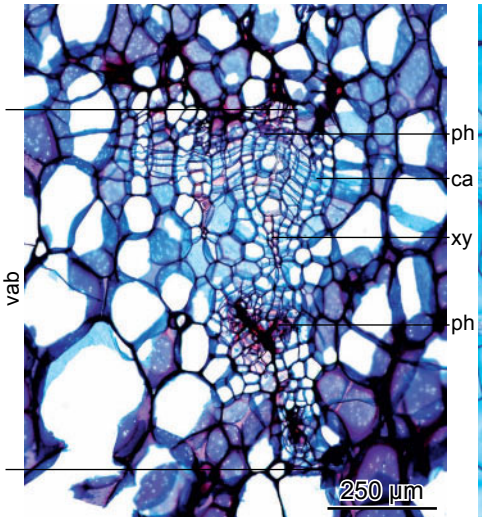



**Fig. 13.** Single bicolateral vascular bundle in a siphonostele. The bundles are laterally unconnected. The centripetal cell groups represent medullary sieve tubes. Succulent plant growing on a rock, dry subtropical climate, Dhofar, Oman. *Caralluma quadrangula*, transverse section.

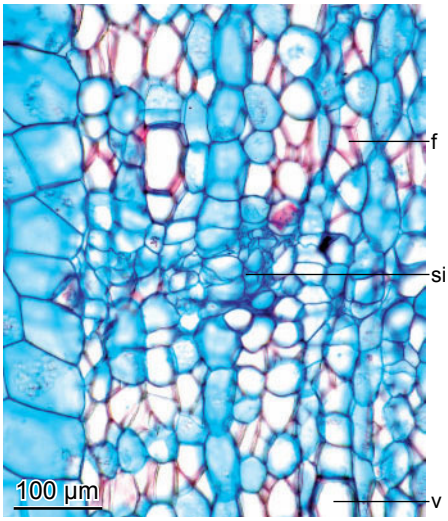



**Fig. 14.** Sieve-tube groups in the xylem. Stem of a succulent shrub on a rock, subtropical climate, Dhofar, Oman. *Adenium obesum*, transverse section.

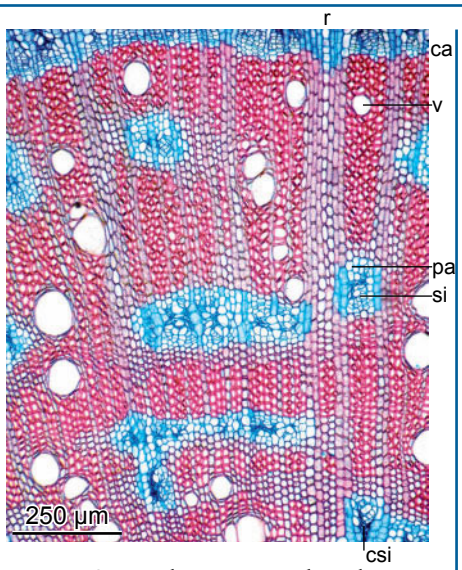



**Fig. 15.** Sieve-tube groups in the xylem are surrounded by parenchymatic cells. Sieve tubes are collapsed in central parts of the stem. Stem of a shrub, hyperarid climate, Algerian desert, Sahara. *Leptadenia pyrotechnica*, transverse section.

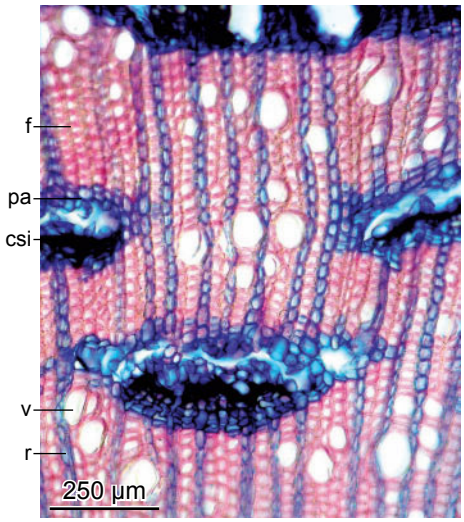



**Fig. 16.** Sieve-tube groups in the xylem are surrounded by parenchymatic cells. Stem of a succulent shrub, subtropical climate, Dhofar, Oman. *Adenium obesum*, transverse section.

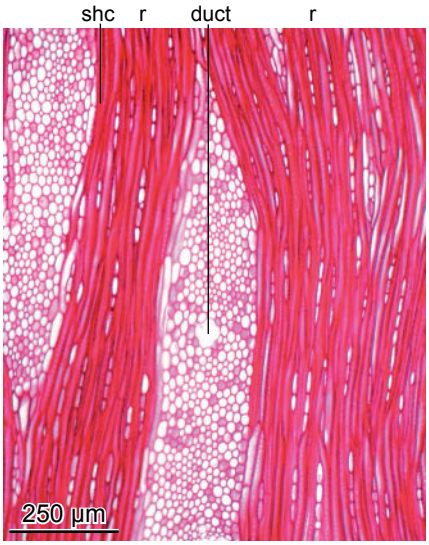



**Fig. 17.** Very large ray with laticifers. Stem of shrub, hyperarid climate, Algerian desert, Sahara. *Leptadenia pyrotechnica*, tangential section.

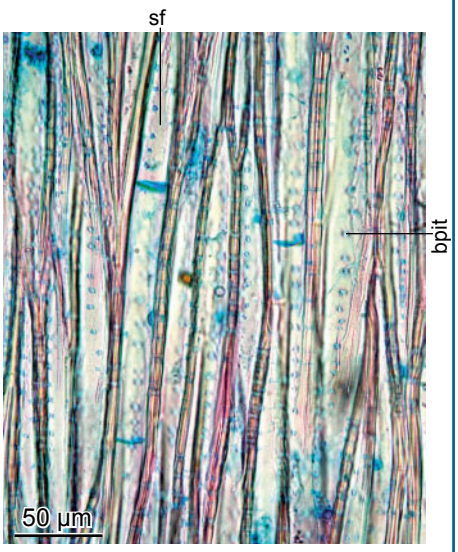



**Fig. 18.** Septate fibers. The horizontal walls in fibers with small, bordered pits are unlignified (blue). Stem of a succulent shrub on a rock, tropical climate, Dhofar, Oman. *Adenium obesum*, radial section.

### Characteristics of the phloem and the cortex

Sclereids in the cortex appear to be almost characteristic of the Apocyanaceae and Asclepiadaceae (**Fig. 19**). They are present throughout all life forms. Crystal druses have been found in the cortex of the hemicryptophytes *Vincetoxicum*, *Asclepias* and *Gomphocarpus* (**Fig. 20**). Prismatic crystals are present in the cortex of *Periploca laevigata*. Laticifers are typical in species of both families (**Figs. 20**, **22** and **23**). They occur in the xylem of *Calotropis* and *Leptadenia* and in the cortex of *Adenium*, *Apocynum*, *Nerium*, *Rhazya*, *Calotropis*, *Ceropegia* and *Periploca*.

### Characteristics of the pith

Characteristic of many genera is the presence of medullary phloem, e.g. in *Ceropegia fusca* (**Fig. 25**), *Calotropis procera* (**Fig. 26**), *Acokanthera*, *Nerium*, *Vinca* (**Fig. 27**), *Vincetoxicum*, *Asclepias*, *Caralluma* and *Periploca*.

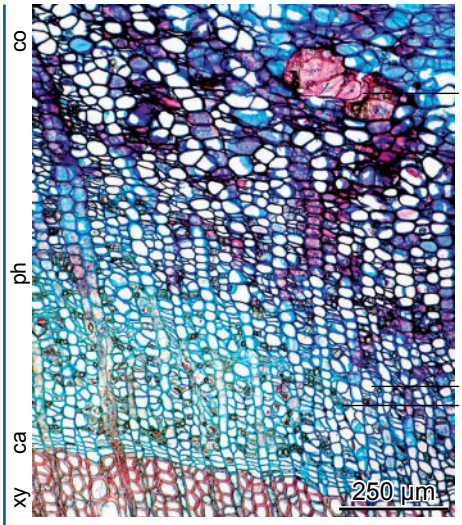



**Fig. 19.** A group of sclerenchymatic cells expands into the cortex. The phloem consists of radially oriented rays, large axial parenchyma cells and small sieve-cell groups. Bark of a shrub in a canyon, succulent zone, subtropical climate, Gomera, Canary Islands. *Nerium oleander*, transverse section.

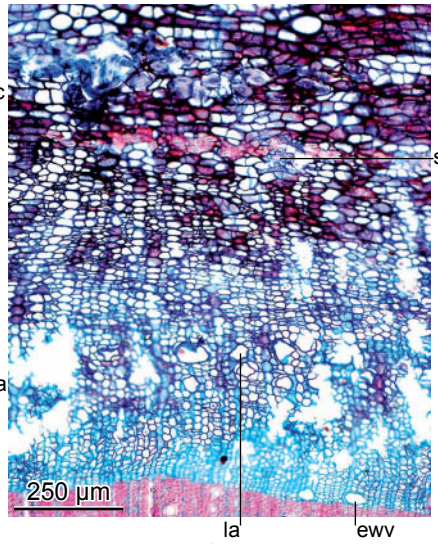



**Fig. 20.** A group of sclerenchymatic cells in a tangential row lies in the cortex. Large laticifers lie in a tangential, simple phloem. Bark of a liana, thermophile zone, subtropical climate, Tenerife, Canary Islands. *Periploca laevigata*, transverse section.

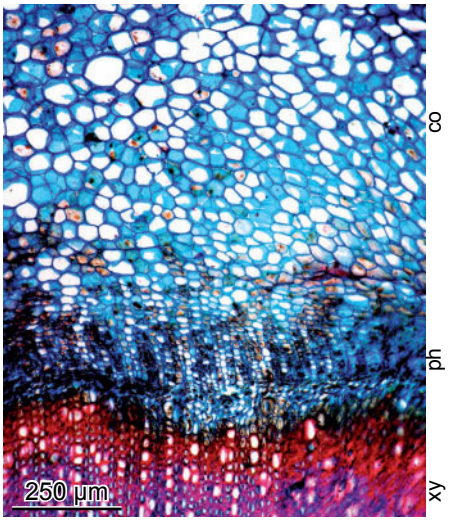
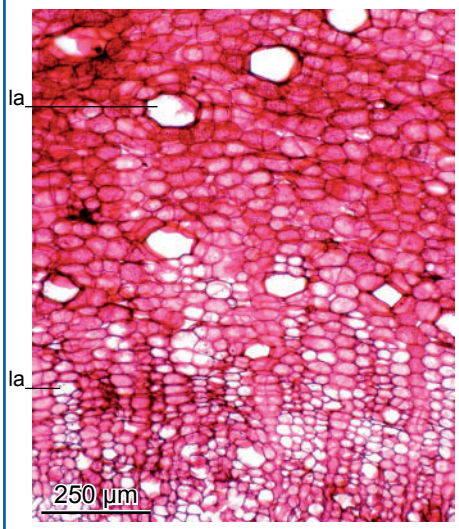
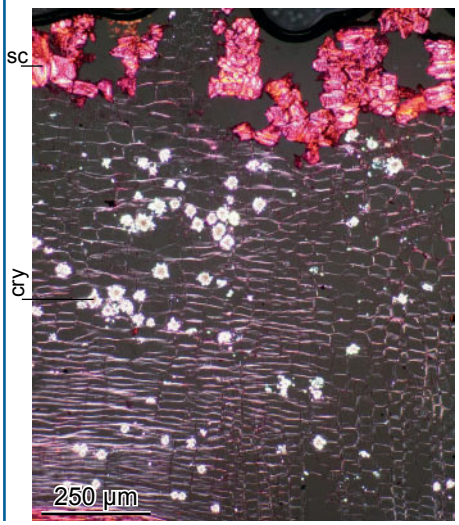


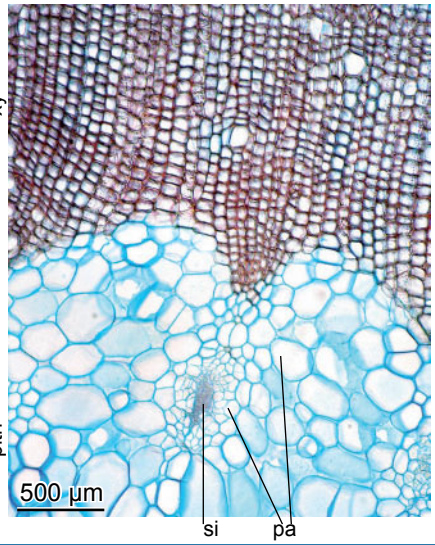

**Fig. 21.** Simple construction of the bark: The cortex consists of large parenchyma cells and the tangential unstructured phloem on small parenchyma and sieve tubes. Laticifers are absent. Rhizome of a perennial herb, garden, mountain subtropical climate, Gomera, Canary Islands. *Vinca major*, transverse section.



**Left Fig. 22.** The large laticifers are mainly in the cortex. 50 cm-high perennial herb in the Botanical Garden of the University of Michigan, Ann Arbour, USA. *Apocynum cannabinum*, transverse section.

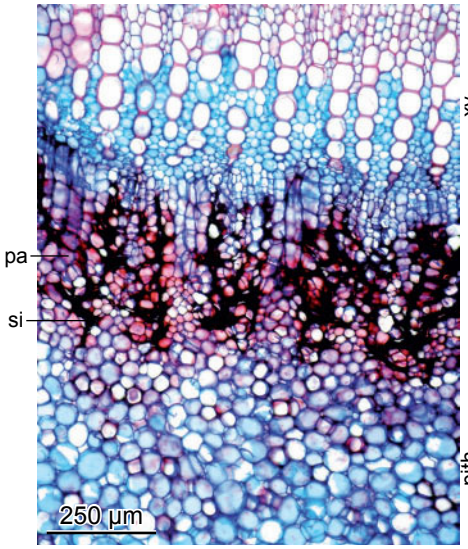
**Right Fig. 23.** Large laticifers in the cortex and the pith. One-year-old long shoot of a cultivated shrub, succulent zone, subtropical climate, Gomera, Canary Islands. *Acokanthera oblongifolia*, transverse section.

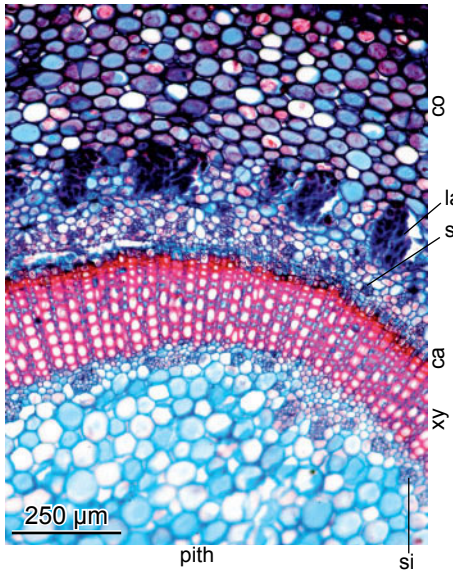



**Left Fig. 24.** Crystal druses in the cortex and the phloem. Rhizome of a 30 cm-high perennial herb, Sage brush steppe, Grand Junction, Colorado, USA. *Asclepias subverticillata*, transverse section, polarized light.

**Right Fig. 25.** Isolated sieve-tube groups (medullary phloem) at the periphery of the pith. Stem of a succulent plant, succulent zone, dry subtropical climate, Canary Islands, Gomera. *Ceropegia fusca*, transverse section.




**Left Fig. 26.** Irregular cell groups filled with dark substances (phenols?) represent medullary phloem. Long shoot of a shrub, arid climate, Arabian desert, Oman. *Calotropis procera*, transverse section.

**Right Fig. 27.** Isolated sieve-tube groups (medullary phloem) at the periphery of the pith. Typical are ducts with One-year-old rhizome of a perennial herb, garden, mountain subtropical climate, Gomera, Canary Islands. *Vinca major*, transverse section.



**Ecological trends in the xylem**

Annual ring width varies between 0.2 and approximately 2 mm. The average ring width increases from 0.53 mm in hemicryptophytes to 0.75 mm in lianas and 1.2 mm in shrubs. Most perennial species have annual growth rings, including those growing in subtropical climates (**Figs. 2-5**). No correlations could be found between the distinctness of growth rings and climatic and vegetation zones. No ecological trends in any anatomical feature of the xylem or bark could be detected.

**Discussion in relation to previous studies**

The anatomy of the following Apocyanaceae and Asclepiadaceae species (8 shrubs, 1 herb) occurring in Europe, the Sahara and the Near East and the Canary Islands has been described by several authors: *Calotropis procera* by Fahn et al. (1986). *Leptadenia pyrotechnica* by Jagiella and Küster (1987), Neumann et al. (2001). *Nerium oleander* by Edlmann et al.(1994), Fahn et al. (1986), Greguss (1959), Neumann et al. (2001), Schweingruber (1990). *Periploca aphylla* by Fahn et al. (1986), Jagiella and Küster (1987). *Pergularia tomentosa* by Neumann et al. (2001). *Periploca graeca* by Huber and Rouschal (1954), Metcalfe and Chalk (1957), Schweingruber (1990). *Periploca laevigata* by Neumann et al. (2001), Schweingruber (1990). *Solenostella argel* by Neumann et al. (2001). Patil and Kishore (2008) described the interxylary phloem in *Leptadenia*.

The present results agree with earlier observations, however, they are more extensive than previous studies, which characterize only shrubs and dwarf shrubs from dry regions. Here we describe semi-herbaceous species, including those of humid regions, and succulent growth forms. The variability of anatomical characteristics of the xylem is higher than expected, e.g. it includes species with very thin-walled fibers (*Adenium*), with septate fibers and with large amounts of thin-walled parenchymatic tissue (*Ceropegia*, *Caralluma*).

The material presented here does not represent the total anatomical spectrum occuring within the family.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of analyzed species** | | **21** |
| 1 | growth rings distinct and recognizable | 25 |
| 2 | growth rings indistinct or absent | 8 |
| 3 | ring-porous | 11 |
| 4 | semi-ring-porous | 8 |
| 5 | diffuse-porous | 7 |
| 6 | vessels in intra-annual tangential rows | 1 |
| 7 | vessels in diagonal and/or radial patterns | 3 |
| 8 | vessels in dendritic patterns | 1 |
| 9 | vessels predominantly solitary | 14 |
| 9.1 | vessels in radial multiples of 2-4 common | 8 |
| 10 | vessels in radial multiples of 4 or more common | 6 |
| 11 | vessels predominately in clusters | 13 |
| 13 | vessels with simple perforation plates | 32 |
| 20 | intervessel pits scalariform | 4 |
| 22 | intervessel pits alternate | 11 |
| 29 | vestured pits | 12 |
| 31 | vessel-ray pits with large apertures, *Salix/Laurus* type | 6 |
| 36 | helical thickenings present | 9 |
| 39.1 | vessel cell-wall thickness >2 µm | 3 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 13 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 9 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 9 |
| 50 | <100 vessels per $mm^2$ in earlywood | 19 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 14 |
| 56 | tylosis with thin walls common | 6 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 15 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 21 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 1 |
| 65 | septate fibers present | 2 |
| 68 | fibers thin-walled | 12 |
| 69 | fibers thick-walled | 3 |
| 70 | fibers thin- to thick-walled | 19 |
| 70.2 | tension wood present | 7 |
| 75 | parenchyma absent or unrecognizable | 9 |
| 76 | parenchyma apotracheal, diffuse in aggregates | 9 |
| 79 | parenchyma paratracheal | 17 |
| 79.1 | parenchyma pervasive | 1 |
| 89 | parenchyma marginal | 3 |
| 89.1 | parenchyma marginal thin-walled, dark in polarized light | 3 |
| 96 | rays exclusively uniseriate | 6 |
| 97 | ray width predominantly 1-3 cells | 19 |
| 98 | rays commonly 4-10-seriate | 5 |
| 99 | rays commonly >10-seriate | 1 |
| 99.1 | vascular-bundle form remaining | 1 |
| 105 | ray: all cells upright or square | 11 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 8 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 10 |
| 117 | rayless | 5 |
| 120 | storied axial tissue (parenchyma, fibers, vessels in tangential section) | 1 |
| 130 | with radial canals | 6 |
| 135 | interxylary phloem present | 3 |
| 136 | prismatic crystals present | 14 |
| 144 | druses present | 5 |
| R1 | groups of sieve tubes present | 9 |
| R2 | groups of sieve tubes in tangential rows | 5 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 7 |
| R6 | sclereids in radial rows | 1 |
| R6.1 | sclereids in tangential rows | 6 |
| R7 | with prismatic crystals | 10 |
| R8 | with crystal druses | 7 |
| R9 | with crystal sand | 1 |
| R10 | phloem not well structured | 2 |
| R12 | with laticifers, oil ducts or mucilage ducts | 16 |
| P1 | with medullary phloem or vascular bundles | 9 |
| P2 | with laticifers or intercellular canals | 3 |

# Aristolochiaceae



### Number of species, worldwide and in Europe

The Aristolochiaceae family includes 7 genera with 460 species. Major genera are *Aristolochia* with 370 and *Asarum* with 70 species. In Europe there are 2 genera (*Aristolochia* and *Asarum*) with 15 species.

### Distribution

Widely distributed in tropical and temperate regions.

### Analyzed material

The xylem and phloem of 6 Aristolochiaceae species has been analyzed here.

| | |
|---|---|
| **Life forms analyzed:** | |
| Phanerophytes >4 m | 1 |
| Liana | 2 |
| Hemicryptophytes and geophytes | 3 |
| **Plants analyzed from different vegetation zones:** | |
| Hill and mountain | 5 |
| Tropical | 1 |

**Analyzed species:**

*Aristolochia clematitis* L.
*Aristolochia gigantea* Mart. *et* Zucc.
*Aristolochia macrophylla* Lam.
*Aristolochia manshuriensis* Kom.
*Aristolochia pallida* Willd.
*Asarum europaeum* L.

*Asarum europaeum*

*Aristolochia macrophylla* (photo: Zinnert)

*Aristolochia clematitis*

**Characteristics of the xylem**

Annual rings are absent in the analysed material of *Asarum europaeum* (**Fig. 1**) and the tropical *Aristolochia gigantea* (**Fig. 2**). Annual rings occur in all other species of the temperate region. Ring boundaries of most species are characterized by semi-ring porosity (**Fig. 3**) or ring-porosity (**Fig. 4**). Vessels are mostly solitary (**Figs. 2** and **3**). Latewood vessels are arranged in tangential uniseriate rows in *Aristolochia manshuriensis* (**Fig. 4**). Vessel diameter varies greatly. Vessels are smaller than 25 µm in the rhizome of *Asarum europaeum* (**Fig. 5**). The earlywood vessel diameter of the rhizomes of the hemicryptophytes *Aristolochia clematitis* and *A. pallida* varies between 50 and 100 µm (**Fig. 3**) and the diameter exceeds 150 µm in the lianas *Aristolochia gigantea*, *A. manshuriensis* and *A. macrophylla* (**Figs. 2, 4**).Vessel density varies in the majority of analyzed species between 50 and 100/mm$^2$. Vessels cell walls are thick-walled (2-3 µm) on *Asarum europaeum*, *Aristolochia clematitis* and *Aristolochia pallida* (**Fig. 5**) and thin-walled on *Aristolochia manshuriensis*. Vessels contain exclusively simple perforations (**Figs. 6** and **7**).

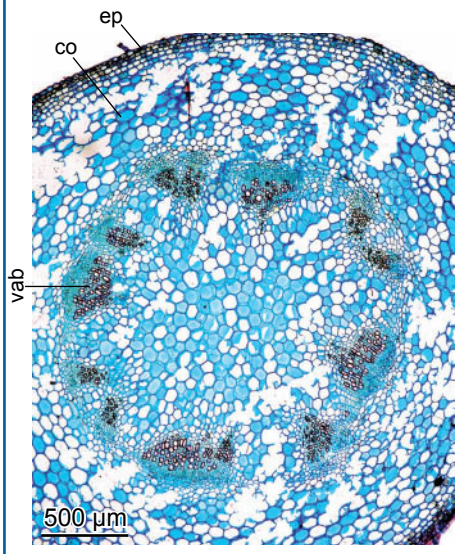



**Fig. 1.** Single vascular bundles without annual rings are arranged in a circle around the pith. A periderm is absent. Rhizome of a 5 cm-high hemicryptophyte, understory of a beech forest, mountain zone, Switzerland. *Asarum europaeum*, transverse section.

**Fig. 2.** The xylem of vascular bundles without annual rings is delimitated by large primary rays with unlignified cell walls. Secondary rays evolve near the periphery. Shoot of a 2 m-high tree, tropical green house, Botanical Garden, Basel, Switzerland. *Aristolochia gigantea*, transverse section.

**Fig. 3.** The xylem of vascular bundles with annual rings is delimitated by large primary rays with unlignified cell walls. Secondary rays evolve continuously with increasing stem diameter. Rhizome of a 40 cm-high hemicryptophyte, abandoned vineyard, hill zone, Austria. *Aristolochia clematitis*, transverse section.

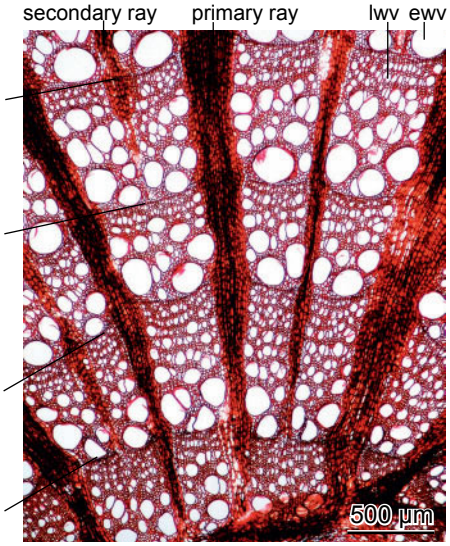



**Fig. 4.** Ring-porous wood with distinct annual rings. Secondary rays evolve continuously with increasing stem diameter. Stem of a 4 m-long liana, hill zone, Botanical Garden, Chabarovsk, Russia. *Aristolochia manshuriensis*, transverse section.

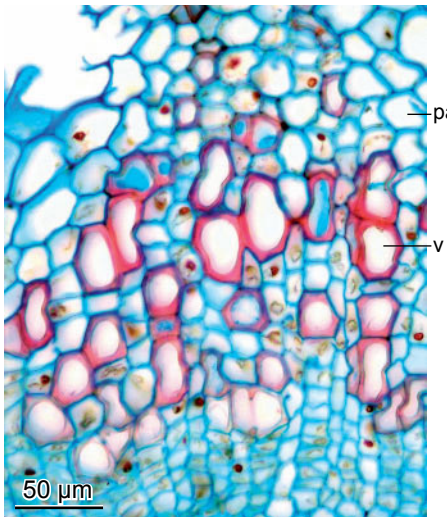



**Fig. 5.** Lignified, thick-walled vessels between living parenchyma cells (pervasive parenchyma). Rhizome of a 5 cm-high hemicryptophyte, understory of a beech forest, mountain zone, Switzerland. *Asarum europaeum*, transverse section.

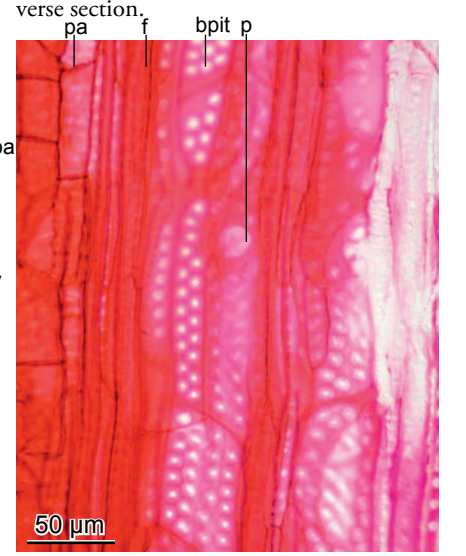



**Fig. 6.** Vessel with a simple perforation and large bordered pits. Stem of a 4 m-long liana, Botanical Garden, Chabarovsk, hill zone, Russia. *Aristolochia manshuriensis*, radial section.

Intervessel pits are predominantly round (**Fig. 6**), but are scalariform on *Asarum europaeum* (**Fig 7**). *Aristolochia clematitis* and *A. pallida* produce thin-walled, unlignified tylosis (**Fig. 8**). Fibers are missing in *Asarum europaeum* (**Fig. 5**). The radial walls of fibers (tracheids) in all other species are perforated by very large round pits (>2 µm). Fibers are mostly thin-walled in *Aristolochia manshuriensis* and thin- to thick-walled in other species. Axial parenchyma is pervasive in *Asarum europaeum* (**Fig. 5**), is diffuse in aggregates (paratracheal and apotracheal) (**Fig. 10** and **11**), and partially marginal on *Aristolochia clematitis* (**Fig. 10**). Axial parenchyma cells and fibers are distinctly storied only in the lianas *Aristolochia gigantea*, *A. manshuriensis* (**Fig. 12**), *A. macrophylla* and vaguely storied in *A. clematitis*. Ray width is large in all species and exceeds 10 cells. Large rays represent intervascular parenchyma in *Asarum europaeum* (**Fig. 1**). Vascular bundle structure is visible in all other species and primary rays therefore represent intervascular parenchyma strands. Rays initiated later are true rays (**Fig. 13** and **14**). Ray cells are square or upright in all species. Crystals (druses) are only present in the rays of *Aristolochia macrophylla* (**Fig. 15**).

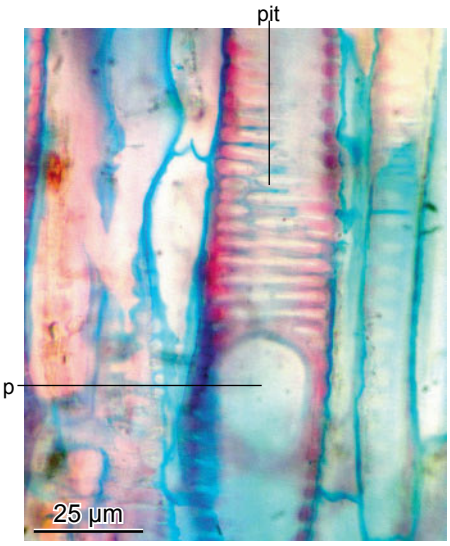



**Fig. 7.** Vessel with a simple perforation and large bordered scalariform intervessel pits. Rhizome of a 5 cm-high hemicryptophyte, understory of a beech forest, mountain zone, Switzerland. *Asarum europaeum*, radial section.

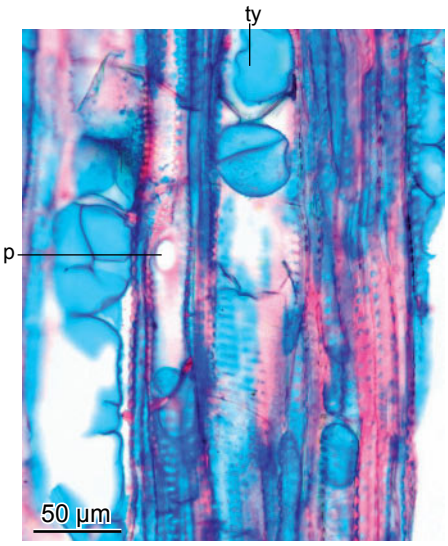



**Fig. 8.** Large vessels with unlignified tylosis. Rhizome of a 40 cm-high hemicryptophyte, abandoned vineyard, hill zone, Austria. *Aristolochia clematitis*, radial section.

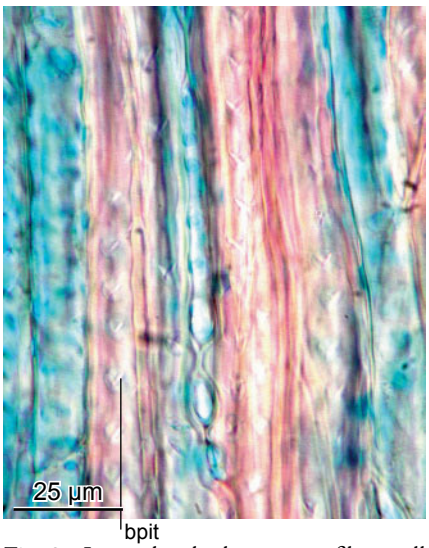



**Fig. 9.** Large borderd pits on fiber cell walls (tracheids). Rhizome of a 40 cm-high hemicryptophyte, abandoned vineyard, hill zone, Austria. *Aristolochia clematitis*, radial section.

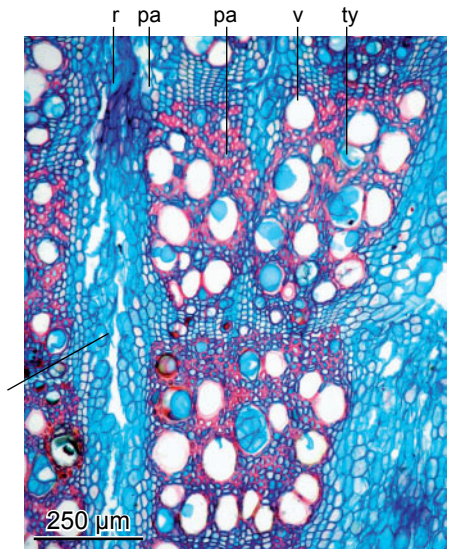



**Fig. 10.** Apotracheal, paratracheal (diffuse in aggregates) and marginal parenchyma. Fibers are thin- to thick-walled. Rhizome of a 40 cm-high hemicryptophyte, abandoned vineyard, hill zone, Austria. *Aristolochia clematitis*, transverse section.

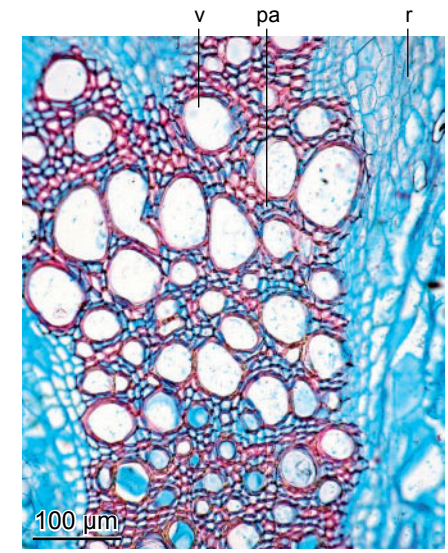



**Fig. 11.** Apotracheal, paratracheal parenchyma (diffuse in aggregates). Fibers are thin- to thick-walled. Rhizome of a 30 cm-high hemicryptophyte, abandoned vineyard, hill zone, Provence, France. *Aristolochia pallida*, transverse section.

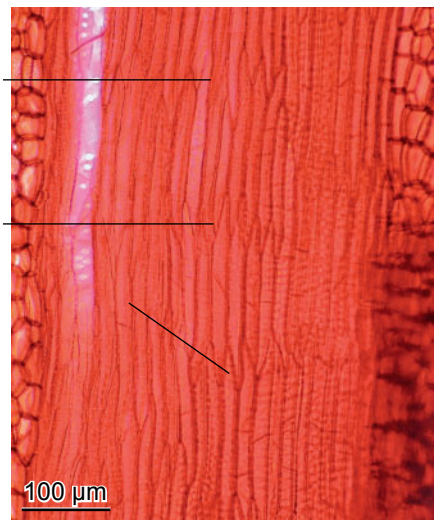



**Fig. 12.** Storied parenchyma cells. Stem of a 4 m-long liana, hill zone, Botanical Garden, Chabarovsk, Russia. *Aristolochia manshuriensis*, tangential section.

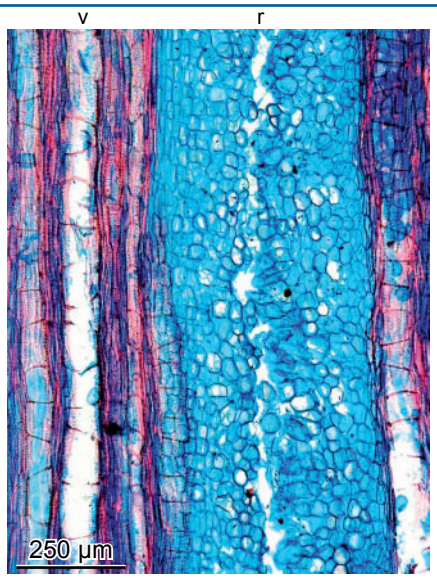



**Fig. 13.** Extremely large ray, >15 cells in width. Rhizome of a 40 cm-high hemicryptophyte, abandoned vineyard, hill zone, Austria. *Aristolochia clematitis*, tangential section.

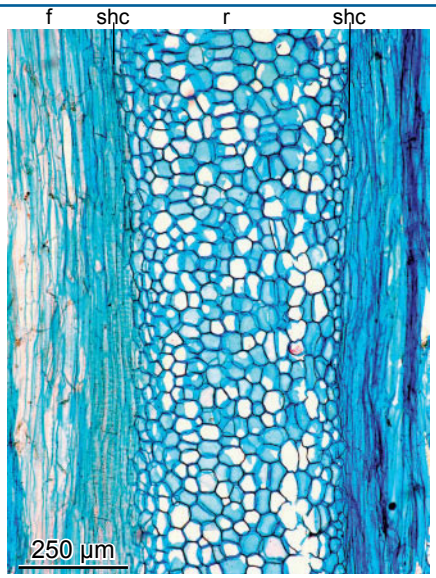



**Fig. 14.** Extremely large ray >15-seriate. It is partially bordered with sheet cells. Shoot of a 2 m-high tree, tropical green house, Botanical Garden, Basel, Switzerland. *Aristolochia gigantea*, tangential section.

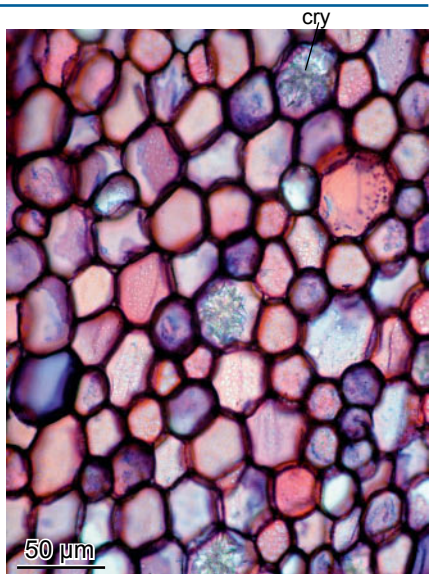



**Fig. 15.** Crystal druses in ray cells. Stem of a 4 m-long liana, Botanical Garden, Bern, hill zone, Switzerland. *Aristolochia macrophylla*, tangential section.

### Characteristic features of taxa

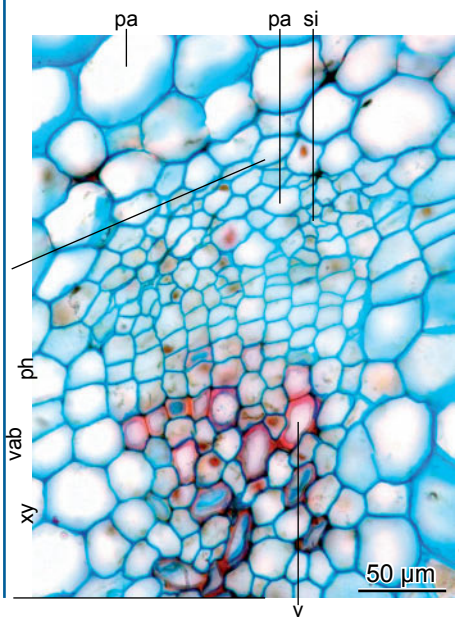
The number of samples analysed here is too small to differentiate species definitely. However, vascular bundles without secondary growth are unique to *Asarum europaeum*. Crystal druses are characteristic of *Aristolochia macrophylla*.

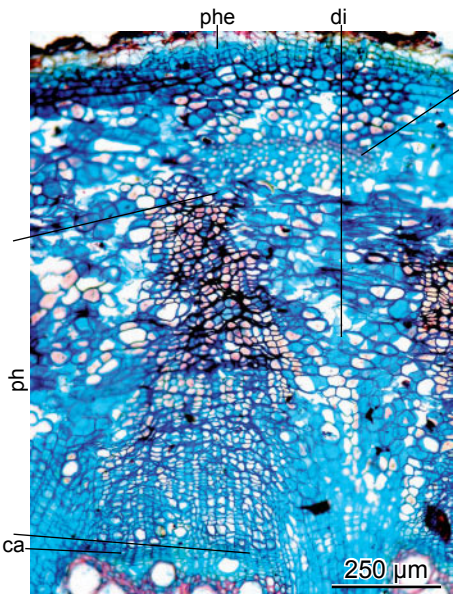
### Ecological trends and relations to life forms

Ecological trends were found concerning earlywood vessel diameter. Large earlywood vessel diameters (>150 µm) are characteristic of the lianas (*Aristolochia gigantea*, *A. manshuriensis*, *A. macrophylla*).

### Characteristics of the phloem and the cortex

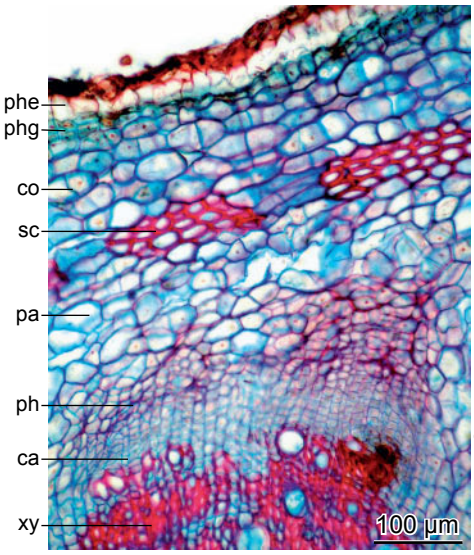
The bark of *Asarum europaeum* is unique: Vascular bundles are isolated in a ring and a peripheral continuous phloem. Cortical fibers and phellem are absent. (**Figs. 1** and **16**). All other species have a cortical fiber band which is broken in older individuals, and a periderm. The periderm is thin in *Aristolochia clematitis* (**Fig. 17**), *Aristolochia pallida* (**Fig. 18**) and large on the lianas *Aristolochia gigantea* (**Fig. 19**), *A. manshuriensis* and *A. macrophylla* (**Fig. 20**). The cortical fibers band consists of septate fibers with small, slit-like pits (**Fig. 21**).

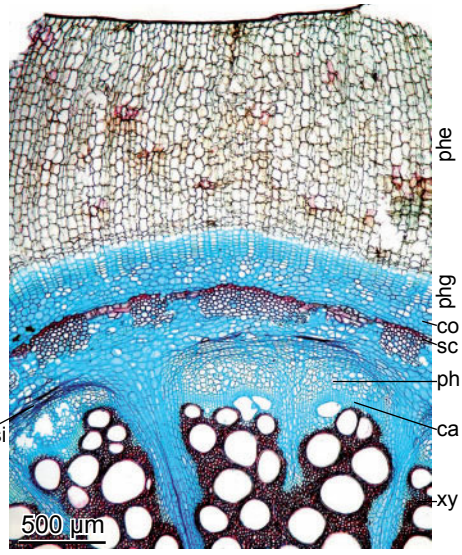



**Left Fig. 16.** Single vascular bundle. The phloem consists of small sieve-tube elements and larger parenchyma cells. The bundle is surrounded by large parenchyma cells. Rhizome of a 5 cm-high hemicryptophyte, understory of a beech forest, mountain zone, Switzerland. *Asarum europaeum*, transverse section.

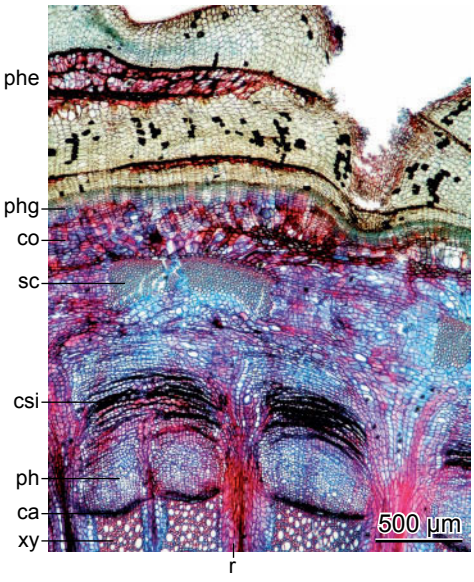
**Right Fig. 17.** Phloem between ray dilatations. Older sieve-tube elements have collapsed (dark irregular zones). A piece of a former fiber-belt is present outside the ray dilatation in the cortex. The periderm is small. Rhizome of a 40 cm-high hemicryptophyte, abandoned vineyard, hill zone, Austria. *Aristolochia clematitis*, transverse section.




**Left Fig. 18.** Pieces of a former fiber belt in the cortex. The phellem is small. Rhizome of a 30 cm-high hemicryptophyte, abandoned vineyard, hill zone, Provence, France. *Aristolochia pallida*, transverse section.

**Right Fig. 19.** Bark with an extremely large phellem. The former fiber belt in the cortex is bridged of sclerenchyma cells. Older sieve-tube elements in the phloem are collapsed. Shoot of a 2 m-high tree, tropical green house, Botanical Garden, Basel, Switzerland. *Aristolochia gigantea*, transverse section.



**Left Fig. 20.** Bark with a multilayered phellem. The former fiber belt is broken and the gaps are filled with thin-walled parenchyma cells. Older sieve-tube elements in the phloem are collapsed. Old stem of a 4 m-long liana, Botanical Garden, Bern, hill zone, Switzerland. *Aristolochia macrophylla*, transverse section.

**Right Fig. 21.** Septate fibers of the fiber belt in the cortex. Shoot of a 2 m-high tree, tropical green house, Botanical Garden, Basel, Switzerland. *Aristolochia gigantea*, radial section.

**Discussion in relation to previous studies**

The only comprehensive wood anatomical study to date was made by Carlquist (1993) on the basis of 12 woody species. Many authors have characterized just a few woody species, see Gregory (1994). Comparable with the present study is *Aristolochia manshuriensis* described by Benkova and Schweingruber (2004).

The present results are mainly compared with the study from Carlquist (1993). Most of his observations could be confirmed. However, we did not find oil cells in the material available. The anatomy of the rhizome of *Aristolochia clematitis* is anatomically related to other species with liana-like growth forms. The anatomy of the rhizome of the small prostrate hemicryptic herb *Asarum europaeum* constrasts all other species by isolated vascular bundles (Metcalfe and Chalk 1957).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of analyzed species** | | **6** |
| 1 | growth rings distinct and recognizable | 4 |
| 2 | growth rings indistinct or absent | 3 |
| 3 | ring-porous | 4 |
| 4 | semi-ring-porous | 2 |
| 6 | vessels in intra-annual tangential rows | 1 |
| 9 | vessels predominantly solitary | 6 |
| 11 | vessels predominately in clusters | 1 |
| 13 | vessels with simple perforation plates | 6 |
| 14 | vessels with scalariform perforation plates | 1 |
| 20 | intervessel pits scalariform | 1 |
| 39.1 | vessel cell-wall thickness >2 µm | 3 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 1 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 2 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 4 |
| 50 | <100 vessels per $mm^2$ in earlywood | 3 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 3 |
| 56 | tylosis with thin walls common | 2 |
| 60.1 | fibers absent | 1 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 5 |
| 69 | fibers thick-walled | 1 |
| 70 | fibers thin- to thick-walled | 4 |
| 76 | parenchyma apotracheal, diffuse in aggregates | 5 |
| 79 | parenchyma paratracheal | 3 |
| 79.1 | parenchyma pervasive | 3 |
| 89 | parenchyma marginal | 1 |
| 99 | rays commonly >10-seriate | 5 |
| 99.1 | vascular-bundle form remaining | 1 |
| 100.2 | rays invisible in in polarized light | 5 |
| 102 | ray height >1 mm | 5 |
| 105 | ray: all cells upright or square | 5 |
| 110 | rays with sheet cells (tangential section) | 1 |
| 117 | rayless | 1 |
| 120 | storied axial tissue (parenchyma, fibers, vessels in tangential section) | 3 |
| 144 | druses present | 1 |
| 153 | crystal sand present | 1 |
| R2 | groups of sieve tubes in tangential rows | 1 |
| R3 | distinct ray dilatations | 1 |
| R7 | with prismatic crystals | 1 |
| R8 | with crystal druses | 3 |
| R12 | with laticifers, oil ducts or mucilage ducts | 3 |

# Berberidaceae



### Number of species, worldwide and in Europe

The Berberidaceae family includes 15 genera with 650 species. The genus *Berberis* is the most representative with 600 species. Widely distributed, especially in temperate regions of the northern hemisphere and the Andes. In Europe there are 5 genera (*Mahonia* is cultivated) with 10 species. The majority belongs to *Berberis* (4 species).

### Analyzed material

The xylem and phloem of 16 Berberidaceae species has been analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 12 | many: several authors |
| Woody chamaephytes | 1 | |
| Hemicryptophytes and geophytes | 3 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 2 | |
| Hill and mountain | 10 | |
| Mediterranean | 3 | |
| Arid | 1 | |

**Analyzed species:**

*Berberis aetnensis* C. Presl.
*Berberis buxifolia* Lam.
*Berberis cretica* L.
*Berberis empetrifolium* Lam.
*Berberis hispanica* Boiss et. Reuter
*Berberis julianae* C.K. Schneid.
*Berberis verruculosa* Hemsl. & E.H.Wilson
*Berberis vulgaris* L.
*Epimedium alpinum* L.
*Epimedium pinnatum* DC.
*Mahonia aquifolium* Nutt.
*Mahonia bealei* Carr.
*Mahonia fremontii* Fedde
*Mahonia nervosa* Pursh.
*Nandina domestica* Thunb.
*Vancouveria planipetala* Calloni

*Berberis vulgaris* (photo: Zinnert)

*Mahonia aquifolium* (photo: Aas)

*Epimedium* sp. (photo: Lauerer)

**Characteristics of the xylem**

Annual rings occur in the present material in all species in most vegetation zones. The ring boundaries of most species are defined by ring-porosity (**Fig. 1**) and semi-ring porosity (**Figs. 2-5**) with different levels of clarity. Rings are often festoon-like indented on *Berberis* (**Fig. 1**). The two *Epimedium* species and *Mahonia nervosa* are diffuse-porous (**Figs. 6** and **7**). Vessels of most species are arranged in oblique to dendritic (**Figs. 1, 4, 5**) or radial patterns (**Figs. 3** and **6**). Vessels are solitary in the stem of the dwarf shrub *Mahonia nervosa* (**Fig. 7**). The primary vascular-bundle form is found in the rhizome of both *Epimedium* species (**Fig. 8**). Vessel diameter varies greatly. Vessels are smaller than 20 µm in the herbs *Epimedium pinnatum* (**Fig. 8**) and *Vancouveria planipetala*, as well in the large shrub *Mahonia bealei*. Earlywood vessel diameter of the majority of species varies between 30 and 60 µm. Vessel density varies in the majority of analyzed species between 200 and 400/mm$^2$. It is only lower in *Vancouveria planipetala* and *Mahonia nervosa*. Vessels contain exclusively simple perforations (**Figs. 8** and **9**).

Inter-vessel pits are predominantly small and round (**Fig. 9**) except in the hemicryptophytic herb *Vancouveria planipetala*, where they are scalariform (**Fig. 10**).Vestured pits have not been observed. Helical thickenings occur in all analyzed species (**Fig. 9**) apart from *Epimedium*. Brown substances in vessels seem to

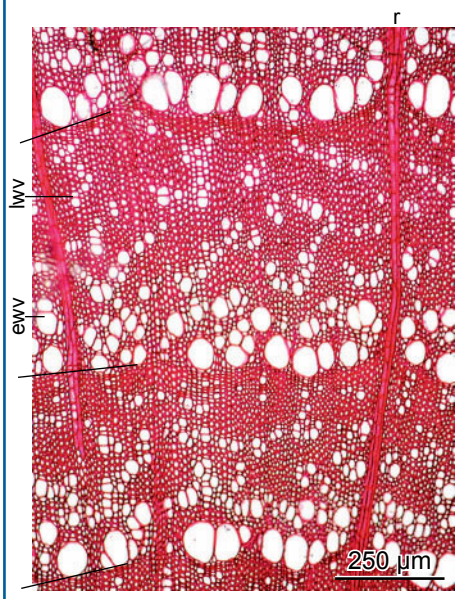



**Fig. 1.** Ring-porous with very distinct rings. Ring boundaries are festoon-like indented. Latewood vessels are arranged in oblique to slightly dendritic groups. Stem of a 60 cm-high shrub on volcanic rocks, subalpine zone, Mt. Etna, Italy. *Berberis aetnensis*, transverse section.

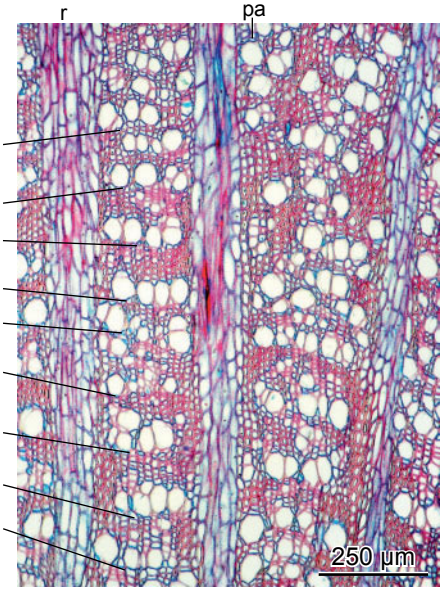



**Fig. 2.** Semi-ring-porous with small rings. Ring boundaries are displaced radially at the borders of large rays. Vessels stay mostly solitary. Stem of a 70 cm-high shrub, volcanic rocks, subalpine zone, Patagonia, Argentina. *Berberis empetrifolium*, transverse section.

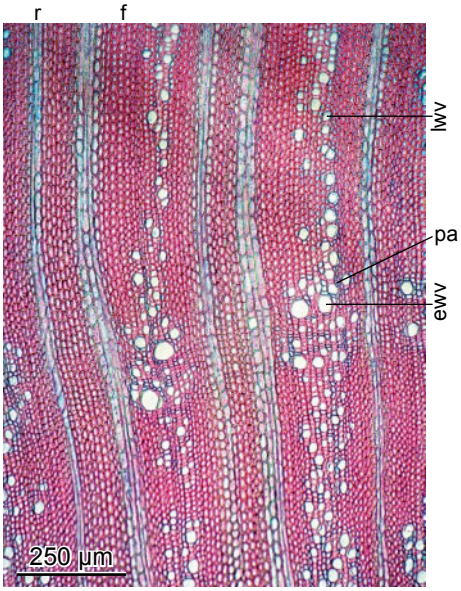
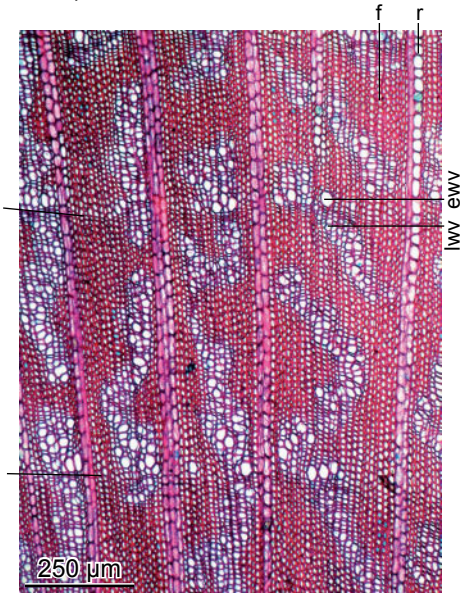
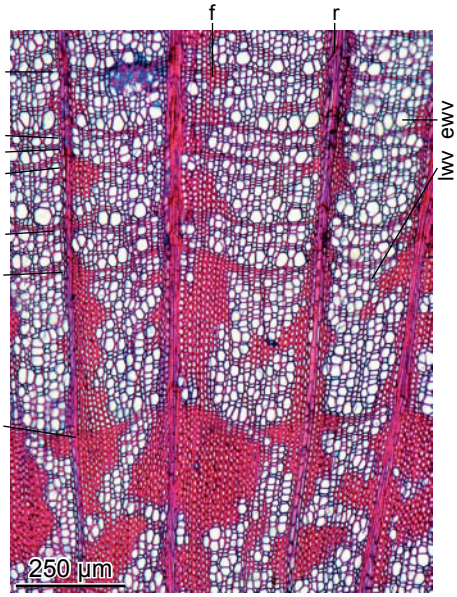



**Fig. 3.** Semi-ring-porous with large rings. Latewood vessels are arranged in long radial groups, Stem of a 1 m-high evergreen shrub, hill zone, Botanical Garden Basel, Switzerland. *Nandina domestica*, transverse section.




**Left Fig. 4.** Diffuse-porous to semi-ring-porous. Latewood vessels are arranged in distinct oblique groups. Stem of a 1.5 m-high evergreen shrub, hill zone, Botanical Garden Basel, Switzerland. *Mahonia bealei*, transverse section.




**Right Fig. 5.** Diffuse-porous to slightly semi-ring-porous wood with large and small rings. Vessel are arranged in dendritic patterns in large rings. Fibers are absent in small rings. Stem of a 1.5 m-high, evergreen shrub, garden, hill zone, Birmensdorf, Switzerland. *Berberis julianae*, transverse section.

be a reaction to mechanical stress and occur in a few species (**Fig. 11**). The radial walls of fibers are perforated by very small slit-like or round pits (<2 µm) of all species. Septate fibers have been found in a few species of *Berberis*, *Mahonia* and *Epimedium* (**Fig. 12**). Fibers are thick- walled (**Fig. 13**) or thin- to thick-walled (**Fig. 14**). Fibers of *Epimedium* are living (with nuclei; **Fig. 15**). Vascular tracheids occur in all shrub species (*Berberis*, *Mahonia*, *Nandina*; **Figs. 13** and **14**). Axial parenchyma is absent or it is a least difficult to recognize (**Fig. 14**).

Ray diversity is high. Rays are absent in *Vancouveria planipetala* (**Figs. 6** and **16**). Three species have rays 1-3 cells wide (**Fig. 17**) and 11 species rays 3-10 cells wide (**Fig. 18**). Ray width of *Nandina domestica* exceeds 10 cells. Ray cells are procumbent in most species. They are exclusively square or upright in *Epimedium* and *Mahonia bealei*. Sheet cells are suggestively present in *Mahonia aquifolium* (**Fig. 18**) and *M. fremontii*. Many species have storied vessels. The ray height exceeds 1 mm in all species. Prismatic crystals have been observed in the rays of *B. buxifolia*, *B. cretica*, *B. empetrifolium*, *B. julianae* and *Mahonia bealei*.

### Taxa characteristic features

Some features characterize single species or groups of species: The absence of annuals (therophytes) is typical for the fam-

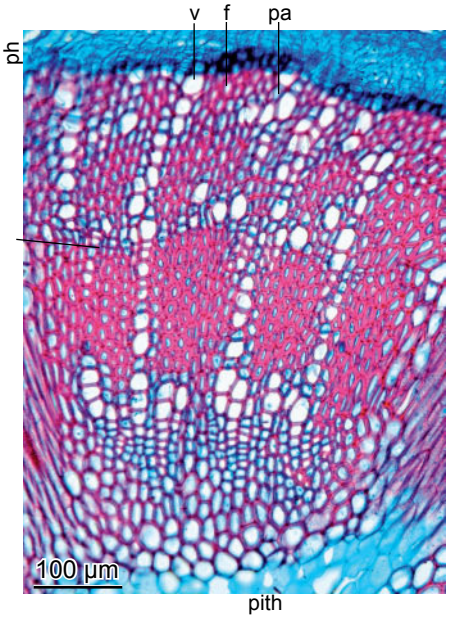



**Fig. 6.** Diffuse-porous to slightly semi-ring-porous wood. Latewood vessels stay in radial rows. Root collar of a 20 cm-high hemicryptophytic herb, Douglas fir forest, hill zone, Cascade Range, Portland, WA, USA. *Vancouveria planipetala*, transverse section.

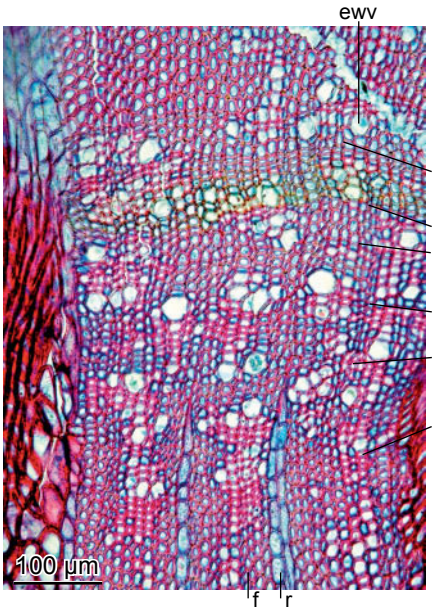



**Fig. 7.** Diffuse-porous wood with solitary vessels. Rings are indistinct. Stem of a 70 cm-high shrub, volcanic rocks, subalpine zone, Cascade Range, Oregon, USA. *Mahonia nervosa*, transverse section.

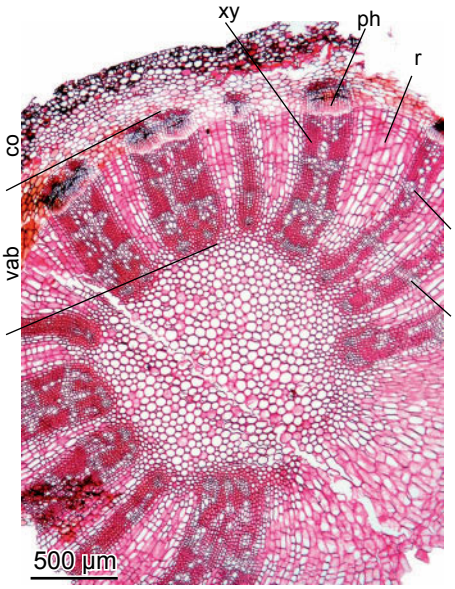
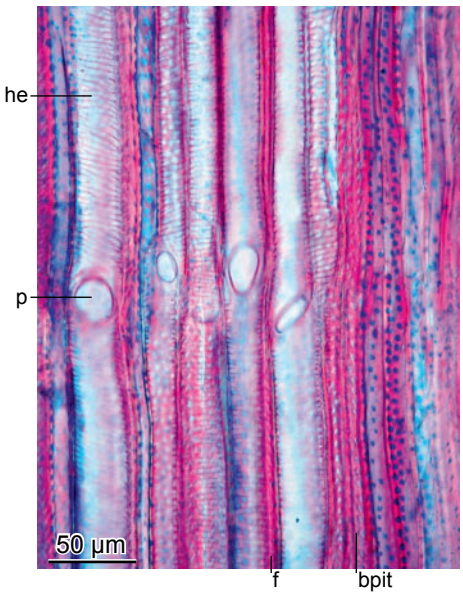
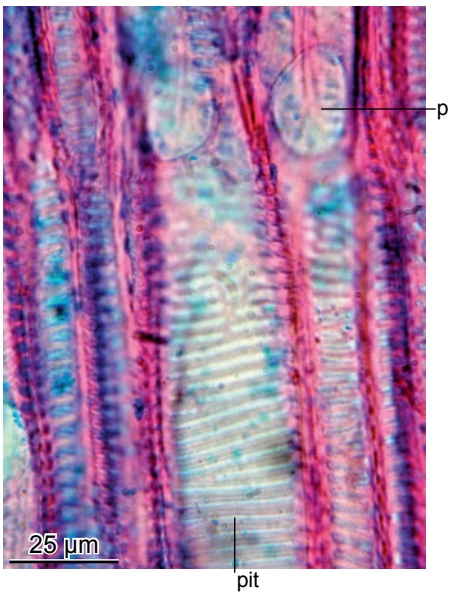



**Fig. 8.** Vascular bundles are separated of large rays. Rhizome of a hemicryptophytic herb, garden, hill zone, Birmensdorf, Switzerland. *Epimedium alpinum*, transverse section.




**Left Fig. 9.** Vessels with simple perforations, small round pits and helical thickenings. Stem of a 1 m-high evergreen shrub, hill zone, Botanical Garden Basel, Switzerland. *Nandina domestica*, radial section.




**Right Fig. 10.** Vessels with simple perforations and scalariform inter-vessel pits. Helical thickenings are absent. Root collar of a 20 cm-high hemicryptophytic herb, Douglas fir forest, hill zone, Cascade Range, Portland, WA, USA. *Vancouveria planipetala*, radial section.

ily of Berberidaceae. Distinct ring-porosity (*Berberis cretica*, *B. vulgaris*) may differentiate others with distinct diffuse porosity (*Berberis julianae*, *B. verruculosa*, *Epimedium*). There is no sufficient material available from different ecological conditions to confirm the hypothesis. Scalariform inter-vessel pits differentiate *Vancouveria planipetala* from all other species in the Berberidaceae family. The occurrenc of vascular bundles differentiate both *Epimedium* species from the genera *Berberis*, *Mahonia* and *Nandina*. We could not find any feature differentiating the genera *Berberis* and *Mahonia*.

Ray width and ray height, as well as the arrangement of vessels (tangential bands, dendritic and radial patterns) might be good features to differentiate species. Very high and large rays as well as small radial vessel groupings are characteristic for *Nandina domestica*.

## Ecological trends and relations to life forms

Anatomical ecological trends were not found. The high age of *Berberis empetrifolium* (53 years) is an indicator of longevity at high altitudes. Basic anatomical structures as radial or dendritic arrangement of vessels and tangential arrangement of sieve-tube/parenchyma bands in the phloem are consistent in all growth forms (shrubs and hemicryptophytes).

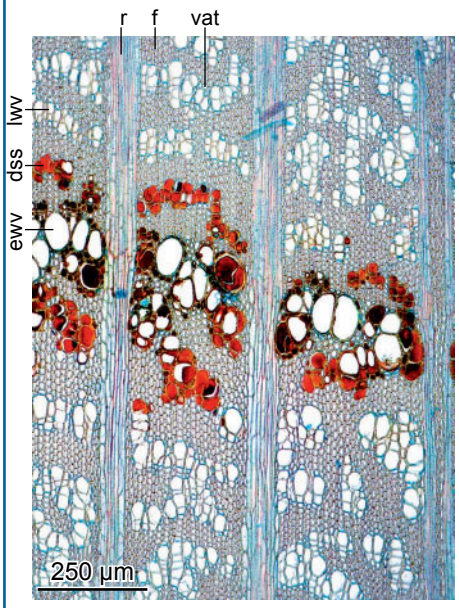



**Fig. 11.** Brown staining substances in vessels are probably a reaction to an injury. Stem of a 1.5 m-high shrub, hedge, mountain zone, Engadin, Switzerland. *Berberis vulgaris*, transverse section.

**Fig. 12.** Septate fibers. The horizontal walls are unlignified. Fibers are perforated by many small slit-like pits. Stem of a 1.5 m-high evergreen shrub, garden, hill zone, Birmensdorf, Switzerland. *Berberis julianae*, transverse section.

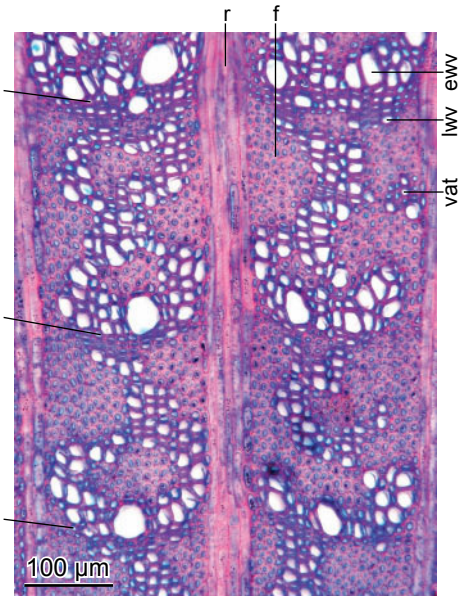
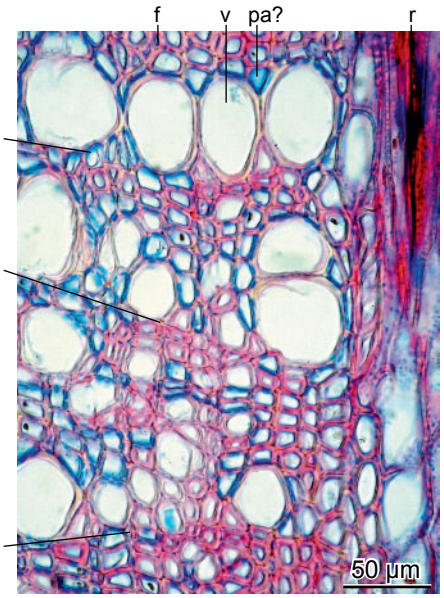
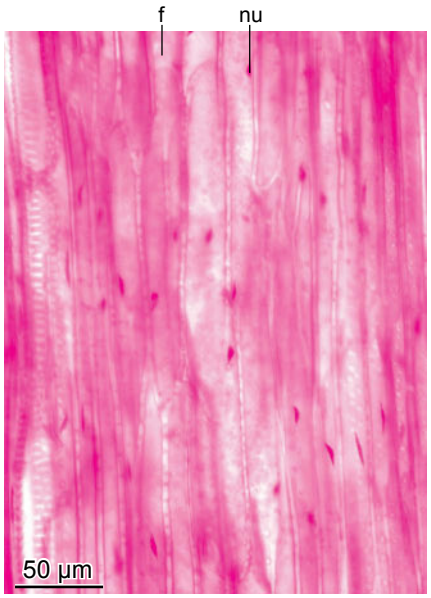



**Fig. 13.** Thick-walled groups of fibers surround vessel groups and vascular tracheids. Stem of a 1 m-high shrub, dry rock, arid zone, Moab, Utah, USA. *Mahonia fremontii*, transverse section.




**Left Fig. 14.** Thin- to thick-walled fibers surround vessel groups. The blue-stained, unlignified fibers represent mostly fibers and tracheids and not parenchyma cells. Stem of a 70 cm-high shrub, volcanic rocks, subalpine zone, Patagonia, Argentina. *Berberis empetrifolium*, transverse section.

**Right Fig. 15.** Fibers with nuclei (living fibers). Rhizome of a hemicryptophytic herb, garden, hill zone, Birmensdorf, Switzerland. *Epimedium pinnatum*, radial section.

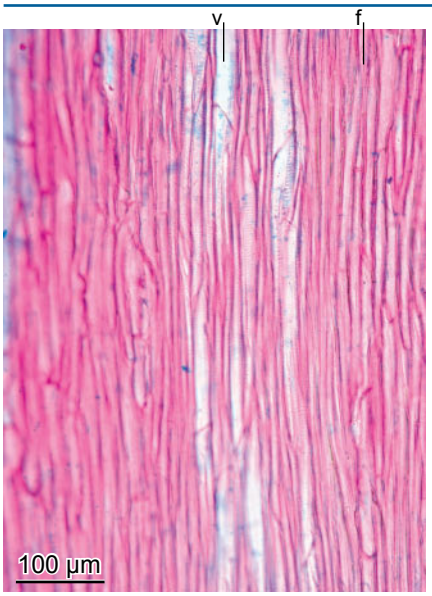



**Fig. 16.** Absent rays. Root collar of a 20 cm-high hemicryptophytic herb, Douglas fir forest, hill zone, Cascade Range, Portland, WA, USA. *Vancouveria planipetala*, tangential section.

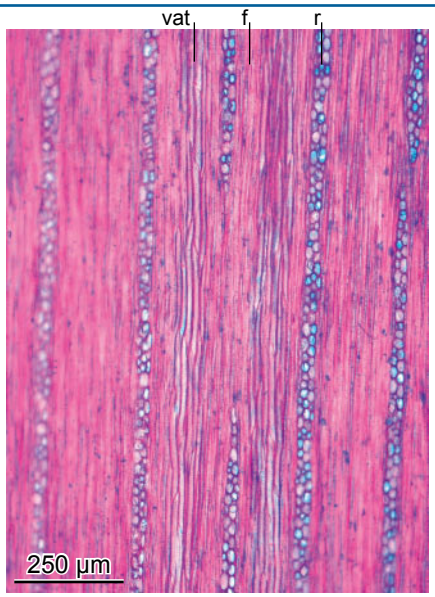



**Fig. 17.** Rays 2-3 cells wide. Ray height up to 8 mm. Stem of a 1.5 m-high evergreen shrub, hill zone, Botanical Garden Basel, Switzerland. *Mahonia bealei*, tangential section.

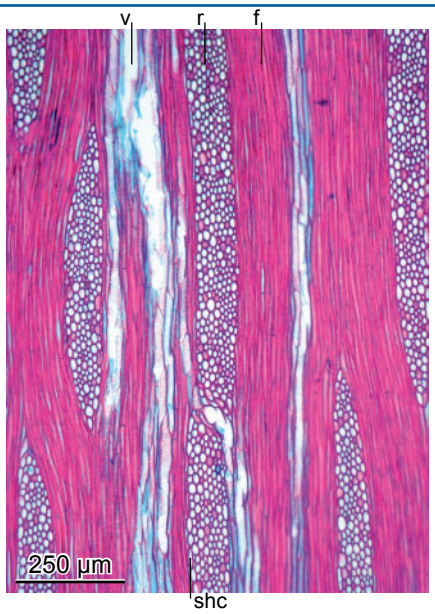



**Fig. 18.** Ray width up to 9 cells, partially with sheet cells. Ray height up to 8 mm. Stem of a 1.5 m-high evergreen shrub, hill zone, garden, Birmensdorf, Switzerland. *Mahonia aquifolium*, tangential section.

**Characteristics of the phloem and the cortex**

The tangential arrangement of sieve tube/parenchyma bands is characteristic of all shrub species (**Figs. 19-21** and **23**). Often they contain a few sclerenchyma fibers (**Figs. 20** and **21**). One to several bands can be formed in one year. Distinct ray dilatations have been observed only on *Berberis empetrifolium* (**Fig. 23**). The phloem of the hemicryptophyte *Epimedium alpinum* consists of small vascular bundle like groups (**Fig. 22**). A few *Berberis* and *Mahonia* species contain prismatic crystals in the rays.

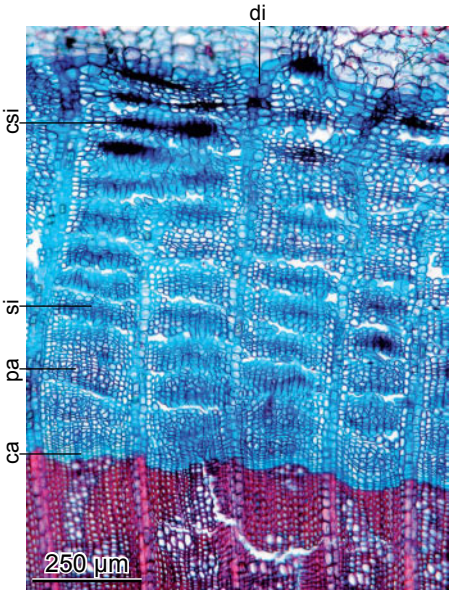



**Fig. 19.** Phloem with tangential sieve-tube/parenchyma layers. Stem of a 1.5 m-high, evergreen shrub, hill zone, Botanical Garden Basel, Switzerland. *Mahonia bealei*, transverse section.

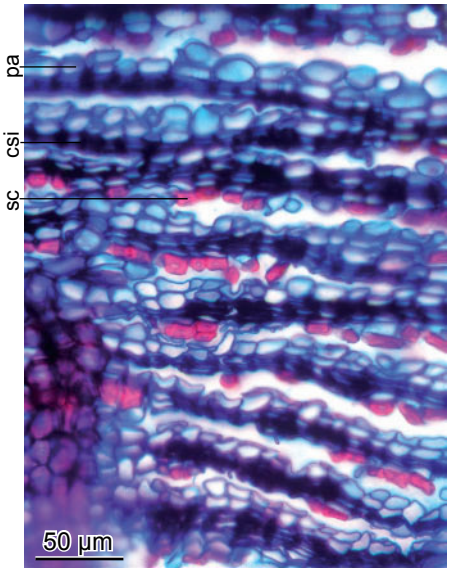



**Fig. 20.** Phloem with tangential sieve-tube/parenchyma layers with a few sclerenchyma fibers in the sieve-cell zone. Phloem cells are mostly collapsed. Stem of a 1.5 m-high evergreen shrub, garden, hill zone, Birmensdorf, Switzerland. *Berberis julianae,* transverse section.

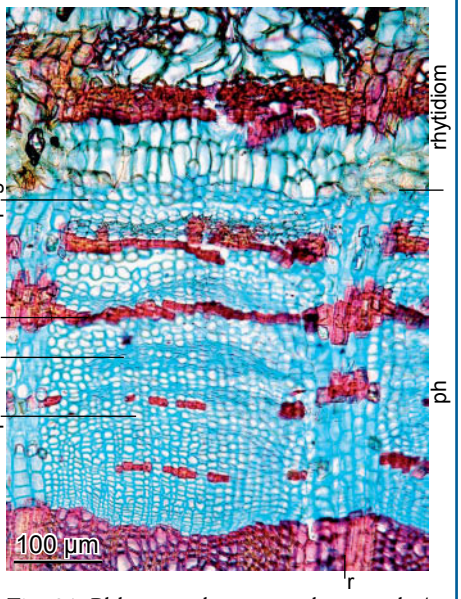
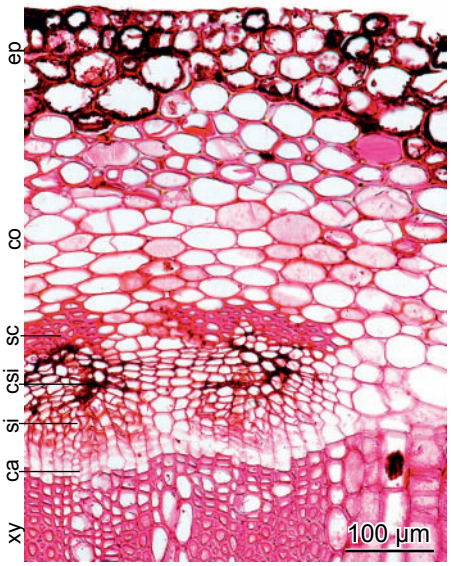
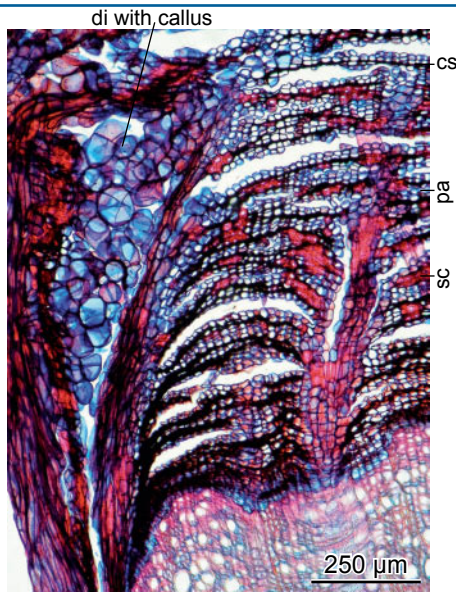



**Fig. 21.** Phloem with tangential sieve-tube/parenchyma layers with a few sclerenchyma fibers in the sieve-cell zone and sclerenchyma-cell groups in the rays. The cortex begins with large thin-walled cells. Stem of a 1 m-high shrub, dry rock, arid zone, Moab, Utah, USA. *Mahonia fremontii*, transverse section.




**Left Fig. 22.** Phloem and cortex. Sieve tubes are collapsed (dark red). Outside the phloem are groups of sclereids. The cortex consists of thin- and thin- to thick-walled parenchyma cells. Rhizome of a hemicryptophytic herb, garden, hill zone, Birmensdorf, Switzerland. *Epimedium alpinum*, transverse section.

**Right Fig. 23.** Phloem with tangential sieve-tube/parenchyma layers with a few sclerenchyma fibers (red, thick-walled cells) in the sieve-cell zone. Phloem cells are mostly collapsed. Rays are intensively dilated and partially filled with thin-walled callus cells. Stem of a 70 cm-high shrub on volcanic rocks, subalpine zone, Patagonia, Argentina. *Berberis empetrifolium*, transverse section.

**Discussion in relation to previous studies**

Carlquist (1995) studied extensively the xylem of the shrubs of *Berberis* and *Mahonia* as well as the rhizomes of the hemicryptophytes *Epimedium pinnatum* and *Jeffersonia diphylla*. Many authors have described the xylem of *Berberis*, e.g. Gregguss (1945), Grosser (1977), Schweingruber (1990). Some authors inspected the genus *Mahonia*, e.g. Kanehira (1921), Gregguss (1945) and Takahashi (1985), and few the genus *Nandina*, e.g. Shen (1954) and Carlquist (1995). For further references see Gregory (1994) and Metcalfe and Chalk (1957). Holdheide (1951) characterised the bark of *Berberis vulgaris*.

Most previous observations could be confirmed. The present study is representative for shrubby life forms of the family however we expect a slightly broader anatomical spectrum by including more herbaceous species. Newly described is *Vancouveria planipetala*.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| | **Total number of analyzed species** | **16** |
| 1 | growth rings distinct and recognizable | 16 |
| 3 | ring-porous | 4 |
| 4 | semi-ring-porous | 14 |
| 5 | diffuse-porous | 4 |
| 7 | vessels in diagonal and/or radial patterns | 10 |
| 8 | vessels in dendritic patterns | 4 |
| 9 | vessels predominantly solitary | 3 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 10 | vessels in radial multiples of 4 or more common | 2 |
| 11 | vessels predominately in clusters | 11 |
| 13 | vessels with simple perforation plates | 16 |
| 20 | intervessel pits scalariform | 1 |
| 36 | helical thickenings present | 13 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 3 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 14 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 7 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 1 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 3 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 13 |
| 58 | dark-stained substances in vessels and/or fibers present (gum, tannins) | 3 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 7 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 16 |
| 65 | septate fibers present | 7 |
| 69 | fibers thick-walled | 5 |
| 70 | fibers thin- to thick-walled | 13 |
| 75 | parenchyma absent or unrecognizable | 16 |
| 79 | parenchyma paratracheal | 1 |
| 97 | rays width predominantly 1-3 cells | 3 |
| 98 | rays commonly 4-10-seriate | 11 |
| 99 | rays commonly >10-seriate | 1 |
| 99.1 | vascular-bundle form remaining | 2 |
| 103 | rays of two distinct sizes (tangential section) | 15 |
| 104 | ray: all cells procumbent (radial section) | 10 |
| 105 | ray: all cells upright or square | 3 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 2 |
| 110 | rays with sheet cells (tangential section) | 4 |
| 117 | rayless | 1 |
| 120 | storied axial tissue (parenchyma, fibers, vessels in tangential section) | 13 |
| 136 | prismatic crystals present | 5 |
| R1 | groups of sieve tubes present | 15 |
| R2 | groups of sieve tubes in tangential rows | 16 |
| R2.1 | groups of sieve tubes in radial rows | 4 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 3 |
| R6.1 | sclereids in tangential rows | 11 |
| R7 | with prismatic crystals | 5 |

# Betulaceae



**Number of species, worldwide and in Europe**

The Betulaceae family, including the Corylaceae, has 6 genera with 157 species. Most of the species grow in the northern hemisphere. In Europe, there are 5 genera with 15 species.

**Analyzed material**

The xylem and phloem of 5 genera with 25 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 10 | >50 |
| Nanophanerophytes 0.5-4 m | 11 | many |
| Woody chamaephytes | 4 | a few |
| **Plants analyzed from different vegetation zones:** | | |
| Boreal and subalpine | 12 | |
| Hill and mountain | 13 | |

**Analyzed species:**

*Alnus crispa* Pursh.
*Alnus glutinosa* (L.) Gaertn.
*Alnus hirsuta* (Spach) Turcz
*Alnus incana* (L.) Moench
*Alnus orientalis* Decne.
*Alnus tenuifolia* Nutt.
*Alnus viridis* (Chaix) DC
*Betula aetnensis* Raf.
*Betula davurica* Pall.
*Betula exilis* Sucachev
*Betula glandulosa* Berl.
*Betula humilis* Schrank
*Betula nana* L.
*Betula pendula* Roth
*Betula pubescens* Erh.
*Betula tortuosa* Ledeb
*Carpinus betulus* L.
*Carpinus orientalis* Mill.
*Corylus avellana* L.
*Corylus colchica* Albov.
*Corylus colurna* L.
*Corylus heterophylla* Fisch ex Trautv.
*Corylus mandshurica* Maxim.
*Corylus maxima* Mill.
*Ostrya carpinifolia* Scop.

*Alnus glutinosa* (photo: Zinnert)

*Alnus viridis*

*Ostrya carpinifolia*

*Corylus avellana* (photo: Zinnert)

*Betula nana* (photo: Lauerer)

*Carpinus betulus*

**Characteristics of the xylem**

All species are diffuse-porous and have annual rings (**Figs. 1-5**). Ring boundaries are generally distinct but rather indistinct in *Ostrya carpinifolia* (**Fig. 3**). Vessels are arranged in short radial rows (*Alnus* and *Betula*; **Figs. 1** and **2**). Long radial rows (**Fig. 3**), often arranged in slightly diagonal patterns, are characteristic of fast growing individuals of *Carpinus*, *Corylus*, *Betula* and *Ostrya* (**Fig. 4**). Ring boundaries are marked by a small zone of flat, thick-walled fibers (**Fig. 5**). The earlywood vessel diameter of tree-like species varies between 50-80 µm in tree-like species and between 30-50 µm in dwarf shrubs. Vessel density varies mostly between 80-150/mm$^2$. Perforations are simple in *Carpinus* and *Ostrya* and scalariform in *Alnus*, *Betula* and *Corylus* (**Figs. 6** and **7**). Inter-vessel pits are arranged in opposite position in *Alnus* (**Fig. 8**), but mostly in alternate position in all other genera (**Fig. 9**). They are round and small (ca. 1 µm in diameter) in *Betula* and *Alnus* (**Fig. 8**). Helical thickenings occur in *Carpi-*

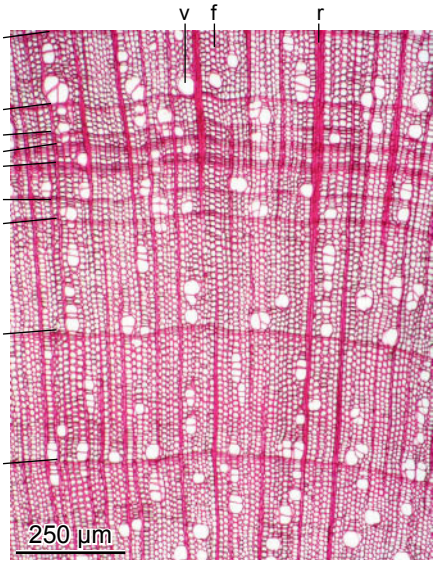



**Fig. 1.** Distinct rings of a diffuse-porous xylem. Vessels are mostly arranged in short radial rows. Stem of a 0.8 m-high shrub, taiga, boreal zone, Taymyr, Russia. *Betula exilis*, transverse section.

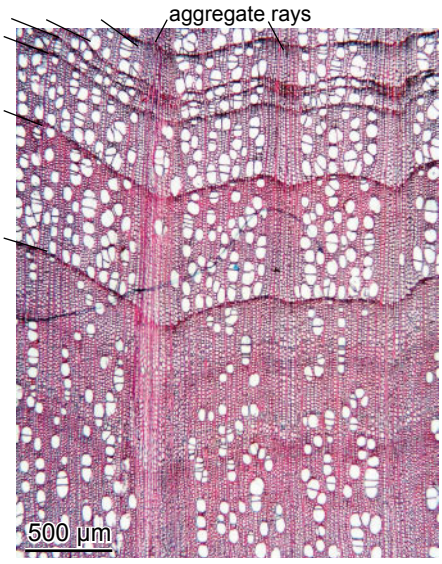



**Fig. 2.** Distinct rings of a diffuse-porous xylem. Vessels are mostly arranged in short radial rows. Vessel-free zones indicate aggregate rays. Stem of a 15 m-high tree, riparian, hill zone, Birmensdorf, Switzerland. *Alnus glutinosa*, transverse section.

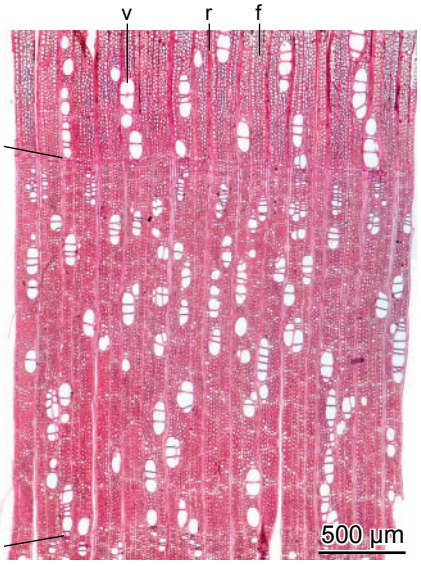



**Fig. 3.** Indistinct rings of a diffuse- to semi-ring-porous xylem with thick-walled fibers. Stem of a 10 m-high tree, *Ostrya* forest, hill zone, Southern Alps, Switzerland. *Ostrya carpinifolia*, transverse section.

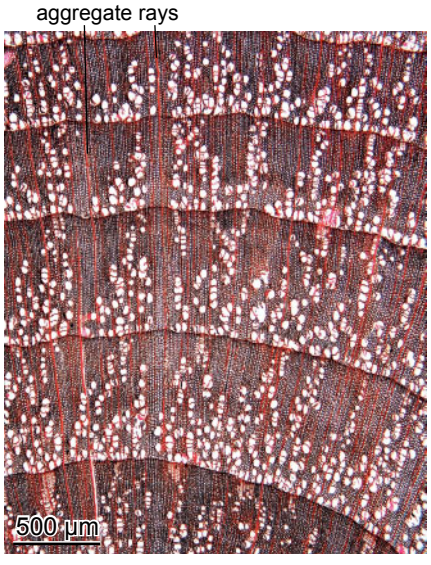



**Fig. 4.** Distinct rings. Vessels are arranged in radial and diagonal patterns. Radial vessel-free zones represent aggregate rays. Stem of a 5 m-high shrub, Botanical Garden, Chabarovsk, Russia. *Corylus heterophylla*, transverse section.

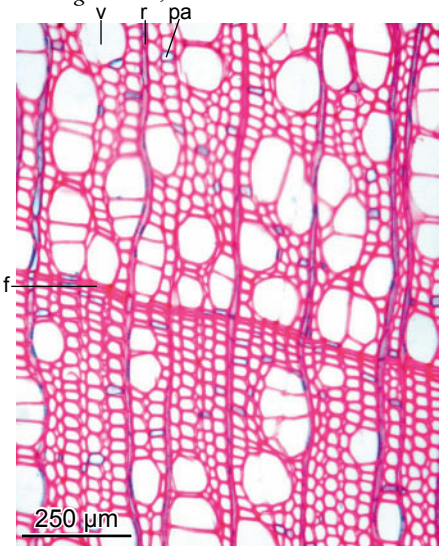



**Fig. 5.** Distinct rings of a diffuse-porous xylem. The ring boundary is indicated by a row of flat marginal fibers in the latewood. Parenchyma is apotracheal diffuse. Stem of a 15 m-high tree, riparian, hill zone, Birmensdorf, Switzerland. *Alnus incana*, transverse section.

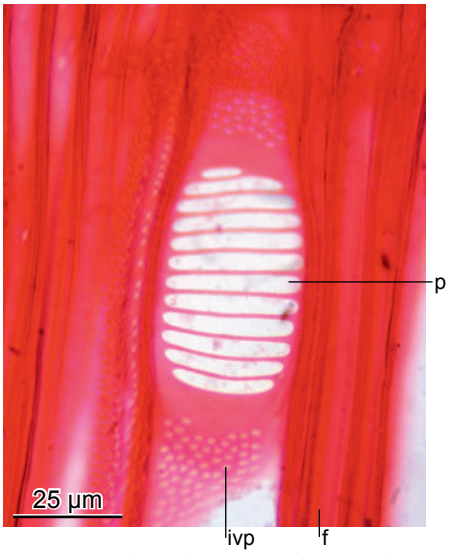



**Fig. 6.** Vessels with a scalariform perforation containing 11 bars and with small, round intervessel pits. Stem of a 1 m-high shrub, bog, hill zone, Masuria, Poland. *Betula humilis*, radial section.

*nus*, *Corylus* and *Ostrya* (**Fig. 9**). Ray-vessel-pits are numerous, small (1-2 µm in diameter) and bordered in *Alnus* and *Betula* (**Fig. 10**). Ray-vessel-pits are large with round apertures and are not bordered in *Carpinus*, *Corylus* and *Ostrya* (**Fig. 7**). Fibers are mostly thin- to thick-walled in *Alnus*, *Betula* and *Corylus* and are rather thick-walled in *Carpinus* and *Ostrya*. Fiber pits are small with a diameter of 2 µm, and have slit-like apertures (**Fig. 11**). Tension wood has been observed in a few individuals of *Alnus* and *Betula* (**Fig. 12**). Parenchyma is primarily apotracheal, diffuse (**Fig. 5**) and diffuse in aggregates (**Fig. 13**) although rarely marginal in uniseriate rows (**Fig. 14**). Rays are uniseriate in *Alnus* and 1-3 seriate in *Betula*, *Carpinus*, *Corylus* and *Ostrya* (**Figs. 15** and **16**). Aggregate rays are characteristic for *Alnus*, *Carpinus* and *Corylus* (**Figs. 17** and **18**). Within the genus *Betula* they occur occasionally in dwarf-shrub-like species. Aggregate rays are absent in *Ostrya* (**Fig. 3**). Rays are mostly homocellular, with procumbent central cells and marginal square cells. Large prismatic crystals have been observed only in *Carpinus betulus*.

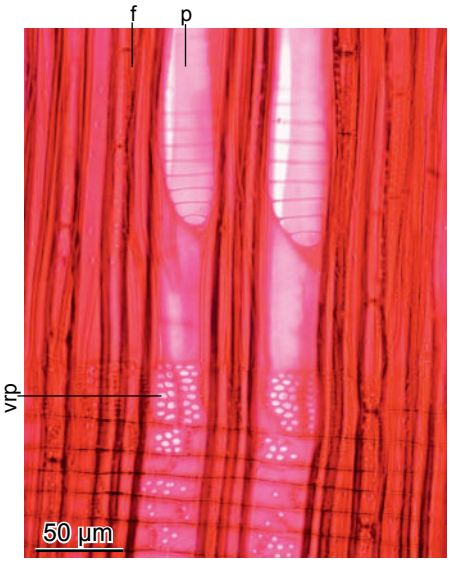



**Fig. 7.** Vessel with scalariform perforations containing <10 bars and with fairly large vessel-ray pits. Stem of a 4 m-high shrub, hedge, hill zone, Birmensdorf, Switzerland. *Corylus avellana*, radial section.

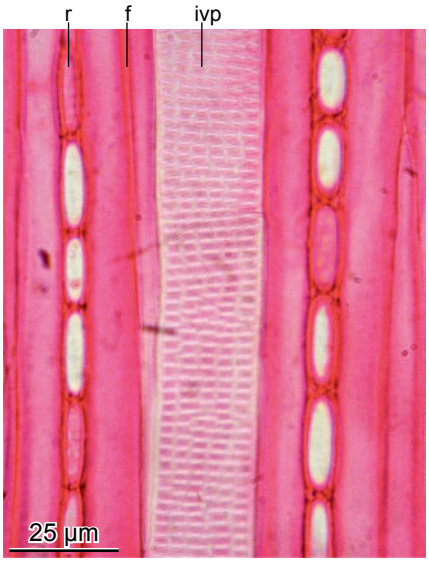



**Fig. 8.** Vessel with small intervessel-pits in opposite position. Stem of a 2 m-high shrub. Bog, boreal zone, Quebec, Canada. *Alnus crispa*, radial section.

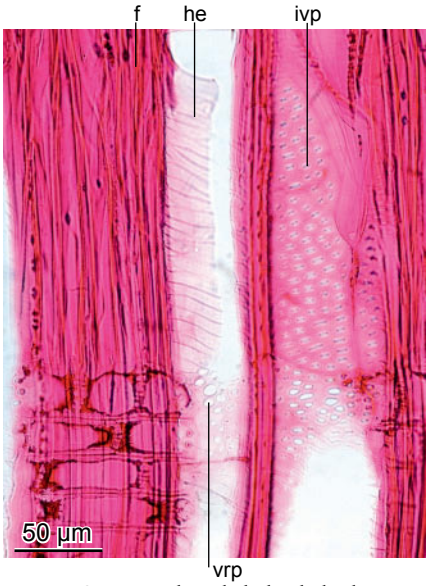



**Fig. 9.** One vessel with helical thickenings and another with large, round intervessel pits. Stem of a 4 m-high shrub, hedge, hill zone, Birmensdorf, Switzerland. *Corylus avellana*, radial section.

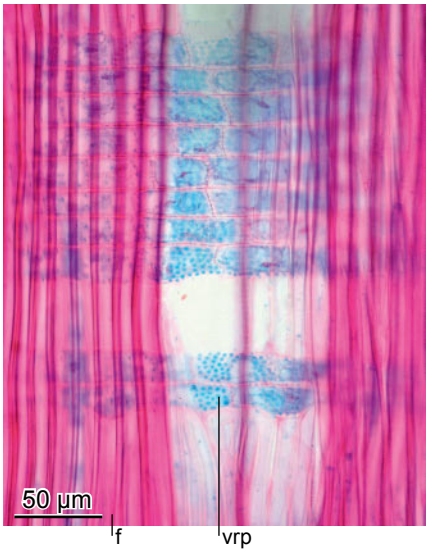



**Fig. 10.** Small vessel-ray pits. Stem of a 2 m-high shrub, avalanche track, subalpine zone, Grisons, Switzerland. *Alnus viridis*, radial section.

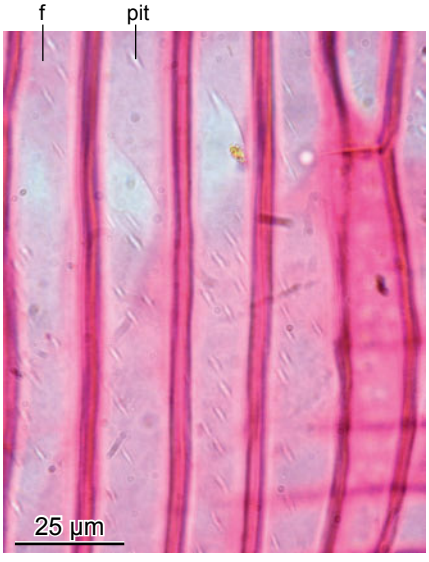



**Fig. 11.** Small fiber pits with slit-like apertures. Stem of a 1 m-high shrub, taiga, boreal zone, Quebec, Canada. *Betula glandulosa*, radial section.

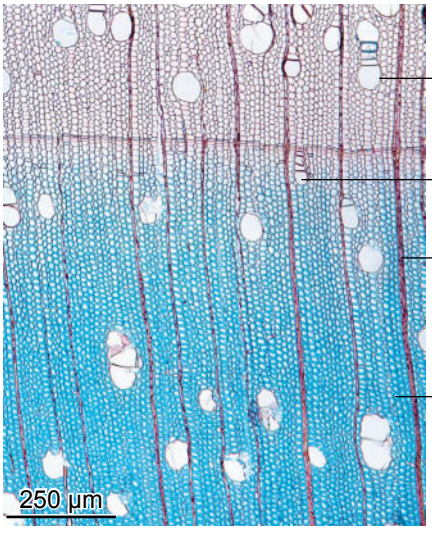



**Fig. 12.** Tension wood in the latewood. Fibers contain unlignified gelatinous fibers. Stem of a 3 m-high tree, avalanche track, subalpine zone, Grisons, Switzerland. *Betula pendula*, transverse section.

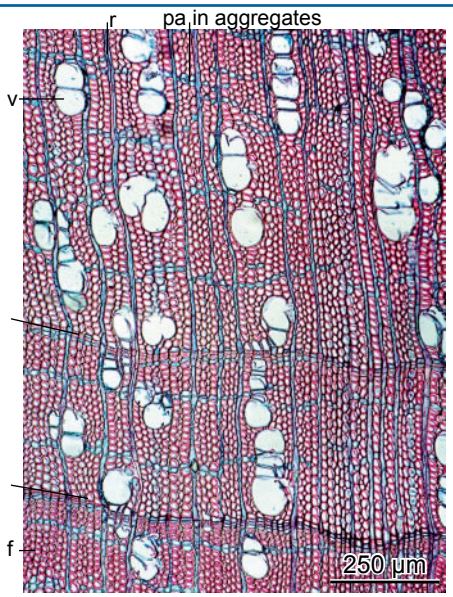



**Fig. 13.** Apotracheal parenchyma, diffuse in aggregates. Parenchyma cells are arranged in uniseriate, tangential bands. Stem of a 10 m-high tree, *Carpinus* forest, hill zone, Zürich, Switzerland. *Carpinus betulus*, transverse section.

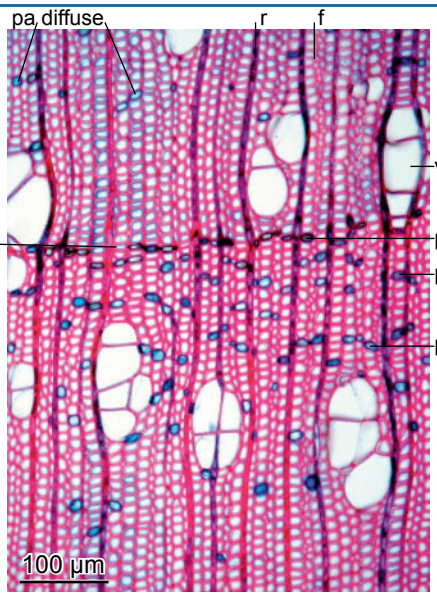



**Fig. 14.** Apotracheal parenchyma, diffuse and marginal. A discontinuous row of parenchyma cells terminates the annual ring. Stem of a 2 m-high shrub, avalanche track, subalpine zone, Grisons, Switzerland. *Alnus viridis*, transverse section.

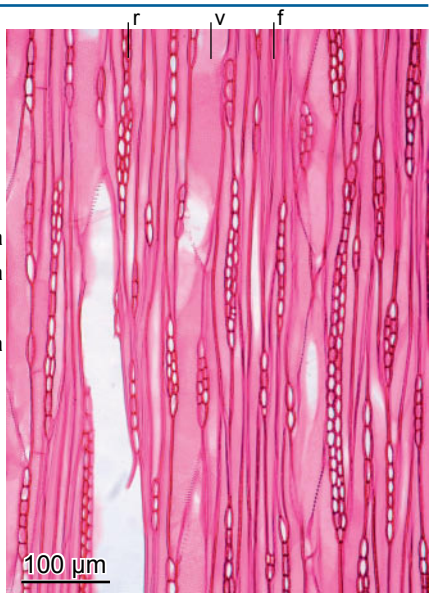



**Fig. 15.** Uni- and biseriate rays. Stem of a 1 m-high shrub, taiga, boreal zone, Quebec, Canada. *Betula glandulosa*, tangential section.

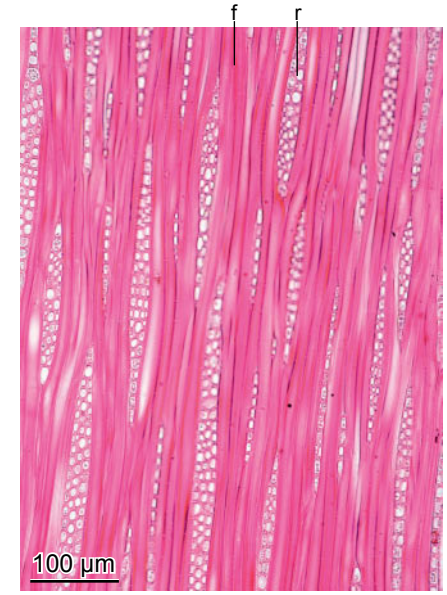



**Fig. 16.** Rays 1-3-seriate. Stem of a 10 m-high tree, *Carpinus* forest, hill zone, Zürich, Switzerland. *Carpinus betulus*, tangential section.

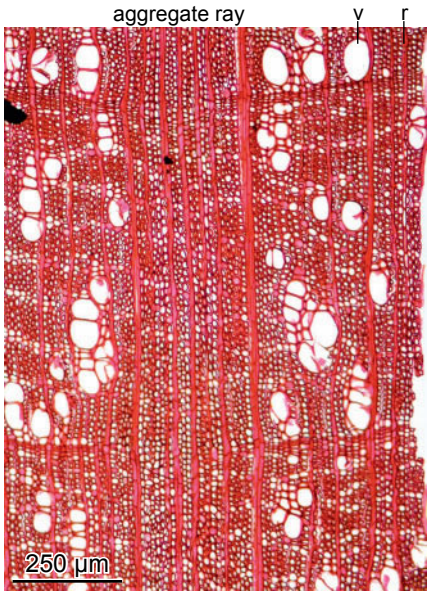



**Fig. 17.** Aggregate ray. A vessel-free zone with a concentration of uniseriate rays. Stem of a 3 m-high tree, *Ostrya* forest, Mediterranean zone, Croatia. *Carpinus orientalis*, transverse section.

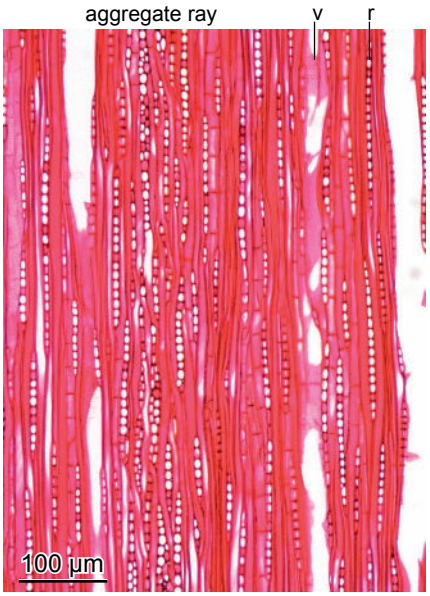



**Fig. 18.** Aggregate ray. A zone with a concentration of uni- and biseriate rays. Stem of a 3 m-high tree, *Ostrya* forest, Mediterranean zone, Croatia. *Carpinus orientalis*, tangential section.

**Characteristic features of taxa**

The anatomical structure within genera is homogeneous. Genera can be differentiated as follows:
Perforations are simple in *Carpinus* and *Ostrya*, scalariform with a few bars in *Corylus* and scalariform with many bars in *Betula* and *Alnus*.

Helical thickenings occur in *Carpinus*, *Corylus* and *Ostrya* and are absent in *Alnus* and *Betula*.
Aggregate rays occur regularly in *Alnus*, *Corylus* and *Carpinus*, but never in *Ostrya*.
Ray-vessel-pits are very small in *Betula* and *Alnus* but are fairly large in *Carpinus*, *Corylus* and *Ostrya*.

**Characteristics of the phloem and the cortex**

Sclereids are present in all species. They occur in large groups in the prolongation of aggregate rays in *Alnus*, *Carpinus* and *Corylus* (**Figs. 19-21**), in round groups in *Betula* (**Fig. 22**) and in laterally elongated groups in *Ostrya* (**Fig. 23**). Sieve tubes and parenchyma are arranged in indistinct tangential layers (**Figs. 19** and **20**). Sieve tubes are mostly collapsed in *Alnus* and *Corylus*. Prismatic crystals and crystal druses are frequent. The phellem consists of a belt of thick-walled, tangentially elongated cells (**Fig. 24**).

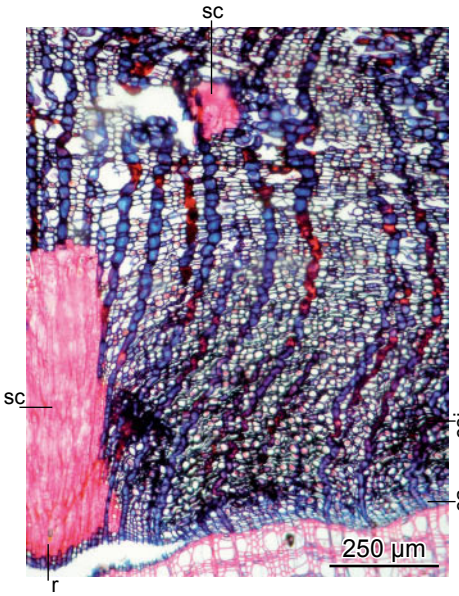



**Fig. 19.** Phloem with indistinct tangential layers of collapsed sieve tubes and round parenchyma cells. The large sclerenchymatic complex lies in the extension of an aggregate ray. Stem of a 15 m-high tree, riparian, hill zone, Birmensdorf, Switzerland. *Alnus incana*, transverse section.

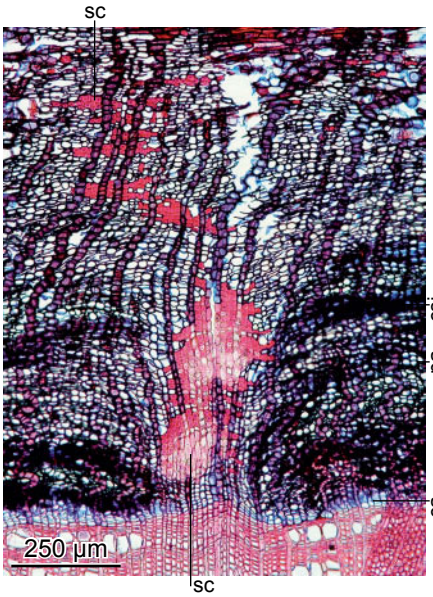



**Fig. 20.** Phloem with indistinct tangential layers of collapsed sieve tubes and round parenchyma cells. The large sclerenchymatic complex in the center lies in the extension of an aggregate ray. Stem of a 4 m-high shrub, hedge, hill zone, Birmensdorf, Switzerland. *Corylus avellana*, transverse section.

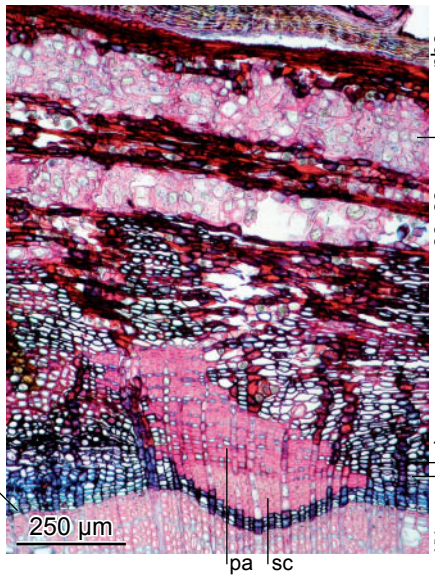



**Fig. 21.** Phloem, cortex and phellem. The large sclerenchymatic complex in the center lies in the extension of an aggregate ray. The cortex is characterized by sclerenchymatic bands containing prismatic crystals. Stem of a 10 m-high tree, *Carpinus* forest, hill zone, Zürich, Switzerland. *Carpinus betulus*, transverse section.

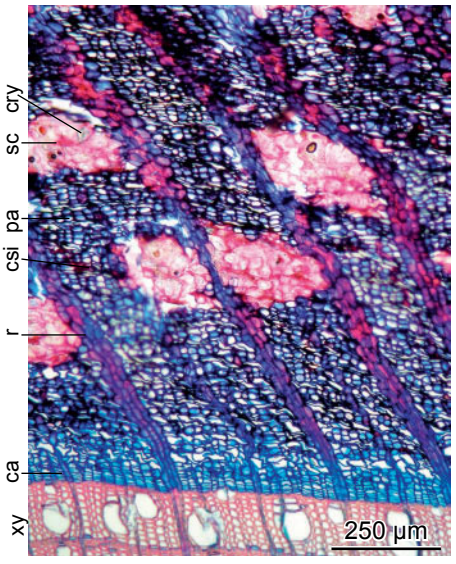



**Fig. 22.** Phloem with indistinct tangential layers of collapsed sieve tubes and round parenchyma cells and with round groups of sclerenchyma cells. Stem of a 3 m-high tree, avalanche track, subalpine zone, Grisons, Switzerland. *Betula pendula*, transverse section.

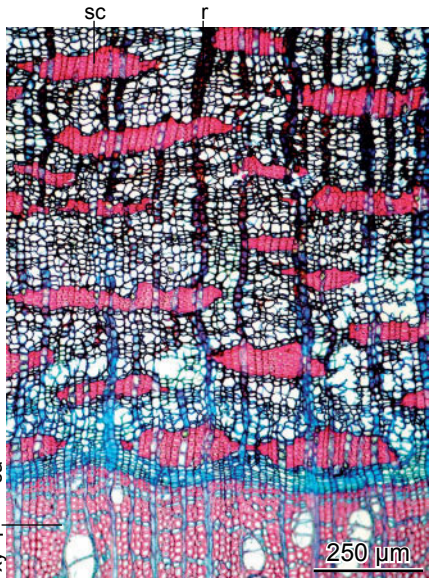



**Fig. 23.** Tangentially elongated groups of sclerenchyma cells are embedded in a tissue consisting of sieve tubes and parenchyma cells. Stem of a 10 m-high tree, *Carpinus* forest, hill zone, Zürich, Switzerland. *Carpinus betulus*, transverse section.

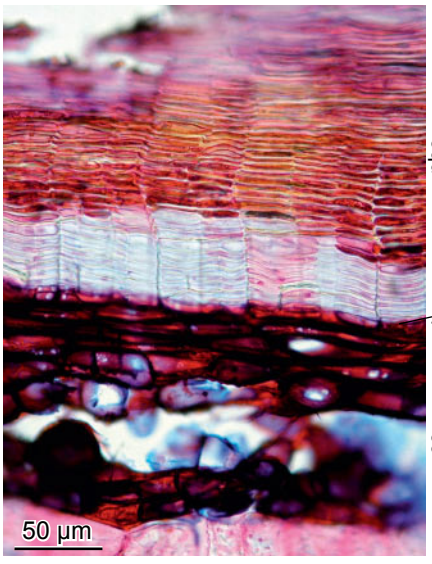



**Fig. 24.** Cortex and phellem. The phellem (top) consists of thick-walled rectangular cork cells. Stem of a 4 m-high shrub, hedge, hill zone, Birmensdorf, Switzerland. *Corylus avellana*, transverse section.

**Ecological trends and relations to life forms**

The diameter of vessels in dwarf shrubs is smaller (30-50 µm) than those in trees (50-80 µm).

**Discussion in relation to previous studies**

Gregory (1994) mentioned more than 87 articles about the xylem of Betulaceae. Holdheide (1951) describes the bark of *Alnus glutinosa*, *Betula pendula*, *Carpinus betulus* and *Ostrya carpinifolia*. The present study summarizes and confirms all previous findings.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **25** |
| 1 | growth rings distinct and recognizable | 25 |
| 5 | diffuse-porous | 25 |
| 7 | vessels in diagonal and/or radial patterns | 7 |
| 9.1 | vessels in radial multiples of 2-4 common | 17 |
| 10 | vessels in radial multiples of 4 or more common | 15 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 3 |
| 14 | vessels with scalariform perforation plates | 22 |
| 21 | intervessel pits opposite | 11 |
| 22 | intervessel pits alternate | 17 |
| 36 | helical thickenings present | 7 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 4 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 21 |
| 50 | <100 vessels per $mm^2$ in earlywood | 17 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 10 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 25 |
| 69 | fibers thick-walled | 1 |
| 70 | fibers thin- to thick-walled | 25 |
| 70.2 | tension wood present | 5 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 25 |
| 89 | parenchyma marginal | 3 |
| 96 | rays uniseriate | 7 |
| 97 | ray width predominantly 1-3 cells | 18 |
| 101 | aggregate rays | 15 |
| 104 | ray: all cells procumbent (radial section) | 22 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 9 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 2 |
| 136 | prismatic crystals present | 1 |
| R2 | groups of sieve tubes in tangential rows | 7 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 9 |
| R6.2 | sclereids in tangentially arranged groups, *Rhamnus* type | 2 |
| R7 | with prismatic crystals | 3 |
| R8 | with crystal druses | 7 |
| R10 | phloem not well structured | 1 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 8 |

# Brassicaceae



### Number of species, worldwide and in Europe

The cosmopolitan Brassicaceae family includes 419 genera with 4130 species. Highest diversity occurs in the Mediterranean region, southwestern and central Asia and western North America. In Europe there are 108 genera with approximately 630 species.

### Analyzed material

The xylem of phloem of 161 species of Brassicaceae has been analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 6 | |
| Semi-woody chamaephytes | 9 | |
| Woody chamaephytes | 7 | ca. 20 |
| Hemicryptophytes and geophytes | 104 | few |
| Therophytes | 35 | 1 (*Arabidopsis*) |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 37 | |
| Hill and mountain | 85 | |
| Mediterranean | 6 | |
| Arid | 19 | |
| Subtropical | 14 | |

**Analyzed species:**

*Aethionema saxatile* R. Br.
*Aethionema thomasiana* J.Gay
*Alliaria officinalis* Cavara & Grande
*Alyssoides utricularia* (L.) Moench
*Alyssum alpestre* L.
*Alyssum alyssoides* (L.) L.
*Alyssum argenteum* All.
*Alyssum ligusticum* Breistr.
*Alyssum montanum* L.
*Alyssum parviflorum* Bieberstein
*Alyssum simplex* Rudolphi
*Anastatica hierochuntica* L.
*Arabidopsis thaliana* (L.) Heyhn.
*Arabis alpina, alpina* L.
*Arabis ciliata* Clairv
*Arabis coerulea* All.
*Arabis hirsuta* (L.) Scop.
*Arabis nova* Vill.
*Arabis procurrens* Waldst. Et Kit.
*Arabis rosea* DC.
*Arabis subcoriaria* Gren
*Arabis sudetica* Tausch
*Arabis turrita* L.
*Aubrieta deltoides* (L.) DC.
*Aurinia saxatilis* Griesb.
*Barbarea intermedia* Boreau
*Barbarea vulgaris* R. Br.
*Berteroa incana* (L.) DC.
*Biscutella brevicaulis* Jord.
*Biscutella cichoriifolia* Lois.
*Biscutella laevigata* L.
*Brassica nigra* (L.) Koch
*Brassica oleracea* L.
*Brassica rapa* L.
*Brassica repanda* (Willd.) DC.
*Braya alpina* Sternb. & Hoppe
*Braya humilis* (C.A. Mey) B.L. Rob.
*Bunias erucago* L.
*Bunias orientalis* L.
*Cakile edentula* Jord.
*Cakile maritima* Scop.
*Calepina irregularis* (Asso) Thell.
*Camelina microcarpa* DC
*Camelina pilosa* (DC) Zinger
*Capsella bursa-pastoris* (L.) Medik.
*Capsella rubella* Reuter
*Cardamine alpina* Willd.
*Cardamine amara* L.
*Cardamine bulbifera* (L.) Crantz
*Cardamine enneaphyllos* L.
*Cardamine flexuosa* With.
*Cardamine halleri* (L.) Hayek
*Cardamine heptaphylla* O.E. Schulz
*Cardamine hirsuta* L.
*Cardamine pentaphyllos* L.
*Cardamine pratensis* L.
*Cardamine resedifolia* L.
*Cardaminopsis arenosa* (L.) Hayek
*Cardaminopsis halleri* (L.) Hayek
*Cardaria draba* (L.) Desv.
*Carrichtera annua* (L.) Asch et GR.
*Clypeola jonthlaspi* L.
*Coincya cheiranthoides* Gr. & Burd.
*Coincya richeri* Gr. & Burd.
*Coronopus didymus* Sm.
*Coronopus squamatus* Asch
*Descurainia bourgeana* O.E. Schulz
*Descurainia millefolia* Webb. et Berth.
*Descurainia preauxina* Webb.
*Descurainia sophia* (L.) Prantl
*Dichroanthus virescens* Webb.
*Diplotaxis harra* (Forssk.) Boiss.
*Diplotaxis muralis* DC.
*Diplotaxis tenuifolia* (L.) DC.
*Draba aizoides* L.
*Draba aurea* Vahl
*Draba dubia* Suter
*Draba nemorosa* L.
*Draba siliquosa* M. Bieb.
*Draba streptocarpa* A. Grey
*Erophila verna* L.
*Eruca sativa* Mill.
*Eruca sativa vesicaria* ssp. *sativa* Thell.
*Erucastrum gallicum* O.E. Schulz
*Erucastrum nasturtifolium* O.E. Schulz
*Erucastrum varium* Webb. ex Christ
*Erysimum asperum* DC.
*Erysimum bicolor* (Hornem.) DC.
*Erysimum capitatum* Greene
*Erysimum cheirii* L.

*Erysimum crepidifolium* Rchb.
*Erysimum montosicola* Jord.
*Erysimum mutabile* Wettst.
*Erysimum nivale* Rydbe
*Erysimum ochroleucum* (Schleich) DC.
*Erysimum odoratum* Erh.
*Erysimum rhaeticum* (Hornem) DC.
*Erysimum scoparium* Wettst.
*Erysimum virgatum* Roth
*Farsetia aegyptica* Turra
*Farsetia ramosissima* Hochst.
*Fourraea alpina* (L.) Greuter et Burdet
*Hirschfeldia incana* (L.) Lagreze-Fossat
*Hornungia petraea* (L.) Rchb.
*Hugueninia tanacetifolia* Rch.
*Iberis sempervirens* L.
*Isatis tinctoria* L.
*Kernera saxatilis* (L.) Sweet
*Lepidium campestre* (L.) R. Br.
*Lepidium densiflorum* Schrad.
*Lepidium perfoliatum* L.
*Lesquerella alpina* Watson
*Lobularia canariensis* (DC.) Borgen
*Lobularia libyca* Meysn
*Lobularia maritima* (L.) Desv.
*Lobularia palmensis* Webb. ex Christ
*Lunaria annua* L.
*Malcolmia aegyptica* Spr.
*Matthiola fruticulosa* (L.) Maire
*Matthiola parviflora* R. Br.
*Matthiola sinuata* R. Br.
*Moricandia arvensis* DC.
*Nasturtium officinale* R. Br.
*Neslia paniculata* (L.) Dedsv.
*Notoceras bicorne* Willk. et Lange
*Oudneya africana* R. Br.
*Parolinia intermedia* Svent & Bramwell
*Parolinia ornata* Webb
*Peltaria alliacea* Jacq.
*Pritzelago alpina* Kunze
*Pseudoerucaria clavata* O.E. Schulz
*Ptilotrichium spinosum* (L.) Boiss.
*Rapistrum rugosum* All.
*Rorippa austriaca* Besser
*Rorippa stylosa* (DC.) Allan.
*Sinapidendron angustifolia* Link
*Sinapidendron frutescens* Link
*Sinapis arvensis* L.
*Sinapis flexuosa* Poir.
*Sisymbrium altissimum* L.
*Sisymbrium andinum* Phil.
*Sisymbrium austriacum* O.E. Schulz
*Sisymbrium irio* L.
*Sisymbrium loeselii* L.
*Sisymbrium officinale* Scop.
*Sisymbrium orientale* L.
*Sisymbrium sophia* L.
*Sisymbrium strictissimum* L.
*Smelowskia calycina* Mey.
*Stanleya pinnata* Britton
*Thlaspi arvense* L.
*Thlaspi bonariense* L.
*Thlaspi caerulescens* Presl.
*Thlaspi perfoliatum* L.
*Thlaspi praecox* Wulfen
*Thlaspi rotundifolium* (L.) Gaudin
*Thlaspi sylvium* Gaudin
*Turritis glabra* L.
*Vella spinosa* Boiss.
*Vella spinosa* ssp. *lucentina* Boiss.
*Zilla spinosa* Prantl

*Brassica oleracea*

*Erysimum rhaeticum*

*Draba aizoides* (photo: Landolt)

*Anastatica hierochuntica*

*Erysimum bicolor*

*Iberis sempervirens*

*Hutchinsia alpina* (photo: Landolt)

**Characteristics of the xylem**

Annual rings occur in the present material of perennial species in all vegetation zones (**Figs. 1-6, 15, 16** and **29**). In 14% (23 species) ring boundaries are absent or indistinct. Ring boundaries of most species are marked by semi-ring-porosity (**Figs. 1-5** and **29**). Ring-porous species are absent. Vessels are frequently solitary (**Figs. 4** and **5**). Most frequent are vessels in radial multiples (**Figs. 1**, **6**, and **7**). Radial multiples predominantly consist of 4 and more vessels (**Fig. 6, 7** and **29**). Distinct intra-annual tangential rows of vessels occur in many species (**Fig. 8**).

Earlywood vessel diameter varies between 15-80 µm. Vessels are frequently exclusively smaller than 20 µm (**Figs. 4** and **5**). Earlywood vessel diameter of the majority of species varies between 35-50 µm. Diameter exceeds 50 µm in a few species.

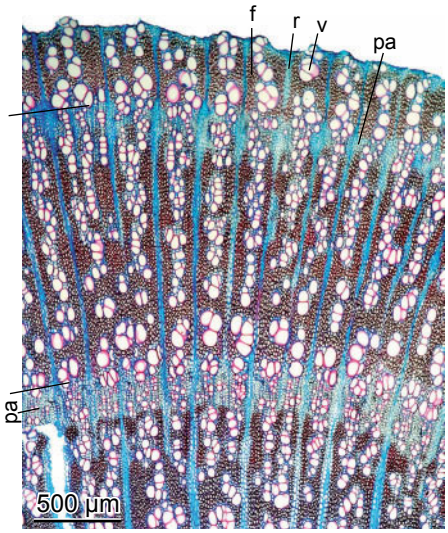



**Fig. 1.** Semi-ring-porous xylem with distinct ring boundaries. The latewood zone is characterised by small vessels, surrounded by thin-walled, unlignified parenchyma cells. Root collar of a 30 cm-high perennial herb, moist meadow, subalpine zone, Alps, France. *Coincya cheiranthoides*, transverse section.

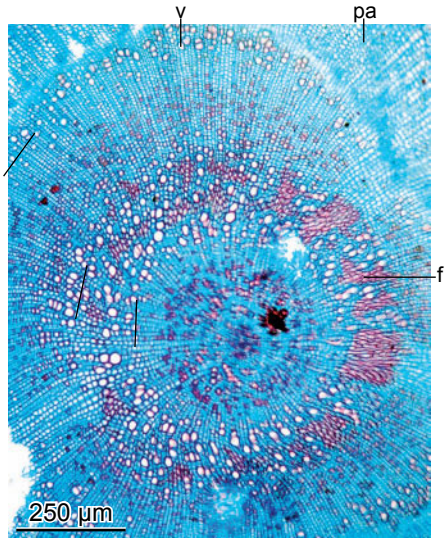



**Fig. 2.** Semi-ring-porous xylem with distinct ring boundaries. The diameter of the earlywood vessels have an average diameter of <20 µm. Fibers are in groups. Rays are unrecognizable. Root collar of an 8 cm-high perennial herb, limestone rock, alpine zone, Switzerland. *Kernera saxatilis*, transverse section.

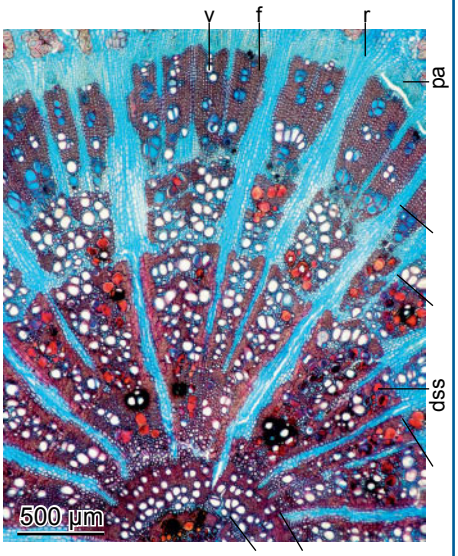



**Fig. 3.** Diffuse- to semi-ring-porous xylem with distinct ring boundaries, defined by a zone of small latewood vessels, surrounded by thin-walled, unlignified parenchyma cells. Vessels partially filled with blue- or red-staining substances. Large rays with unlignified cells. Root collar of a 40 cm-high perennial herb, meadow, hill zone, Burgenland, Austria. *Cardaria draba*, transverse section.

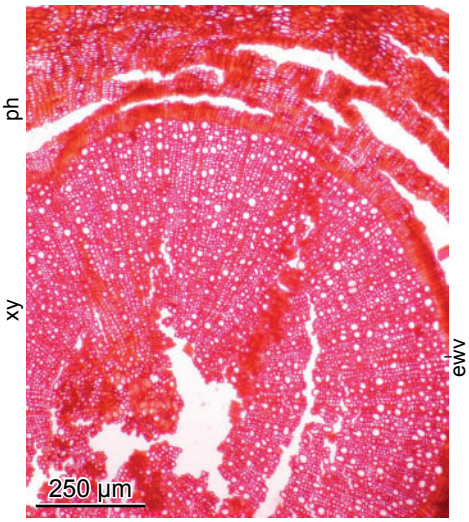



**Fig. 4.** Diffuse- to slightly semi-ring-porous xylem with ring boundaries. Ring boundaries are indicated by slightly enlarged earlywood vessels. The vessels are mostly solitary. Root collar of a 5 cm-high cushion-plant, meadow, alpine zone, Switzerland. *Draba aizoides*, transverse section.

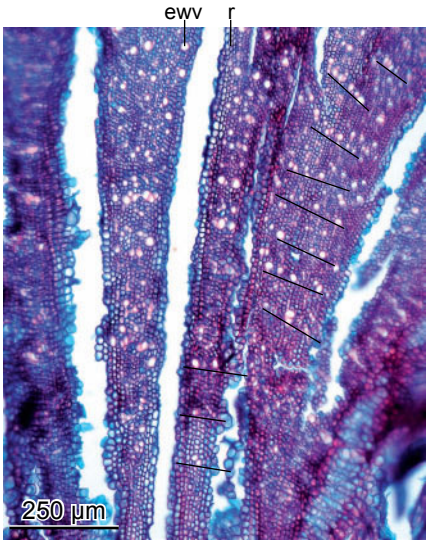



**Fig. 5.** Diffuse- to slightly semi-ring-porous xylem with indistinct ring boundaries indicated by few slightly enlarged earlywood vessels. Vessels are mostly solitary. Root collar of a 5 cm-high cushion plant, meadow, alpine zone, Rocky Mountains, Colorado, USA. *Smelowskia calycina*, transverse section.

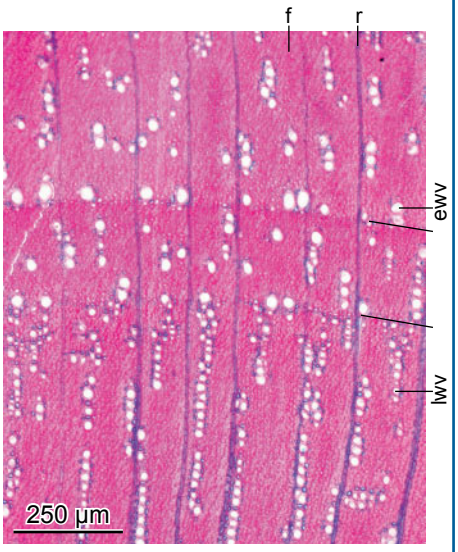



**Fig. 6.** Two growth zones, probably not annual rings. The lower boundary is marked by a change of vessel arrangement and the second by a dense latewood fiber zone. Stem of a 80 cm-high shrub, arid belt, subtropical climate, Tenerife, Canary Islands. *Parolinia intermedia*, transverse section.

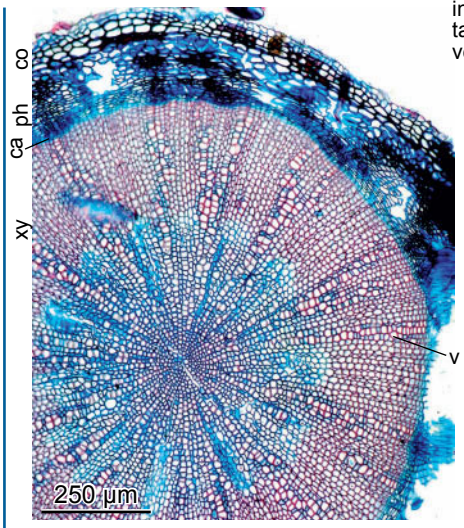



**Fig. 7.** Annual herb with one ring. Vessels are arranged in long radial multiples. Fiber/parenchyma cell walls in the centre of the stem are unlignified. Root collar of a 10 cm-high annual plant, meadow, hill zone, Switzerland. *Thlaspi perfoliatum*, transverse section.

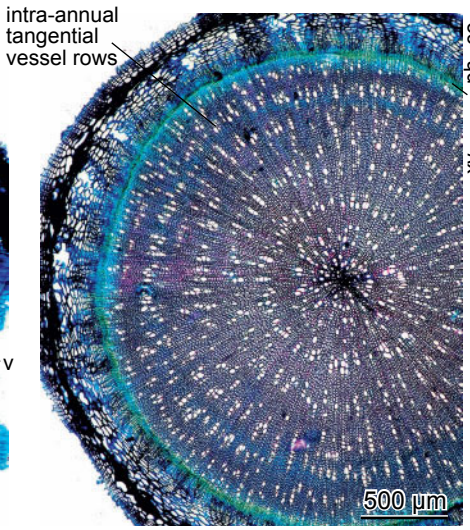



**Fig. 8.** Herb with one ring. Vessels are arranged in intra-annual tangential rows. Root collar of a 10 cm-high, annual plant, ruderal site, hill zone, Switzerland. *Capsella bursa-pastoris*, transverse section.

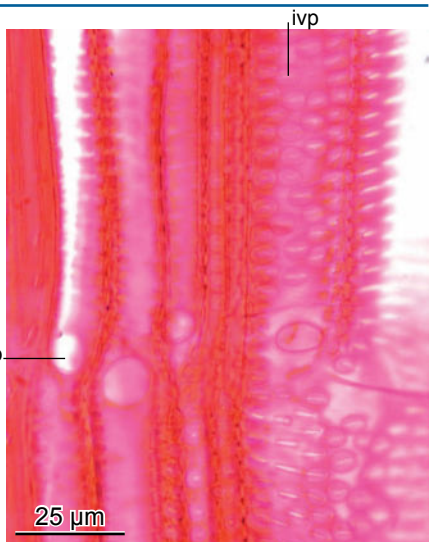
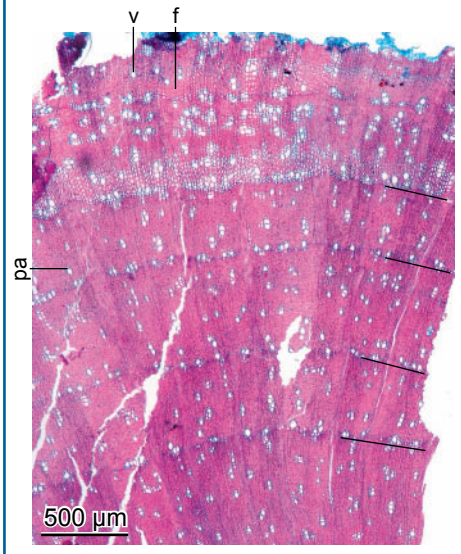
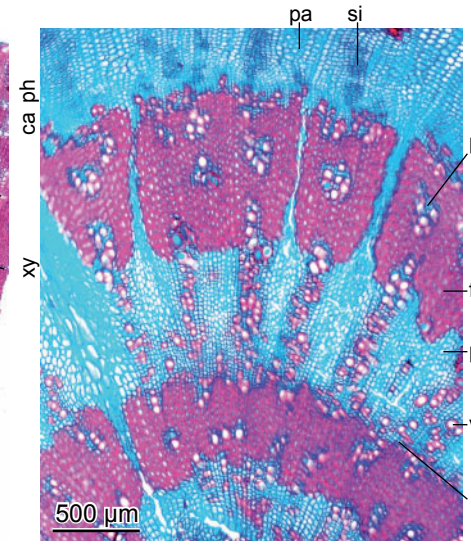


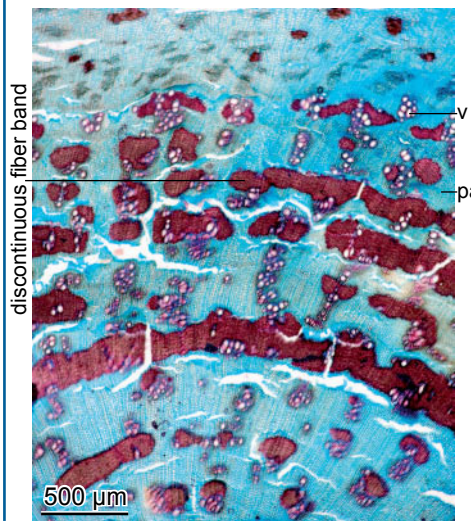

**Fig. 9.** Vessels with simple perforations and large, bordered intervessel pits. Xylem of a 30 cm-high dwarf shrub, volcanic rock, subtropical mountain zone, Tenerife, Canary Islands. *Descurainia millefolia*, radial section.

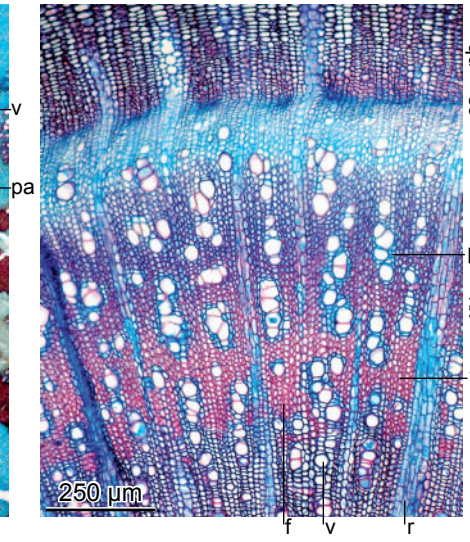



**Left Fig. 10.** Xylem with very thick-walled fibers. Wood density is >1 g/cm³. Xylem of a 40 cm-high dwarf shrub, volcanic rock, subtropical mountain zone, Gran Canaria, Canary Islands. *Descurainia preauxina*, transverse section.

**Right Fig. 11.** Intra-annual continuous fiber bands alternate with parenchymatic zones. Parenchyma is paratracheal in the earlywood and pervasive in the latewood. Root collar of a 40 cm-high perennial herb, meadow, hill zone, Swiss Southern Alps. *Rorippa stylosa*, transverse section.




**Left Fig. 12.** Xylem with many discontinuous fiber bands and one continuous fiber band. Vessels occur only in the fiber zones. In June, the xylem is in the formation process. Stem of a 25 cm-high perennial chamaephyte, rock, hill zone, Switzerland. *Aurinia saxatilis*, transverse section.

**Right Fig. 13.** Paratracheal parenchyma, distinct in the fiber-zone. Root collar of a 25 cm-high annual herb of the subtropical mountain zone, Gomera, Canary Islands. *Eruca sativa*, transverse section.

Vessel density varies in most species between 100-500/mm$^2$. Vessels are absent in *Erophila verna*. Vessels of all species have simple perforations (**Fig. 9**). Inter-vessel pits are predominantly small and round or scalariform to various degrees (**Fig. 9**). Very fine helical thickenings are almost absent in the family of Brassicaceae but occur sporadically in some individuals of *Descurainia millefolia*. Vestured pits seem to occur in most species but quantification is difficult because their size is at the limit of the optical resolving capacity. Some species contain dark-stained substances spot-like in the center of the stem (heartwood; **Fig. 3**). Tylosis does not exist.

The radial walls of fibers in all species are perforated by very small slit-like or round pits (<2 µm). Septate fibers are absent. Fiber thickness varies from thin- to thick-walled in all vegetation zones (thin-walled 24, thick-walled 36, thin- to thick-walled 84 species). Fibers are grouped often in continuous or interrupted tangential bands (**Figs. 11** and **12**).

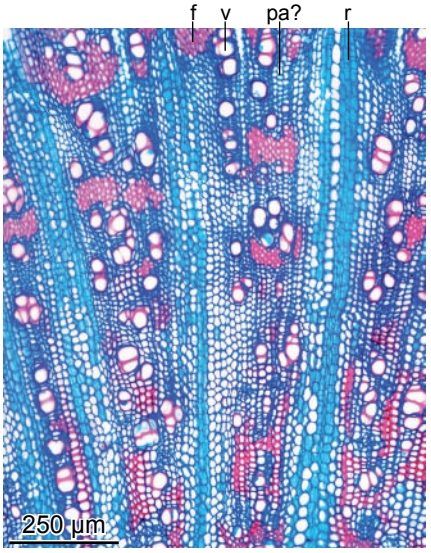



**Fig. 14.** Pervasive parenchyma in an annual herb. Unlignified fibers and parenchyma cells cannot be distinguished. Large rays separate radial vessel/fiber/parenchyma strips. Root collar of a 15 cm-high annual herb, rock, arid zone, subtropical climate, Gomera, Canary Islands. *Hirschfeldia incana*, transverse section.

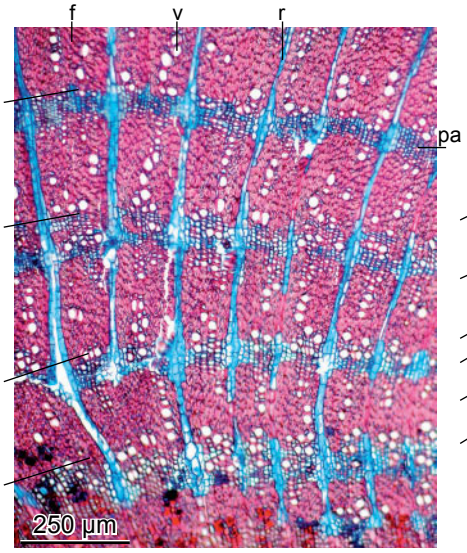



**Fig. 15.** Marginal parenchyma of a semi-ring-porous xylem with distinct annual rings and large rays. Stem of a 40 cm-high dwarf shrub, rock, arid zone, Southern Spain. *Vella spinosa* ssp. *lucentina*, transverse section.

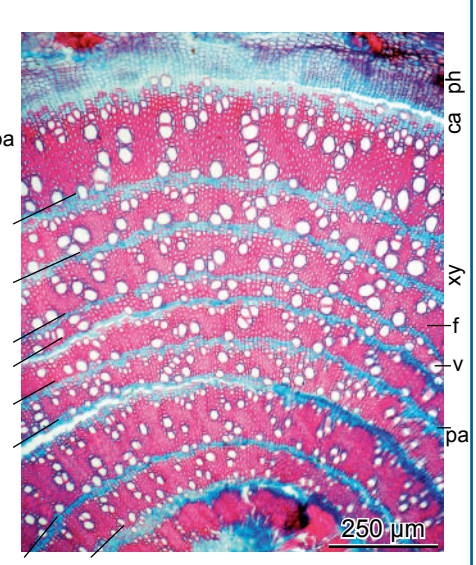



**Fig. 16.** Marginal parenchyma of a more or less diffuse-porous xylem with distinct annual rings and absent rays. Stem of a 40 cm-high dwarf shrub, rock, arid zone, Southern Spain. *Ptilotrichum spinosum*, transverse section.

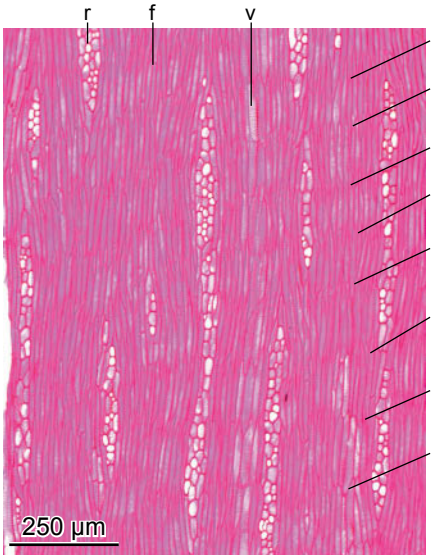



**Fig. 17.** Storied fiber/parenchyma structure. Stem of a 1 m-high perennial plant, volcanic rock, arid zone, subtropical climate, Madeira, Portugal. *Sinapidendron angustifolia*, tangential section.

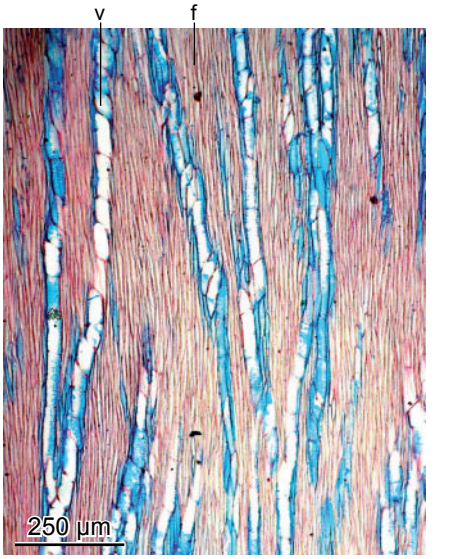



**Fig. 18.** Rayless xylem. Root collar of a 10 cm-high annual herb, ruderal site, arid zone, subtropical climate, Tenerife, Canary Islands. *Notoceras bicorne*, tangential section.

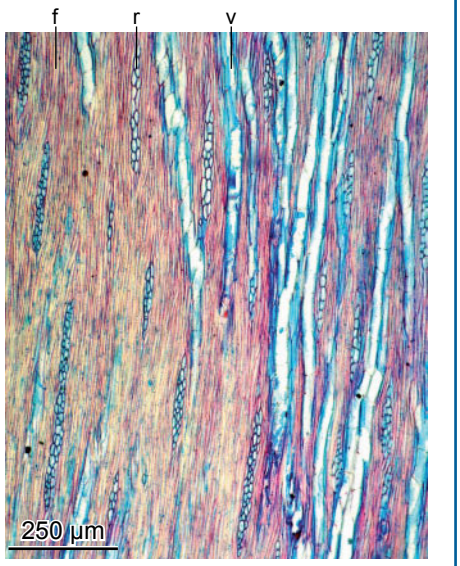



**Fig. 19.** Xylem with 1- to 3-seriate rays. Root collar of a 30 cm-high annual herb, ruderal site, hill zone, Switzerland. *Sinapis arvensis*, tangential section.

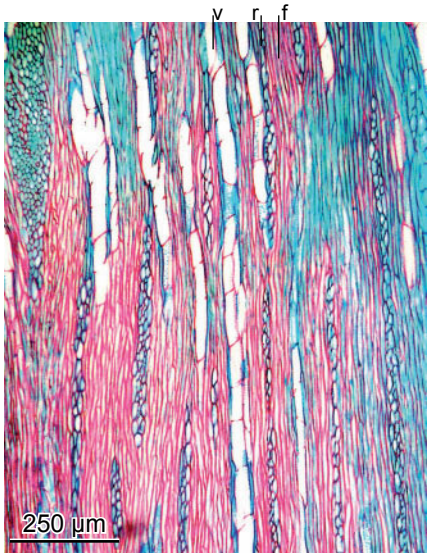



**Fig. 20.** Xylem with mainly 2- to 10-seriate rays. Root collar of a 60 cm-high biannual herb, dry field, hill zone, Switzerland. *Isatis tinctoria*, tangential section.

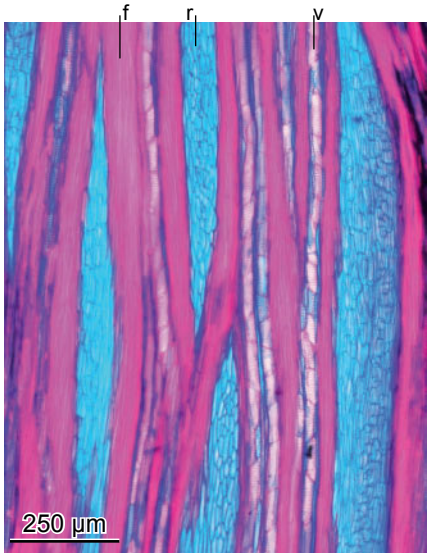



**Fig. 21.** Xylem with mainly >10-seriate unlignified rays. Root collar of a 40 cm-high perennial herb, rock, mountain zone, Pyrenees, France. *Sisymbrium austriacum*, tangential section.

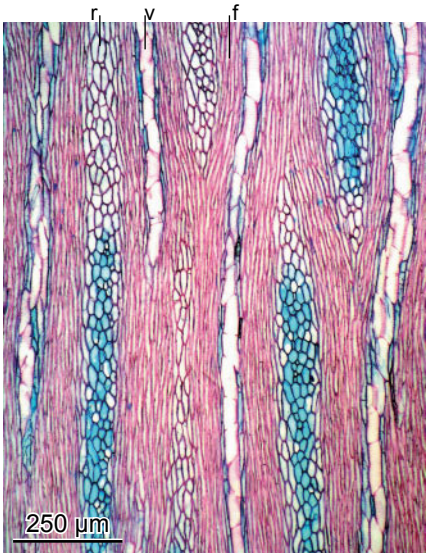
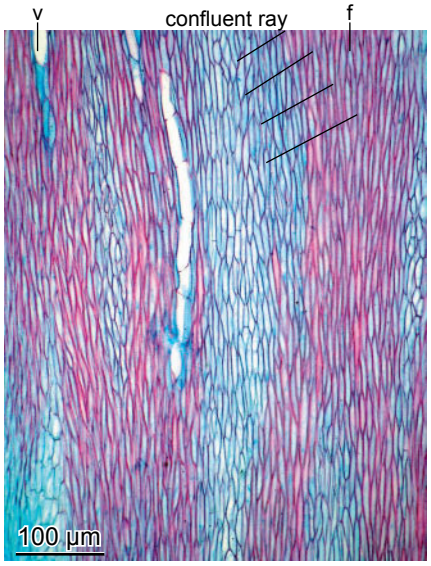
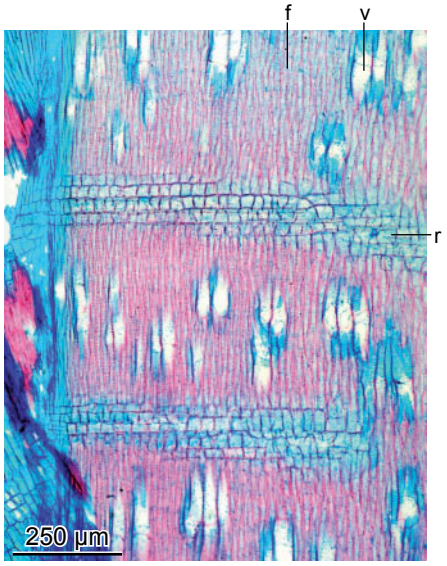


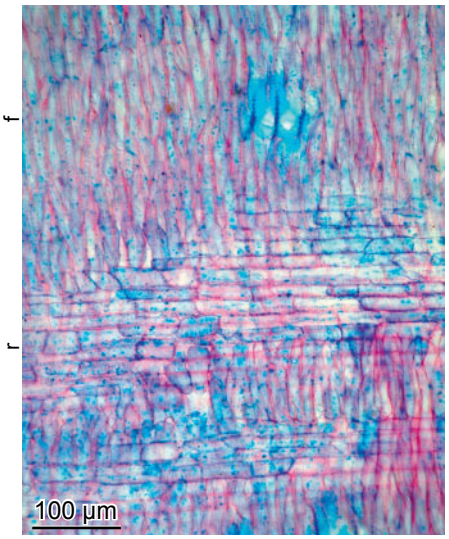

**Fig. 22.** Xylem with mainly 4- to 6-seriate rays with sheet cells. Root collar of a perennial herb, meadow, mountain zone, Botanical Garden Champex, Switzerland. *Hugueninia tanacetifolia*, tangential section.

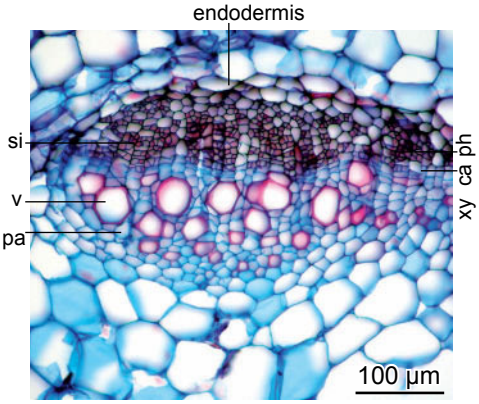



**Left Fig. 23.** Rays not distinctly delimitated from the axial fiber tissue (confluent). Root collar of a 40 cm-high biannual herb, deciduous forest, hill zone, Ticino, Switzerland. *Fourraea alpina*, tangential section.

**Right Fig. 24.** Ray with square and upright cells. Root collar of a 30 cm-high annual herb, dry meadow, hill zone, Ticino, Switzerland. *Erucastrum nasturtifolium*, radial section.




**Left Fig. 25.** Ray with procumbent cells. Root collar of a 30 cm-high biannual herb, dry meadow, Burgenland, Austria. *Sisymbrium orientale*, radial section.

**Right Fig. 26.** Single collateral vascular bundle at the periphery of a rhizome. Solitary vessels are surrounded by pervasive parenchyma and an endodermis. Rhizome of a 30 cm-high perennial herb, deciduous forest, hill zone, Ticino, Switzerland. *Cardamine bulbifera*, transverse section.

There is a predominance of paratracheal parenchyma (**Fig. 13**). Pervasive parenchyma is characteristic of 31 species (**Fig. 14**). Marginal parenchyma is present in 48 species and occurs in most vegetation zones except the arid zone (**Figs. 15** and **16**). A few species have storied parenchyma/fiber structures (**Fig. 17**).

Ray diversity is high in all vegetation zones. Rays are absent in 52 species (**Fig. 18**), 1- to 3-seriate in 41 species (**Fig. 19**), 4-10-seriate in 52 species (**Fig. 20**) and >10-seriate in 11 species (**Fig. 21**). The occurrence of unlignified rays of many species is characteristic (**Fig. 21**). Sheet cells occur in 9 species (**Fig. 22**). Rays are often not distinctly delimitated from the axial fiber-tissue (**Fig. 23**). Ray cells are uniquely square or upright in 87 species (**Fig. 24**). Rays with central procumbent and marginal square cells and 3 to many upright cells have been observed in 15 species (**Fig. 25**). Rays do not reflect polarized light and are unlignified in 39 species (**Fig. 21**). The primary vascular-bundle form is found in 6 species (**Figs. 26-29**). In such cases ray width exceeds 10 cells. Included phloem is present in one herb species (*Hirschfeldia incana*). Crystals are absent in most species. Prismatic crystals have been found in only 4 shrubs and dwarf shrubs of dry regions (*Parolinia intermedia*, *P. ornata*, *Malcolmia aegyptica* and *Descurainia bourgeana*).

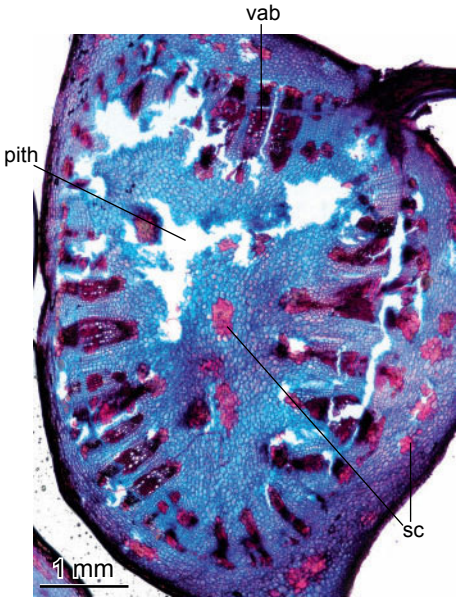



**Fig. 27.** Collateral vascular bundles at the periphery of a rhizome. Rhizome of a 30 cm-high perennial herb, deciduous forest, mountain zone, Jura, Switzerland. *Cardamine enneaphyllos*, transverse section.

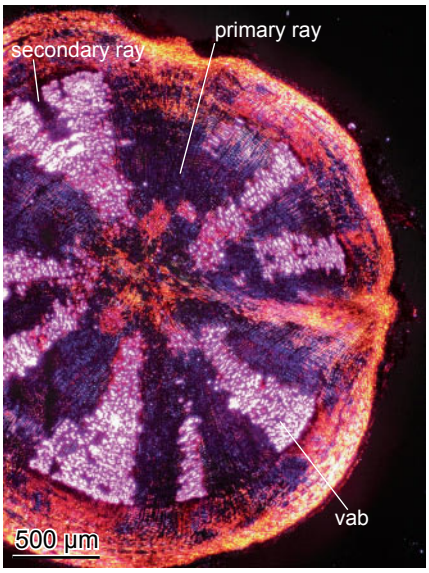



**Fig. 28.** Radial dilated strips of vessel/fiber/parenchyma tissue between very large dilated rays. The strips represent the xylem of initial vascular bundles. Root collar of perennial herb, snow bed, alpine zone, Davos, Switzerland. *Cardamine alpina*, transverse section, polarized light.

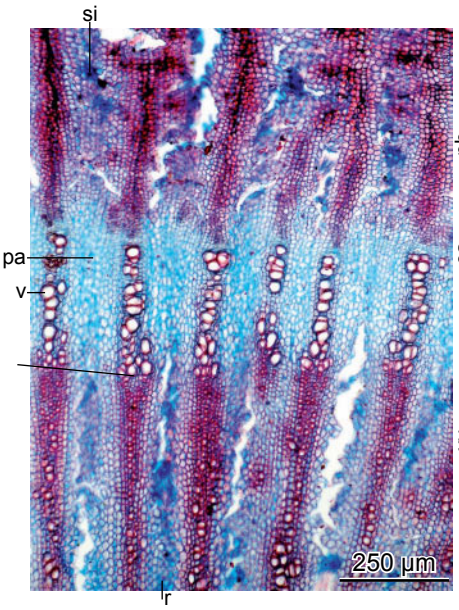



**Fig. 29.** Small radial strips of vessel/fiber/parenchyma tissue between large rays. The strips represent the xylem of initial vascular bundles. Root collar of a 10 cm-high perennial herb, rock field, alpine zone, Rocky Mountains, Colorado, USA. *Erysimum nivale*, transverse section.

**Characteristic features of taxa**

Characteristics for the species are mainly the distribution of vessels (e.g. solitary or radial multiples), ray features (e.g. absent or >4-seriate), and the presence of storied parenchyma/fiber structures, marginal parenchyma and the presence of prismatic crystals.

**Ecological trends in the xylem**

Differences between the alpine zone (cold environment with a vegetation period of 1-4 month) and the hill zone (warm environment with a vegetation period of 6-7 months) are in focus of this study.
No shrubs or dwarf shrubs from this family occur in the alpine region. In contrast, dwarf shrubs (9 species) and shrubs (2 species, *Parolinia ornata* and *P. intermedia*) occur only in dry regions. Therophytes are rare in alpine regions (2 species). Hemicryptophytes are dominant in the hill zone.

Alpine plants are, on average, older than those in the hill zone. Maximum ages occur in the alpine species *Draba aizoides* with 40 years, *Smelowskia calycina* (26 years) and *Thlaspi sylvium* (25 years). Plants with distinct rings are more frequent in the alpine zone than in the hill zone.

### Characteristics of the phloem and the cortex

Crystals are absent in almost every species. Sieve tubes and companion cells are primarily grouped in small clusters, which are often arranged in tangential rows (**Figs. 30** and **31**). Sclereids are very frequent in the cortex and the phloem (**Figs. 32–35**). Parenchyma cells are mostly enlarged due to cell wall dilation towards the primary bark, but the size of the sieve tubes remains constant. Ray dilatations occur in most species with large xylem rays (**Fig. 34**).

### Ecological trends in the phloem and the cortex

Sclereids in the bark are much less frequent in plants in the alpine zone (4 of 35 species) than in the hill zone (33 of 88 species). It is difficult to quantify the presence of sclerenchyma since it occurs more frequent in fast- than in slow-growing individuals. Species with tangential rows of sieve-tube groups are more frequent in the alpine zone (23 of 35 species) than in the hill zone (30 of 88 species). This feature is absent in the arid zone.

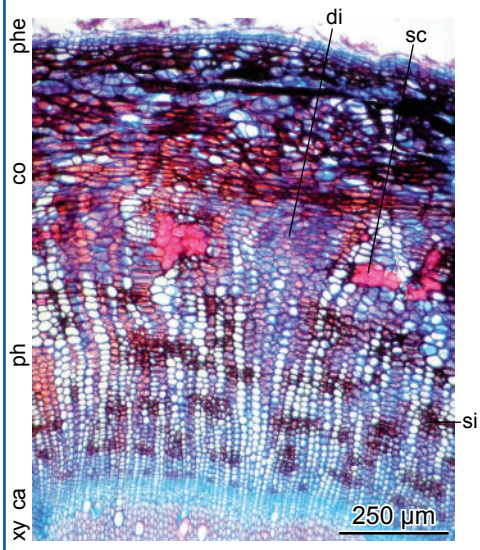



**Fig. 30.** The phloem is characterised by distinct sieve-tube groups arranged in tangential rows, with a few sclerenchyma groups and dilatations. Bark of the root collar of a 40 cm-high biannual herb, ruderal site, mountain zone, Wyoming, USA. *Berteroa incana*, transverse section.

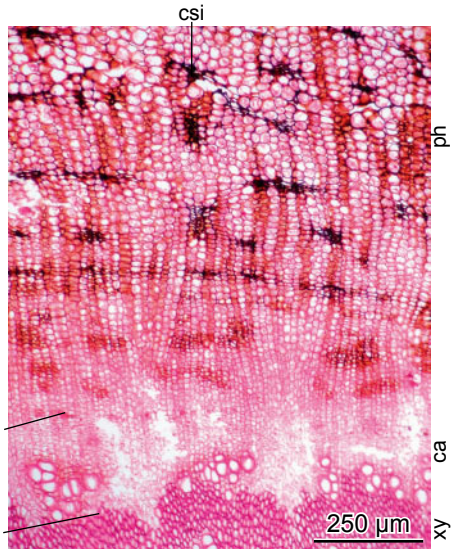



**Fig. 31.** Phloem with distinct sieve-tube groups arranged in tangential rows. They are compressed in external parts. A few sclerenchyma groups and dilatations occur in the cortex. Bark of the root collar of a 40 cm-high biannual herb, ruderal site, mountain zone, Switzerland. *Barbarea vulgaris*, transverse section.

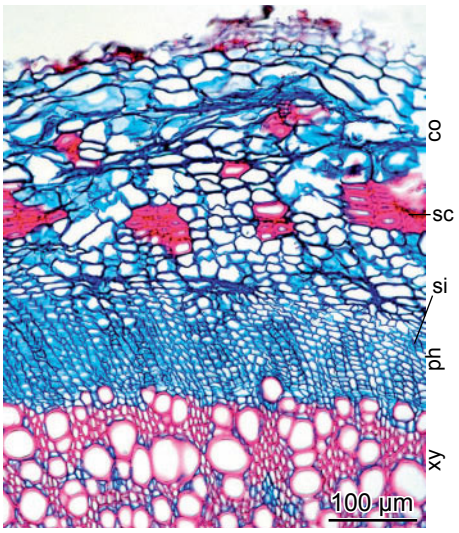



**Fig. 32.** Cortex with isolated, small groups of sclerenchyma cells. The phloem contains indistinct groups of sieve tubes. Bark of the root collar of a 8 cm-high annual herb, coastal line, Cornwall, England. *Coronopus didymus*, transverse section.

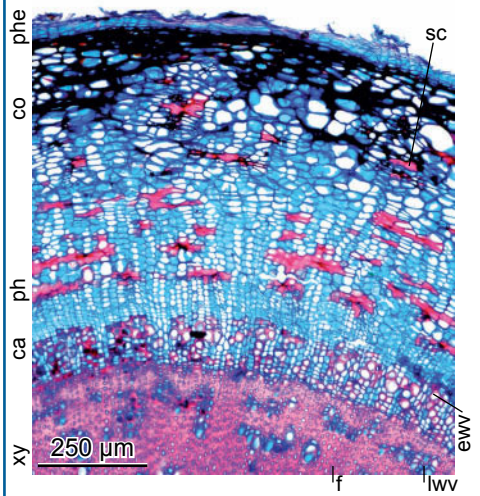



**Fig. 33.** Phloem with groups of sclerenchyma cells, which are arranged in tangential rows. Bark of the root collar of a 15 cm-high perennial herb, rock, hill zone, Switzerland. *Arabis hirsuta*, transverse section.

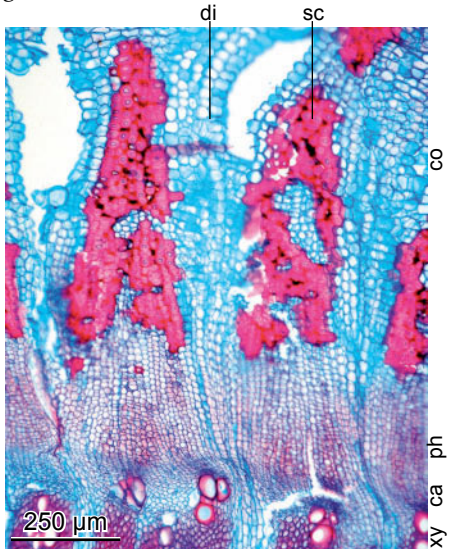



**Fig. 34.** Phloem with large radial groups of sclerenchyma which are divided by ray dilatations. Phloem of a 30 cm-high perennial herb, ruderal site, hill zone, Switzerland. *Diplotaxis tenuifolia*, transverse section.

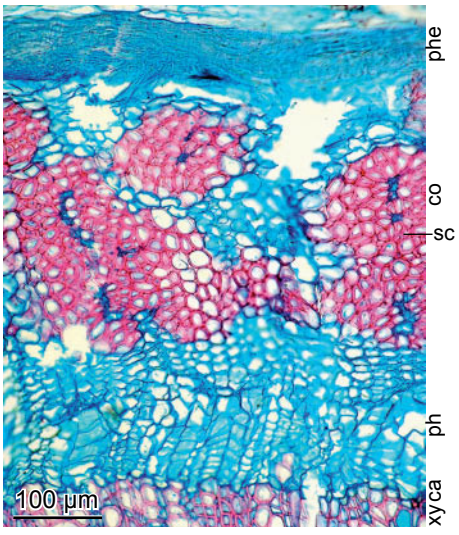



**Fig. 35.** Irregular, dense zone of sclerenchyma in the cortex. Phloem of a 20 cm-high annual herb, oak forest, mediterranean climate, Provence, France. *Bunias erucago*, transverse section.

**Discussion in relation to previous studies**

Hollendonner (1909), Betts (1918), Rollins (1939) and Messeri (1957) described the vegetative anatomy of a few herbaceous plants and of the dwarf shrub *Schouwia schimperi*, from the arid zone Fezzan in Northern Niger. More recent studies concentrate on *Arabidopsis thaliana*, e.g. Busse et al. (1999), Dolan et al. (1995), Chengsong et al. (2000), Kontratieva-Melville et al. (1982) and Lev Yadun et al. (1994). Carlquist (1971) characterized eighteen "woody insular representatives" belonging to seven genera from Macaronesia, mainly growing on subtropical climates on dry sites on the Canary Islands. Wood anatomical descriptions of 3 dwarf shrubs exist for Russia (Benkova and Schweingruber 2004), for 7 from the Sahara and Sahel zone (Neumann et al. 2001) and 7 from western Europe (Schweingruber 1990). The characterisation of the Brassicaceae is an intensively modified version of the article by Schweingruber (2006).

Results from this study are mainly compared with those from Carlquist (1971) and from Metcalfe and Chalk (1957). Carlquist primarily analyzed woody species from the Canary Islands and Metcalfe and Chalk investigated a few annual and perennial herbs as well as dwarf shrubs from different vegetation zones of the hyperarid zone to the moderate temperate zone. Most of their observations could be confirmed in the present study: i.e the exclusive presence of simple perforations, the predominance of square and upright ray cells and the paratracheal parenchyma, the sporadic presence of vestured pits, marginal parenchyma, storied fibers, prismatic crystals in some shrubs, isolated perennial vascular bundles and the absence of rays in a few herbs. Included phloem has been found only in one species (*Hirschfeldia incana*).

All earlier studies are mostly based on only a few shrubby species. That explains most inconsistenceies between the present and earlier studies. Only on the basis of an ecological stratification of a large amount of material, morphological and ecological trends within the family can be recognized. Taxonomic related intra-family groupings would be possible on the basis of more material.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **161** |
| 1 | growth rings distinct and recognizable | 105 |
| 2 | growth rings indistinct or absent | 18 |
| 2.1 | only one ring | 36 |
| 4 | semi-ring-porous | 92 |
| 5 | diffuse-porous | 31 |
| 6 | vessels in intra-annual tangential rows | 51 |
| 9 | vessels predominantly solitary | 53 |
| 9.1 | vessels in radial multiples of 2-4 common | 59 |
| 10 | vessels in radial multiples of 4 or more common | 56 |
| 11 | vessels predominantely in clusters | 57 |
| 13 | vessels with simple perforation plates | 139 |
| 20 | intervessel pits scalariform | 11 |
| 20.1 | intervessel pits pseudoscalariform to reticulate | 1 |
| 39.1 | vessel cell-wall thickness >2 µm | 12 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 29 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 127 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 12 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 114 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 49 |
| 58 | dark-stained substances in vessels and/or fibers present (gum, tannins) | 22 |
| 59 | vessels absent or indistinguishable from fibers | 1 |
| 60.1 | fibers absent | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 160 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 1 |
| 67 | thick- and thin-walled fiber bands, *Acer* type | 1 |
| 68 | fibers thin-walled | 27 |
| 69 | fibers thick-walled | 37 |
| 70 | fibers thin- to thick-walled | 86 |
| 70.1 | intra-annual thick-walled tangential fiber bands | 32 |
| 75 | parenchyma absent or unrecognizable | 3 |
| 79 | parenchyma paratracheal | 140 |
| 79.1 | parenchyma pervasive | 30 |
| 89 | parenchyma marginal | 42 |
| 89.1 | parenchyma marginal thin-walled, dark in polarized light | 19 |
| 89.2 | ring shake, *Saxifraga* type | 2 |
| 97 | ray width predominantly 1-3 cells | 40 |
| 98 | rays commonly 4-10-seriate | 52 |
| 99 | rays commonly >10-seriate | 11 |
| 99.1 | vascular-bundle form remaining | 8 |
| 100.1 | rays confluent with ground tissue | 14 |
| 100.2 | rays invisible in in polarized light | 38 |
| 105 | ray: all cells upright or square | 85 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 14 |
| 110 | rays with sheet cells (tangential section) | 9 |
| 117 | rayless | 63 |
| 120 | storied axial tissue (parenchyma, fibers, vessels in tangential section) | 6 |
| 135 | interxylary phloem present | 1 |
| 136 | prismatic crystals present | 4 |
| R1 | groups of sieve tubes present | 90 |
| R2 | groups of sieve tubes in tangential rows | 57 |
| R2.1 | groups of sieve tubes in radial rows | 7 |
| R3 | distinct ray dilatations | 58 |
| R4 | sclereids in phloem and cortex | 47 |
| R6 | sclereids in radial rows | 19 |
| R6.1 | sclereids in tangential rows | 31 |
| R7 | with prismatic crystals | 3 |
| R7.1 | with acicular crystals | 2 |
| R10 | phloem not well structured | 15 |

# Buxaceae



**Number of species, worldwide and in Europe**

The cosmopolitean Buxaceae family includes 5 genera with 60 species. *Buxus sempervirens* and *B. balearica* occur in Europe.

**Analyzed material**

The xylem and phloem of 6 Buxaceae species were analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 2 | 5, div. authors |
| Woody chamaephytes | 4 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 5 | |
| Mediterranean | 1 | |

**Analyzed species:**

*Buxus sempervirens* L.
*Pachysandra stylosa* Dunn.
*Pachysandra terminalis* S. *et* Z.
*Sarcococca saligna* Müll. Arg.
*Sarcococca hookeriana* R. Fehder *et* Wilson
*Styloceras brokawii* All. Gentry *et* Foster

*Buxus sempervirens* (photo: Zinnert)

*Pachysandra stylosa* (photo: Zinnert)

*Sarcococca confusa*

**Characteristics of the xylem**

In the present material, the genera *Buxus*, *Pachysandra*, *Sarcococca*, and *Styloceras* represent an anatomical unit. Annual rings occur in all species of the temperate zones (*Buxus* **Fig. 1**, *Sarcococca* **Fig. 2**). Density fluctuations instead of rings occur in the tropical *Styloceras brokawii* (**Fig. 3**). Annual rings are often indistinct in *Pachysandra* (**Fig. 4**). A band of latewood with few vessels and a small band of radially flat fiber cells mark ring boundaries of most species. All species are diffuse-porous and have solitary vessels (**Figs. 1-6**). Vessel diameter varies between 15 and 40 µm. Vessels are extremely small (<20 µm) in *Pachysandra stylosa* (**Fig. 4**) and in *Sarcococca hookeriana* (**Fig. 2**). All species contain scalariform perforations: with few bars in *Buxus* (**Fig. 6**), which has less than 10 while and all others more than 20 (**Fig. 7**). Plugs of dark-stained substances are present in vessels of *Buxus sempervirens*. Vessel density varies from 300-500/mm$^2$. Intervessel pits are predominantly small and round. The radial walls of fibers are typically thick (**Figs. 1, 2** and **5**) and perforated by round pits with a diameter of 2-3 µm (**Fig. 8**). Fibers are thin- to thick-walled in *Styloceras brokawii* (**Fig. 3**). Axial parenchyma is usually apotracheal diffuse or unrecognizable (**Fig. 5**). The rays of both *Pachysandra* species are exclusively uniseriate with upright cells (**Fig. 9**). The rays of *Buxus*, *Sarcococca* and *Styloceras* have 1-2 cells (**Figs. 10** and **11**). Rays of *Buxus sempervirens* are heterocellular (1-3 marginal, square and upright cells, **Fig. 10**). Central cells in rays of *Sarcococca* and *Styloceras* are square in the interior and upright at the margins (**Fig. 11**).

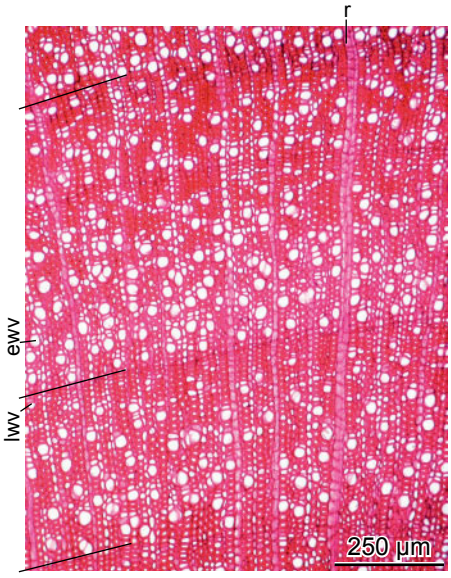



**Fig. 1.** Diffuse-porous wood. Ring boundaries are defined by a zone with few vessels. Stem of a 2 m-high shrub, dry site on limestone, submediterranean climate, Niaux, Pyrenees, France. *Buxus sempervirens*, transverse section.

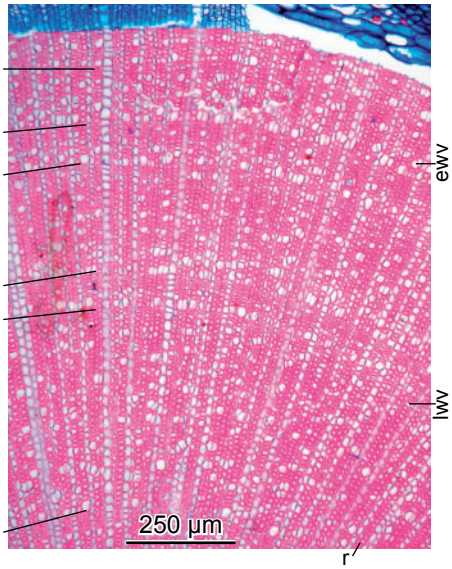



**Fig. 2**. Diffuse-porous wood. Ring boundaries are defined by a zone with few vessels. Vessel diameter is small (<20 µm). Stem of a 60 cm-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Sarcococca hookeriana*, transverse section.

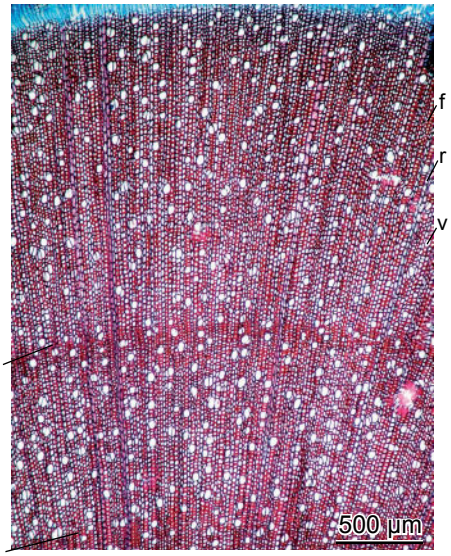
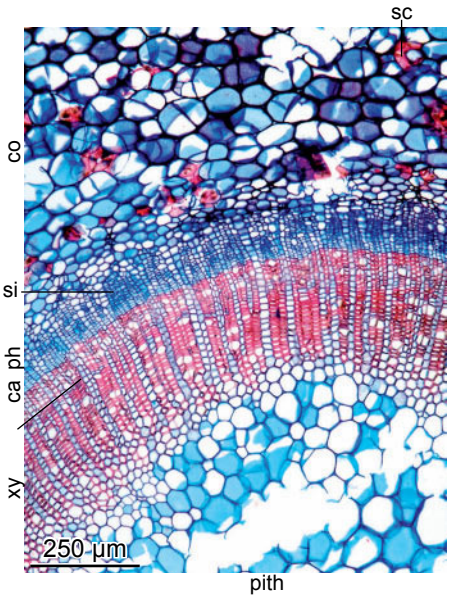
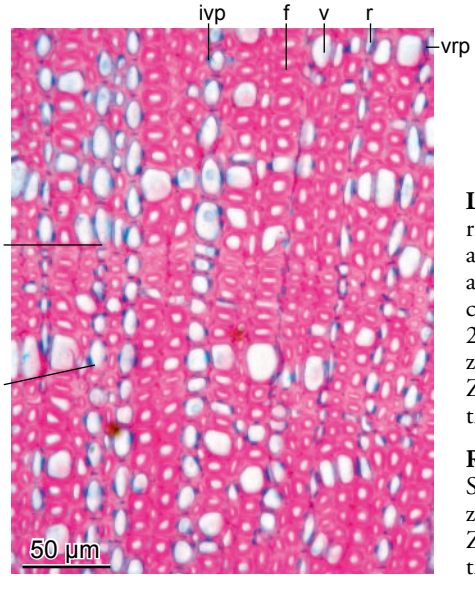



**Fig. 3.** Wood with indistinct rings. Zones with more or fewer vessels and thicker fiber cell walls indicate growing zones. Stem of a 1.5 m-high shrub, cultivated, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Styloceras brokawii*, transverse section.




**Left Fig. 4.** Diffuse-porous wood with two rings. The second is very small. Vessel diameter is small (<20 µm). Ray cells have a short radial expansion. Isolated sclerenchyma cells occur in the cortex. Stem of a 25 cm-high chamaephyte, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Pachysandra stylosa*, transverse section.

**Right Fig. 5.** Parenchyma unrecognizable. Stem of a 60 cm-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Sarcococca hookeriana*, transverse section.

**Taxa characteristic features**

*Buxus* is characterized by perforations with few bars and heterocellular rays. Many bars are typical for all other species. Rays are uniseriate in *Pachysandra* and biseriate in *Sarcococca* and *Styloceras*.

**Ecological trends and relations to life forms**

Ecological trends are absent or could not be detected.

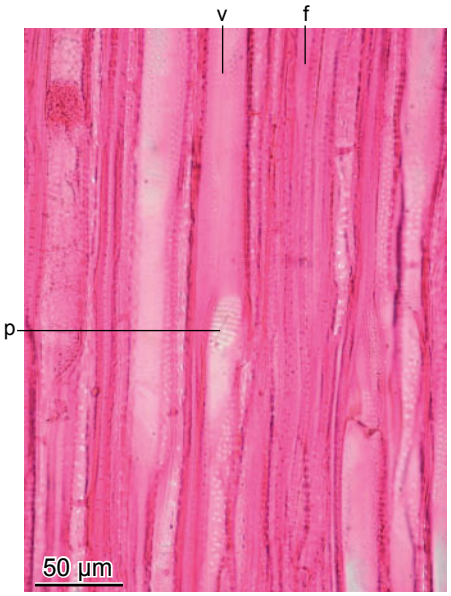



**Fig. 6.** Scalariform perforation with few bars (<10). Stem of a 2 m-high shrub, dry site on limestone, submediterranean climate, Niaux, Pyrenees, France. *Buxus sempervirens*, radial section.

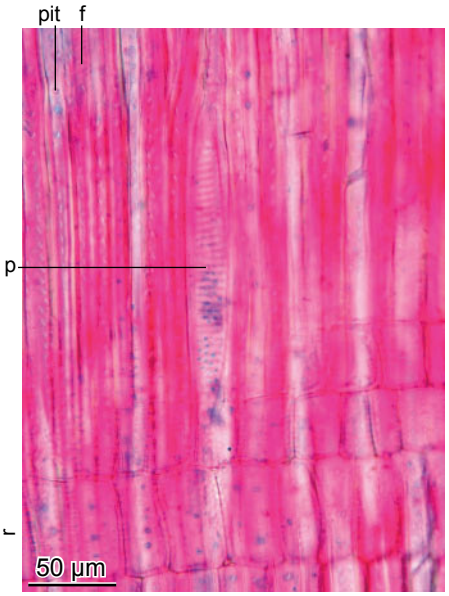



**Fig. 7.** Scalariform perforation with many bars (<20). Stem of a 60 cm-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Sarcococca hookeriana*, radial section.

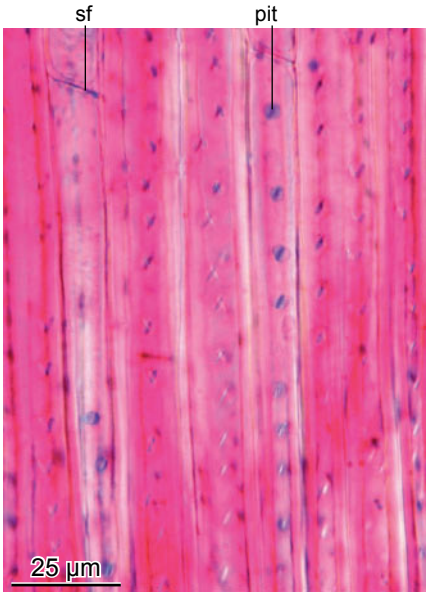



**Fig. 8.** Fibers with large, round pits and slit-like apertures. Stem of a 60 cm-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Sarcococca hookeriana*, radial section.

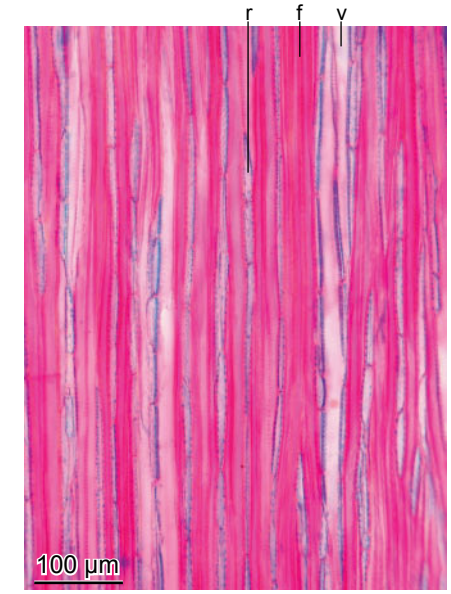



**Fig. 9.** Uniseriate rays with axially elongated cells. Stem of a 30 cm-high chamaephyte, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Pachysandra terminalis*, tangential section.

**Fig. 10.** Heterocellular, uniseriate and biseriate rays. Central ray cells are much smaller than the marginal cells. Stem of a 2 m-high shrub, dry site on limestone, submediterranean climate, Niaux, Pyrenees, France. *Buxus sempervirens*, tangential section.

**Fig. 11.** Heterocellular, uniseriate and biseriate rays. Central ray cells are much smaller than marginal cells. Stem of a 60 cm-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Sarcococca hookeriana*, tangential section.

**Characteristics of the phloem and the cortex**

All genera can be differentiated by bark characteristics. The phloem of *Buxus sempervirens* has a uniform phloem and distinct phellem layers (**Fig. 12**). The phloem of *Pachysandra* is very small (**Fig. 13**). The cortex of *Pachysandra stylosa* and of *Sarcococca saligna* contains isolated sclerenchyma cells (**Figs. 14** and **15**). The phloem of *Sarcococca saligna* is similar to *Buxus*. The phloem of *Styloceras* is characterized by isolated, round groups of sclereids (**Figs. 15** and **16**) and by the absence of a phellem. Prismatic crystals have been observed in *Buxus* (**Fig. 17**) but they are rare in *Pachysandra stylosa*. Isolated crystal druses have been found in *Pachysandra stylosa* and *Sarcococca hookeriana*.

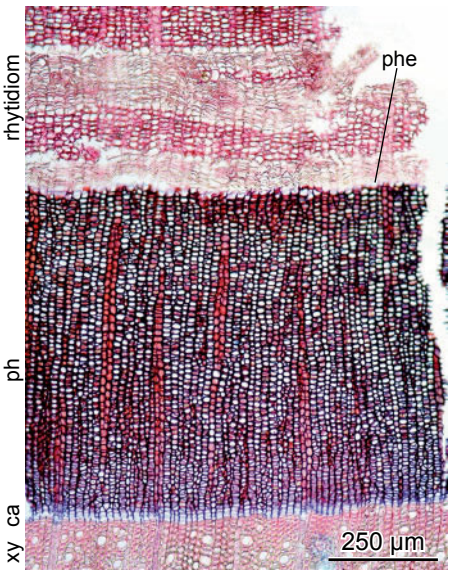



**Fig. 12.** Uniform phloem and layers of phellem zones. Stem of a 2 m-high shrub, dry site on limestone, submediterranean climate, Niaux, Pyrenees, France. *Buxus sempervirens*, transverse section.

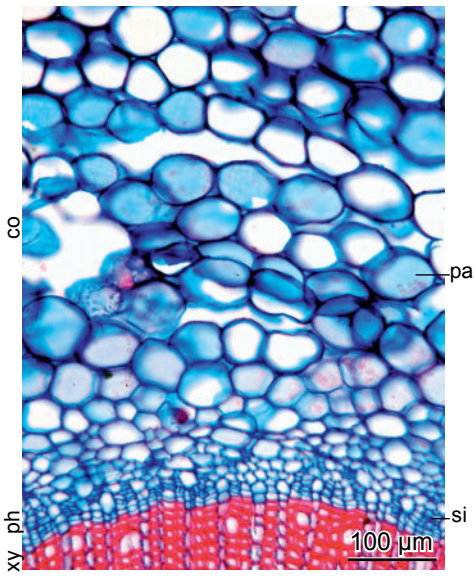



**Fig. 13.** Small phloem. Sclereids are absent from the phloem and from the cortex. Stem of a 25 cm-high chamaephyte, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Pachysandra terminalis*, transverse section.

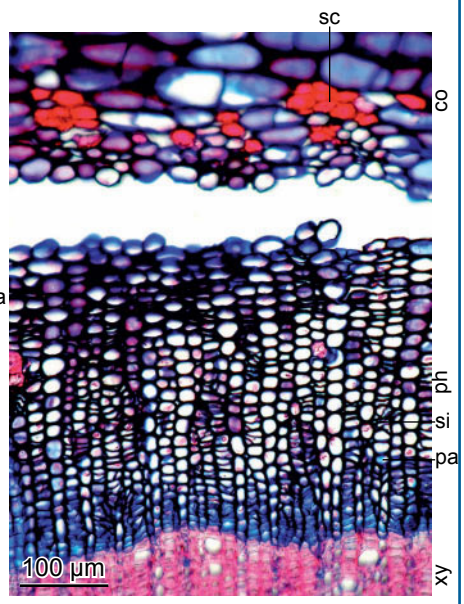



**Fig. 14.** Uniform phloem with few groups and some isolated thick-walled sclerenchyma cells in the cortex. Stem of a 80 cm-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Sarcococca saligna*, transverse section.

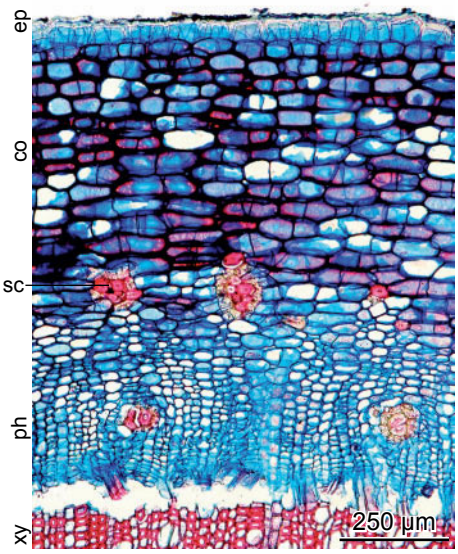



**Fig. 15.** Phloem and cortex with round groups of sclereids. Stem of a 1.5 m-high shrub, cultivated, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Styloceras brokawii*, transverse section.

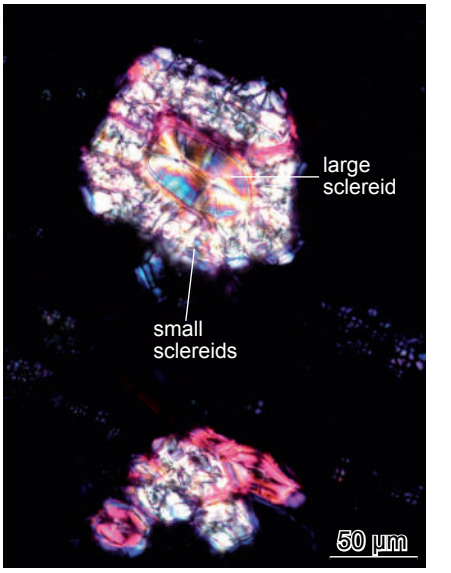



**Fig. 16.** A group of sclereids in the phloem. Small sclereids surround a large central sclereid cell. Stem of a 1.5 m-high shrub, cultivated, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Styloceras brokawii*, transverse section, polarized light.

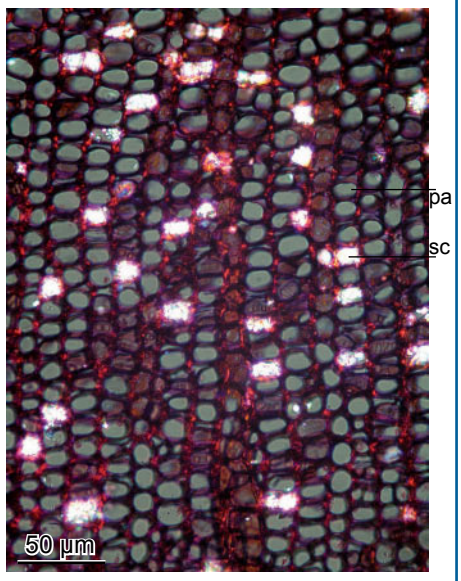



**Fig. 17.** Crystals exist in parenchyma cells of the phloem. Stem of a 2 m-high shrub, dry site on limestone, submediterranean climate, Niaux, Pyrenees, France. *Buxus sempervirens*, transverse section.

**Discussion in relation to previous studies**

The only existing study was made by Carlquist (1982), on the basis of 5 genera (*Buxus*, *Notobuxus*, *Sarcococca*, and *Styloceras*). Many authors described *Buxus sempervirens*. Gregory (1994) and Metcalfe and Chalk (1957) provide many further references. The present confirms observations from earlier studies.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **6** |
| 1 | growth rings distinct and recognizable | 3 |
| 2 | growth rings indistinct or absent | 2 |
| 2.1 | only one ring | 1 |
| 5 | diffuse-porous | 3 |
| 9 | vessels predominantly solitary | 6 |
| 11 | vessels predominantely in clusters | 2 |
| 14 | vessels with scalariform perforation plates | 6 |
| 20 | intervessel pits scalariform | 1 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 4 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 4 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 5 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 1 |
| 58 | dark-stained substances in vessels and/or fibers present (gum, tannins) | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 6 |
| 69 | fibers thick-walled | 4 |
| 70 | fibers thin- to thick-walled | 3 |
| 76 | parenchyma apotracheal, diffuse in aggregates | 6 |
| 96 | rays exclusively uniseriate | 2 |
| 97 | ray width predominantly 1-3 cells | 4 |
| 105 | ray: cells upright or square | 5 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| R1 | groups of sieve tubes present | 5 |
| R3 | distinct ray dilatations | 2 |
| R4 | sclereids in phloem and cortex | 3 |
| R6.1 | sclereids in tangential rows | 2 |
| R7 | with prismatic crystals | 2 |
| R8 | with crystal druses | 2 |
| R10 | phloem not well structured | 1 |

# Cannabaceae

### Number of species, worldwide and in Europe

The Cannabaceae family is distributed in the northern hemisphere and includes 2 genera with 4 species. In Europe, there are 2 genera (*Cannabis*, *Humulus*) with 3 species.

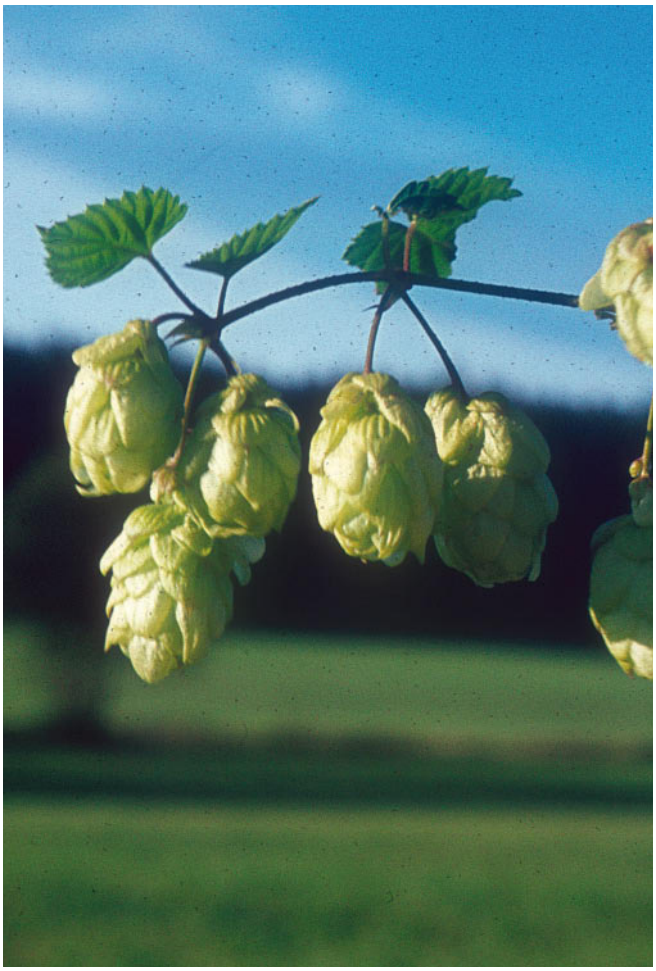
**Analyzed species:**
*Cannabis sativa* L.
*Humulus lupulus* L. annual liana-like shoot
*Humulus lupulus* L. rhizome

### Analyzed material

The xylem and phloem of 2 genera with 2 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Hemicryptophyte rhizome | 1 | 0 |
| Hemicryptophyte with annual, liana-like shoots | 1 | 1 |
| Therophytes | 1 | 1 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 2 | |

*Cannabis sativa* (photo: Zinnert)



*Humulus lupulus*

**Characteristics of the xylem, phloem and cortex**

The stem-anatomy of the 2 species is very different.

***Cannabis sativa***

*Cannabis sativa* is an annual plant and has only one ring (**Fig. 1**). Vessels occur in radial multiples (**Fig. 2**) which are arranged in more-or-less distinct tangential rows (**Fig. 1**). Vessel diameter varies between 50-90 µm, decreasing from the center to the periphery. Vessels have exclusively simple perforations, and pits are scalariform or round in opposite position. Ray-vessel pits of different forms are enlarged (**Fig. 3**). Vessels contain thin-walled tylosis (**Fig. 2**). Fibers are thin- to thick-walled (**Figs. 2**, **4** and **5**). Fiber pits are difficult to recognize. *Cannabis sativa* produces tension wood (**Fig. 4**). The distribution of axial parenchyma is paratracheal (**Fig. 5**). The 2-3 seriate rays (**Fig. 6**) are heterocellular, with procumbent central cells and a few square, upright marginal cells (**Fig. 6**). Rectangular, prismatic crystals

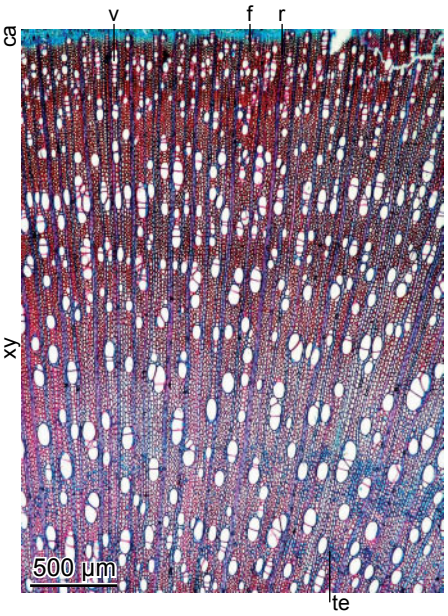



**Fig. 1.** Annual plant with one ring. Vessels are partially arranged in tangential rows. Vessel size continuously decreases from the center to the periphery. Stem of a 1.5 m straight monopodial therophyte, cultivated, hill zone, Zürich, Switzerland. *Cannabis sativa*, transverse section.

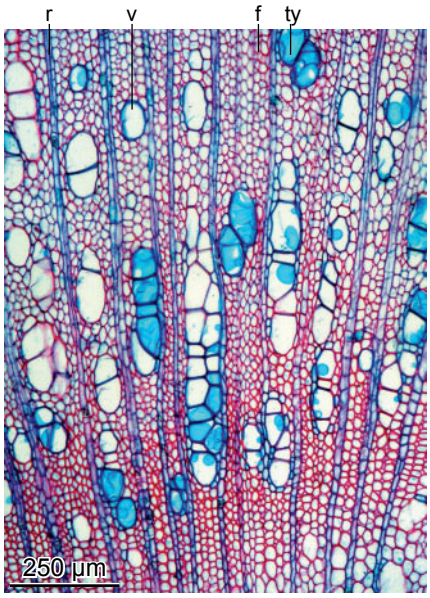



**Fig. 2.** Vessels contain tylosis (blue) and are arranged in long radial multiples. Fibers are thin- to thick-walled. Species and site as described in **Fig. 1**, transverse section.

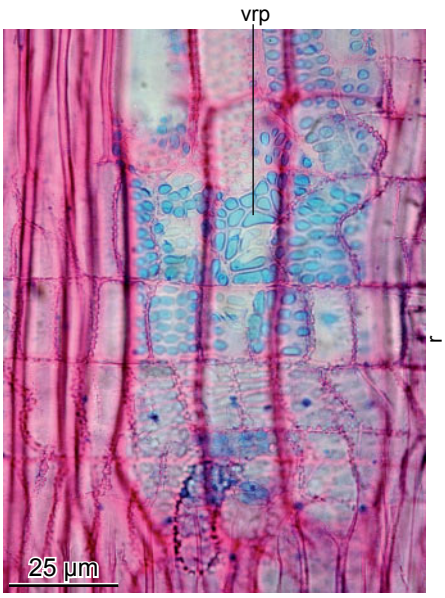



**Fig. 3.** Vessel-ray pits with large apertures of various forms. Species and site as described in **Fig. 1**, radial section.

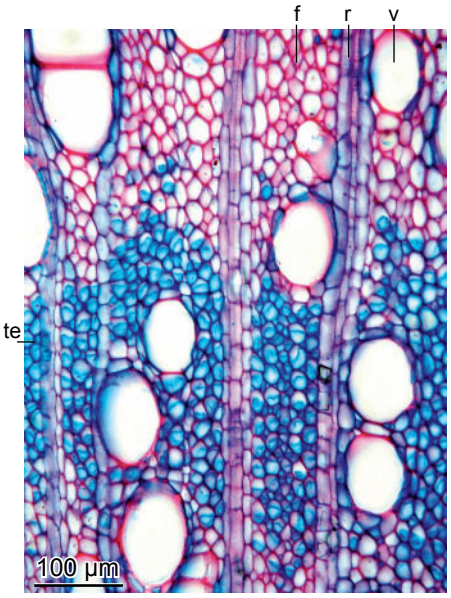



**Fig. 4.** Fibers with gelatinous fibers (tension wood). Species and site as described in **Fig. 1**, transverse section.

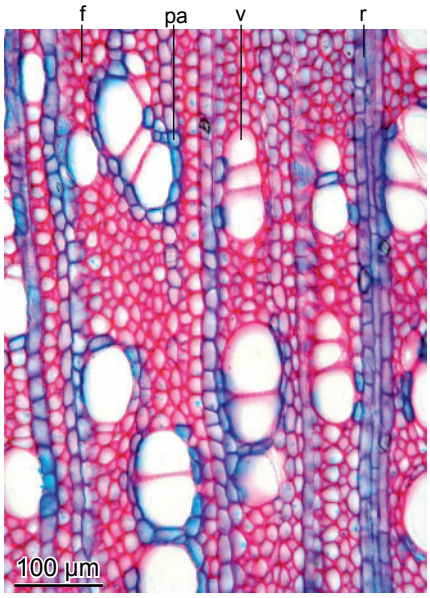



**Fig. 5.** Paratracheal parenchyma. Species and site as described in **Fig. 1**, transverse section.

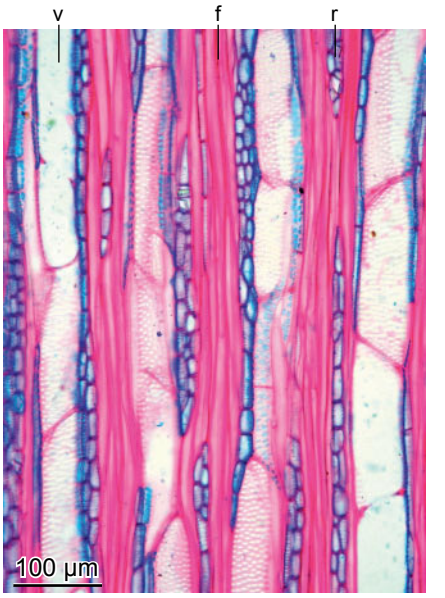



**Fig. 6.** Uni- and biseriate rays. Intervessel pits are arranged in alternate and opposite position. Species and site as described in **Fig. 1**, tangential section.

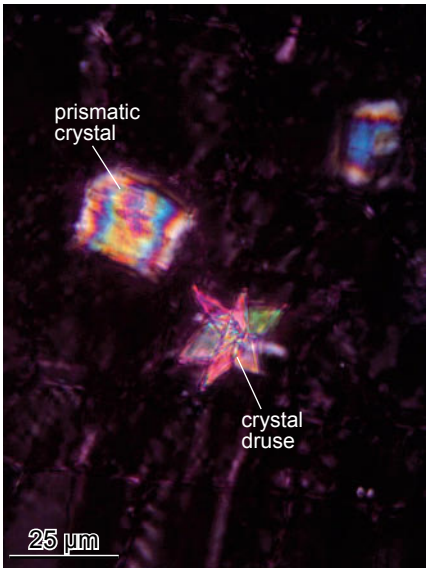
and crystal druses occur in ray cells (**Fig. 7**). Bark: Groups of sclerenchyma near the cambium are arranged in a tangential band and in triangles between ray dilatations (**Fig. 8**). Crystal druses are very frequent.

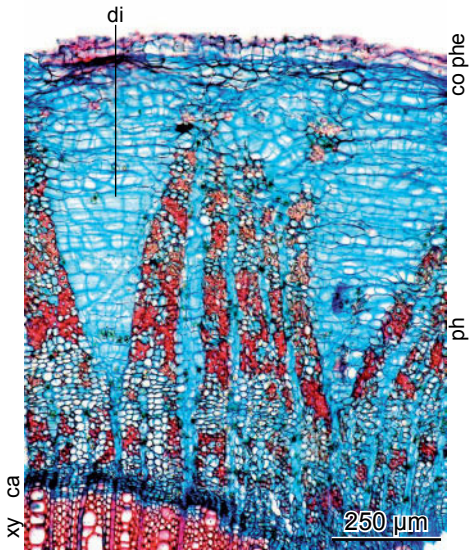
***Humulus lupulus***

The xylem of *Humulus lupulus* has two vessel systems: vessels in the annual liana-like shoot are small at their initial zone and in the later formed part of the second ring (40-60 µm). The second ring contains many large vessels with diameters up to 200 µm (first zone produced by secondary growth; **Fig. 9**). The xylem of the rhizome is ring-porous (**Fig. 10**). Vessels are thick-walled and contain tylosis (**Fig. 9**). Perforations are simple, intervessel-pits are mostly scalariform (**Fig. 11**) and vessel-ray pits are large with an irregular form (**Fig. 12**). Thick-walled vessels are arranged in spots between thin-walled apotracheal and paratracheal parenchyma and large vessels (**Fig. 10**). Ray-width varies between 3-8 cells (**Fig. 13**). Prismatic crystals are frequent and arranged in long axial chains (**Fig. 14**).

The form of parenchyma cells and sieve tubes is similar. Horizontally oriented sieve-plates often characterize sieve tubes in the transverse section (red). Thick-walled fiber bands occur in the phloem and in the cortex (**Fig. 15**).






**Left Fig. 7.** Prismatic crystal and crystal druse in a ray cell. Species and site as described in **Fig. 1**, radial section.

**Right Fig. 8.** Phloem and cortex with radial stripes of fibers between large ray dilatations. Species and site as described in **Fig. 1**, transverse section.

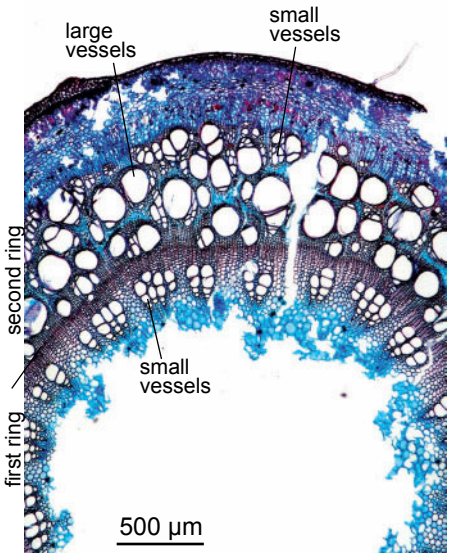



**Fig. 9.** Stem with two rings showing vessel dimorphism. The fist consists of vascular bundles with vessels in radial multiples, whereas the second consists of solitary, large vessels and groups of small vessels. Stem of a 4 m-long winding shoot, *Quercus petraea* forest, mountain zone, Ticino, Switzerland. *Humulus lupulus*, transverse section.

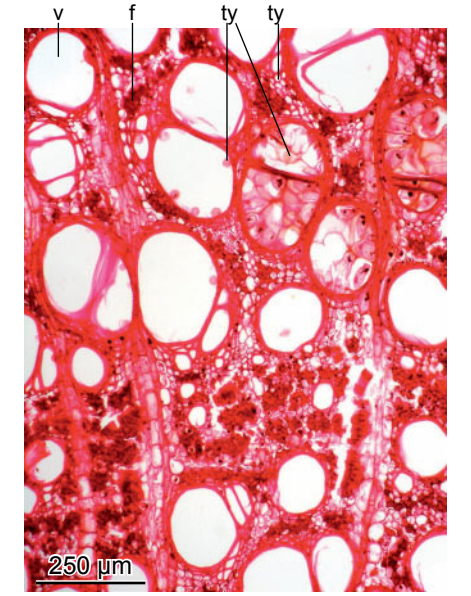



**Fig. 10.** Large thick-walled vessels with tylosis are surrounded by thin-walled parenchyma and thick-walled fibers. Rhizome of a hemicryptophyte with long, annual, liana-like shoots, riparian, mountain zone, Grisons, Switzerland. *Humulus lupulus*, transverse section.

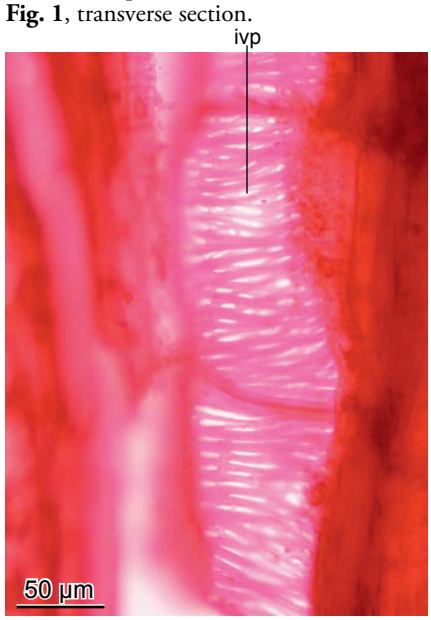
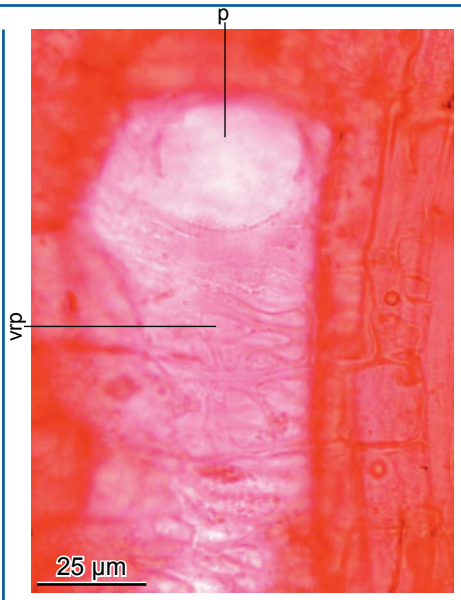
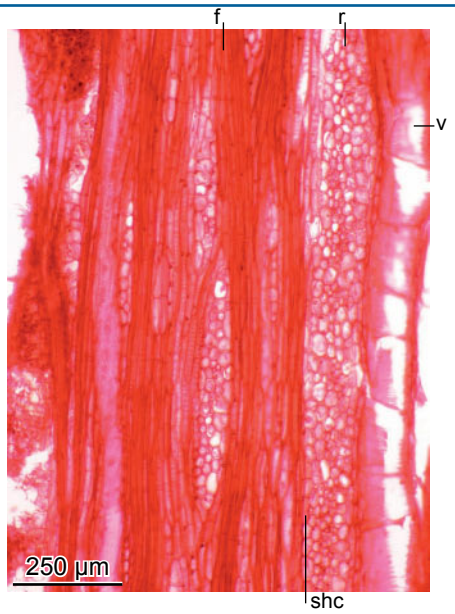


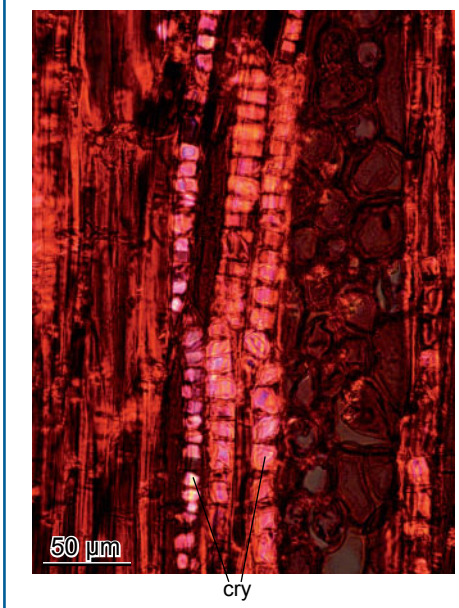

**Fig. 11.** Vessels with scalariform intervessel-pits. Rhizome of a hemicryptophyte with long, annual liana-like shoots, riparian, mountain zone, Grisons, Switzerland. *Humulus lupulus*, radial section.

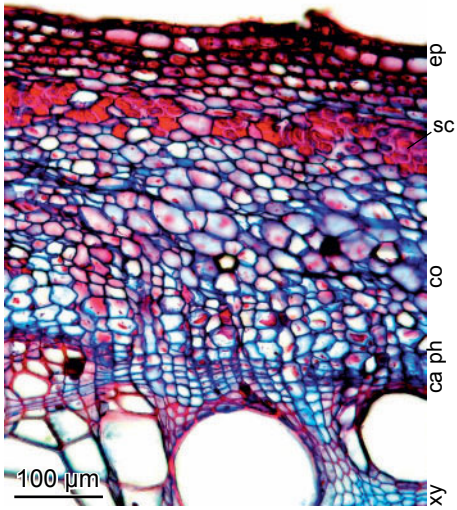



**Left Fig. 12.** Vessel-ray pits with large, irregular apertures. Rhizome of a hemicryptophyte with long, annual liana-like shoots, shoot, riparian, mountain zone, Grisons, Switzerland. *Humulus lupulus*, radial section.

**Right Fig. 13.** 2-8-seriate rays. Rhizome of a hemicryptophyte with long, annual liana-like shoots, hedge, mountain zone, Valais, Switzerland. *Humulus lupulus*, tangential section.




**Left Fig. 14.** Prismatic crystals of various sizes in long chains near a ray. Rhizome of a hemicryptophyte with long, annual liana-like shoots, hedge, mountain zone, Valais, Switzerland. *Humulus lupulus*, tangential section.

**Right Fig. 15.** Phloem with thin-walled sieve tubes and rudiments of sieve-plates (red). Cortex with a tangential band of fibers. Bi-annual winding shoot of a hemicryptophyte, riparian, mountain zone, Grisons, Switzerland. *Humulus lupulus*, transverse section.

**Discussion in relation to previous studies**

Cross-sections of both species have been described by Metcalfe and Chalk (1957). Miller (1959) studied the stem anatomy of *Cannabis sativa* and Anderson (1974) studied that of *Humulus lupulus*.

Growth form specific features characterize stem anatomy. Large vessels, ring-porosity and thin-walled, unlignified strands of parenchyma are characteristic of the liana *Humulus lupulus*. In contrast, the compact, regularly formed, column-like xylem is characteristic of the large, upright *Cannabis sativa*. Common for both species are vessels with simple perforation and large vessel-ray pits.

**Present features in relation to the number of analyzed specimens**

| IAWA code | | frequency |
|---|---|---|
| **Total number of specimens** | | |
| **(2 species; *Humulus lupulus* rhizome and shoot)** | | **3** |
| 1 | growth rings distinct and recognizable | 1 |
| 2.1 | only one ring | 2 |
| 3 | ring-porous | 1 |
| 9 | vessels predominantly solitary | 1 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 10 | vessels in radial multiples of 4 or more common | 1 |
| 13 | vessels with simple perforation plates | 3 |
| 20 | intervessel pits scalariform | 2 |
| 21 | intervessel pits opposite | 1 |
| 22 | intervessel pits alternate | 2 |
| 31 | vessel-ray pits with large apertures, *Salix/Laurus* type | 1 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 2 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 2 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 1 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 2 |
| 50 | <100 vessels per $mm^2$ in earlywood | 3 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 1 |
| 56 | tylosis with thin walls common | 3 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 3 |
| 69 | fibers thick-walled | 1 |
| 70 | fibers thin- to thick-walled | 2 |
| 70.2 | tension wood present | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 79 | parenchyma paratracheal | 3 |
| 97 | ray width predominantly 1-3 cells | 2 |
| 98 | rays commonly 4-10-seriate | 1 |
| 100.2 | rays not visible in polarized light | 1 |
| 103 | rays of two distinct sizes (tangential section) | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 3 |
| 110 | rays with sheet cells (tangential section) | 1 |
| 136 | prismatic crystals present | 3 |
| R2 | groups of sieve tubes in tangential rows | 1 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 3 |
| R6 | sclereids in radial rows | 1 |
| R6.1 | sclereids in tangential rows | 3 |
| R7 | with prismatic crystals | 1 |
| R8 | with crystal druses | 3 |
| R12 | with laticifers, oil ducts or mucilage ducts | 1 |

# Capparaceae



**Number of species, worldwide and in Europe**

The cosmopolitean Capparaceae family includes 42 genera with 800 species. In Europe, there are 2 genera with 4 endemic species.

**Analyzed material**

The xylem and phloem of 5 genera with 8 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 1 | many |
| Nanophanerophytes 0.5-4 m | 6 | many |
| Hemicryptophytes | 1 | 0 |
| **Plants analyzed from different vegetation zones:** | | |
| Arid | 6 | |
| Mediterranean | 1 | |
| Subtropical | 1 | |

**Analyzed species:**
*Boscia arabica* L.
*Cadaba longifolia* DC .
*Cadaba rotundifolia* Forsk.
*Capparis spinosa* L.
*Cleome arabica* Pestalozzi
*Cleome brachyphylla* Vahl ex DC.
*Cleome isomeris* Greene
*Maerua crassifolia* Forssk.

**Below:** *Capparis spinosa;* **Right:** *Cleome diandra*

**Characteristics of the xylem**

Growth ring boundaries are rather indistinct in most species (**Figs. 1** and **2**) except *Capparis spinosa* (**Fig. 3**). Ring boundaries are absent in *Cadaba rotundifolia*, *Cleome brachyphylla* and *Cleome isomeris* (**Fig. 2**). *Capparis spinosa* is ring-porous to semi-ring-porous (**Fig. 3**), diffuse-porous are *Cadaba longifolia*, *Cleome arabica* and *Maerua crassifolia*. Vessels are arranged in radial multiples of various length (**Figs. 1-3**, **6** and **7**). Earlywood vessels with a diameter between 100-200 µm are characteristic of *Capparis spinosa* (**Fig. 3**). The diameter of all other species varies from 50-100 µm (**Figs. 1** and **2**). Vessels of all species have simple perforations and small intervessel pits in alternating or opposite position (**Fig. 4**). Vessels of most species are thick-walled (**Fig. 5**). Fibers containing large pits with slit-like apertures occur in the radial walls of all species. The distribution of axial parenchyma is paratracheal (**Figs. 6** and **7**). Rays are species-specific: uniseriate, homocellular with square and upright cells in *Cadaba longifolia* (**Fig. 8**), heterocellular with one to several square and upright marginal cells and 2-3-seriate in all other species (**Figs. 9-11**). Particular is the occurrence of included phloem in *Cadaba longifolia*, *Cadaba rotundifolia* (**Fig. 12**), *Cleome brachyphylla* (**Fig. 13**) and *Maerua crassifolia*. Large prismatic crystals are present in ray cells of *Cadaba longifoilia*, *Cadaba rotundifolia* and *Maerua crassifolia* (**Fig. 14**).

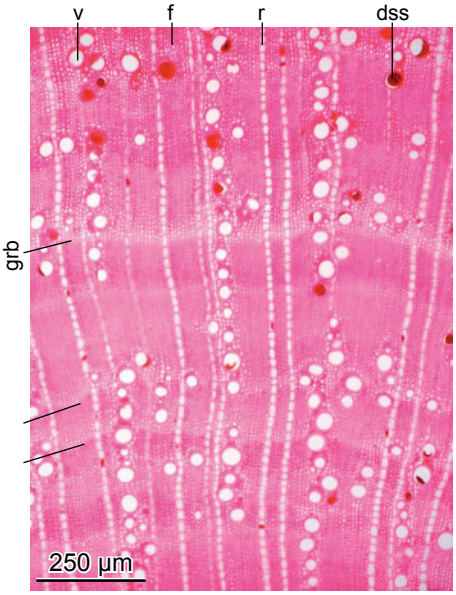



**Fig. 1.** Diffuse-porous xylem with growth zones. Vessels are arranged in long, loose radial multiples. Stem of a 1 m-high shrub, Savannah, arid zone, Saudi Arabia. *Cadaba longifolia*, transverse section.

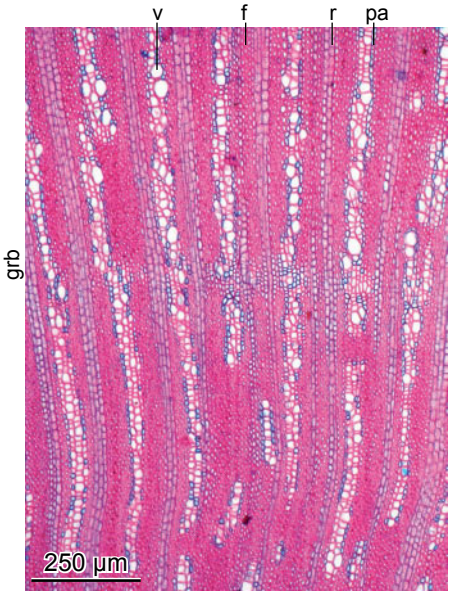



**Fig. 2.** Diffuse-porous xylem with growth zones. Vessels are arranged in long straight radial multiples. Stem of a 1 m-high shrub, desert, arid zone, Twentynine Palms, California, USA. *Cleome isomeris*, transverse section.

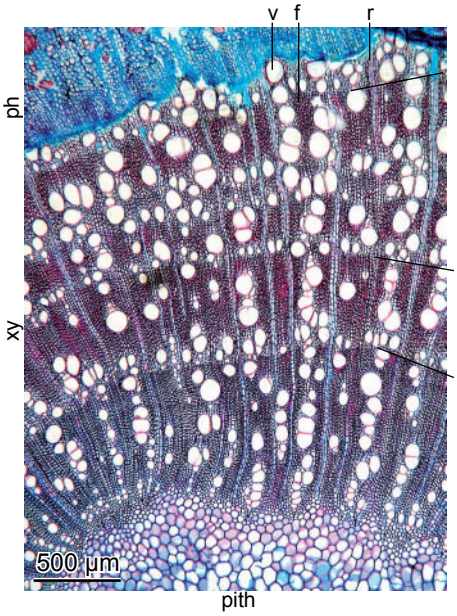
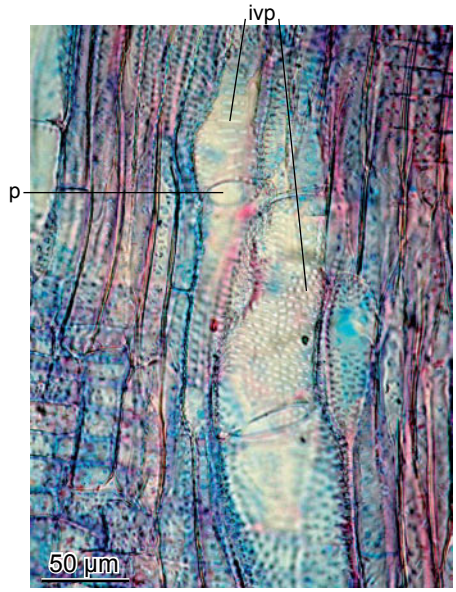
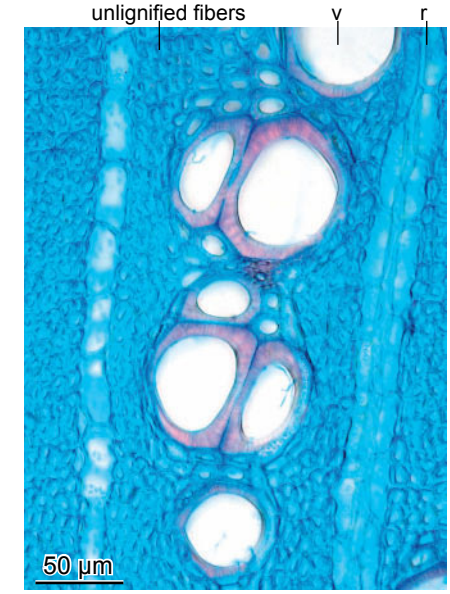



**Fig. 3.** Ring-porous to semi-ring-porous xylem. Vessels are arranged solitary or in irregular radial multiples. Stem of a 1-2 m-high shrub with long, liana-like twigs, on rock, Mediterranean zone, Catalonia, Spain. *Capparis spinosa*, transverse section.




**Left Fig. 4.** Vessels with simple perforations and small intervessel pits. Stem of a 1 m-high shrub, succulent zone, subtropical climate, Gran Canaria, Canary Islands. *Cleome brachyphylla*, radial section.




**Right Fig. 5.** Vessels with very thick, lignified walls. Stem of a 1 m-high shrub, desert, arid zone, Saudi Arabia. *Cadaba rotundifolia*, transverse section.

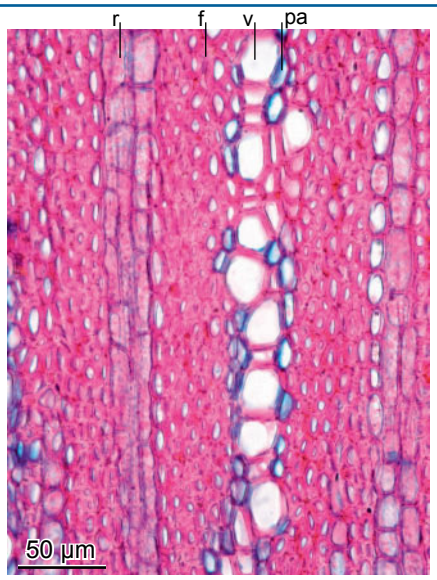



**Fig. 6.** Paratracheal parenchyma. Stem of a 1 m-high shrub, desert, arid zone, Twenty-nine Palms, California, USA. *Cleome isomeris*, transverse section.

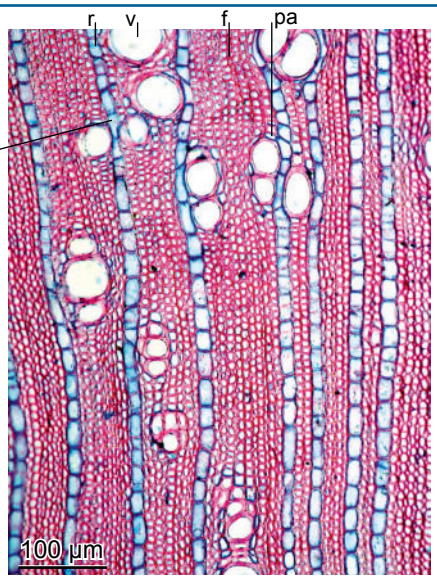
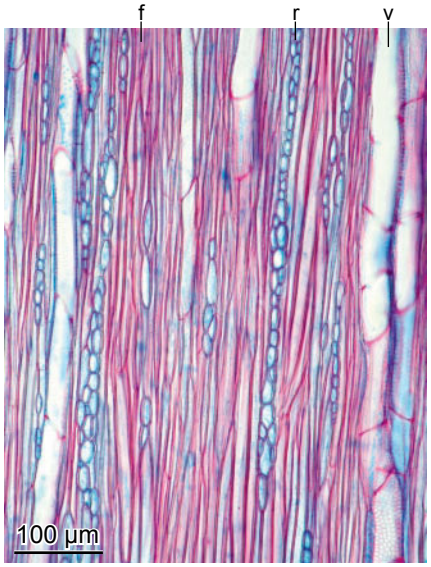


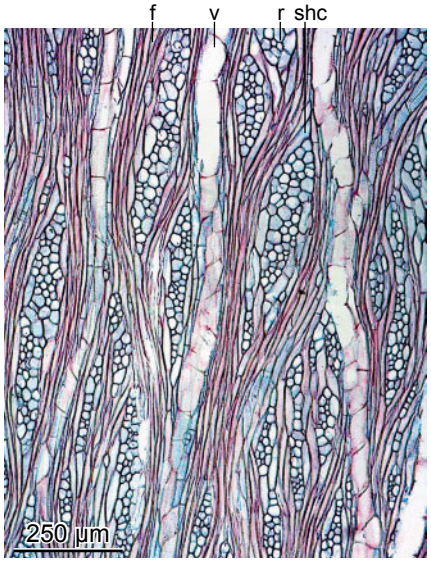

**Fig. 7.** Paratracheal parenchyma. Rays are unlignified. Stem of a 2 m-high shrub, desert, arid zone, Fezzan, Libya. *Maerua crassifolia*, transverse section.

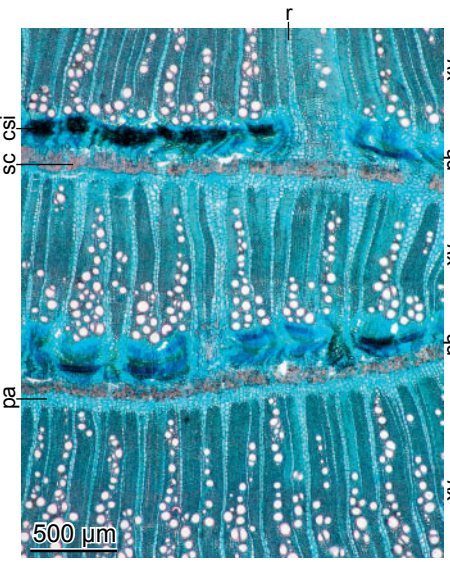
**Fig. 8.** Uniseriate homocellular rays. Stem of a 5 m-high tree, Savannah, arid zone, Sudan. *Boscia arabica*, tangential section.



**Left Fig. 9.** Uni- and biseriate rays. Root collar of a 0.5 m-high hemicryptophyte, ruderal site, arid zone, Fezzan, Libya. *Cleome arabica*, tangential section.

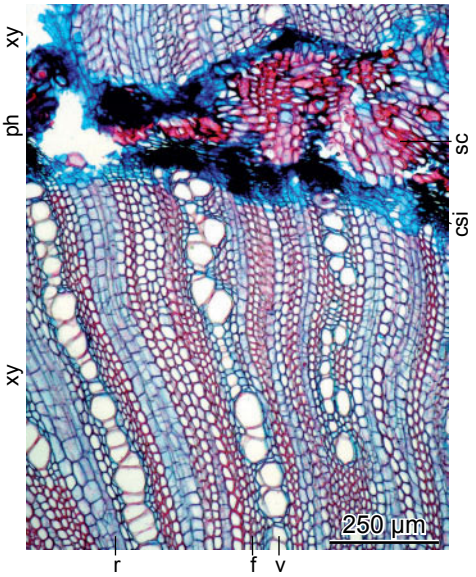
**Right Fig. 10.** 2-3 seriate rays. Stem of a 1-2 m-high shrub with long, liana-like twigs, on rock, Mediterranean zone, Catalonia, Spain. *Capparis spinosa*, tangential section.

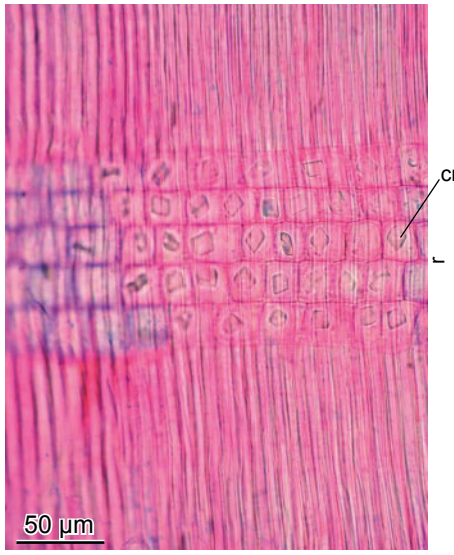



**Left Fig. 11.** 3-6 seriate rays with sheet cells, in a plant with a bent stem. Stem of a 1 m-high shrub, succulent zone, subtropical climate, Gran Canaria, Canary Islands. *Cleome brachyphylla*, tangential section.

**Right Fig. 12.** Included phloem consisting of a tangential band of thin-walled parenchyma, of thick-walled fibers and collapsed sieve tubes. Stem of a 1 m-high shrub, desert, arid zone, Saudi Arabia. *Cadaba rotundifolia*, transverse section.




**Left Fig. 13.** Included phloem consisting of two marginal, tangential bands of collapsed sieve tubes and groups of irregularly-formed lignified parenchyma cells or/and sclerenchyma in the center. Stem of a 1 m-high shrub, succulent zone, subtropical climate, Gran Canaria, Canary Islands. *Cleome brachyphylla*, transverse section.

**Right Fig. 14.** Large prismatic crystals in ray cells. Stem of a 2 m-high shrub, desert, arid zone, Fezzan, Libya. *Maerua crassifolia*, radial section.



### Characteristics of the phloem and the cortex

Irregularly formed groups of sclerenchyma and ray dilatations are characteristic of most species (**Figs. 15-17**). Irregularly formed groups of collapsed sieve tubes have been observed in *Cleome isomeris* and *Capparis spinosa* (**Figs. 15** and **16**). Crystals are absent in all species.

### Discussion in relation to previous studies

All species described here occur in warm and dry regions or sites. Fahn et al. (1986) and Neumann et al. (2001) describe all trees and shrubs characterized here. New to this study are the descriptions of a North American shrub (*Cleome isomeris*) and a hemicryptophyte from the Sahara (*Cleome arabica*) as well as all bark descriptions. The present results are in accordance with previous findings. Particular is the presence of included phloem in some species. Anatomical structures related to environmental conditions were not recognizable. Hall et al. (2002) relate the Capparaceae to Brassicaceae.

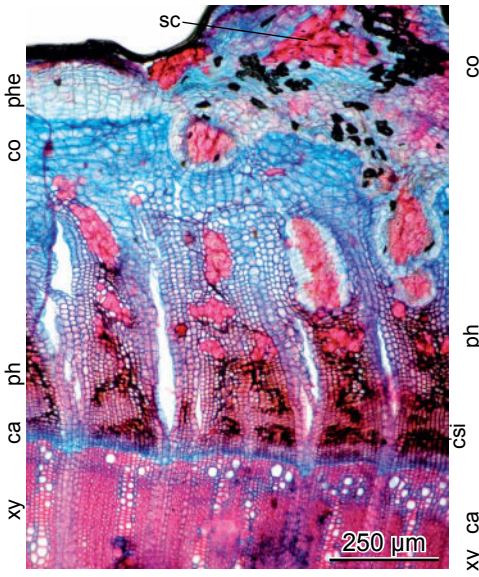



**Fig. 15.** The inner part of the phloem consists of collapsed sieve tubes, surrounded by parenchyma cells. Groups of sclerenchyma cells are located in the outer part of the phloem. Stem of a 1 m-high shrub, desert, arid zone, Twentynine Palms, California, USA. *Cleome isomeris*, transverse section.

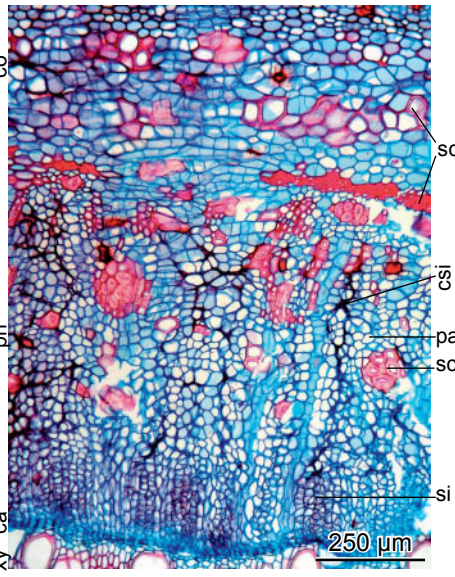



**Fig. 16.** The phloem consists of thin-walled, irregularly formed parenchyma cells, collapsed sieve tubes and groups of sclerenchyma cells. Stem of a 1-2 m-high shrub with long, liana-like twigs, on rock, Mediterranean zone, Catalonia, Spain. *Capparis spinosa*, transverse section.

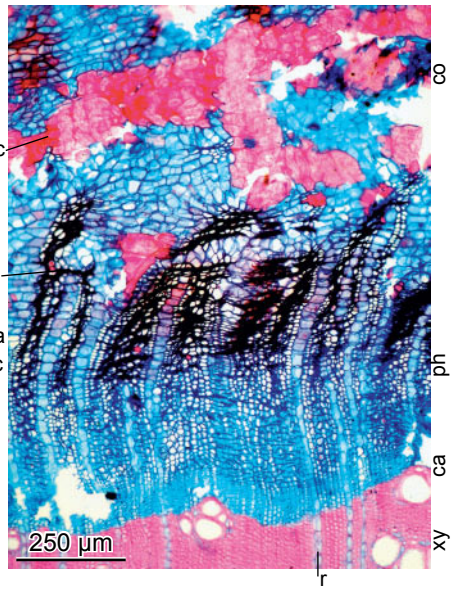



**Fig. 17.** The inner part of the phloem consists of collapsed sieve tubes, surrounded by parenchyma cells. Groups of sclerenchyma cells are located in the outer part of the phloem and in the cortex. Stem of a 2 m-high shrub, desert, arid zone, Fezzan, Libya. *Maerua crassifolia*, transverse section.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **8** |
| 1 | growth rings distinct and recognizable | 5 |
| 2 | growth rings absent | 3 |
| 3 | ring-porous | 1 |
| 4 | semi-ring-porous | 1 |
| 5 | diffuse-porous | 4 |
| 10 | vessels in radial multiples of 4 or more common | 8 |
| 11 | vessels predominantely in clusters | 1 |
| 13 | vessels with simple perforation plates | 8 |
| 22 | intervessel pits alternate | 8 |
| 39.1 | vessel cell-wall thickness >2 µm | 4 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 6 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 2 |
| 42 | earlywood vessels: tangential diameter 100.200 µm | 1 |
| 50 | <100 vessels per $mm^2$ in earlywood | 3 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 5 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 2 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 8 |
| 69 | fibers thick-walled | 3 |
| 70 | fibers thin- to thick-walled | 5 |
| 79 | parenchyma paratracheal | 8 |
| 96 | rays uniseriate | 1 |
| 97 | ray width predominantly 1-3 cells | 6 |
| 98 | rays commonly 4-10-seriate | 4 |
| 104 | ray: all cells procumbent (radial section) | 1 |
| 105 | ray: all cells upright or square | 1 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 3 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 3 |
| 110 | rays with sheet cells (tangential section) | 1 |
| 133 | successive cambia: Caryophyllaceae type | 4 |
| 136 | prismatic crystals present | 2 |
| R1 | groups of sieve tubes present | 5 |
| R3 | distinct ray dilatations | 4 |
| R4 | sclereids in phloem and cortex | 4 |
| R6.2 | sclereids in tangentially arranged groups, *Rhamnus* type | 2 |

# Caryophyllaceae

### Number of species, worldwide and in Europe

The northern hemispheric Caryophyllaceae family includes 86 genera and 2200 species (Bittrich, 1993). In Europe occur 37 genera with 652 species.

### Analyzed material

Analyzed are a total of 100 species of Caryophyllaceae. The subfamilies include the following numbers of species: *Alsinoideae* 28, *Caryophylloideae* 52 and *Paronychoideae* 20 species.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Semi-woody chamaephytes | 1 | ca. 25 |
| Hemicryptophytes and geophytes | 85 | |
| Therophytes | 14 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 27 | |
| Boreal | 4 | |
| Hill and mountain | 52 | |
| Mediterranean | 4 | |
| Arid | 4 | |
| Subtropical | 9 | |

*Silene adscendens*

**Analyzed species:**

*Acanthophyllum microcephalum* Boiss. (Paronychioideae)
*Agrostemma ghitago* L. (Caryophylloideae)
*Arenaria aggregata* L. (Lois.) (Alsinoideae)
*Arenaria biflora* L. (Alsinoideae)
*Arenaria ciliata* L. (Alsinoideae)
*Arenaria serpyllifolia* L. (Alsinoideae)
*Bufonia paniculata* Dubois (Alsinoideae)
*Cerastium alpinum* L. (Alsinoideae)
*Cerastium arvense* L. (Alsinoideae)
*Cerastium fontanum* Baumg. (Alsinoideae)
*Cerastium glomeratum* Thuill. (Alsinoideae)
*Cerastium latifolium* L. (Alsinoideae)
*Cerastium semidecandrum* L. (Alsinoideae)
*Cerastium* sp. (Alsinoideae)
*Cucubalus baccifer* L. (Caryophylloideae)
*Dianthus armeria* L. (Caryophylloideae)
*Dianthus balbisii* Ser. in DC. (Caryophylloideae)
*Dianthus carthusianorum* L. (Caryophylloideae)
*Dianthus caryophyllus* L. (Caryophylloideae)
*Dianthus deltoids* L. (Caryophylloideae)
*Dianthus furcatus* Balb (Caryophylloideae)
*Dianthus hispanicus* Asso (Caryophylloideae)
*Dianthus lumnitzeri* Wierb (Caryophylloideae)
*Dianthus pavonius* Tausch (Caryophylloideae)
*Dianthus repens* Willd. (Caryophylloideae)
*Dianthus seguieri* Vill. (Caryophylloideae)
*Dianthus silvestris* Wulfen (Caryophylloideae)
*Dianthus superbus* ssp. *alpestris* L. (Caryophylloideae)
*Dicheranthus plocamoides* Webb. (Alsinoideae)
*Gypsophila muralis* L. (Caryophylloideae)
*Gypsophila repens* L. (Caryophylloideae)
*Herniaria alpina* Chaix (Paronychioideae)
*Herniaria glabra* L. (Paronychioideae)
*Herniaria hirsuta* L. (Paronychioideae)
*Herniaria incana* Lam. (Paronychioideae)
*Holosteum umbellatum* L. (Alsinoideae)
*Minuartia arctica* (Ser.) Graebner (Alsinoideae)
*Minuartia capillaceae* Graebn. (Alsinoideae)
*Minuartia cherlerioides* (Hope) Bech. (Caryophylloideae)
*Minuartia laricifolia* (L.) Schinz and Thell. (Caryophylloideae)
*Minuartia recurva* (All) Schinz and Thell. (Alsinoideae)
*Minuartia rostrata* (Pers) Rchb. (Alsinoideae)
*Minuartia rubella* Graebn. (Caryophylloideae)
*Minuartia rubra* (Scop) McNeil (Alsinoideae)
*Minuartia sedoides* (L.) Hiern. (Caryophylloideae)
*Minuartia verna* (L.) Hiern. (Caryophylloideae)
*Moeringia ciliata* Dalla Torre (Caryophylloideae)
*Moeringia muscosa* L. (Caryophylloideae)
*Paronychia canariensis* Juss. (Paronychioideae)
*Paronychia glabrata* L. (Paronychioideae)
*Paronychia kapela* (Hacq.) A. Kern (Paronychioideae)
*Paronychia kapela* ssp. *serpyllifolia* (Chaix) Graebn.
*Petrorhagia nanteulii* Ballet *et* Heyw. (Caryophylloideae)
*Petrorhagia prolifera* (L.) Ballet *et* Heyw. (Caryophylloideae)
*Petrorhagia saxifraga* (L.) Link (Caryophylloideae)
*Polycarpaea aristata* DC. (Paronychioideae)
*Polycarpaea carnosa* S. ex Busch (Paronychioideae)
*Polycarpaea divaricata* Poir. (Paronychioideae)
*Polycarpaea latifolia* Poir. (Paronychioideae)
*Polycarpaea nivea* (Aiton) Webb (Paronychioideae)
*Sagina apetala* Ard. (Alsinoideae)
*Sagina maritima* G. Don (Alsinoideae)
*Saponaria lutea* L. (Caryophylloideae)
*Saponaria ocymoides* L. (Caryophylloideae)

*Silene acaulis* (photo: Landolt)

*Silene coronaria* (photo: Landolt)

*Silene vulgaris* (photo: Landolt)

*Dianthus gratianopolitanus*

*Cerastium latifolium* (photo: Landolt)

*Petrorhagia prolifera*

*Cucubalus baccifer* (photo: Landolt)

*Scleranthus annuus*

*Saponaria officinalis* L. (Caryophylloideae)
*Scleranthus annuus* L. (Alsinoideae)
*Scleranthus perennis* L. (Alsinoideae)
*Silene acaulis* (L.) Jacq. (Caryophylloideae)
*Silene arctica* (Caryophylloideae)
*Silene coronaria* (L.) Clairv. (Caryophylloideae)
*Silene dioeca* (L.) Clairv. (Caryophylloideae)
*Silene excapa* All. (Caryophylloideae)
*Silene flos-cuculi* (L.) Clairv. (Caryophylloideae)
*Silene flos-jovis* (L.) Clairv. (Caryophylloideae)
*Silene gallica* L. (Caryophylloideae)
*Silene italica* (L.) Pers. (Caryophylloideae)
*Silene latifolia* ssp. *alba* (Mill.) Greuter *et* Burdet (Caryophylloideae)
*Silene maritima* With. (Caryophylloideae)
*Silene noctiflora* L. (Caryophylloideae)
*Silene nutans* ssp. *nutans* L. (Caryophylloideae)
*Silene otites* (L.) Wibel (Caryophylloideae)
*Silene pauciflora* Ledeb. (Caryophylloideae)
*Silene petrarchae* Ferrini *et* Cecchi (Caryophylloideae)
*Silene pseudovelutina* Rothm. (Caryophylloideae)
*Silene pusilla* Waldst. *et* Kit. (Caryophylloideae)
*Silene rupestris* L. (Caryophylloideae)
*Silene saxifraga* L. (Caryophylloideae)
*Silene scouleri* Hook (Caryophylloideae)
*Silene suecica* Greuter *et* Burdet (Caryophylloideae)
*Silene tridentata* Desf. (Caryophylloideae)
*Silene viscaria* (L.) Borkh. (Caryophylloideae)
*Silene vulgaris* Garcke (Caryophylloideae)
*Silene vulgaris* ssp. *canariensis* Garcke (Caryophylloideae)
*Spergula arvensis* L. (Paronychioideae)
*Spergula morisonii* Bor. (Paronychioideae)
*Spergularia marina* (L.) Griesb. (Paronychioideae)
*Spergularia media* (L.) C. Presl (Paronychioideae)
*Spergularia rubra* (L.) J. Presl *et* Presl (Paronychioideae)
*Stellaria media* (L.) Vill (Alsinoideae)
*Vaccaria hispanica* (Mill.) Rauschert (Caryophylloideae)

*Illecebrum* sp. (photo: Zinnert)

*Sagina saginoides*

**Characteristics of the xylem**

The presence of annual rings in the xylem of perennial plants is characteristic of most species and individuals growing in the distinct seasonal climates of the temperate zone (**Figs. 1** and **2**) and even in the subtropical climate on the Canary Islands (**Fig. 3**). Ring boundaries of most species are defined by semi-ring porosity (**Figs. 1-4**). A thin-walled marginal parenchyma enhances the visibility of the ring boundary in a few species, e.g. *Dianthus hispanicus* (**Fig. 4**). Annual plants (therophytes) contain one ring (**Figs. 5** and **6**). However, those germinating in fall and flowering in spring of the following year have two rings. Only a few features were found to be common to most of the Caryophyllaceae specimens analyzed: The presence of simple vessel perforations, a high number of vessels (>100/mm$^2$) and small vessel diameters (<50 µm). Vessels stay in the majority of analyzed species solitary or are grouped in small clusters or in radial multiples. The absence of spiral thickenings and vestured inter-vessel pits is striking. Fibers, if present, have pointed ends and small slit-like pits (<3 µm). Most of the species are rayless.

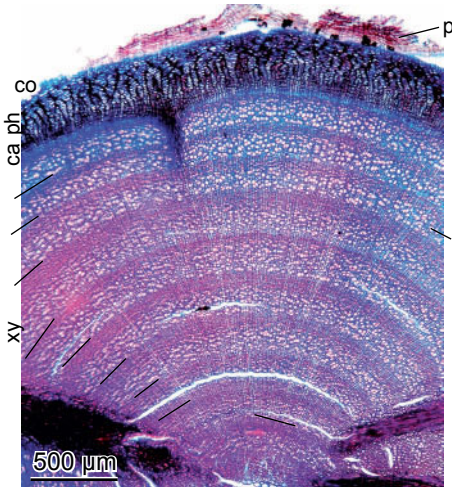



**Fig. 1.** Perennial herb with 11 rings. The wood is distinctly semi-ring-porous. Root collar of a 6 cm-high plant, dry limestone rock, submediterranean region of the Alps, France. *Minuartia rostrata* (Alsinoideae), transverse section.

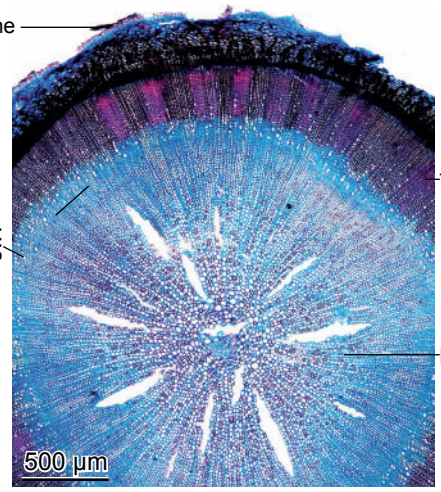



**Fig. 2.** Perennial herb with 2 rings. The wood is slightly semi-ring-porous, the vessels in the first ring are surrounded by pervasive parenchyma, those in the second ring by fibers. Root collar of a 25 cm-high hemicryptophyte on a field, hill zone, Alps, France. *Dianthus armeria* (Caryophylloideae), transverse section.

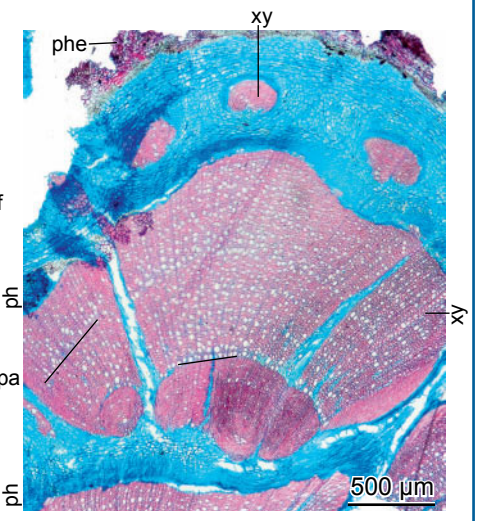



**Fig. 3.** Perennial small dwarf shrub with annual rings. The ring boundaries of the slightly semi-ring-porous wood are in the xylem. Root collar of a 10 cm-high chamaephyte, rock, pine belt, subtropical climate, Tenerife, Canary Islands. *Polycarpaea aristata* (Paronychioideae), transverse section.

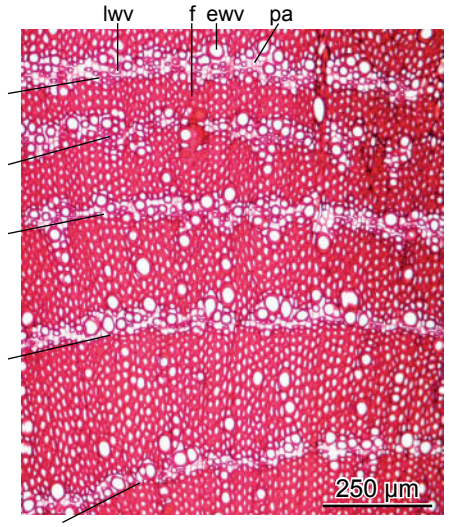



**Fig. 4.** Xylem of a dwarf shrub. Ring boundaries of the diffuse-porous wood are defined by a small marginal parenchymatic band. Vessels are surrounded by fibers. Root collar of a 40 cm-high chamaephyte, rock, Mediterranean zone, Spain. *Dianthus hispanicus* (Caryophylloideae), transverse section.

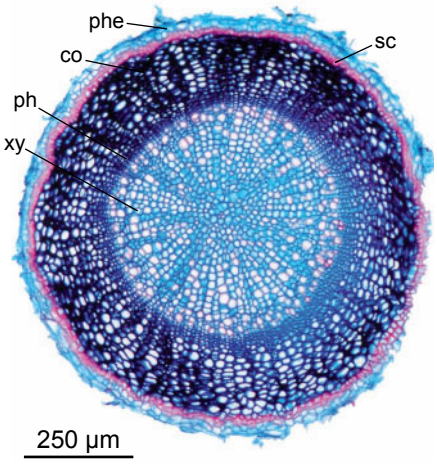



**Fig. 5.** Annual herb with one ring. The vessels are surrounded by a pervasive parenchyma. Root collar of a 5 cm-high plant, vineyard, hill zone, dry Central Alpine Valais of Switzerland. *Cerastium semidecandrum* (Alsinoideae), transverse section.

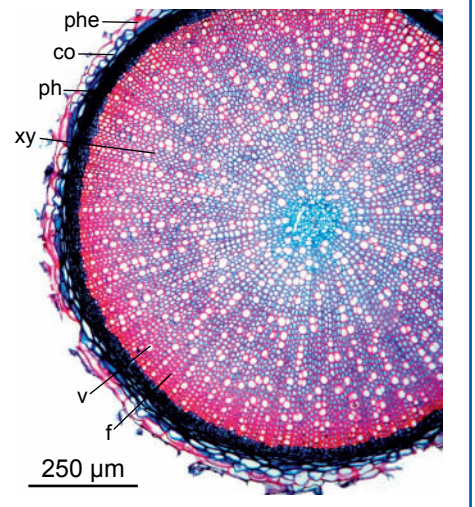



**Fig. 6.** Annual herb with one ring. The vessels are surrounded by fibers. Root collar of a 8 cm-high plant, dry gravel place, hill zone, Alps in Switzerland. *Minuartia rubra* (Alsinoideae), transverse section.

**Characteristics of the xylem of the subfamily Alsinoideae**

Anatomical xylem characteristics are uniform: All perennial species are semi-ring-porous. The small thick-walled solitary vessels (2 µm; **Fig. 1**) with diameters of 15-30 µm remain solitary and are in many species surrounded by a pervasive parenchyma (**Fig. 5**), rarely by fibers (**Fig. 6**). Inter-vessel pitting is pseudoscalariform (**Fig. 7**) and/or scalariform (**Fig. 8**). A few species contain fibers e.g. *Minuartia rubra* (**Fig. 6**), *Scleranthus annuus* and *S. perennis*. Rays and crystals are absent (**Figs. 1**, **5** and **6**). Ring boundaries are mechanically very weak (ring shake) and break apart in some species e.g. *Arenaria biflora* (**Fig. 9**). The anatomical structure of the root collar of the annual plant *Sagina maritima* and the perennial *Minuartia artica* are different from all other species: they contain successive cambia.

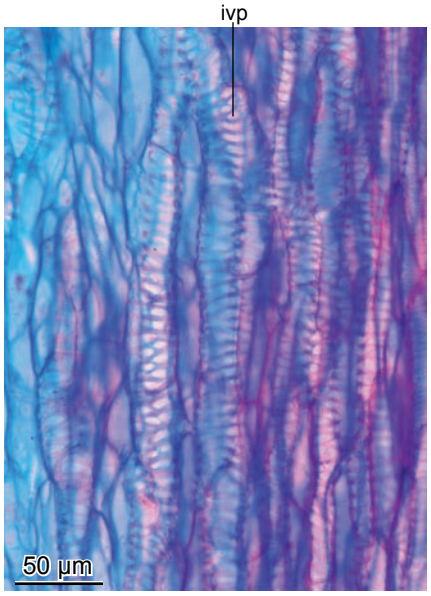



**Fig. 7.** Pseudoscalariform (reticulate) inter-vessel pitting. Radial cell walls of vessels look like a net. Root collar of a 10 cm-high annual plant, ruderal site, hill zone, Alps, Switzerland. *Stellaria media* (Alsinoideae), radial section.

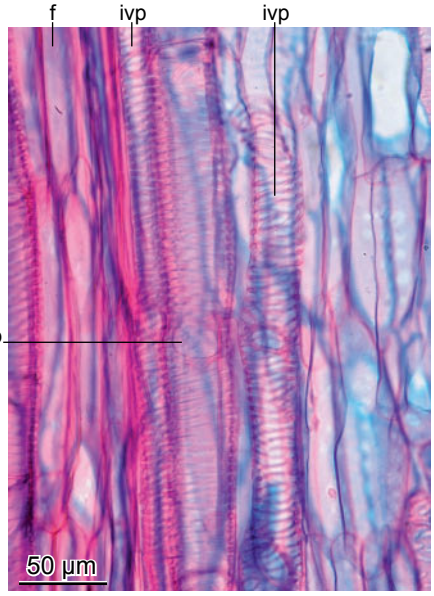



**Fig. 8.** Scalariform inter-vessel pitting. Radial cell walls of vessels are perforated by pits with slit-like apertures. Root collar of a 100 cm-high perennial plant (liana), hedge, hill zone, Alps, Switzerland. *Cucubalus baccifer* (Caryophylloideae), radial section.

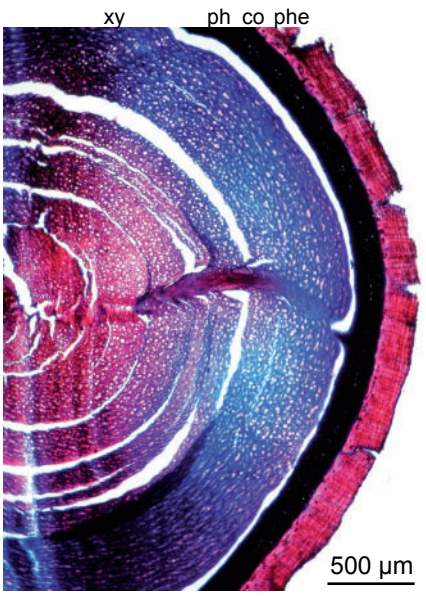



**Fig. 9.** Ring shake, the rings fall apart. Root collar of a cushion plant, rock, alpine zone, Alps, Switzerland. *Arenaria biflora* (Alsinoideae), transverse section.

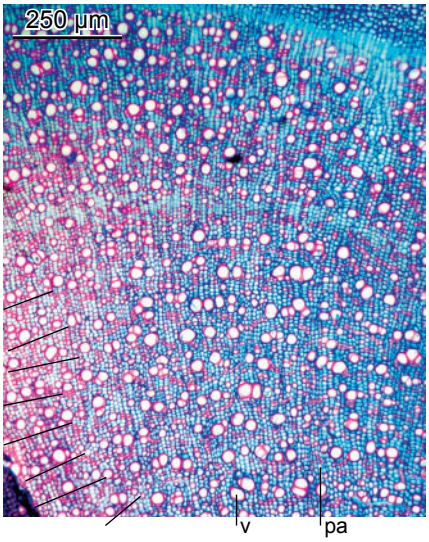
**Characteristics of the xylem of the subfamily Caryophylloideae**

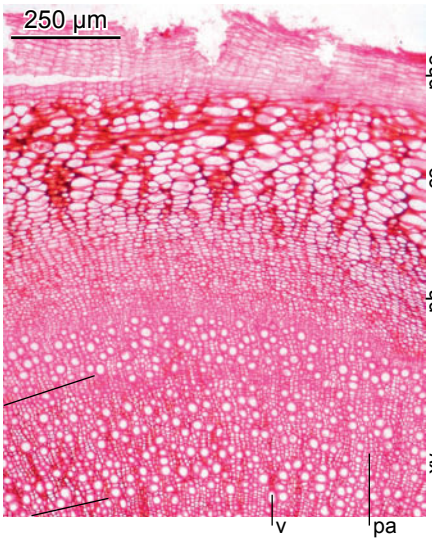
There are anatomical similarities between the genera *Dianthus*, *Gypsophila*, *Saponaria* and *Silene* (**Figs. 10-13**), whereas the genera *Agrostemma*, *Petrorhagia*, *Vaccaria*, and *Cucubalus* (**Figs. 14-17**) are different.

The first group is characterized by thick-walled solitary vessels (2 µm; **Fig. 10**) with diameters of 15-50 µm. The liana *Cucubalus baccifer* shows unusually large vessels (60-80 µm; **Fig. 17**). All species have scalariform (**Fig. 8**) and many also pseudoscalariform (**Fig. 7**) inter-vessel pits. The ground tissue of dwarf shrubs is composed of thick-walled fibers (*Dianthus hispanicus*; **Fig. 4**) and many hemicryptophytes of the genera *Dianthus* and *Silene* contain intra-annual thick-walled tangential fiber bands (**Fig. 18**). They are absent in the genera *Gypsophila* and *Saponaria*. Parenchyma appears in three forms: pervasive parenchyma is present in most species (**Figs. 10**, **25** and **27**), it occurs in a small marginal band in *Dianthus hispanicus* and it is paratracheal surrounded by thick-walled fiber bands in *Dianthus seguieri* (**Fig. 18**).

The majority of species in the subfamily is characterized by the absence of rays, e.g. *Silene italica* (Fig. 19. Caryophyllaceae), but some have rays with one to three cell rows. A few have rays with 3-10 cell rows, e.g. *Saponaria officinalis*, *Dicheranthus plocamoides* and *Silene nutans* (**Figs. 20** and **25**) and some have very large rays, e.g. *Silene vulgaris* (**Fig. 21**). All species analyzed showed rays with quadrangular or upright ray cells (radial section). Crystal druses (**Fig. 22**) are very frequent in rays and in the parenchyma cells of the genera *Dianthus*, *Gypsophila*, *Saponaria* and *Silene*. Crystal druses sometimes expand parenchyma cells, e.g. in *Silene latifolia* and *Gypsophila repens* (**Fig. 22**). The presence of successive cambia in the alpine cushion plants *Silene acaulis* and *Silene excapa* is special for the Caryophylloideae (**Fig. 23**). Crystal druses are missing in *Cucubalus baccifer*.

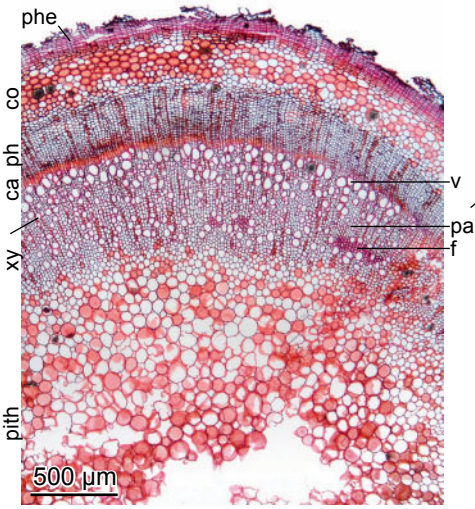
The second group - *Agrostemma*, *Petrorhagia* and *Vaccaria* - are different from the other genera. Characteristically they contain radially grouped (2-6) thin-walled vessels (1.5-2 µm) and are embedded in thin-walled fiber tissue (**Figs. 14-16**). Pseudoscalariform inter-vessel pits, rays and crystals are absent.

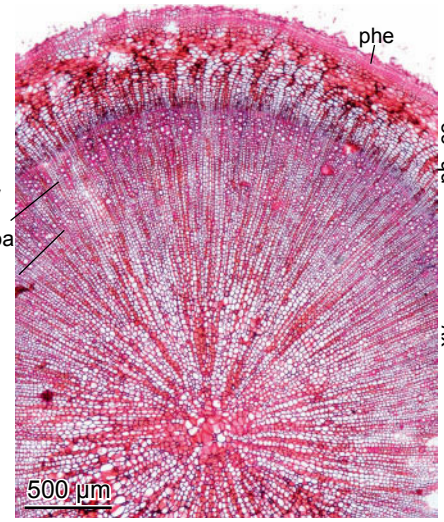



**Left Fig. 10.** Semi-ring-porous xylem with small (<20 µm), thick-walled vessels, embedded in pervasive parenchyma. Root collar of a 10 cm-high plant, rock, alpine zone of the Alps, France. *Dianthus furcatus* (Caryophylloideae), transverse section.

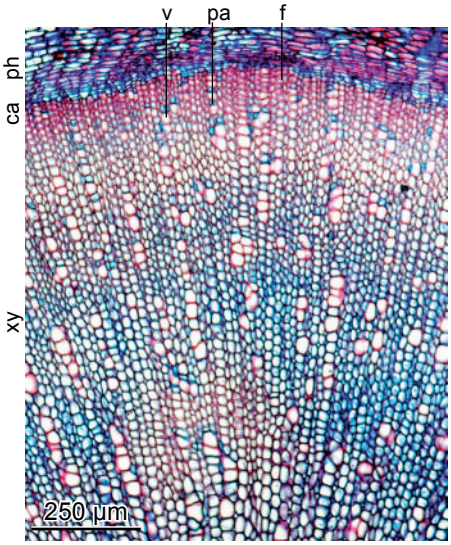
**Right Fig. 11.** Semi-ring-porous xylem with small (<20 µm), thick-walled vessels, embedded in pervasive parenchyma. The bark has a simple construction. It is divided into a phloem with small parenchyma und sieve tubes, a cortex with large parenchyma cells and a phellem with small, radially flat cells. Root collar of a 15 cm-high plant, alpine zone, dry valley, Valtellina, Italian Alps. *Gypsophila muralis* (Caryophylloideae), transverse section.

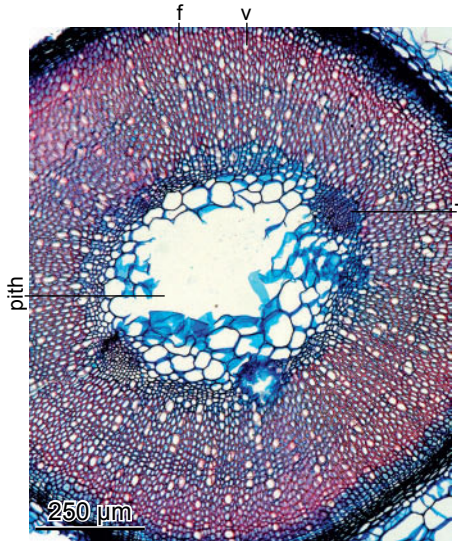



**Left Fig. 12.** Semi-ring-porous xylem with small vessels, embedded in pervasive parenchyma and some groups of fibers. The bark has principally the same construction as shown in **Figs. 11** and **13**. Root collar of a 40 cm-high, 2-year-old plant, vineyard, hill zone, dry valley, Valtellina, Alps, Italy. *Saponaria officinalis* (Caryophylloideae), transverse section.

**Right Fig. 13.** Semi-ring-porous xylem with small vessels, embedded in pervasive parenchyma. Root collar of a 40 cm-high 3-year-old plant, ruderal site, alpine zone, Alps, Switzerland. *Silene dioeca* (Caryophylloideae), transverse section.



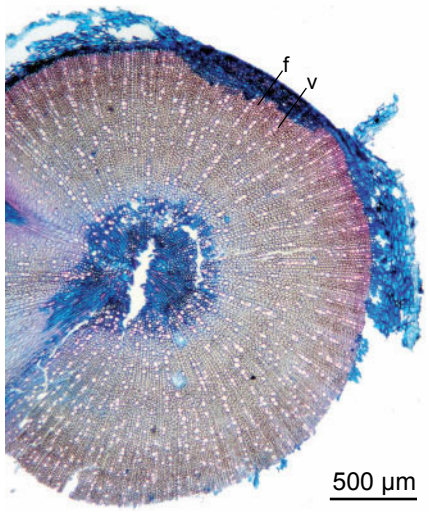
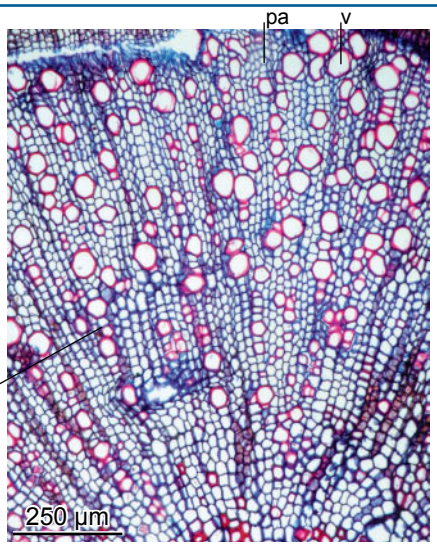
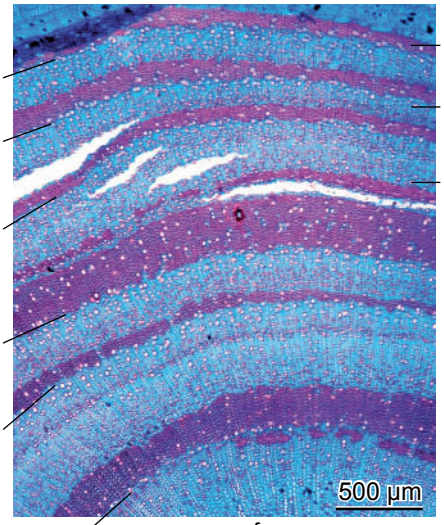




**Fig. 14.** Xylem with vessels in radial multiples, embedded in a fiber tissue. Root collar of a 40 cm-high annual plant, field, hill zone in the Alps, France. *Agrostemma ghitago* (Caryophylloideae), transverse section.

**Fig. 15.** Xylem with vessels in short radial multiples, embedded in a fiber tissue. Root collar of a 20 cm-high annual plant, meadow, thermophiloe zone, subtropical climate, Gomera, Canary Islands. *Petrorhagia nanteulii* (Caryophylloideae), transverse section.

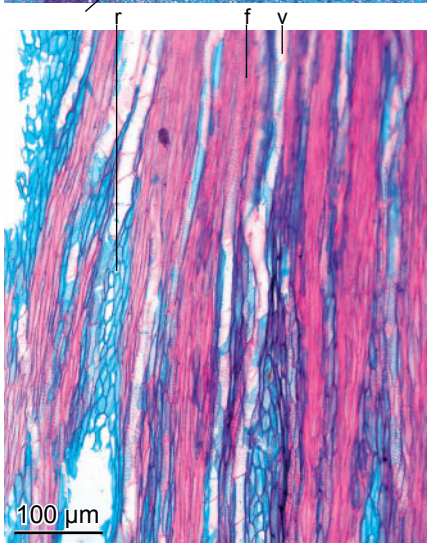
**Fig. 16.** Xylem with vessels in long radial multiples, embedded in a fiber tissue. Root collar of a 30 cm-high annual plant, garden, hill zone, Alps, Switzerland. *Vaccaria hispanica* (Caryophylloideae), transverse section.



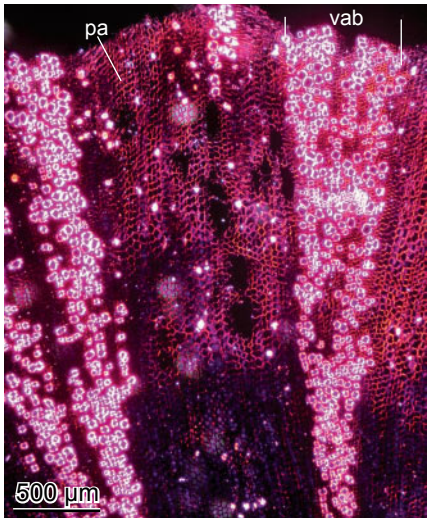

**Left Fig. 17.** Semi-ring-porous xylem with large vessels (50-70 µm), embedded in a pervasive parenchyma. Stem of a 100 cm-high liana, hedge, hill zone of the Alps, Switzerland. *Cucubalus baccifer* (Caryophylloideae), transverse section.

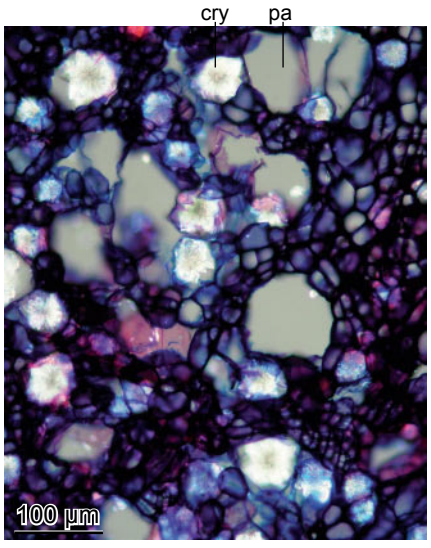
**Right Fig. 18.** Diffuse-porous to slightly semi-ring-porous xylem with tangential intra-annual fiber bands (red) of a 7-year-old plant. Root collar of a 25 cm-high perennial plant, dry meadow, hill zone, Alps, Italy. *Dianthus seguieri* (Caryophylloideae), transverse section.




**Left Fig. 19.** Rays indistinct or absent. Root collar of a 20 cm-high perennial plant, dry meadow, mountain zone, Alps, France. *Silene italica* (Caryophylloideae), tangential section.

**Right Fig. 20.** Rays 3-10 cell rows in width. The walls are unlignified (blue). Root collar of a 40 cm-high, 2-year-old plant, vineyard, hill zone, dry alpine valley, Valtellina, Alps, Italy. *Saponaria ocymoides* (Caryophylloideae), tangential section.



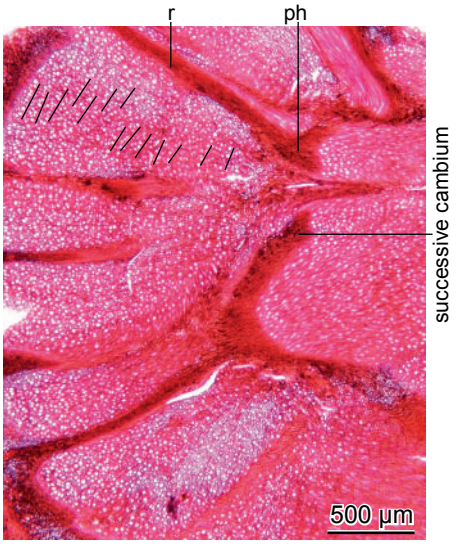




**Fig. 21.** Parenchymatic ray-like zones between radial strips of vessels. Root collar of a 20 cm-high perennial plant, thermophile zone, subtropical climate, Tenerife, Canary Islands. *Silene vulgaris* (Caryophylloideae), transverse section, polarized light.

**Fig. 22.** Crystal druses in enlarged parenchymatic cells in the cortex. Root collar of a 15 cm-high perennial plant, subalpine zone, Alps, Switzerland. *Gypsophila repens* (Caryophylloideae), transverse section.

**Fig. 23.** Stem with successive cambia (Caryophyllaceae type). Root collar of a 5 cm-high perennial cushion plant, subalpine zone, Alps, Switzerland. *Silene acaulis* (Caryophylloideae), transverse section.

**Characteristics of the xylem of the subfamily Paronychioideae**

Anatomical structures in this subfamily are very heterogeneous. The 6 genera are mainly characterized by the following features:

*Acanthophyllum*: Presence of thick-walled vessels, pervasive parenchyma, successive cambia and crystal druses in the cortex and the absence of rays (**Fig. 24**).

*Dicheranthus*: Presence of tangential bands of fibers and parenchyma, and large rays with unlignified cell walls. The vessels are very small (**Fig. 25**).

*Herniaria*: Presence of thick-walled vessels (2 µm), pervasive parenchyma, absence of rays (**Fig. 26**). Sclereids and crystal druses are, in contrast to the species in the Alsinoideae, present in the cortex.

*Paronychia*: Presence of thin-walled vessels, variable parenchyma, absence of rays (**Fig. 27**).

*Polycarpaea*: Presence of thin-walled vessels, large rays, successive cambia and unrecognizable parenchyma (**Fig. 3**).

*Spergularia*: Presence of thin-walled vessels, successive cambia and prismatic crystals in the cortex. That feature is unique for the whole family of Caryophyllacea (**Fig. 28**).

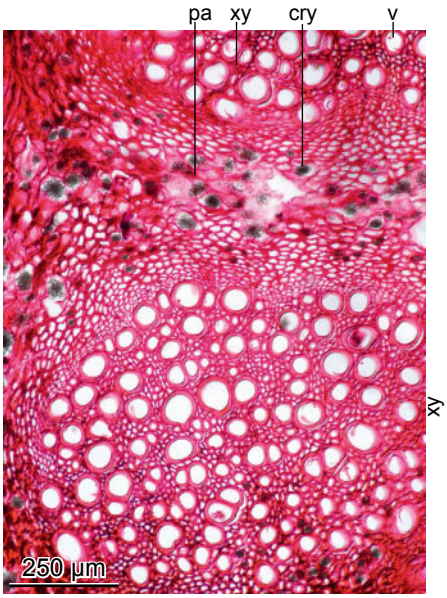



**Fig. 24.** Stem with large, thick-walled vessels and successive cambia with crystal druses. Stem of a 50 cm-high perennial cushion-like dwarf shrub, dry subalpine zone, Iranian mountains. *Acanthophyllum microcephalum* (Paronychioideae), transverse section.

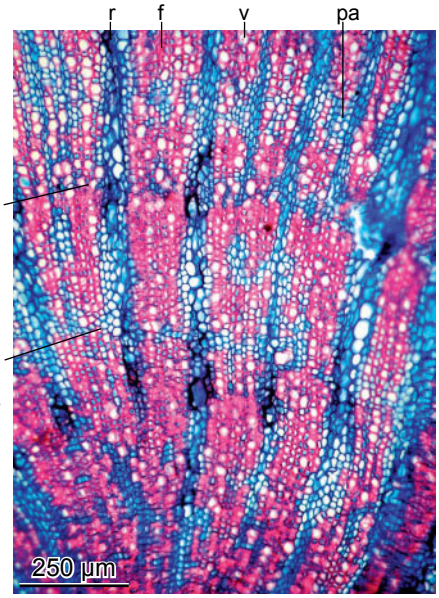



**Fig. 25.** Xylem with groups of fibers and paratracheal, pervasive parenchyma. Typical are large rays with unlignified cell walls. Stem of a 20 cm-high dwarf shrub, dry bush zone, subtropical climate, Gomera, Canary Islands. *Dichantherus plocamoides* (Paronychioideae), transverse section.

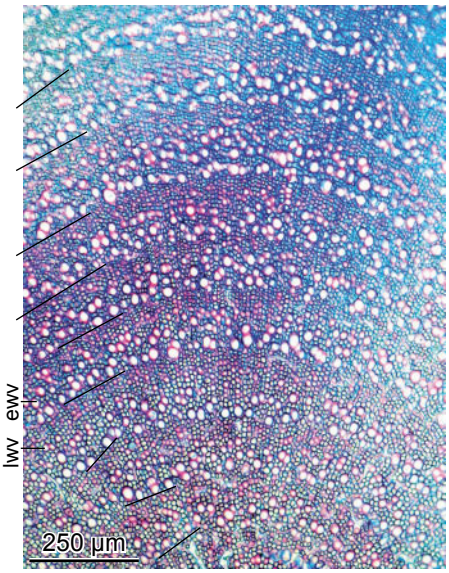
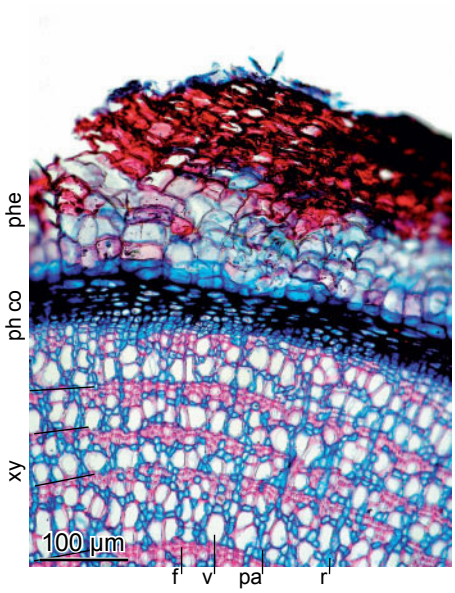
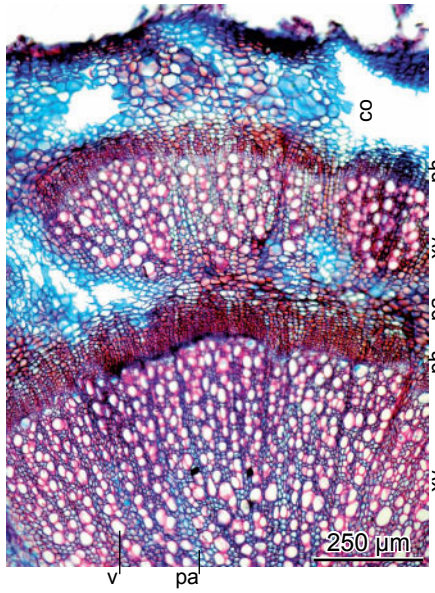



**Fig. 26.** Semi-ring-porous xylem with small vessels (<20 µm) and pervasive parenchyma. Root collar of a prostrate, 5 cm-high perennial plant, limestone gravel, alpine zone, Alps, France. *Herniaria alpina* (Paronychioideae), transverse section.




**Left Fig. 27.** Semi-ring-porous xylem with small vessels (<20 µm), pervasive parenchyma in the earlywood and fibers in the latewood. The very thick phellem is a reaction to the stem being wind-exposed. Root collar of a 5 cm-high, prostrate perennial plant, limestone gravel, alpine zone, Alps, France. *Paronychia kapela* (Paronychioideae), transverse section.

**Right Fig. 28.** Stem with successive cambia, numerous, small vessels embedded in pervasive parenchyma. Root collar of a prostrate 8 cm-high annual plant, ruderal site, hill zone, Alps, France. *Spergula arvensis* (Paronychioideae), transverse section.

**Characteristics of the bark of the subfamily Alsinoideae**

Anatomical bark characteristics are uniform. Typical are radial rows of parenchyma and small groups of sieve tubes. Phloem and cortex do not contain sclereids and crystals (**Figs. 1**, **5** and **29**). There is little structural variability.

**Characteristics of the bark of the subfamily Caryophylloideae**

Ray dilatations and crystal druses in the phloem and the cortex are frequent, but sclereids are mostly absent (**Figs. 11**-13 and **30-32**). Only *Silene coronaria* shows very distinct radial sclereid groups (**Fig. 33**).

**Characteristics of the bark of the subfamily Paronychioideae**

There are no special features for the subfamily of Paronychioideae (**Figs. 28** and **35**).

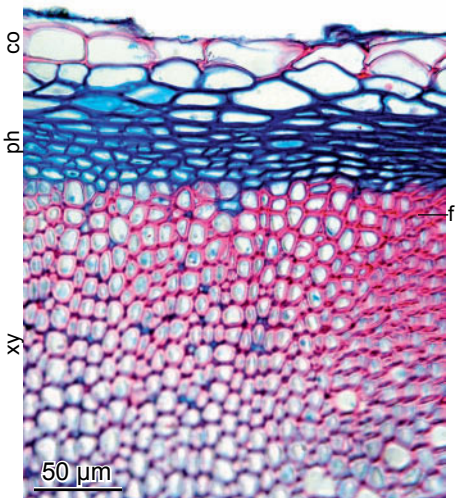



**Fig. 29.** Simple bark structure. The phloem and the cortex are continuous. Sieve tubes in the phloem are unrecognizable. Root collar of a 8 cm-high annual plant, dry gravel place, hill zone, Alps, Switzerland. *Minuartia rubra* (Alsinoideae), transverse section.

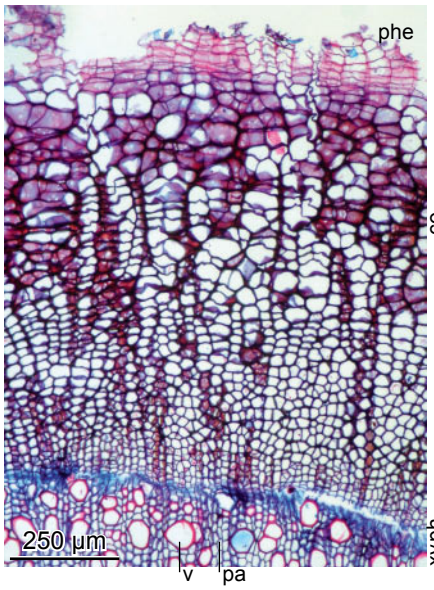



**Fig. 30.** Small phloem and a very large cortex. Root collar of a 100 cm-high liana, hedge, hill zone in the Alps, Switzerland. *Cucubalus baccifer* (Caryophylloidaea), transverse section.

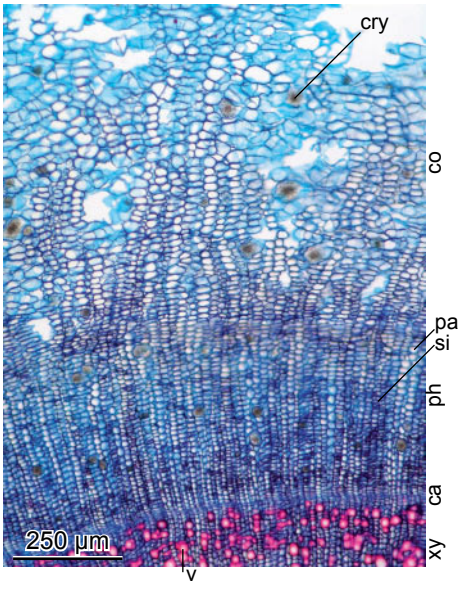
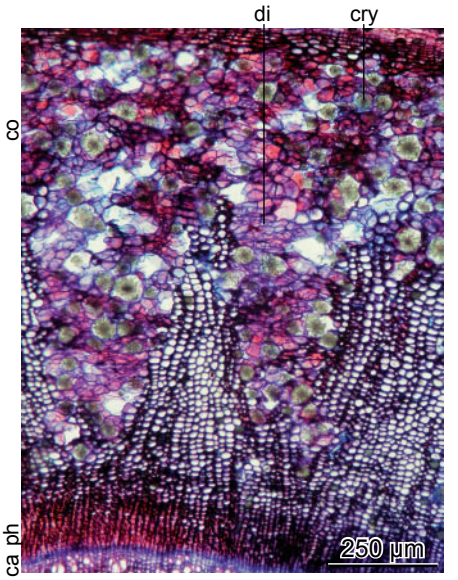
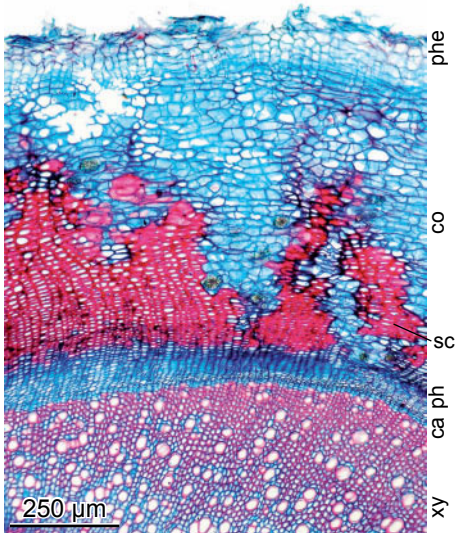


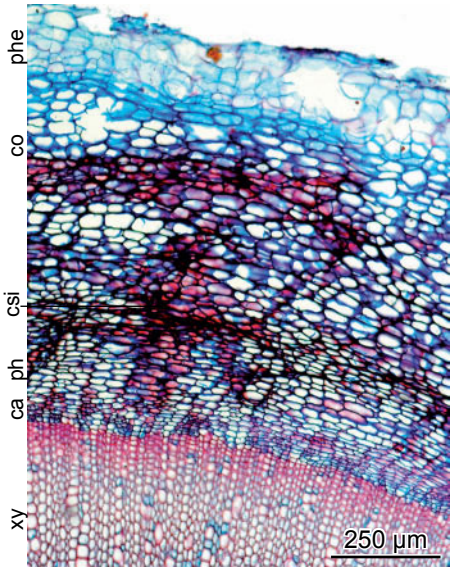

**Fig. 31.** Distinct radial rows of parenchyma with very small groups of sieve tubes characterize the phloem. Crystal druses occur in the phloem and the cortex. Root collar of a 30 cm-high, perennial plant, dry meadow, dry valley, Valais, Switzerland. *Silene otites* (Caryophylloidaea), transverse section.

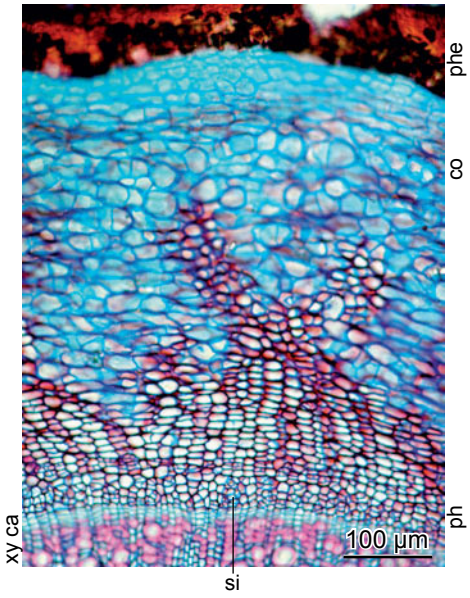



**Left Fig. 32.** Distinct ray dilatation in the cortex. Crystal druses occur in large parenchyma cells. Root collar of a 15 cm-high perennial plant, subalpine zone, Alps, Switzerland. *Gypsophila repens* (Caryophylloidaea), transverse section, polarized light.

**Right Fig. 33.** Distinct radial zones of sclereids in the older phloem and the cortex. Crystal druses occur in the parenchyma cells of dilatations in the cortex. Root collar of a 30 cm-high perennial plant, garden, hill zone, Alps, Switzerland. *Silene coronaria* (Caryophylloidaea), transverse section.




**Left Fig. 34.** Phloem with small groups of sieve tubes and a large cortex. Root collar of a 40 cm-high annual plant, field, hill zone, Alps, France. *Agrostemma ghitago* (Caryophylloidaea), transverse section.

**Right Fig. 35.** Small phloem with small groups of sieve tubes and large dilated cortex. Root collar of a 5 cm-high, prostrate perennial plant, limestone gravel, alpine zone, Alps, France. *Herniaria alpina* (Paronychioideae), transverse section.



**Anatomical structures in relation to ecological conditions, and life and growth-forms**

Ecological trends are clearly expressed in the age of plants and the average annual radial growth rates. The age of perennial herbaceous plants decreases (hemicryptophytes) from the alpine to the hill zone (14.6 to 4.0 years) and is slightly higher in the submediterranean zone (5.6 years).

Maximum individual age decreases from the alpine and subalpine to the hill and submediterranean zone. The maximum ages of the oldest individuals in different vegetation zones are as follows:

Alpine and subalpine zone: *Arenaria biflora* 40 years, *Minuartia sedoides* 40 years,

Hill/mountain and sub-mediterranean zone: *Minuartia laricifolia* 20 years, *Silene vulgaris* 20 years.

Annual plants are almost absent in the alpine and subalpine zone and rare in the mountain and submediterranean zone.

Growth rates decrease from the hill zone to the alpine zone (0.66 mm/year to 0.08 mm/year). Ring distinctness in all vegetation zones is very high (>80%). The average radial diameter of earlywood vessels in the smaller species is approximately 20 µm and that of tall *Silene* species 40-50 µm. The largest vessels were observed in the dwarf shrub *Acanthophyllum microcephalum* and the liana *Cucubalus baccifer* (60-75 µm).

The data basis is too small to identify significant ecological effects on vessel size frequency and distribution since plant size plays an important role. A clear pattern is the dominance of species with intra-annual fiber bands in the hill and mountain zones (80%; **Fig. 18**). The presence of intra-annual fiber bands corresponds with the presence of paratracheal parenchyma (80% in the hill and mountain zones and 8% in the subalpine and alpine zones). Large rays appear in the Caryophylloideae (except for *Cucubalus*, *Agrostemma* and *Petrorhagia*) growing in the lowland (35%) rather than in higher altitudes (8%). This corresponds with the presence of distinct ray dilatations in the cortex. Crystal druses in the xylem and the cortex of the Caryophylloideae are concentrated in lowland species (61% and 52%) and are rare in subalpine species (38% and 8%). No ecological trends were found in the Alsinoideae. For Paronychioideae the databasis is too small and the anatomical structures are too heterogeneous to detect ecological trends.

**Discussion in relation to previous studies**

The most extensive wood anatomical study of woody species is that of Carlquist (1995). It includes a total of 16 species from Hawaii (7), Californian natural sites (3), California Botanical Garden (3), the Canary Islands (2), Lake Baikal (1) and Armenia (1). Fahn *et al.* (1986) described one dwarf shrub in Israel and Schweingruber 1990 the 4 species from Southern Spain and the Alps. Pfeiffer (1926) and Metcalfe and Chalk (1957) mention the successive cambia in some species of 19 genera, and Tellini (1939) provided a full description of the dwarf shrub *Dianthus arboreus*. Millner (1934) characterised in detail the root anatomy of *Silene maritima* and *Silene vulgaris*, and Kutschera and Sabotik (1992) described primarily the thin roots from 9 central European species. The present study is a converted version of the study from Schweingruber (2007).

The analyzed material of all earlier studies is heterogeneous in relation to life forms and geographical and climatic provenance. Despite the limited material, major family characteristics have been detected i.e successive cambia and imperforate tracheary elements.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of analyzed species** | | **100** |
| 1 | growth rings distinct and recognizable | 78 |
| 2 | growth rings indistinct or absent | 13 |
| 2.1 | only one ring | 9 |
| 4 | semi-ring-porous | 67 |
| 5 | diffuse-porous | 10 |
| 9 | vessels predominantly solitary | 96 |
| 9.1 | vessels in radial multiples of 2 to 4 common | 8 |
| 10 | vessels in radial multiples of 4 or more common | 2 |
| 11 | vessels predominantely in clusters | 16 |
| 13 | vessels with simple perforation plates | 100 |
| 20 | intervessel pits scalariform | 71 |
| 20.1 | intervessel pits pseudoscalariform to reticulate | 58 |
| 21 | intervessel pits opposite | 1 |
| 39.1 | vessel cell-wall thickness >2 µm | 83 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 37 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 71 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 1 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 20 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 80 |
| 60.1 | fibers absent | 53 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 42 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 6 |
| 68 | fibers thin-walled | 6 |
| 69 | fibers thick-walled | 27 |
| 70 | fibers thin- to thick-walled | 16 |
| 70.1 | intra-annual thick-walled tangential fiber bands | 21 |
| 75 | parenchyma absent or unrecognizable | 4 |
| 79 | parenchyma paratracheal | 26 |
| 79.1 | parenchyma pervasive | 82 |
| 89 | parenchyma marginal | 2 |
| 89.2 | ring shake, *Saxifraga* type | 7 |
| 96 | rays exclusively uniseriate | 2 |
| 97 | ray width predominantly 1-3 cells | 8 |
| 98 | rays commonly 4-10-seriate | 10 |
| 99 | rays commonly >10-seriate | 5 |
| 99.1 | vascular-bundle form remaining | 1 |
| 100.2 | rays invisible in in polarized light | 5 |
| 105 | ray: all cells upright or square | 15 |
| 110 | rays with sheet cells (tangential section) | 1 |
| 117 | rayless | 86 |
| 120 | storied axial tissue (parenchyma, fibers, vessels in tangential section) | 10 |
| 133 | successive cambia: Caryophyllaceae type | 14 |
| 136 | prismatic crystals present | 2 |
| 144 | druses present | 26 |
| R1 | groups of sieve tubes present | 7 |
| R2 | groups of sieve tubes in tangential rows | 5 |
| R3 | distinct ray dilatations | 18 |
| R4 | sclereids in phloem and cortex | 3 |
| R6.1 | sclereids in tangential rows | 6 |
| R7 | with prismatic crystals | 54 |
| R8 | with crystal druses | 26 |
| R9 | with crystal sand | 8 |
| R10 | phloem not well structured | 82 |

# Celastraceae



### Number of species, worldwide and in Europe

The pantropical Celastraceae family includes 55 genera with 855 species. Mayor genera are *Maytenus* with 200 species and *Euonymus* with 200 species. In Europe, there are 2 genera with 6 species. *Maytenus canariensis* is endemic to Macaronesia.

### Analyzed material

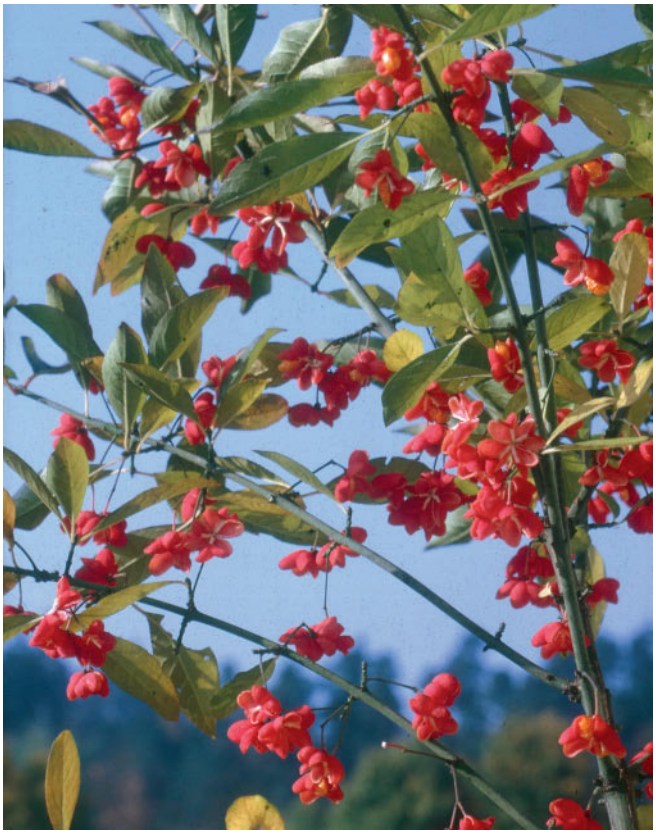
The xylem and phloem of 5 genera with 10 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 3 | ca. 40 genera |
| Liana | 2 | |
| Nanophanerophytes 0.5-4 m | 4 | |
| Woody chamaephytes | 1 | |
| **Plants analyzed from different vegetation zones:** | | Studies from other authors: |
| Alpine and subalpine | 1 | |
| Hill and mountain | 7 | |
| Arid | 2 | |
| Tropical | 0 | ca. 30 genera |

**Analyzed species:**
*Canotia holocantha* Torr
*Celastrus flagellaris* Rupr.
*Celastrus orbiculatus* Thunb.
*Euonymus europaeus* L.
*Euonymus latifolius* (L.) Miller
*Euonymus verrucosus* Scop.
*Maytenus canariensis* (Loisl.) Kunk et Sund.
*Maytenus dhofarensis* Sebsebe
*Maytenus senegalensis* (Lam.) Exell
*Pachystima myrsinithes* (Pursh) Raf.

*Euonymus europaeus*

*Celastrus orbiculatus*



*Euonymus europaeus* (photo: Landolt)

**Characteristics of the xylem**

Annual rings are present in most species (**Figs. 1-5**), but not in *Maytenus dhofarensis* and *M. senegalensis*. Rings are very small in *Pachystima myrsinithes* (**Fig. 4**). Ring boundaries, if present, are characterized by ring-porosity (**Figs. 1** and **2**), semi-ring-porosity (**Figs. 3** and **4**) or just bands of thick-walled latewood fibers (**Fig. 5**).

Vessels are arranged mostly solitary (**Figs. 1-4**) or are arranged in short rows (**Fig. 5**). The earlywood vessel diameter of the majority of species varies between 30-60 µm but is very large in the liana *Celastrus flagellaris* (150-200 µm; **Fig. 1**). Vessel density varies in most cases between 200-300/mm$^2$ (**Figs. 1-5**). Vessels contain exclusively simple perforations (**Figs. 6** and **7**). Intervessel pits are predominantly small and round in alternating position but are large and scalariform in the earlywood vessels of *Celastrus flagellaris* (**Fig. 7**). Tylosis occur in *Celastrus flagellaris* (**Fig. 8**) and dark-staining substances are present in *Maytenus senegalensis* and *Pachystima myrsinithes*.

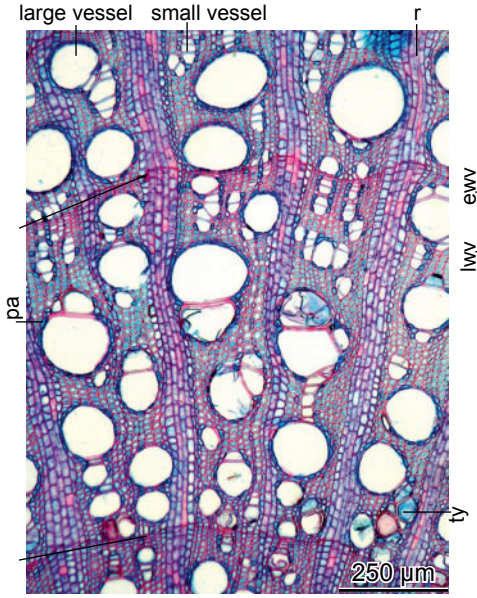



**Fig. 1.** Xylem with large and small vessels surrounded by paratracheal parenchyma. Annual ring boundaries consist of a few rows of thick-walled fibers. Stem of a 3 m-long liana, on a wall in the Botanical Garden Halle, Germany. *Celastrus flagellaris*, transverse section.

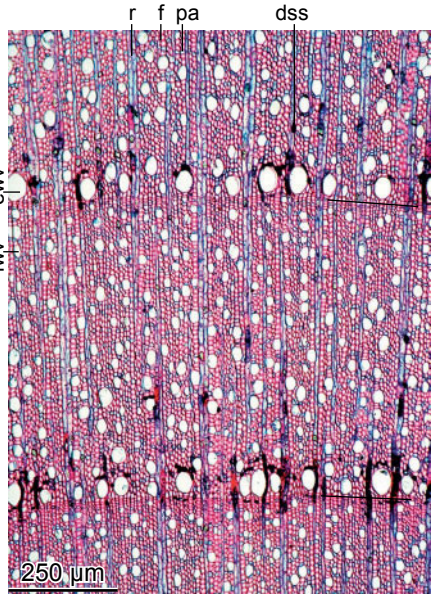



**Fig. 2.** Ring-porous xylem with one row of large earlywood vessels. Annual ring-boundaries consist of thick-walled fibers. Stem of a 50 cm-high shrub, shrub-desert, arid zone, Kingman, Arizona, USA. *Canotia holocantha*, transverse section.

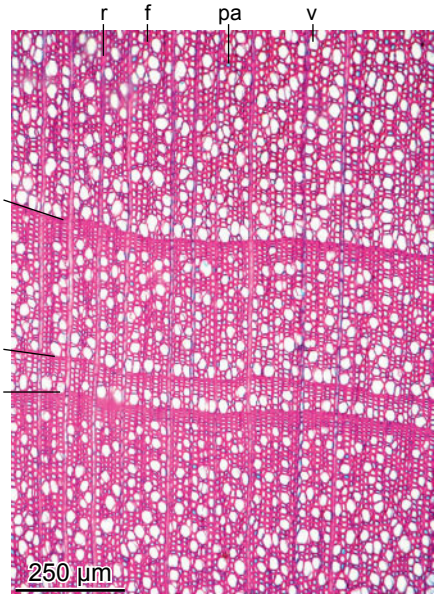
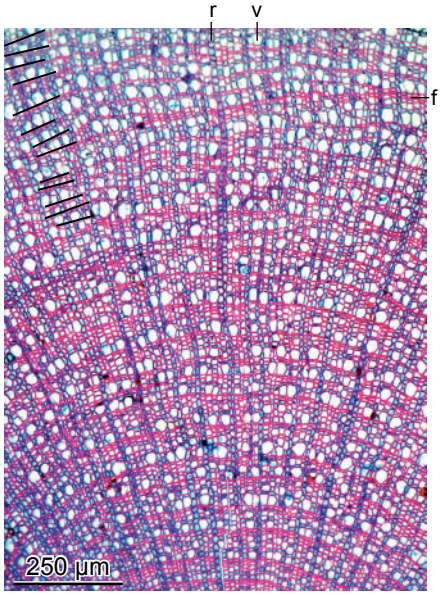
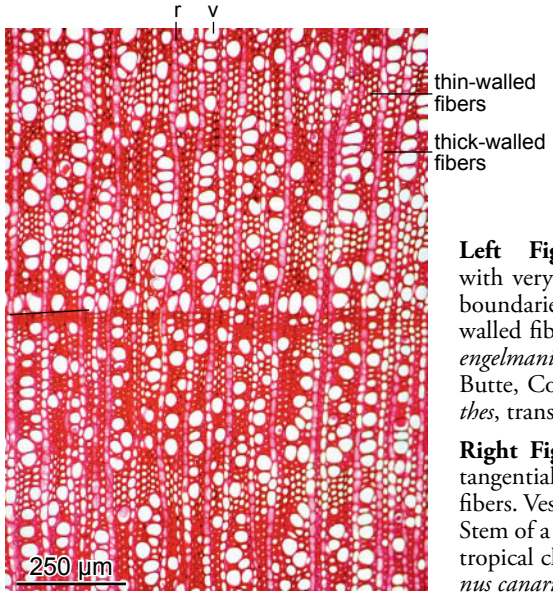



**Fig. 3.** Semi-ring-porous xylem. Annual ring boundaries consist of thick-walled fibers. Stem of a 2 m-high shrub, hedge, hill zone, Birmensdorf, Switzerland. *Euonymus europaeus*, transverse section.




**Left Fig. 4.** Semi-ring-porous xylem with very small annual rings. Annual ring boundaries consist of 1-2 rows of thick-walled fibers. Stem of a dwarf shrub, *Picea engelmanii*-forest, subalpine zone, Crested Butte, Colorado, USA. *Pachystina myrsinithes*, transverse section.

**Right Fig. 5.** Diffuse-porous xylem with tangential bands of thin- and thick-walled fibers. Vessels are mostly in radial multiples. Stem of a 3 m-high shrub, ruderal site, subtropical climate, Madeira, Portugal. *Maytenus canariensis*, transverse section.

Thin- and thick-walled fibers are arranged in multiseriate tangential bands. Thick-walled fibers have large round pits (2-3 µm in diameter) and thin-walled fibers have small pits (<2 µm); both fibertypes have slit-like apertures (**Fig. 8**). Septate fibers are present in most species (**Figs. 8** and **9**), but are absent in *Canotia holocantha*, *Euonymus verrucosus* and *Pachystima myrsinithes*.

Parenchyma is absent or rarely occurs. It is distinctly apotracheal in *Pachystima myrsinithes* and is paratracheal in *Celastrus flagellaris*. Rays are uniseriate, 1-3 cells wide (**Figs. 10-12**), or very large with sheet cells as in *Celastrus flagellaris* (**Fig. 13**). Rays are homocellular in *Canotia holocantha* (**Fig. 14**) and heterocellular to a varying degree in all other species. Prismatic crystals occur in rays of *Canotia holocantha*, *Euonymus europaeus*, and all *Maytenus* species (**Fig. 14**). A few crystal druses have been observed in *Euonymus europaeus*.

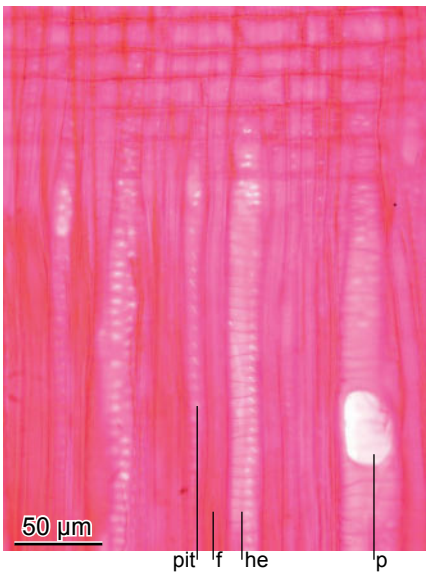



**Fig. 6.** Simple perforation and thick helical thickenings. Stem of a 2 m-high shrub, hedge, hill zone, Fluelen, Switzerland. *Euonymus latifolius*, radial section.

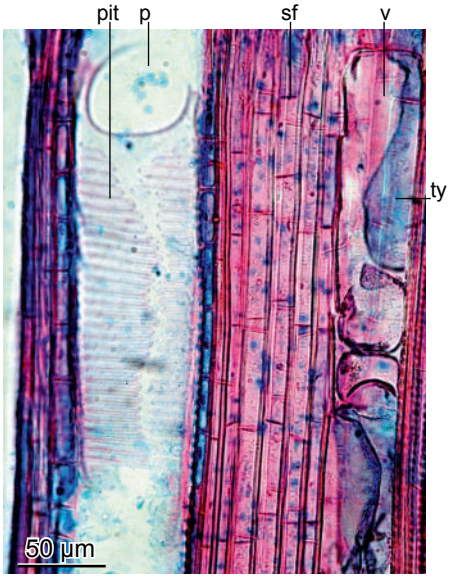



**Fig. 7.** Vessel with a simple perforation and scalariform inter-vessel pits. Septate fibers are arranged in strands. Stem of a 3 m-long liana, on a wall in the Botanical Garden Halle, Germany. *Celastrus flagellaris*, radial section.

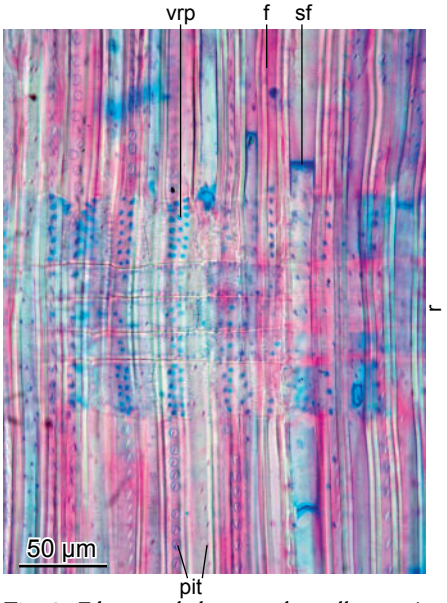



**Fig. 8.** Fibers with large and small pits. A few fibers are septate. Heterocellular ray with one row of upright cells. Stem of a 2 m-high, shrub, hedge, hill zone, Fluelen, Switzerland. *Euonymus latifolius*, radial section.

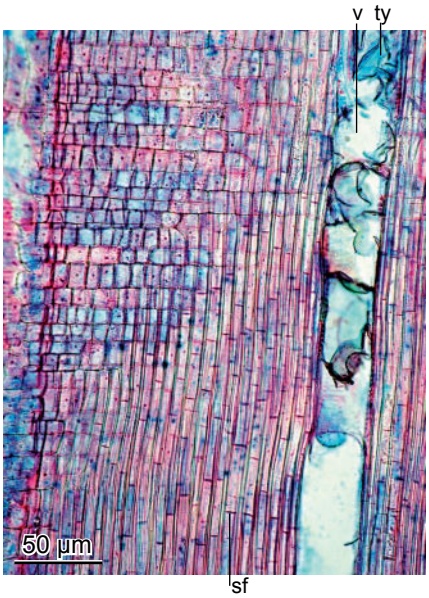



**Fig. 9.** Thin-walled tylosis in a large earlywood vessel. Rays consist of square and upright cells. Stem of a 3 m-long liana, on a wall in the Botanical Garden Halle, Germany. *Celastrus flagellaris*, radial section.

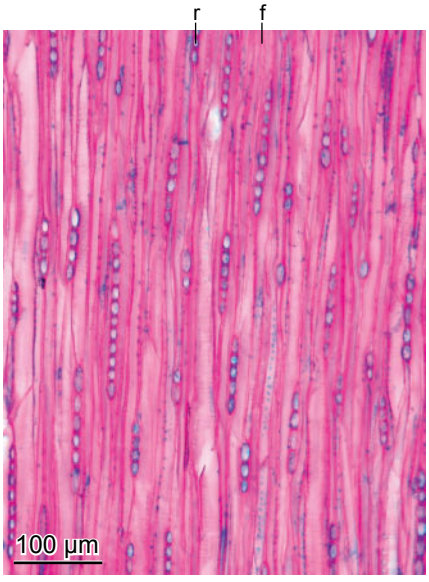



**Fig. 10.** Uniseriate, homocellular rays. Stem of a 2 m-high shrub, hedge, hill zone, Birmensdorf, Switzerland. *Euonymus europaeus*, tangential section.

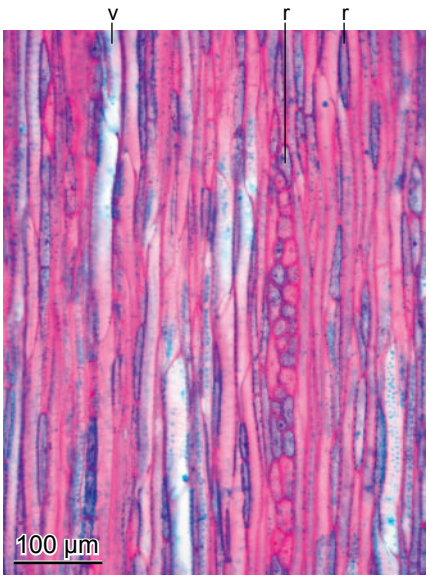



**Fig. 11.** Uni- and biseriate rays with axially elongated cells. Stem of a dwarf shrub, *Picea engelmanii*-forest, subalpine zone, Crested Butte, Colorado, USA. *Pachystina myrsinithes*, tangential section.

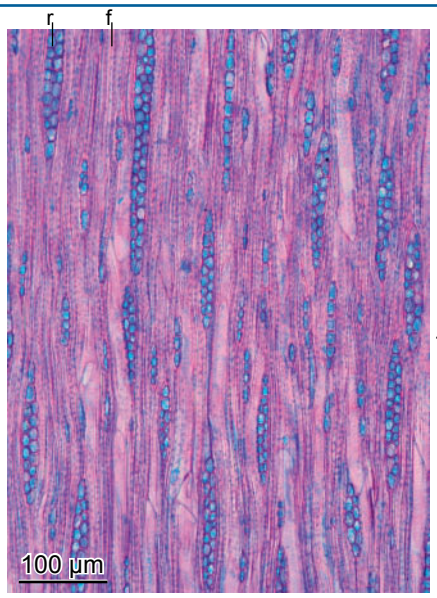



**Fig. 12.** Biseriate rays. Stem of a 50 cm-high, stiff, spiny shrub, shrub desert, arid zone, Kingman, Arizona, USA. *Canotia holacantha*, tangential section.

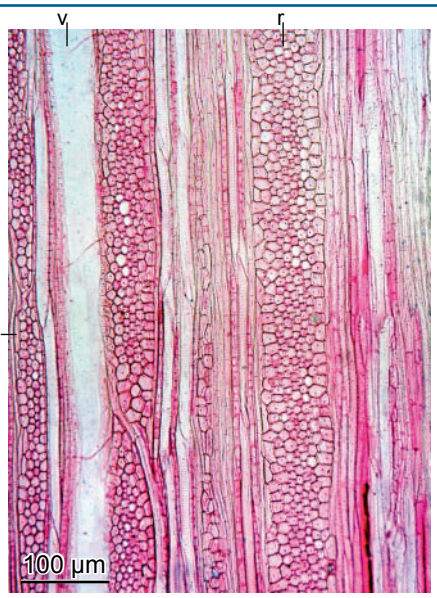



**Fig. 13.** Very large and high rays, partially composed of sheet cells. Stem of a 3 m-long liana, on a wall in the Botanical Garden Halle, Germany. *Celastrus flagellaris*, tangential section.

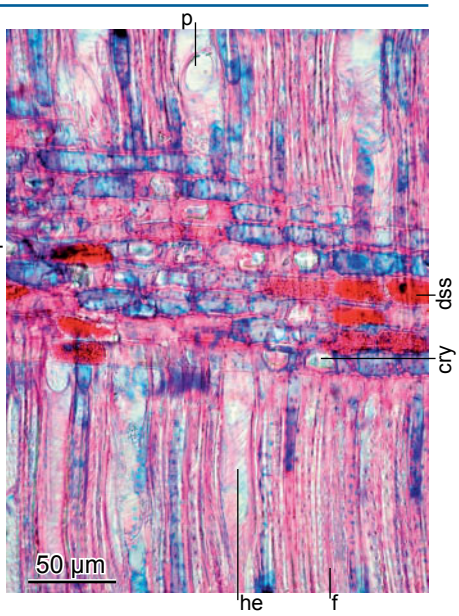



**Fig. 14.** Large prismatic crystals and red-staining substances in rays. Stem of a 50 cm-high shrub, shrub desert, arid zone, Kingman, Arizona, USA. *Canotia holacantha*, radial section.

### Characteristic features of taxa

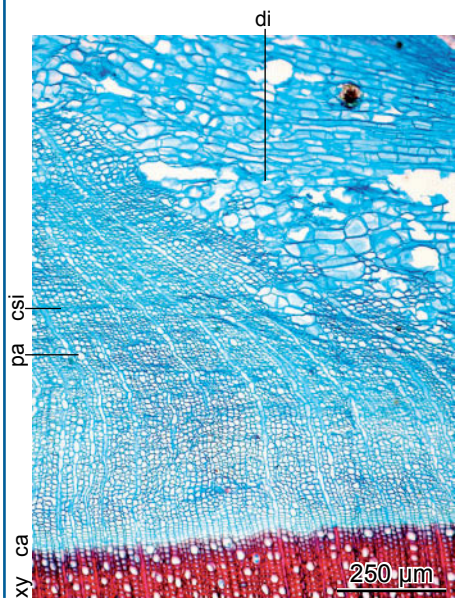
The anatomical structure of the present material is very heterogeneous. All genera are characterized by particular features, e.g. *Celastrus* by ring-porosity and very large rays, *Euonymus* and *Pachystema* by semi-ring-porosity and small rays, and *Maytenus* by tangential bands of thin- and thick-walled fibers.

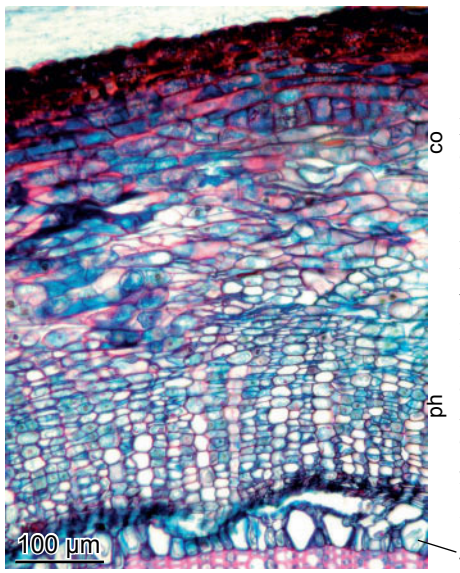
### Ecological trends and relation to life forms

There is not enough material available to recognize ecological trends.

### Characteristics of the phloem and the cortex

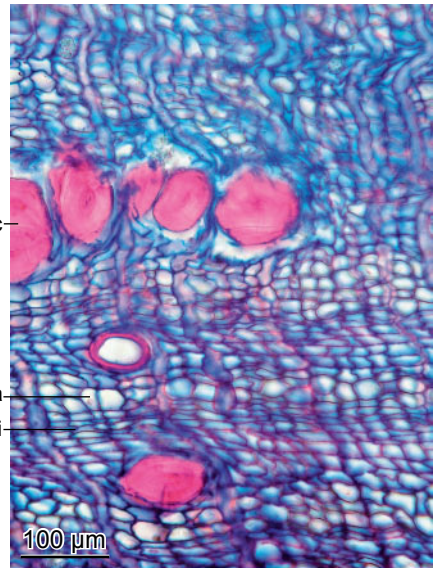
Tangential layers of parenchyma cells and sieve tubes are characteristic of the genus *Euonymus* (**Figs. 15**, **17** and **18**). The phloem is uniform in *Pachystina myrsinithes* (**Fig. 16**). Sclereids are absent in *Euonymus europaeus* (**Fig. 15**), *E. latifolius* and *Pachystina myrsinithes* (**Figs. 15** and **16**). *Euonymus verrucosus* has a few isolated sclereids (**Fig. 17**), and *Canotia holacantha* has many sclereids arranged in tangential bands (**Fig. 18**). Dilatations occur in *Euonymus europaeus* (**Fig. 15**) and *E. latifolius*.

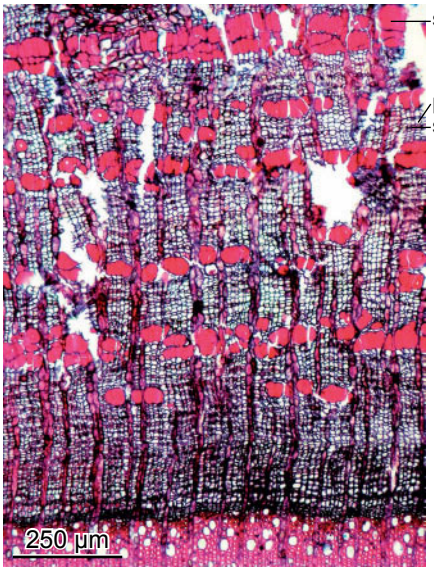



**Left Fig. 15.** Tangentially layered phloem consisting of round parenchyma cells and irregularly formed sieve tubes. Sclereids are absent. Laterally of the layered phloem is a large dilatation. Stem of a 2 m-high shrub, hedge, hill zone, Birmensdorf, Switzerland. *Euonymus europaeus*, transverse section.

**Right Fig. 16.** Fairly uniform phloem. Parenchyma cells and sieve tubes are not well distinguished. The cortex consist of irregularly formed, large parenchyma cells. Stem of a dwarf shrub, *Picea engelmanii*-forest, subalpine zone, Crested Butte, Colorado, USA. *Pachystina myrsinithes*, transverse section.




**Left Fig. 17.** Tangentially layered phloem consisting of round parenchyma cells and rectangularly-shaped sieve tubes. A few very large, very thick-walled sclereids expand the soft parenchyma/sieve-tube tissue. Stem of a 2 m-high, shrub, *Quercus pubescens*-forest, hill zone, Vienna, Austria. *Euonymus verrucosus*, transverse section.

**Right Fig. 18.** Tangentially layered phloem consisting of round parenchyma cells and rectangular shaped sieve tubes. Thick-walled sclereids are arranged in tangential bands. Stem of a 50 cm-high shrub, desert, arid zone, Kingman, Arizona, USA. *Canotia holocantha*, transverse section.



## Discussion in relation to previous studies

Gregory (1994) mentioned 74 wood anatomical studies for the family of Celastraceae that focused on tropical, commercial species. Most genera described here have been characterized before: the genus *Euonymus* has been extensively described by various authors, e.g. Greguss (1945), Benkova and Schweingruber (2004; 7 Siberian species), Edlmann et al. (1994) and Grosser (1977). As Benkova and Schweingruber (2004) mentioned, the 7 *Euonymus* species cannot be distinguished anatomically. Itoh (1998) described Japanese shrub and liana species: 7 *Euonymus*, 1 *Microtopis*, 1 *Celastrus*, and 1 *Tripterygium* species. Neumann et al. (2001) studied *Maytenus senegalensis* and Gibson (1979) *Canotia holocantha*. The present study is novel for the description of *Pachystima myrsinithes*. Holdheide (1951) characterized the bark of *Euonymus europaeus*.

The xylem and phloem anatomy within the Celastraceae family is extremely heterogeneous; corresponding to the occurrence of various life forms (lianas, shrubs and trees) growing in different vegetation zones (tropical rain forest to the subalpine zone).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **10** |
| 1 | growth rings distinct and recognizable | 9 |
| 2 | growth rings absent | 2 |
| 3 | ring-porous | 3 |
| 4 | semi-ring-porous | 4 |
| 5 | diffuse-porous | 4 |
| 9 | vessels predominantly solitary | 10 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 10 | vessels in radial multiples of 4 or more common | 1 |
| 13 | vessels with simple perforation plates | 10 |
| 21 | intervessel pits opposite | 2 |
| 22 | intervessel pits alternate | 7 |
| 31 | vessel-ray pits with large apertures, *Salix/Laurus* type | 2 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 2 |
| 36 | helical thickenings present | 7 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 7 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 3 |
| 50 | <100 vessels per mm$^2$ in earlywood | 1 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 8 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 1 |
| 56 | tylosis with thin walls | 2 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 3 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 3 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 8 |
| 65 | septate fibers present | 6 |
| 67 | thick- and thin walled fiber bands, *Acer* type | 3 |
| 70 | fibers thin- to thick-walled | 7 |
| 70.2 | tension wood present | 1 |
| 75 | parenchyma absent or unrecognizable | 6 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 4 |
| 79 | parenchyma paratracheal | 2 |
| 96 | rays uniseriate | 3 |
| 97 | ray width predominantly 1-3 cells | 6 |
| 98 | rays commonly 4-10-seriate | 2 |
| 99 | rays commonly >10-seriate | 1 |
| 103 | rays of two distinct sizes (tangential section) | 2 |
| 102 | ray height >1 mm | 1 |
| 104 | ray: all cells procumbent (radial section) | 4 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 2 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 3 |
| 110 | rays with sheet cells (tangential section) | 2 |
| 142 | prismatic crystals in axial chambered cells | 6 |
| 149 | rhaphides present | 2 |
| R2 | groups of sieve tubes in tangential rows | 7 |
| R2.1 | groups of sieve tubes in radial rows | 6 |
| R4 | sclereids in phloem and cortex | 3 |
| R6 | sclereids in radial rows | 4 |
| R7 | with prismatic crystals | 3 |
| R7.1 | with acicular crystals | 3 |
| R9 | with crystal sand | 3 |
| R11 | with rhaphides | 1 |

# Ceratophyllaceae



**Number of species, worldwide and in Europe**

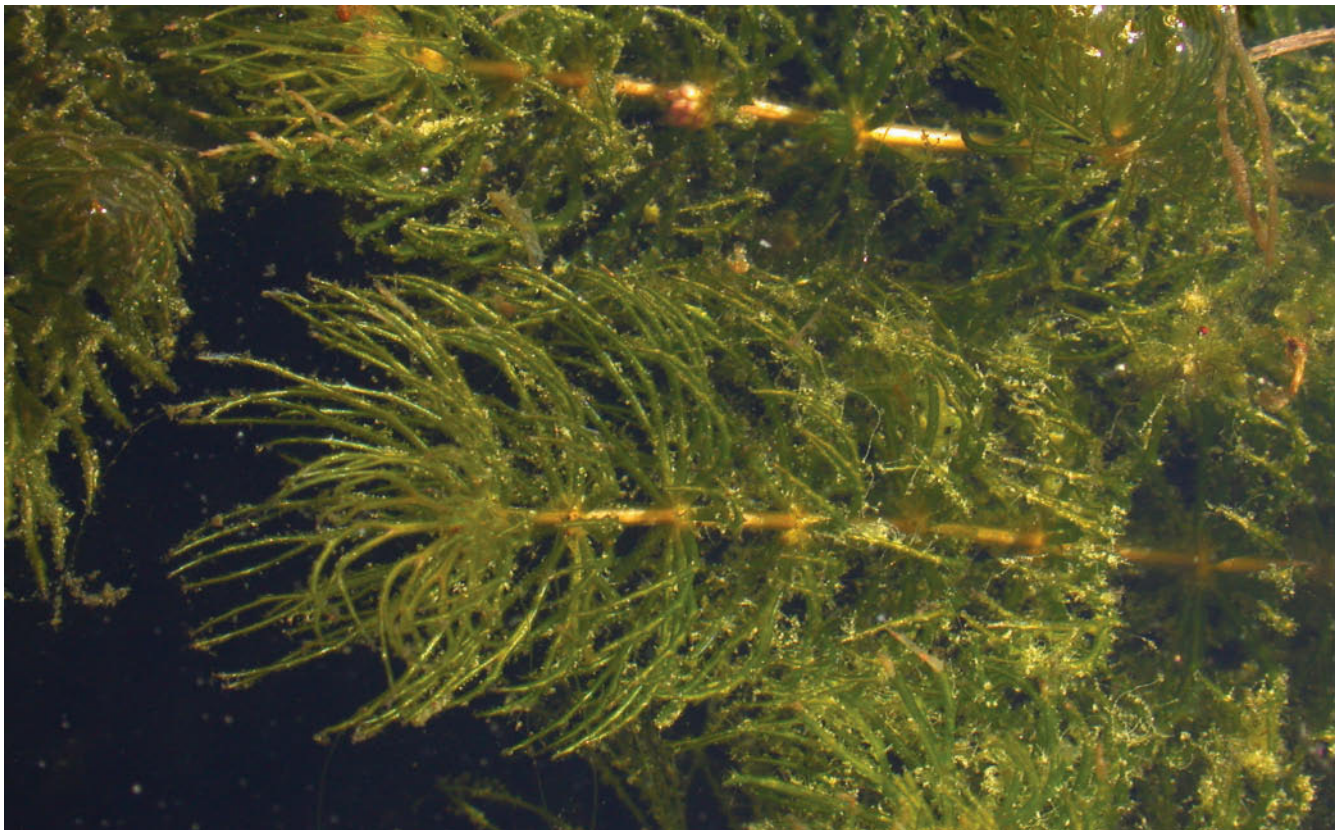
The cosmopolitan Ceratophyllaceae family includes 1 genus (*Ceratophyllum*) with 6 species. In Europe there are 4 species.

**Analyzed material**

Analyzed is one hydrophyte from Central Europe: *Ceratophyllum demersum* L.; previous authors described the same species.

**Analyzed species:**
*Ceratophyllum demersum* L.

*Ceratophyllum demersum* (photos: Stützel)



**Characteristics of the stem**

Secondary growth is absent. The stem is composed of a central vascular cylinder and a peripheral cortex (**Fig. 1**). The cylinder consists of a central air canal, surrounded by some thin-walled cells (**Fig. 2**). Outside them is parenchymatic tissue with slightly lignified cell walls. In this tissue there are a few larger cells, which can be interpreted as vessels. Since these cells do not have any cell-wall structure it is difficult to identify them. Fibers and rays are absent. Therefore Schneider and Carlquist 1996 conclude that a xylem is absent in *Ceratophyllum demersum* (**Fig. 3**). Some elongated cells contain scattered sieve-tube elements. Phloem and xylem, if occurring, cannot be differentiated. The cylinder is surrounded by a one-cell-wide thin-walled endodermis containing starch. The epidermis has no stomata (**Figs. 1** and **4**). The structure is adapted to submerse conditions: absent are stomata, secondary walls and cell-wall thickenings and cells are unlignified.

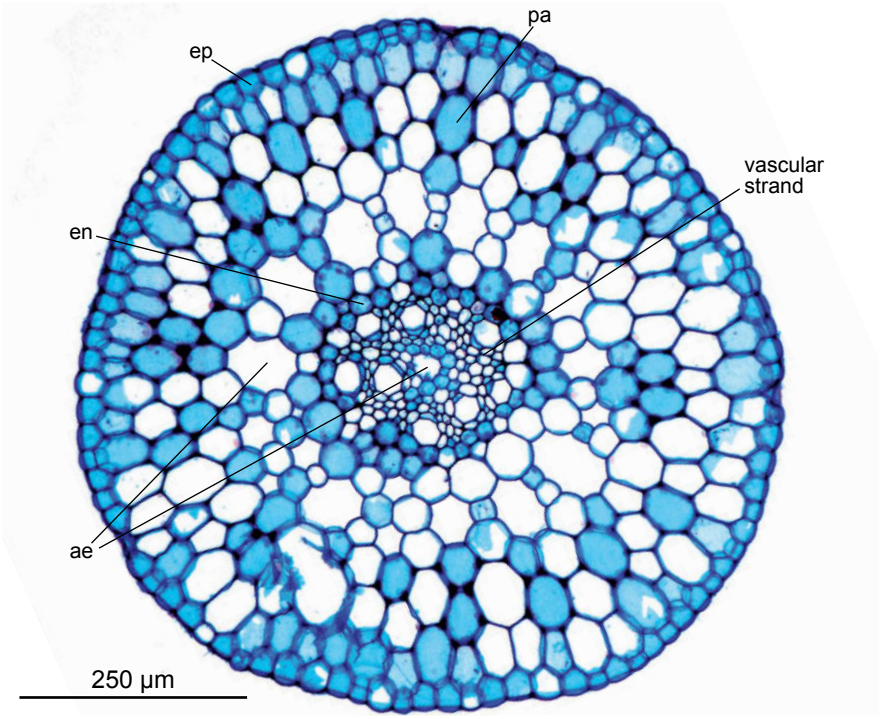



**Fig. 1.** The central vascular strand is surrounded by an endodermis and a large parenchymatic cortex with slightly enlarged air canals. Stem of a submerse plant in a pond, hill zone, cultivated, Botanical Garden Basel, Switzerland. *Ceratophyllum demersum*, transverse section.

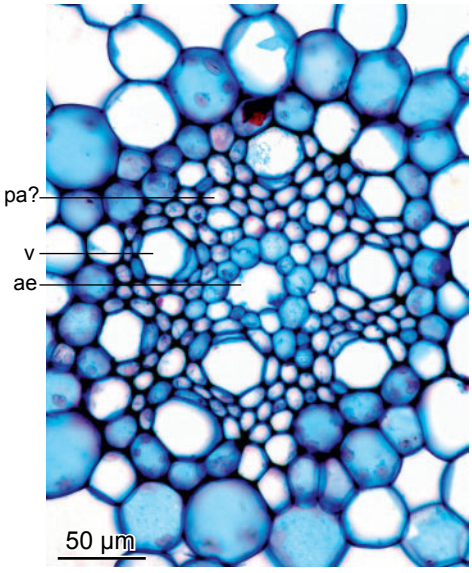



**Fig. 2.** In the center of the vascular strand is an air canal. Vessel-like cells are embedded in small, probably parenchymatic cells. Structured, lignified secondary cell walls are absent in all cells. Origin see **Fig. 1**. Transverse section.

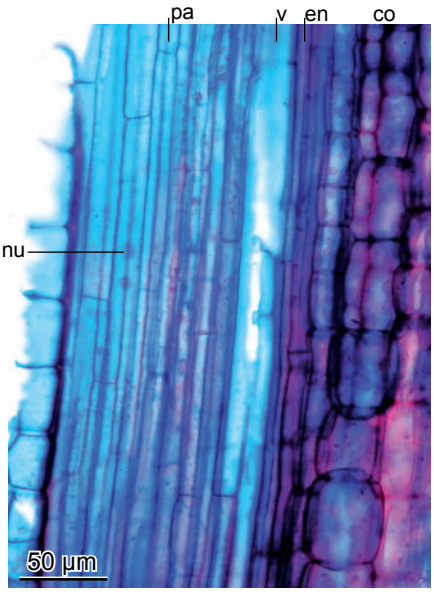



**Fig. 3.** Longitudinal section through the central vascular strand. All cells are rectangular and elongated along the axis. Cell walls are unstructured. Origin see **Fig. 1**. Radial section.

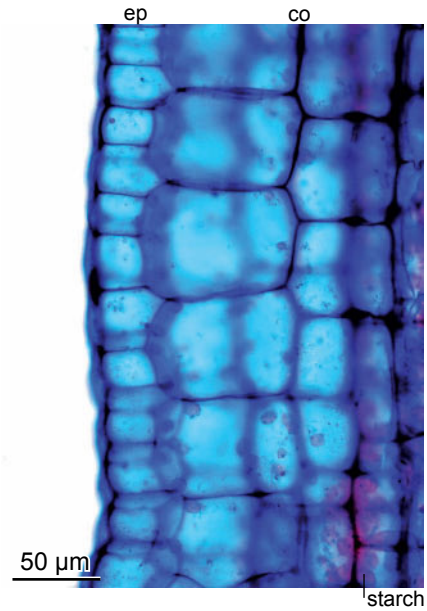



**Fig. 4.** Epidermis without stomata and parenchyma cells of the cortex. Origin see **Fig. 1**. Radial section.

**Discussion in relation to previous studies**

Metcalfe and Chalk (1957), based on Solereder (1908) as well as Schneider and Carlquist (1996) describe the stem of *Ceratophyllum demersum*.

The present study is in agreement with previous findings.

# Cercidiphyllaceae



### Number of species, worldwide and in Europe

The Cercidiphyllaceae family includes 1 genus with 2 species. No represantives of the family Cercidiphyllaceae are found in Europe. The origin of the species is SW-Asia, Japan and Taiwan.

### Analyzed material

The xylem and phloem of one Cercidiphyllaceae species (a tree) were analyzed. The material was collected in the Botanical Gardens of Basel and Zürich, Switzerland.

**Analyzed species:**
*Cercidiphyllum japonicum* Sieb. et Zucc.

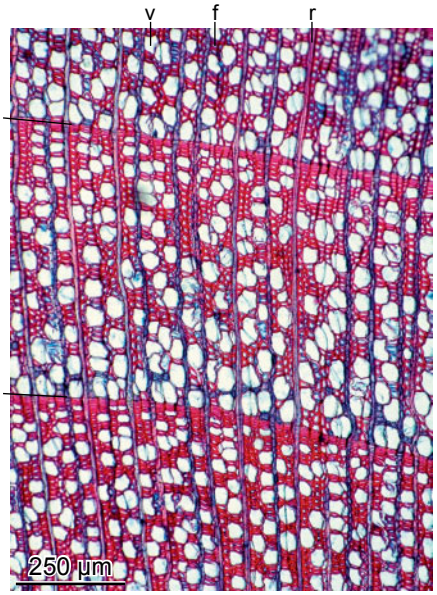
*Cercidiphyllum japonicum* (photo: Holdenrieder)

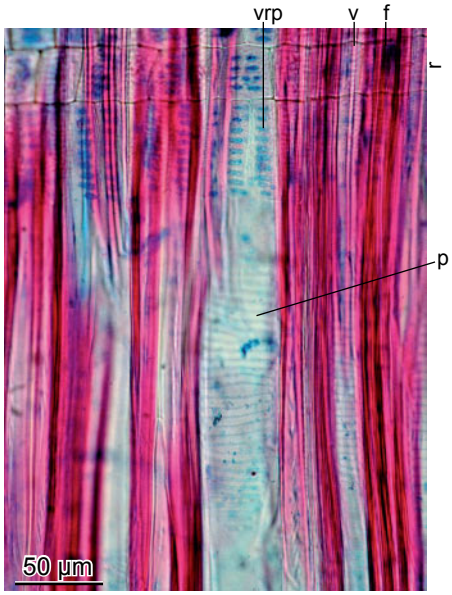
### Characteristics of the xylem

The anatomical structure of this species fits perfectly in that of the family of Hamamelidaceae. The diffuse-porous wood with mostly solitary vessels has distinct rings (**Fig. 1**). Perforations are scalariform with >20 bars and ray-vessel pits are round and scalariform (horizontal, gash-like; **Fig. 2**). Fibers are thin- to thick-walled, with distinctly bordered, round pits. The parenchyma is apotracheal. The heterocellular rays (2-4 upright cells) are 1-2 cells in width (**Fig. 3**). A few prismatic crystals have been observed.

### Characteristics of the phloem and the cortex

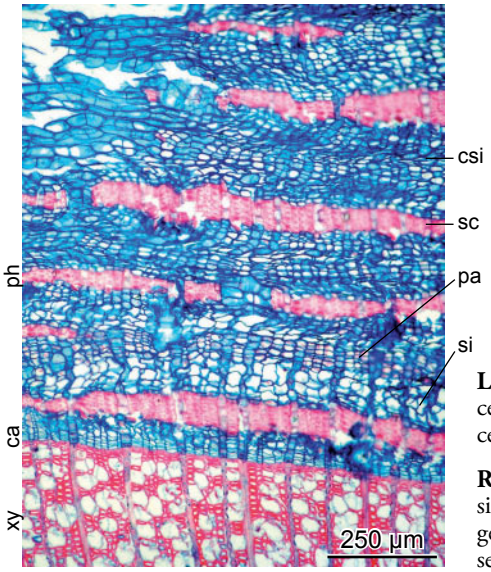
The bark is similar to that of *Liquidambar styraciflua*. The phloem has distinct tangential layers of sieve tubes, parenchyma cells and small tangential band of sclerenchyma cells (**Fig. 4**). A few ray dilatations occur. Prismatic crystals are frequent.




**Left Fig. 1.** Diffuse to slightly semi-ring-porous wood with distinct rings and small rays. Branch of a 5 m-high tree, hill zone, cultivated, Botanical Garden Zürich, Switzerland. *Cercidiphyllum japonicum*, transverse section.

**Right Fig. 2.** Heterocellular rays, 1-2 cells in width. Ray cells with horizontally enlarged ray-vessel pits and vessel with a scalariform perforation. Origin see **Fig. 1**. Radial section.




**Left Fig. 3.** Heterocellular ray with small central cells and axial elongated marginal cells. Origin see **Fig. 1**. Tangential section.

**Right Fig. 4.** Phloem with tangential layers sieve tubes and parenchyma cells and tangential groups of sclerenchyma cells. Origin see **Fig. 1**. Transverse section.

**Discussion in relation to previous studies**

Gregory (1994) mentions 27 articles in which *Cercidiphyllum* is described. A good description and an IAWA code classification is given by Richter and Dallwitz. http://www.biologie.uni-hamburg.de/b-online/wood/german/trotrara.htm

The present study is in agreement with previous observations.

# Cistaceae



**Number of species, worldwide and in Europe**

The cosmopolitean Cistaceae family includes 8 genera with 200 species. In Europe, there are 5 genera with 74 species.

**Analyzed material**

The xylem and phloem of 4 genera with 35 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 10 | 3 genera |
| Dwarf shrubs | 24 | 3 genera |
| Hemicryptophytes | 1 | |
| **Plants analyzed from different vegetation zones:** | | |
| Subalpine | 2 | |
| Hill and mountain | 4 | |
| Mediterranean | 27 | |
| Subtropical | 2 | |

**Analyzed species:**

*Cistus albidus* L.
*Cistus clusii* Dunal
*Cistus creticus* L.
*Cistus crispus* L.
*Cistus ladanifer* L.
*Cistus laurifolius* L.
*Cistus monspeliensis* L.
*Cistus palhinae* Ingram
*Cistus salvifolius* L.
*Cistus symphytifolius* Lam.
*Fumana ericoides* Pau
*Fumana procumbens* Gren. et Godron
*Fumana thymifolia* Spach
*Halimium atriplicifolium* Spach
*Halimium halimifolium* (L.) Willk.
*Halimium ocymoides* Willk.
*Halimium viscosum* (Willk.) P. Silva
*Helianthemum almeriense*
*Helianthemum alpestre* Rchb.
*Helianthemum apenninum* D.C.
*Helianthemum canariense* Pers.
*Helianthemum canum* (L.) Boiss.
*Helianthemum caput-felis* Boiss.
*Helianthemum croceum* (Desf.) Pers.
*Helianthemum hirtum* (L.) Mill.
*Helianthemum italicum* Pers.
*Helianthemum lavandulifolium* Miller
*Helianthemum ledifolium* Spach
*Helianthemum leptophyllum* Pers.
*Helianthemum nummularium* Mill.
*Helianthemum rufficonum* Spreng
*Helianthemum squamatum* (L.) Pers.
*Helianthemum umbellatum* Mill.
*Tuberaria guttata* (L.) Fourr.
*Tuberaria lignosa* Samp.

*Cistus monspeliensis*

*Helianthemum album*

*Helianthemum nummularium*

**Characteristics of the xylem**

Annual rings are mostly distinct (**Figs. 1** and **2**). Ring distinctness is indicated by tangential flat fibers in diffuse and semi-ring-porous species (**Figs. 1-3**). Earlywood vessel diameter varies from 15-30 µm in the genera *Helianthemum* and *Tuberaria* and from 20-50 µm in the genera *Cistus*, *Halimium* and *Fumana*. Vessel density varies from of 300-500/mm$^2$. All species have simple perforations and small, round intervessel pits (**Fig. 4**). Fine helical thickenings have been observed in *Cistus laurifolius* and *C. monspeliensis* (**Fig. 4**). Fibers have large pits and are fairly thick-walled in most species (**Figs. 1**, **2** and **5**). Parenchyma is apotracheal, diffuse and scanty paratracheal (**Figs. 6** and **7**). Rays of all *Helianthemum* and *Tuberaria* species are uniseriate (**Fig. 8**). Rays are 1-3- (-4) seriate in the genera *Cistus*, *Fumana* and *Halimium* (**Figs. 9** and **10**). Most species have homogeneous rays with square and upright cells (**Fig. 5**). Procumbent cells in the center zone, square and upright cells in the marginal zones have been observed in a few *Cistus* and *Halimium* species. Crystals are rare in ray cells of the xylem. Prismatic crystals occur in *Cistus ladanifer*, *C. laurifolius* and *Halimium viscosum* (**Fig. 5**) and crystal druses are present in *Helianthemum umbellatum*.

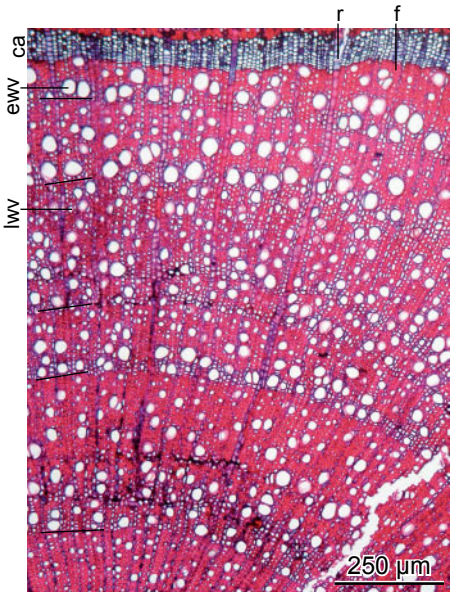



**Fig. 1.** Semi-ring-porous xylem with distinct rings and thick-walled fibers. Stem of an 80 cm-high shrub, garigue, Mediterranean zone, Andalusia, Spain. *Cistus crispus*, transverse section.

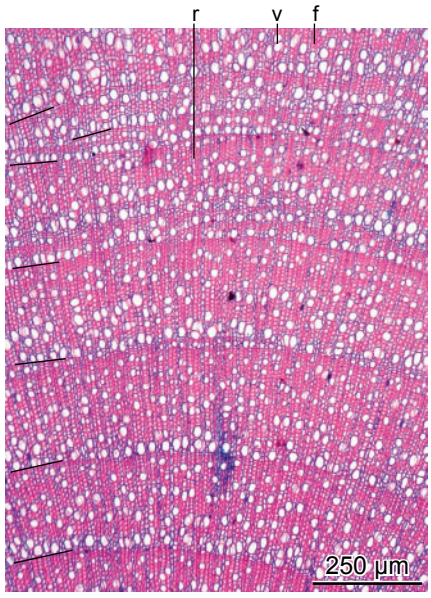



**Fig. 2.** Semi-ring-porous xylem with distinct rings and thick-walled fibers. A few rings are wedging. Root collar of a 20 cm-high dwarf shrub, dry meadow, Mediterranean zone, Valencia, Spain. *Helianthemum canum*, transverse section.

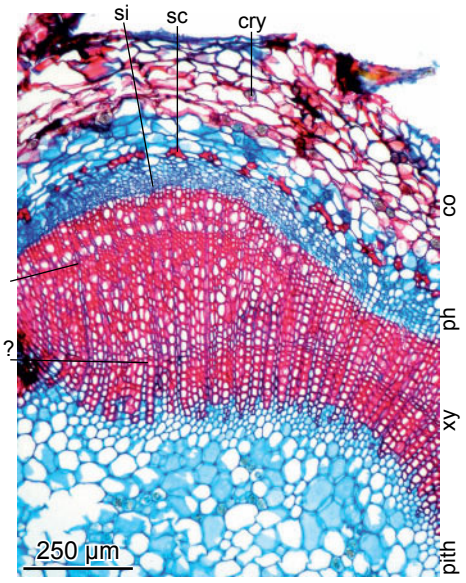
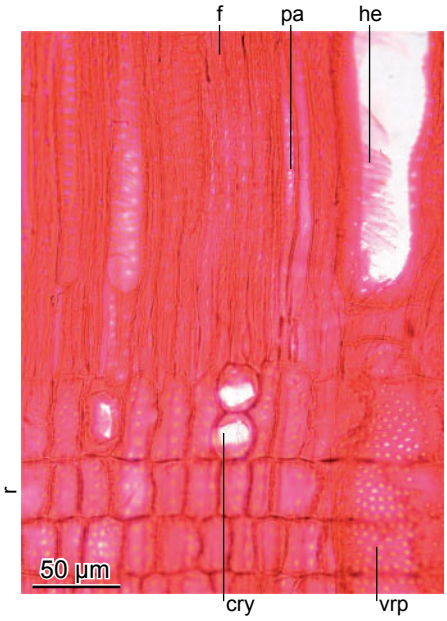
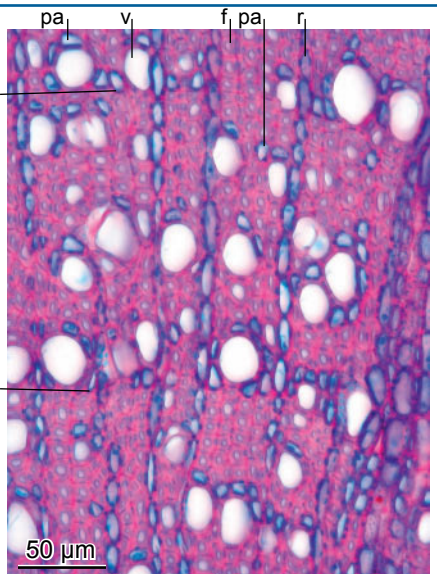


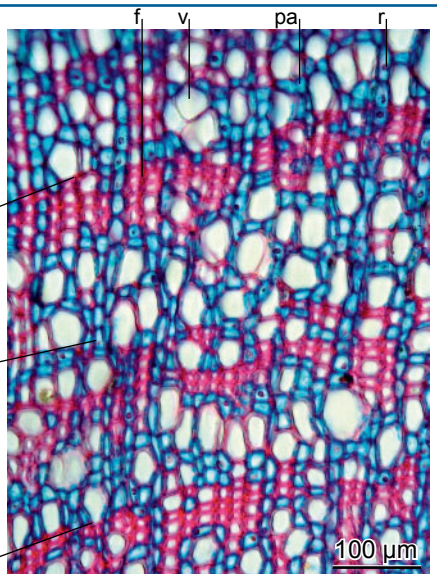

**Fig. 3.** Semi-ring-porous xylem with a first indistinct and second distinct ring boundary. Root collar of a 20 cm-high hemicryptophyte, exposed rock, Mediterranean zone, Estremadura, Spain. *Tuberaria guttata*, transverse section.

**Left Fig. 4.** Vessels with simple perforations and small, round pits in alternating position. Stem of a 40 cm-high dwarf shrub, garigue, Mediterranean zone, Andalusia, Spain. *Cistus salvifolius*, radial section.




**Right Fig. 5.** Vessel with thin helical thickenings and upright ray cells containing prismatic crystals. Stem of an 80 cm-high shrub, maccia, Mediterranean zone, Zaragoza, Spain. *Cistus laurifolius*, radial section.




**Left Fig. 6.** Apotracheal diffuse and scanty paratracheal parenchyma. Fibers are thick-walled. Root collar of a 10 cm-high dwarf shrub, garigue, Mediterranean zone, Provence, France. *Fumana ericoides*, transverse section.

**Right Fig. 7.** Earlywood with paratracheal, and latewood with mainly apotracheal parenchyma. Root collar of a 10 cm-high chamaephyte, meadow, subalpine zone, Provence, France. *Helianthemum hirtum*, transverse section.

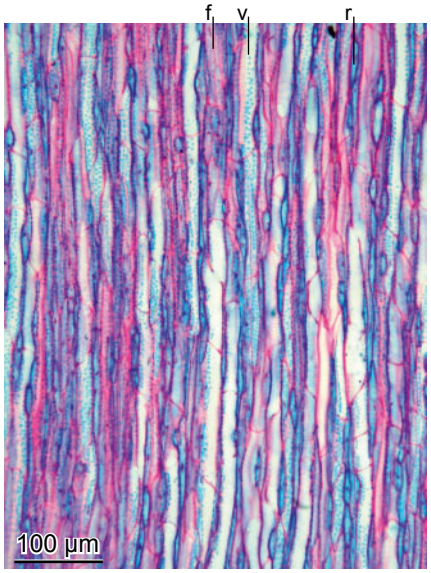



**Fig. 8.** Uniseriate rays with elongated cells. Root collar of a 10 cm-high chamaephyte, meadow, subalpine zone, Provence, France. *Helianthemum hirtum*, tangential section.

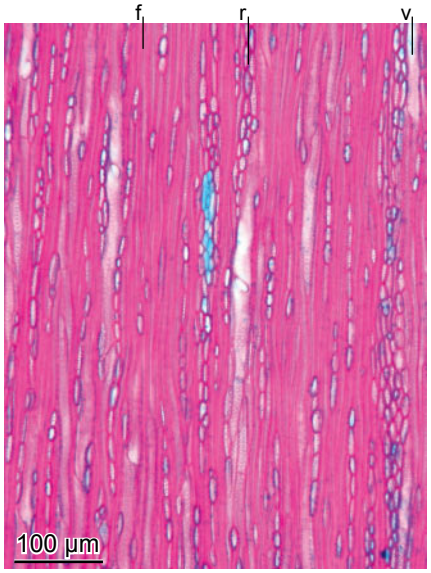



**Fig. 9.** 1-3- (-4) seriate rays. Root collar of a 10 cm-high dwarf shrub, dry slope, hill zone, Valais, Switzerland. *Fumana procumbens*, tangential section.

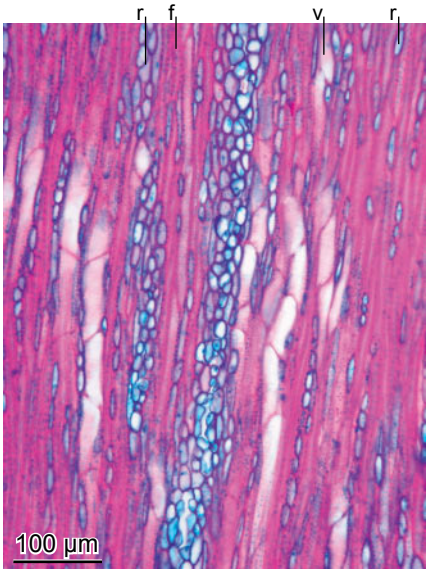



**Fig. 10.** Uni- and multiseriate rays. Root collar of a 10 cm-high dwarf shrub, garigue, Mediterranean zone, Provence, France. *Fumana ericoides*, tangential section.

### Characteristics of the phloem and the cortex

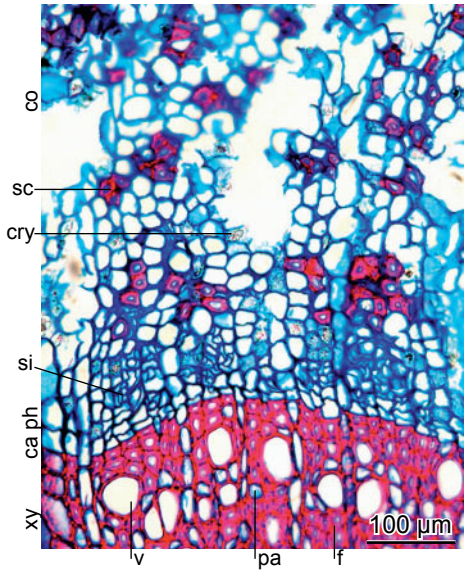
Phloem structures are relatively uniform. Sieve-tubes and parenchyma cells are arranged in small groups in a few species (**Fig. 11**), but sieve-tubes and parenchyma cells are often difficult to differentiate in transverse sections (**Figs. 12-14**). Sclereids are arranged in small groups (**Fig. 11**) and in tangential bands (**Figs. 12** and **13**). Ray dilatations are rare (**Fig. 13**). Most species contain crystals (**Fig. 14**). Prismatic forms are concentrated in the genus *Cistus*, and crystal druses are common in *Helianthemum* and *Fumana* (**Fig. 14**).

### Ecological trends in the xylem and the bark

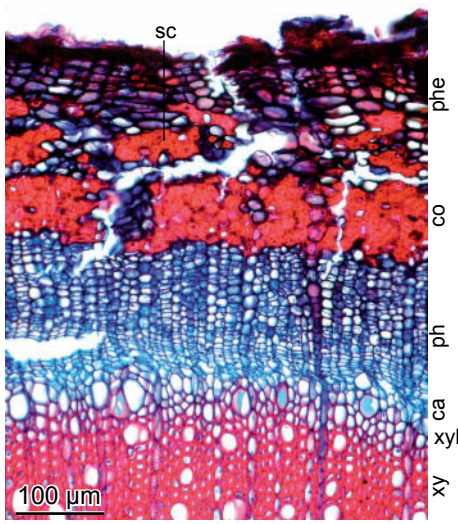
Uniseriate rays occur often in small plants especially in *Helianthemum* and 2-3-seriate rays in larger dwarf shrubs or small shrubs of the genera *Cistus* and *Halimium*. Fiber-cell walls of the subalpine species are generally thinner than those in plants of the Mediterranean zone.

### Discussion in relation to previous studies

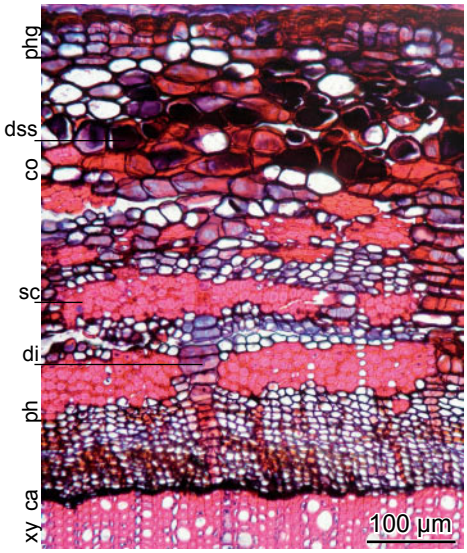
A few species of the genera *Cistus*, *Fumana*, *Halimium* and *Helianthemum* have been described by Huber and Rouschal (1954), Greguss (1945), Fahn (1986) and Schweingruber (1990). Most species of this study have not been described before.

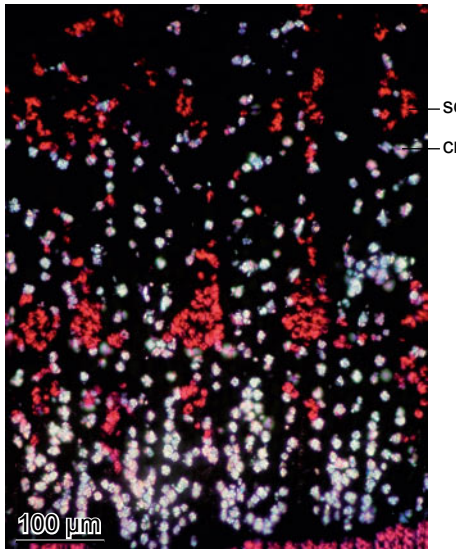



**Left Fig. 11.** Phloem with small groups of sieve-tubes and fibers. Some parenchyma cells contain crystals druses. Root collar of a 10 cm-high dwarf shrub, garigue, Mediterranean zone, Provence, France. *Fumana ericoides*, transverse section.




**Right Fig. 12.** Phloem with small groups of sieve-tubes and a dense tangential band of thick-walled sclerenchyma cells. Stem of a 40 cm-high dwarf shrub, meadow, Mediterranean zone, Andalusia, Spain. *Halimium halimifolium*, transverse section.




**Left Fig. 13.** Uniform phloem near the cambium and tangential strips of thick-walled sclerenchyma cells. Stem of a 40 cm-high dwarf shrub, garigue, Mediterranean zone, Tarragona, Spain. *Cistus creticus*, transverse section.

**Right Fig. 14.** Phloem with tangentially arranged groups of sclerenchyma. Most parenchyma-cells contain crystal druses. Root collar of a 10 cm-high dwarf shrub, dry slope, hill zone, Valais, Switzerland. *Fumana procumbens*, polarized light, transverse section.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **35** |
| 1 | growth rings distinct and recognizable | 35 |
| 4 | semi-ring-porous | 21 |
| 5 | diffuse-porous | 26 |
| 9 | vessels predominantly solitary | 35 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 35 |
| 21 | intervessel pits opposite | 1 |
| 22 | intervessel pits alternate | 34 |
| 36 | helical thickenings present | 2 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 7 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 32 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 16 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 25 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 17 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 35 |
| 69 | fibers thick-walled | 30 |
| 70 | fibers thin- to thick-walled | 10 |
| 75 | parenchyma absent or unrecognizable | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 34 |
| 79 | parenchyma paratracheal | 34 |
| 96 | rays uniseriate | 21 |
| 97 | ray width predominantly 1-3 cells | 16 |
| 98 | rays commonly 4-10-seriate | 5 |
| 100.2 | rays not visible in polarized light | 2 |
| 102 | ray height >1 mm | 4 |
| 105 | ray: all cells upright or square | 26 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 3 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 5 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 6 |
| 110 | rays with sheet cells (tangential section) | 1 |
| 136 | prismatic crystals present | 5 |
| 144 | druses present | 2 |
| R1 | groups of sieve tubes present | 7 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 23 |
| R6 | sclereids in radial rows | 1 |
| R6.1 | sclereids in tangential rows | 2 |
| R6.2 | sclereids in tangential arranged groups, *Rhamnus* type | 17 |
| R7 | with prismatic crystals | 7 |
| R8 | with crystal druses | 15 |
| R9 | with crystal sand | 1 |
| R10 | phloem not well structured | 2 |

# Clusiaceae



## Number of species, worldwide and in Europe

The Clusiaceae family includes 38 genera with 1100 species. Most of the species grow in the tropics of the southern hemisphere. In Europe, there is 1 genus (*Hypericum*) with 62 species. Three species are endemic on the Canary Islands.

## Analyzed material

The xylem and phloem of one genus with 18 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | | ca. 40 genera (tropical) |
| Nanophanerophytes 0.5-4 m | 4 | 2 |
| Dwarf shrubs | 14 | 1 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 12 | |
| Mediterranean | 2 | |
| Subtropical | 4 | |

**Analyzed species:**

*Hypericum androsaemum* L.
*Hypericum balearicum* L.
*Hypericum canariense* L.
*Hypericum coris* L.
*Hypericum empetrifolium* Willd.
*Hypericum grandifolium* Choisy
*Hypericum hirsutum* L.
*Hypericum humifusum* L.
*Hypericum inodorum* Mill.
*Hypericum maculatum* Crantz
*Hypericum montanum* L.
*Hypericum perforatum* L.
*Hypericum polygonifolium* Rupr.
*Hypericum ptarmicifolium* Spach
*Hypericum reflexum* L. fil.
*Hypericum revolutum* R. Keller
*Hypericum richeri* Vill.
*Hypericum tomentosum* L.

*Hypericum coris* (photo: Landolt)

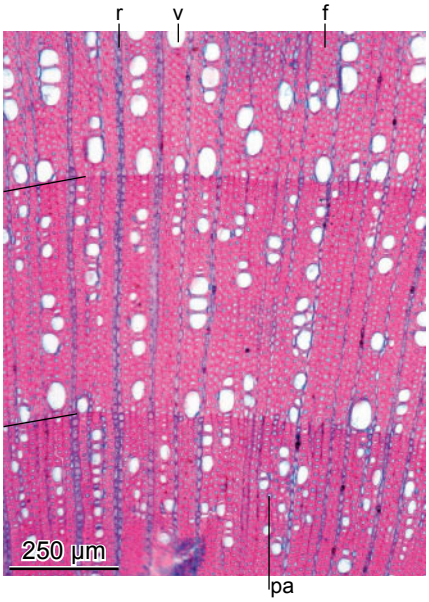
*Hypericum calycina* (photo: Aas)

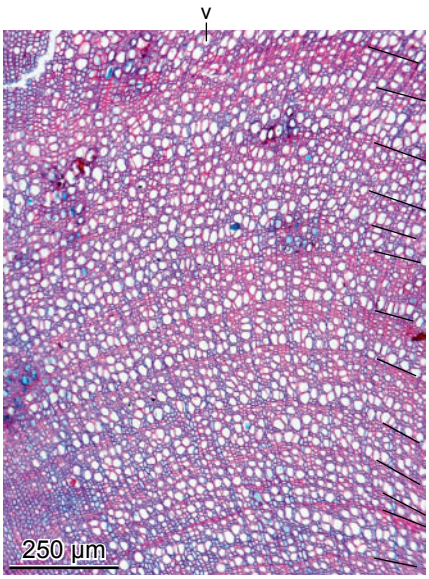
*Hypericum perforatum*

**Characteristics of the xylem**

Annual rings are present in most species (**Figs. 1-3**) but are indistinct in *Hypericum androsaemum* (**Fig. 4** and **5**). Rings are very small in *Hypericum coris* (**Fig. 2**). Ring boundaries, are marked by semi-ring-porosity (**Figs. 1-4**). Vessels are arranged mostly solitary (**Figs. 3** and **4**) or are arranged in short radial rows (**Fig. 1**). The earlywood vessel diameter of the majority of species varies between 30-60 µm and vessel density mostly between 200-300/mm$^2$. Vessels contain exclusively simple perforations (**Fig. 5**). Inter-vessel pits are small (<2 µm) and round in alternating position but are larger (3-4 µm) in a few species, e.g. *Hypericum polygonifolium*. Vessels of a few species tend to be thick-walled (3-4 µm). Vessels of some species, e.g. *Hypericum coris*, contain dark-staining substances.

Fibers are mostly thin- to thick-walled (**Figs. 2** and **4**), but are also occasionally thick-walled (**Fig. 1**) or thin-walled (**Fig. 3**). Septate fibers are present in 7 of 16 species (**Fig. 6**). Some species contain distinct tension wood (**Fig. 7**). Parenchyma is absent or rare in most species (**Figs. 1**, **3** and **4**) and it tends to be paratracheal in *Hypericum coris* (**Fig. 2**). Rays are uniseriate (**Fig. 8**) or 1-3 cells wide (**Fig. 9**). Rays are mostly homocellular with square and upright cells (**Fig. 10**), rarely with procumbent cells as in *Hypericum coris* (**Fig. 11**). Ray-vessel-pits are small and round (**Fig. 11**). Crystals don't occur in any species. Oil drops have been found in *Hypericum grandifolium* (**Fig. 12**).




**Left Fig. 1.** Distinct rings of a semi-ring-porous xylem. Vessels are mostly arranged in short radial rows. Fibers are thick-walled. Axial parenchyma cells are absent or rare. Stem of a 1 m-high shrub, thermophile belt, subtropical climate, Tenerife, Canary Islands. *Hypericum canariense*, transverse section.

**Right Fig. 2.** Very small distinct rings of a semi-ring-porous xylem with a high vessel density. Stem of a 20 cm-high dwarf shrub, on limestone rock, submediterranean zone, Provence, France. *Hypericum coris*, transverse section.

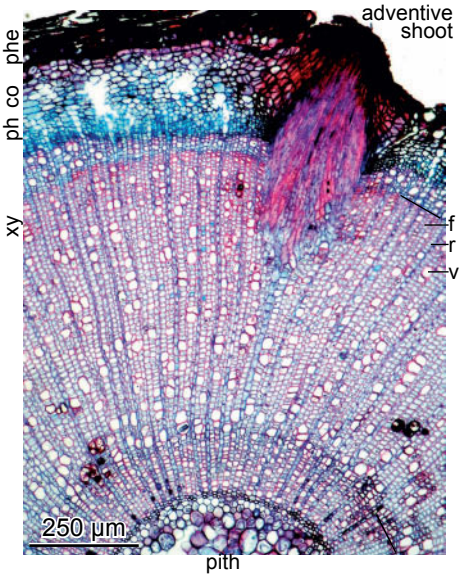



**Fig. 3.** Distinct rings of a semi-ring-porous xylem with thin-walled fibers. Root collar of a 20 cm-high hemicryptophyte, meadow, subalpine zone, little Caucasus, Georgia. *Hypericum hirsutum*, transverse section.

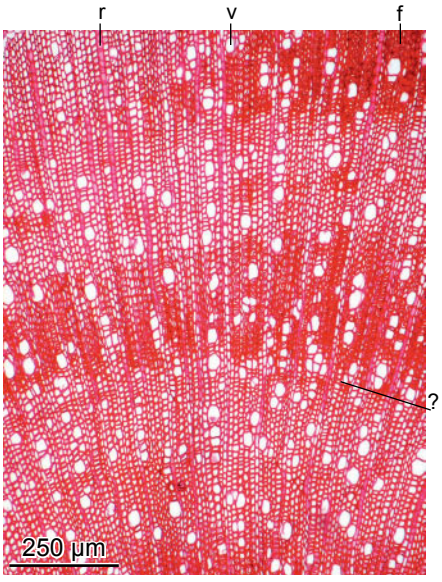



**Fig. 4.** Indistinct rings. Vessels are mostly solitary. Root collar of a 20 cm-high chamaephyte, cultivated, Birmensdorf, Switzerland. *Hypericum androsaemum*, transverse section.

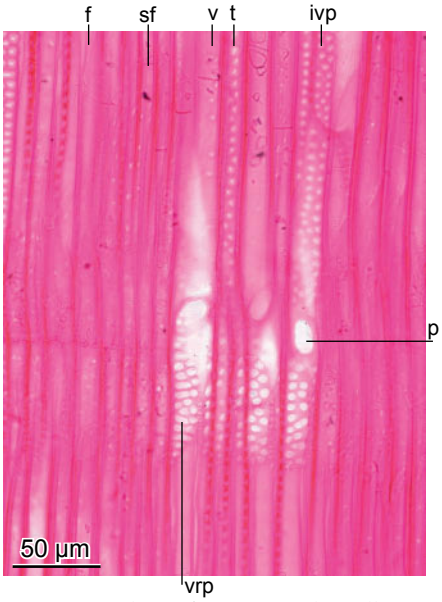



**Fig. 5.** Simple perforations and small ray-intervessel pits. Stem of a 1 m-high shrub, thermophile belt, subtropical climate, Tenerife, Canary Islands. *Hypericum reflexum*, radial section.

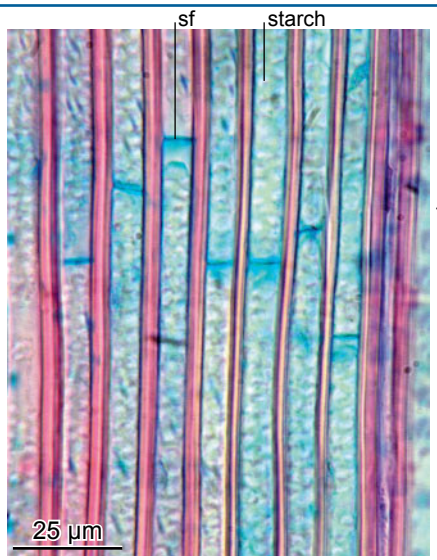



**Fig. 6.** Septate fibers with thick, lignified axial and thin, unlignified horizontal walls. Stem of a 1 m-high shrub, thermophile belt, subtropical climate, Tenerife, Canary Islands. *Hypericum grandifolium*, radial section.

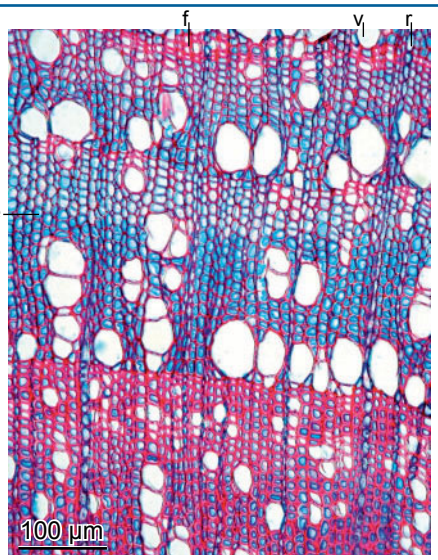



**Fig. 7.** Tension wood, mainly in the earlywood (blue cell contents in fibers). Stem of a 1 m-high shrub, thermophile belt, subtropical climate, Tenerife, Canary Islands. *Hypericum inodorum*, transverse section.

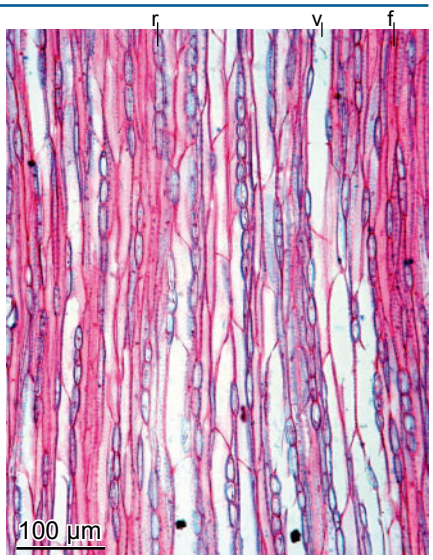
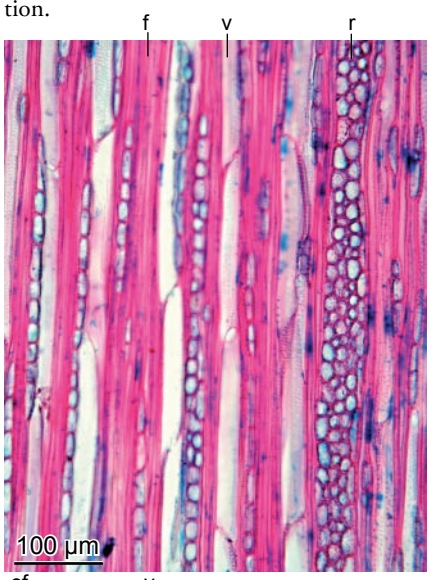
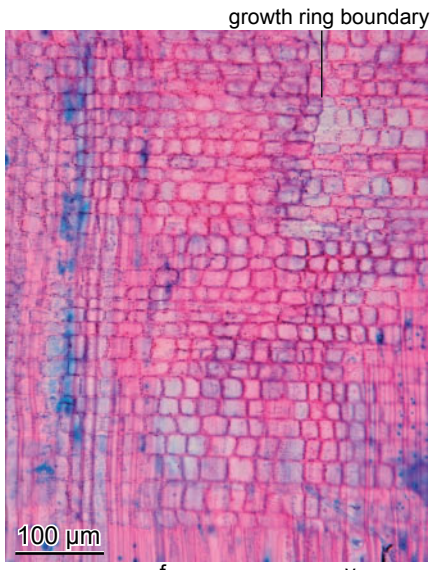


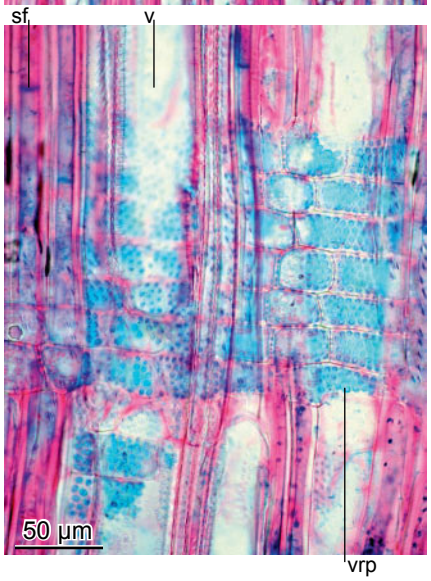

**Fig. 8.** Uniseriate rays. Stem of a 20 cm-high dwarf shrub, on limestone rock, submediterranean zone, Provence, France. *Hypericum coris*, tangential section.

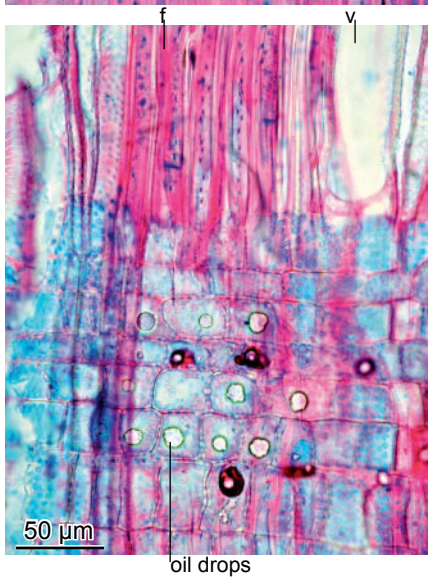



**Left Fig. 9.** Uniserate and 2-4 cells-wide rays. Stem of a 1 m-high shrub, thermophile belt, subtropical climate, Tenerife, Canary Islands. *Hypericum reflexum*, tangential section.

**Right Fig. 10.** Homocellular ray with mainly square cells. Stem of a 1 m-high shrub, thermophile belt, subtropical climate, Tenerife, Canary Islands. *Hypericum reflexum*, radial section.




**Left Fig. 11.** Homocellular ray with procumbent cells. Ray-intervessel pits are small and round. Stem of a 1 m-high shrub, thermophile belt, subtropical climate, Tenerife, Canary Islands. *Hypericum canariense*, radial section.

**Right Fig. 12.** Ray cells with oil drops. Fibers with small pits. Stem of a 1 m-high shrub, thermophile belt, subtropical climate, Tenerife, Canary Islands. *Hypericum canariense*, radial section.

### Characteristic features of taxa

The anatomical structure of the present material is homogeneous. Rays tend to be smaller in dwarf shrubs and hemicryptophytes, e.g. *Hypericum coris* or *Hypericum humifusum* than in shrubs, e.g. *Hypericum inodorum*.

### Characteristics of the phloem and the cortex

The phloem is mostly uniform. Parenchyma cells and sieve tubes cannot to be distinguished (**Fig. 13**). Intercellular canals, surrounded by a few secretory cells are characteristic of 13 of 16 species (**Figs. 14** and **15**).

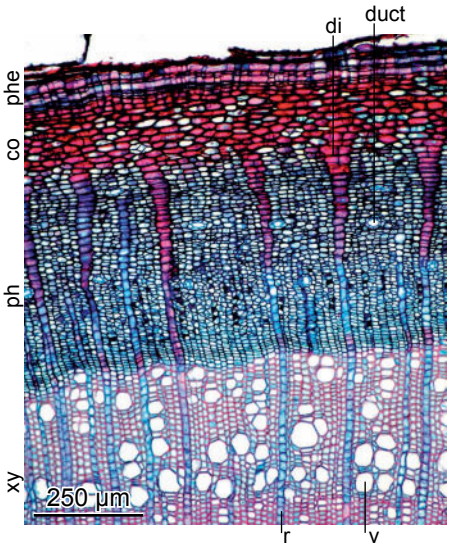



**Fig. 13.** Fairly uniform phloem with slight ray dilatations and small secretory ducts. The phellem consists of small rectangular cork cells. Stem of a 1 m-high shrub, thermophile belt, subtropical climate, Tenerife, Canary Islands. *Hypericum inodorum*, transverse section.

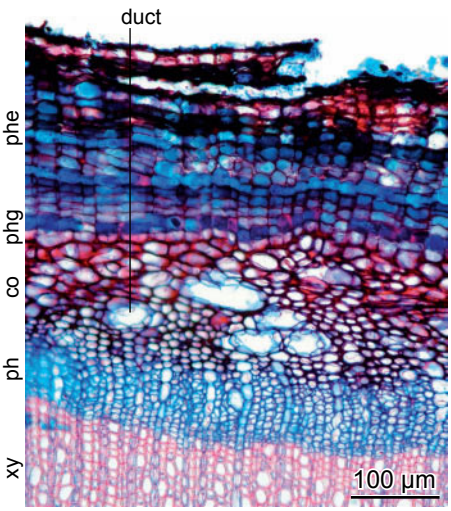



**Fig. 14.** Cortex and phloem with secretory ducts. The phellem consists of four layers of small rectangular cork cells. Stem of a 20 cm-high dwarf shrub, on limestone rock, submediterranean zone, Provence, France. *Hypericum coris*, transverse section.

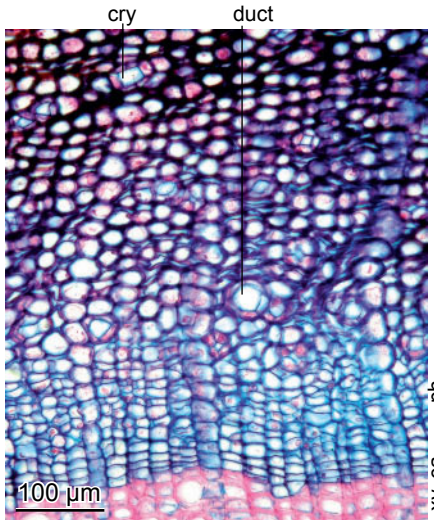



**Fig. 15.** Fairly uniform phloem with one distinct and a few indistinct, small secretory ducts. Stem of a 1 m-high shrub, thermophile belt, subtropical climate, Tenerife, Canary Islands. *Hypericum inodorum*, transverse section.

### Ecological trends and relations to life forms

There is not enough material available to distinguish ecological trends.

### Discussion in relation to previous studies

Gregory (1994) mentioned more than 100 articles about the xylem of Guttiferae. Most of them characterize the xylem of tropical tree species, but only 3 describe *Hypericum* species. Due to the homogeneity of the genus, the present characterization simply adds details, e.g with the description of *Hypericum coris*.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **18** |
| 1 | growth rings distinct and recognizable | 16 |
| 2 | growth rings absent | 1 |
| 4 | semi-ring-porous | 14 |
| 5 | diffuse-porous | 3 |
| 6 | vessels in intra-annual tangential rows | 1 |
| 9 | vessels predominantly solitary | 15 |
| 9.1 | vessels in radial multiples of 2-4 common | 8 |
| 11 | vessels predominantly in clusters | 2 |
| 13 | vessels with simple perforation plates | 17 |
| 22 | intervessel pits alternate | 17 |
| 39.1 | vessel cell-wall thickness >2 µm | 8 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 14 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 4 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 11 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 5 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 4 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 13 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 4 |
| 65 | septate fibers present | 8 |
| 68 | fibers thin-walled | 3 |
| 69 | fibers thick-walled | 2 |
| 70 | fibers thin- to thick-walled | 13 |
| 70.2 | tension wood present | 7 |
| 75 | parenchyma absent or unrecognizable | 15 |
| 79 | parenchyma paratracheal | 2 |
| 96 | rays uniseriate | 4 |
| 97 | ray width predominantly 1-3 cells | 12 |
| 100.2 | rays not visible in polarized light | 2 |
| 104 | ray: all cells procumbent (radial section) | 1 |
| 105 | ray: all cells upright or square | 13 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| R2 | groups of sieve tubes in tangential rows | 3 |
| R4 | sclereids in phloem and cortex | 14 |
| R11 | with rhaphides | 16 |
| R13 | tannins in parenchyma cells | 15 |

# Cneoraceae



**Number of species, worldwide and in Europe**

The Cneoraceae family includes 2 genera with 3 species occurring in Cuba, on the Canary Islands and in SW-Europe.

**Analyzed species:**
*Cneorum tricoccum* L.
*Neochamaelea pulverulenta* Ertm.

**Analyzed material**

The xylem and phloem of 2 genera with 2 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 2 | 2 |
| **Plants analyzed from different vegetation zones:** | | |
| Mediterranean | 1 | |
| Subtropical | 1 | |

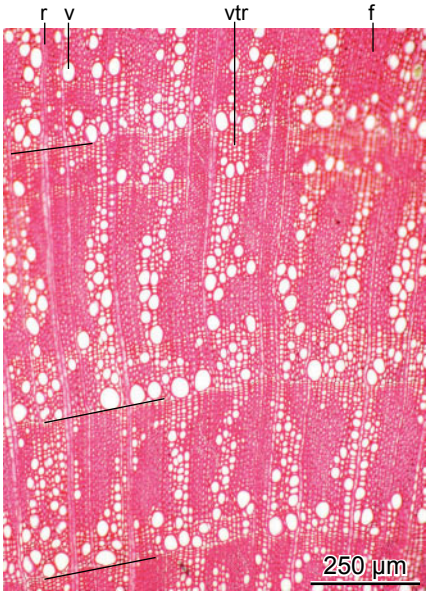
**Right:** *Cneorum tricoccum* (photo: Stützel)

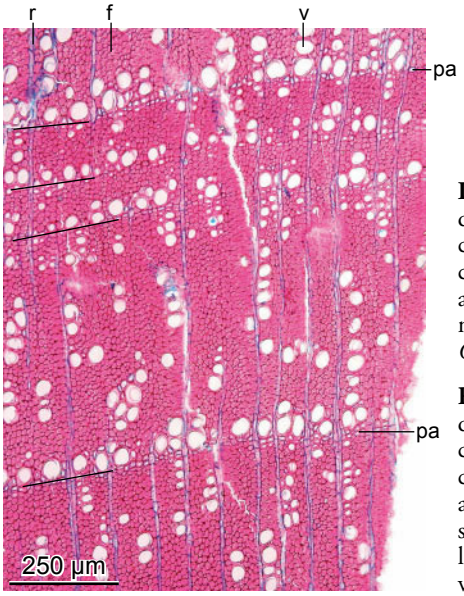
*Neochlamaea pulverulenta*

**Characteristics of the xylem**

Both species are semi-ring-porous and have distinct annual rings (**Figs. 1** and **2**). Ring boundaries are indicated by a discontinuous row of terminal parenchyma cells. Latewood vessels are arranged in radial and, occasionally, slightly diagonal patterns. Earlywood vessel diameter varies from 20-40 µm and vessel density from of 200-300/mm$^2$ (**Figs. 1** and **2**). Vessels have simple perforations and large intervessel pits (**Figs. 3** and **4**). Helical thickenings occur in *Cneorum tricoccum* (**Fig. 3**).

Parenchyma is scanty paratracheal, terminal or apotracheal diffuse and often difficult to recognize (**Figs. 1** and **2**). Both species have homocellular rays with procumbent cells (**Figs. 3** and **4**). Rays are 1-3-seriate in *Cneorum triccocum* (**Fig. 5**) and are mostly uniseriate in *Neochamaelea pulverulenta* (**Fig. 6**). Large prismatic crystals are very frequent in rays of *Cneorum tricoccum* (**Fig. 7**) and in axial chambered cells in *Neochamaelea pulverulenta* (**Fig. 8**).




**Left Fig. 1.** Semi-ring-porous xylem with distinct rings. Ring boundaries are indicated by thin-walled terminal parenchyma cells. Latewood vessels are arranged in radial multiples. Stem of an 80 cm-high shrub, maccia, Mediterranean zone, Mallorca. *Cneorum tricoccum*, transverse section.

**Right Fig. 2.** Semi-ring-porous xylem with distinct rings. Ring boundaries are indicated by thin-walled terminal parenchyma cells. Fibers are very thick-walled. Stem of an 80 cm-high shrub, dry succulent zone, subtropical climate, Gomera, Canary Islands. *Neochamaelea pulverulenta*, transverse section.

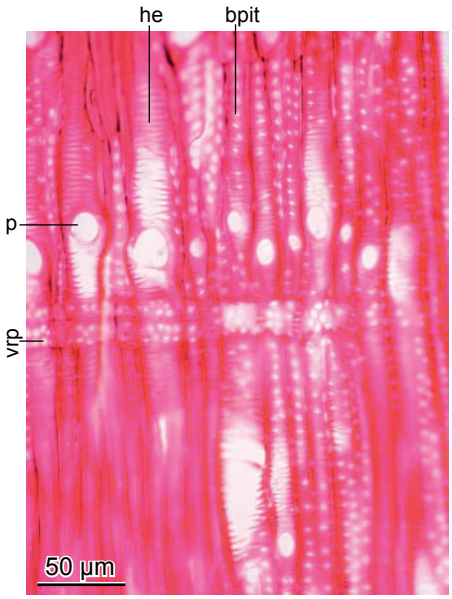



**Fig. 3.** Vessels with simple perforations and helical thickenings. Stem of an 80 cm-high shrub, maccia, Mediterranean zone, Mallorca. *Cneorum tricoccum*, radial section.

**Fig. 4.** Vessels with simple perforations. Helical thickenings are absent. Stem of an 80 cm-high shrub, dry succulent zone, subtropical climate, Gomera, Canary Islands. *Neochamaelea pulverulenta*, radial section.

**Fig. 5.** 1-3-seriate rays. Stem of an 80 cm high shrub, maccia, Mediterranean zone, Mallorca. *Cneorum tricoccum*, tangential section.

**Fig. 6.** Uniseriate rays. Stem of an 80 cm-high shrub, dry succulent zone, subtropical climate, Gomera, Canary Islands. *Neochamaelea pulverulenta*, tangential section.

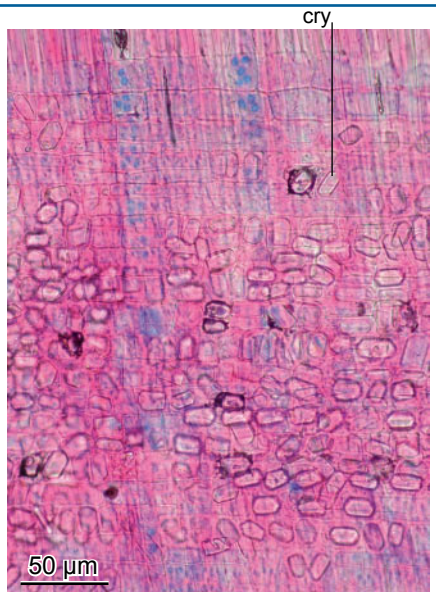



**Fig. 7.** Large prismatic crystals in ray cells. Stem of an 80 cm-high shrub, maccia, Mediterranean zone, Mallorca. *Cneorum tricoccum*, radial section.

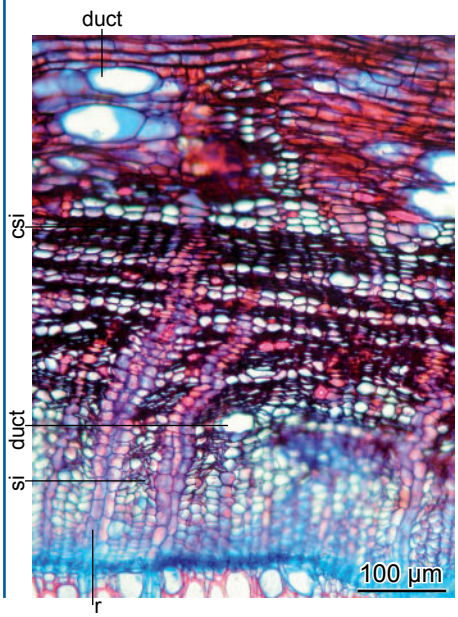
**Fig. 8.** Large prismatic crystals in axial chambered cells. Stem of an 80 cm-high shrub, dry succulent zone, subtropical climate, Gomera, Canary Islands. *Neochamaelea pulverulenta*, radial section, polarized light.

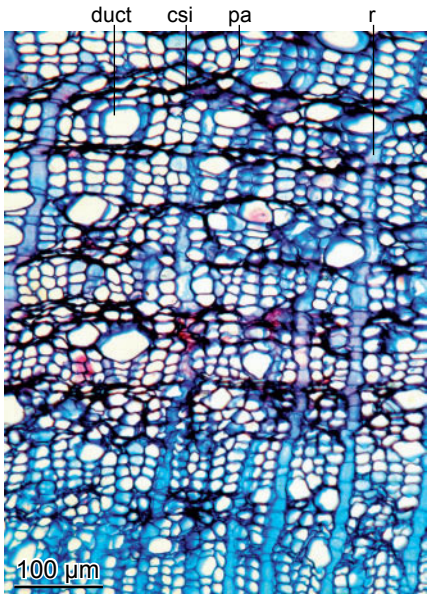
### Characteristics of the phloem and the cortex

Phloem structures of both species are similar. Sieve-tubes and parenchyma cells are arranged in tangential rows. Sieve-tubes collapse in older parts (**Figs. 9** and **10**). Irregularly distributed sclerenchyma cells occur solitarily or in small groups. Ducts are characteristic (**Figs. 9** and **10**). Small prismatic crystals are frequent.

### Discussion in relation to previous studies

The xylem of *Cneorum tricoccum* has been described by several authors, e.g. by Huber and Rouschal (1954), Greguss (1945), Carlquist (1988) and Schweingruber (1990). Described for the first time are the xylem of *Neochamaelea pulverulenta* and the phloem of *Cneorum* and *Neochamaelea*. Radial vessel-distribution, helical thickenings, ray structure, the paratracheal parenchyma and the occurrence of ducts in the bark show taxonomic relationships to the genus *Ruta*.




**Left Fig. 9.** Phloem with tangential layers of parenchyma, collapsed sieve tubes. Stem of an 80 cm-high shrub, maccia, Mediterranean zone, Mallorca. *Cneorum tricoccum*, transverse section.

**Right Fig. 10.** Phloem with tangential layers of parenchyma, collapsed sieve tubes, and tangentially arranged ducts. Stem of an 80 cm-high shrub, dry succulent zone, subtropical climate, Gomera, Canary Islands. *Neochamaelea pulverulenta*, transverse section.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **2** |
| 1 | growth rings distinct and recognizable | 2 |
| 4 | semi-ring-porous | 2 |
| 7 | vessels in diagonal and/or radial patterns | 1 |
| 10 | vessels in radial multiples of 4 or more common | 2 |
| 13 | vessels with simple perforation plates | 2 |
| 22 | intervessel pits alternate | 2 |
| 36 | helical thickenings present | 1 |
| 39.1 | vessel cell-wall thickness >2 µm | 2 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 2 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 2 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 2 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 2 |
| 69 | fibers thick-walled | 2 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 79 | parenchyma paratracheal | 2 |
| 89 | parenchyma marginal | 2 |
| 96 | rays uniseriate | 2 |
| 97 | ray width predominantly 1-3 cells | 1 |
| 104 | ray: all cells procumbent (radial section) | 2 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 1 |
| 136 | prismatic crystals present | 1 |
| 142 | prismatic crystals in axial chambered cells | 1 |
| R2 | groups of sieve tubes in tangential rows | 2 |
| R3 | distinct ray dilatations | 2 |
| R4 | sclereids in phloem and cortex | 2 |
| R7 | with prismatic crystals | 2 |
| R12 | with laticifers, oil ducts or mucilage ducts | 2 |

# Crassulaceae



**Number of species, worldwide and in Europe**

The Crassulaceae family includes 35 genera with 1500 species. In Western Europe there are 12 genera with 101 species. The majority belongs to *Sedum* (57) and *Sempervivum* (23). Most of the species are widespread from tropical to boreal regions and often grow in arid habitats (Judd et al. 2002). Four genera with 75 species are endendemic to Macaronesia, from which the majority belongs to *Aeonium* (35), *Monanthes* (16) and *Aichryson* (4).

**Analyzed material**

The xylem and phloem from 31 species of Crassulaceae are analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 3 | 16 |
| Semi-woody chamaephytes | 1 | |
| Woody chamaephytes | 5 | |
| Hemicryptophytes and geophytes | 21 | 1 |
| Therophytes | 2 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 3 | |
| Hill and mountain | 15 | |
| Mediterranean | 1 | |
| Subtropical | 13 | |

**Analyzed species:**

*Aeonium arboreum* (L.) Webb *et* Berth.
*Aeonium decorum* Webb ex Christ
*Aeonium simsii* (Sw.) Stern
*Aeonium smithii* Webb ex Berth.
*Aeonium spathulatum* (Hornem.) Praeg
*Aeonium undulatum* Webb
*Aeonium urbicum* (Chr. S.) Webb
*Aeonium viscatum* Bolle
*Aichryson parlatorei* Bolle
*Amerosedum lanceolatum* Löve and Löve
*Greenovia diplocyla* Bolle
*Jovibarba arenaria* W.D. J. Koch
*Jovibarba hirta* (L.) Opiz
*Monanthes brachycaulon* Lowe
*Monanthes pallens* (Webb) Christ
*Rhodiola integrifolia* (Raf.) Löve and Löve
*Rhodiola rosea* L.
*Sedum album* L.
*Sedum alpestre* Vill.
*Sedum anopetalum* DC
*Sedum atratum* L.
*Sedum cepaea* L.
*Sedum dasyphyllum* L.
*Sedum reflexum* L.
*Sedum rupestre* L.
*Sedum telephium* L.
*Sempervivum arachnoideum* L.
*Sempervivum montanum* L.
*Sempervivum tectorum* L.
*Sempervivum wulfenii* Met. et W.D. J. Koch
*Umbilicus rupestris* (Salis.) Dandy

*Aeonium* sp.

*Jovibarba* sp. (photo: Lauerer)

*Sedum acre* (photo: Landolt)

*Rhodiola rosea* (photo: Landolt)

*Sedum telephium* (photo: Zinnert)

*Sempervivum montanum* (photo: Zinnert)

**Characteristics of the xylem**

Annual rings occur in the present material in most genera apart from *Umbilicus* and *Monanthes*. Rings are distinct and frequent in the temperate zone in most *Sedum* (**Fig. 1**) and *Rhodiola* (**Fig. 2**) but indistinct in *Jovibarba* and *Sempervivum* species. Ring distinctness is indicated by semi-ring porosity (**Figs. 1**, **2** and **4**), or radially flat latewood fibers (**Fig. 3**). Annual rings are less frequent in the subtropical climate and have been found only in *Greenovia brachycaule*, *Aeonium arboreum* and *A. urbicum* (**Fig. 3**). The diameter of the small, round and fairly thick-walled vessels (1.5-2 µm) is 15-35 µm (**Fig. 4**). Sometimes the vessels can hardly be distinguished from the fiber tissue (*Sedum anopetalum*; **Fig. 5**). Vessel density varies from 200-500/mm$^2$. Vessels contain exclusively simple perforations. Imperforate vessel cell walls (annular to slightly reticulate thickening) and simple perforations are characteristic of all members of the Crassulaceae (**Fig. 6**).

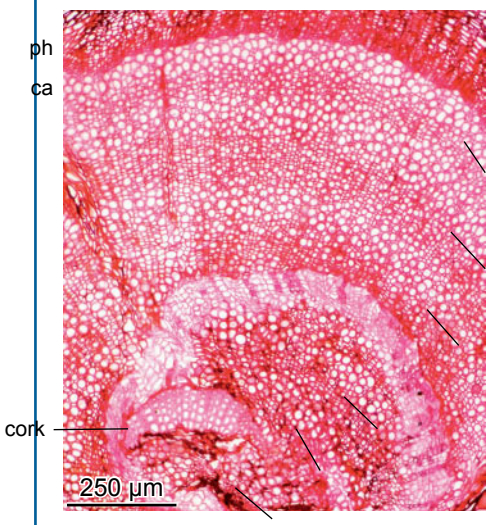



**Fig. 1.** Six recognizable annual rings in a semi-ring-porous, rayless xylem; ring boundaries are marked by the difference in pore size between latewood and earlywood. A closed ring of cork delimits the inner and outer part of the stem. Rhizome of a 10 cm-high succulent herb, dry rock, hill zone, Alps, Switzerland. *Sedum album*, transverse section.

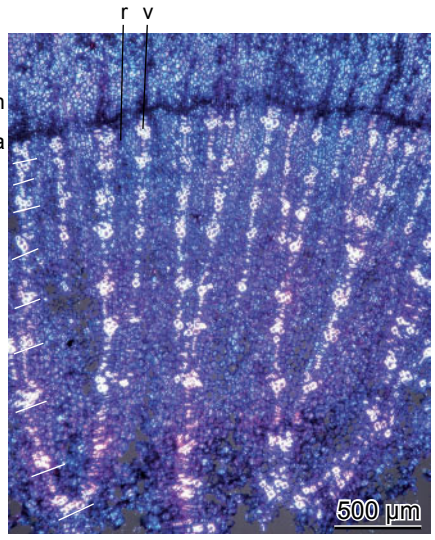



**Fig. 2.** Distinct annual rings in a semi-ring-porous xylem. Between the radial vessel/parenchyma strips are very large rays with thin-walled cells. See also **Fig. 7**. Rhizome of a 20 cm-high succulent herb, dry rock, mountain zone, Alps, Switzerland. *Rhodiola rosea*, transverse section, polarized light.

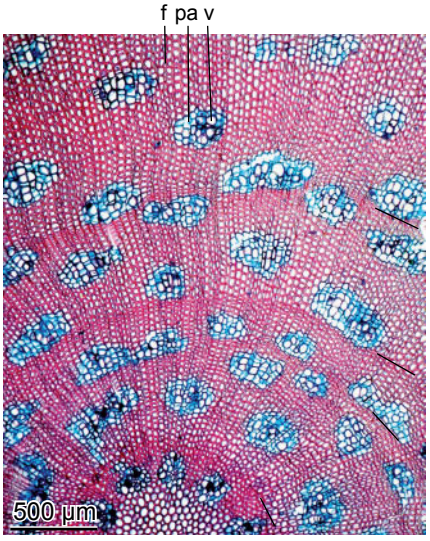



**Fig. 3.** Distinct rings in the fiber zone. Ring boundaries are marked by the radial flat fibers in the latewood. Stem of a 60 cm-high succulent shrub, seasonal dry subtropical climate, dry volcanic rock, succulent zone, Tenerife, Canary Islands. *Aeonium urbicum*, transverse section.

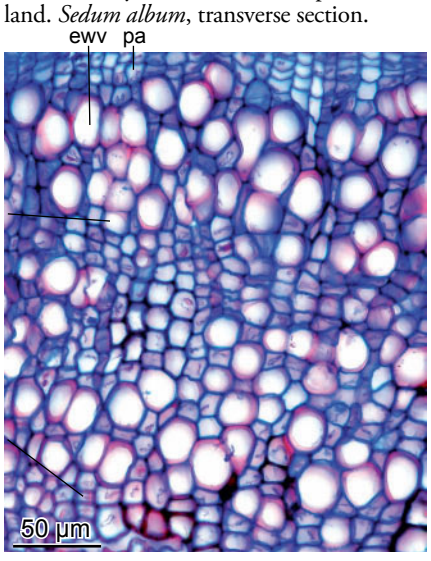



**Fig. 4.** Round, fairly thick-walled, lignified vessels with a diameter of appr. 25 µm are characteristic of most species of the Crassulaceae family. Vessels are surrounded by thin-walled unlignified parenchyma (perivasive). Stem of a 15 cm-high succulent herb, dry rock, hill zone, Alps, Switzerland. *Sedum rupestre*, transverse section.

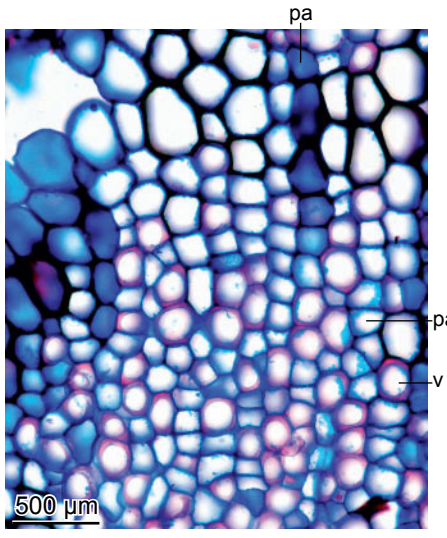



**Fig. 5.** Round, fairly thick-walled, lignified vessels with a diameter of approximately <20 µm have approximately the same size as the surrounding unlignified parenchyma cells. Polar root of a 15 cm-high succulent herb, dry rock, hill zone, Alps, France. *Sedum anopetalum*, transverse section.

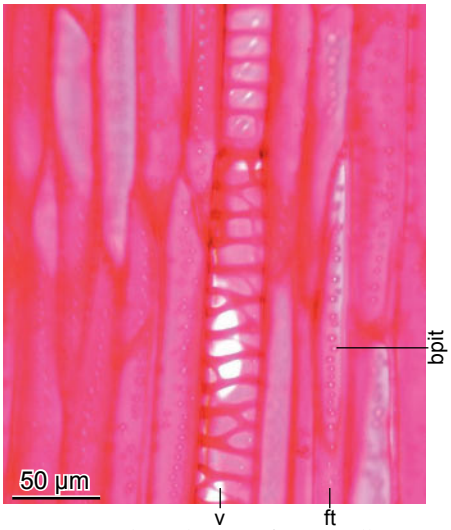



**Fig. 6.** Vessels with imperforate walls (reticulate pitting) and libriform fibers with many, very small (<2 µm), slightly bordered pits. Stem of a succulent 60 cm-high shrub, seasonal dry subtropical climate, dry volcanic rock, Tenerife, Canary Islands. *Aeonium undulatum*, radial section.

Fibers are short, and the radial walls are perforated by very small slit-like or round pits (<2 µm; **Fig. 6**). Occurrence and fiber distribution is very variable:

*Type 1:* Fibers, if present, are thin-walled in *Sedum album* (**Fig. 1**), *Sempervivum arachnoideum*, *S. wulfenii*, *Rhodiola* (**Fig. 7**) and *Monanthes*.

*Type 2:* A closed latewood-like ring of fibers is characteristic of *Jovibarba* (**Fig. 8**), *Umbilicus*, *Sedum alpestre*, *S. atratum* and *S. cepaea* and *Aichryson* (**Fig. 9**).

*Type 3:* Intra-annual fiber bands are characteristic of *Greenovia*, *Sedum anopetalum*, *S. dasyphyllum*, *S. reflexum*, *S. rupestre* (**Fig. 10**) and *Aeonium simsii*.

*Type 4:* Tangential bands of fiber groups are characteristic of *Rhodiola* and *Sempervivum tectorum* (**Fig. 11**).

*Type 5:* A dense fiber-tissue with enclosed vessel-parenchyma spots is characteristic of all *Aeonium* species (**Fig. 12**) and the annual shoots of *Sedum telephium* (intervascular axial parenchyma, Carlquist 2001). The anatomy of the xylem of *Sedum telephium* (**Fig. 13**) is more closely related to *Aeonium* than to *Sedum*.

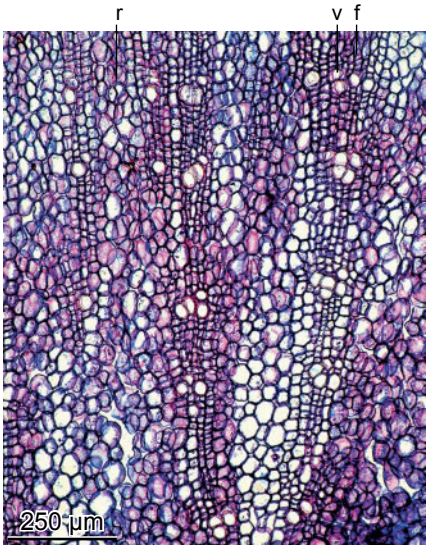



**Fig. 7.** *Fiber type 1.* Thin-walled fibers and vessels, arranged in radial strips between large rays. Fibers not distinguishable from parenchyma in the transverse section. Rhizome of a 20 cm-high succulent herb, dry rock, mountain zone, Alps, Switzerland. *Rhodiola rosea*, transverse section, polarized light.

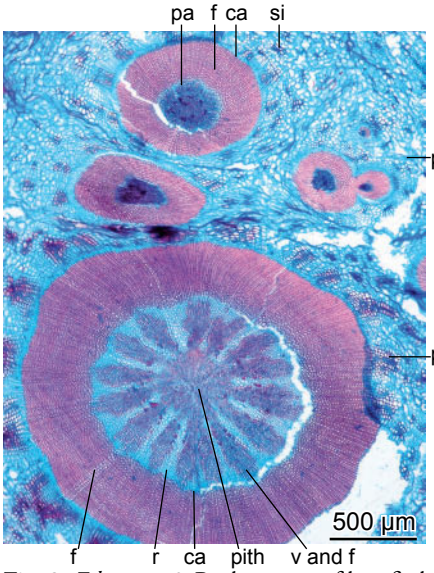



**Fig. 8.** *Fiber type 2.* Rayless rings of lignified fibers surround the central parts, consisting of large rays and a fiber/parenchyma tissue. Rootstock of a 20 cm-high succulent herb, dry rock, mountain zone, Little Carpathians, Slovakia. *Jovibarba hirta*, transverse section.

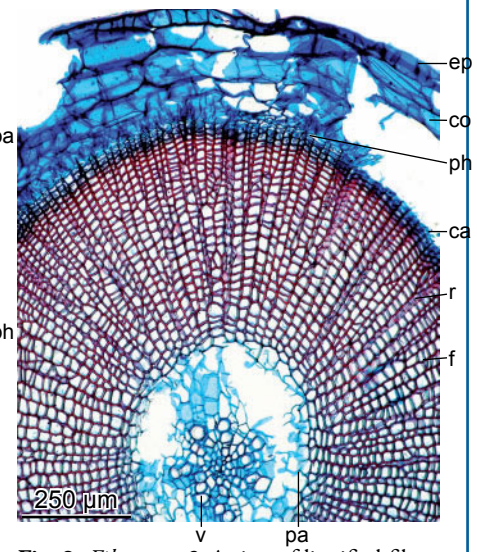



**Fig. 9.** *Fiber type 2.* A ring of lignified fibers without rays and vessels surrounds the central part consisting of a rayless fiber/parenchyma tissue. Root collar of a succulent 10 cm-high herb, seasonal dry subtropical climate, moist volcanic rock, Gomera, Canary Islands. *Aichryson parlatorei*, transverse section.

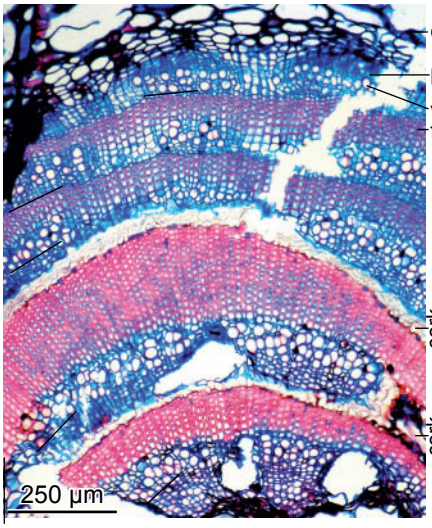



**Fig. 10.** *Fiber type 3.* Alternating zones of vesselless fibers, vessel/parenchyma and cork. Root collar of a perennial succulent 10 cm-high herb, hill zone, dry meadow, Alps, France. *Sedum rupestre*, transverse section.

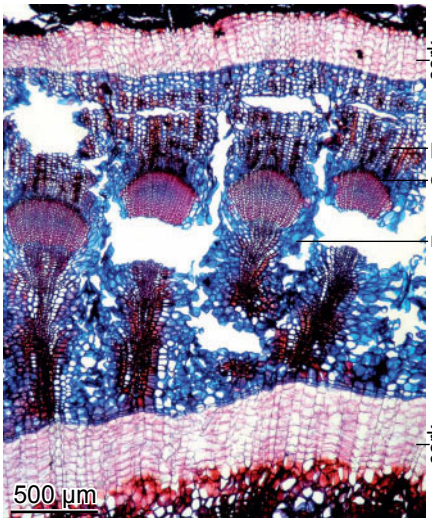



**Fig. 11.** *Fiber type 4.* Between 2 cork bands is a circle of thick-walled fibers and, centripetally, strips of vessel/parenchyma cells. Ray-like zones limit the radial-oriented zones. Root collar of a perennial, succulent 15 cm-high herb, hill zone, dry rock, Alps, France. *Sempervivum tectorum*, transverse section.

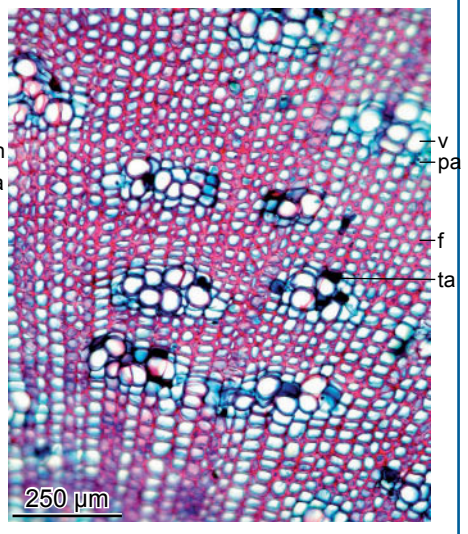


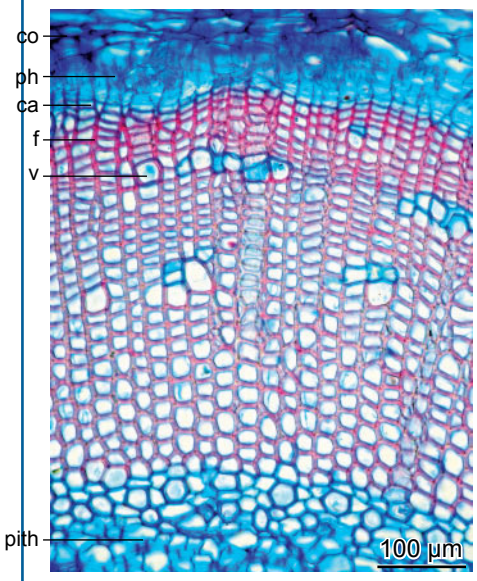

**Fig. 12.** *Fiber type 5.* Vessel/parenchyma groups of cells are embedded in a rayless fiber zone. Some cells contain tannins (dark brown). Stem of a succulent 50 cm-high shrub, laurel zone, subtropical climate, volcanic rock, Gomera, Canary Islands. *Aeonium viscatum*, transverse section.

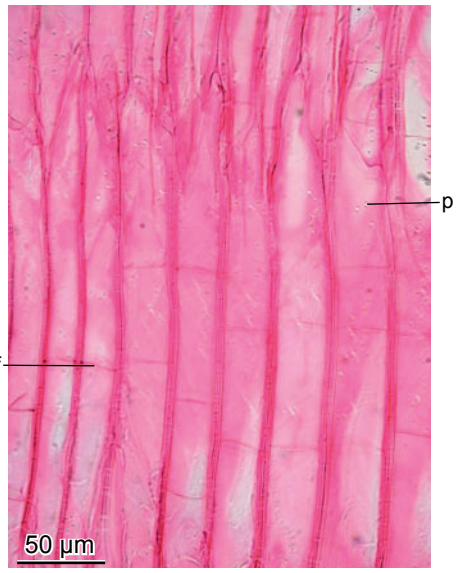
Septate fibers have been found in *Sedum reflexum* and *Aeonium smithii* (**Fig. 14**). If the fibers are thin-walled, it is difficult to distinguish them from parenchyma cells, e.g. in *Sedum cepaea*, *Sempervivum arachnoideum* and *Rhodiola*.

The distribution of axial parenchyma varies greatly. It is typically pervasive in species without distinct fibers, e.g. in *Sedum album* (fiber type 1). It occurs only in the center of the stems (fiber type 2), between tangential fiber bands (fiber type 3), on radial strips (fiber type 4) or around vessels embedded in a dense fiber tissue (fiber type 5).

Rays are mostly absent. Small and large rays have been observed only in *Rhodiola rosea* (**Fig. 15**). Exclusively large rays occur in *Rhodiola integrifolia* (**Fig. 16**). Large rays in the thin-walled vessel/parenchyma tissue (fiber type 4) occur in *Sedum anopetalum* and *Sempervivum tectorum* (**Fig. 11**). Large rays rarely occur in the thin-walled tissue (fiber type 1), e.g in *Jovibarba* (**Fig. 17**).

Cells of large rays are always square or upright in radial section. Interxylary cork layers have been found in *Sedum* and *Sempervivum* species (**Figs. 10** and **11**).




**Left Fig. 13.** *Fiber type 5.* Vessel groups are embedded in a rayless fiber zone. Annual flowering shoot of a 40 cm-high succulent herb, cultivated, garden, hill zone, Switzerland. *Sedum telephium*, transverse section.

**Right Fig. 14.** Septate fibers of the vesselless fiber zone. Stem of a succulent 40 cm-high shrub, thermophile zone, subtropical climate, volcanic rock, Gomera, Canary Islands. *Aeonium smithii*, radial section.

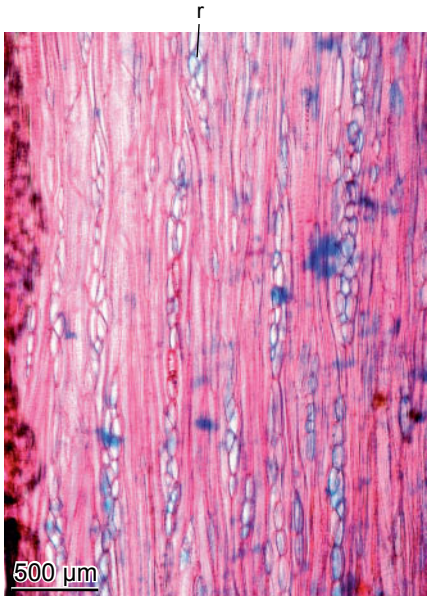



**Fig. 15.** 1-3-seriate rays with upright and square cells in the fiber zone. It is the only plant in the family of Crassulaceae with such rays. Rhizome of a 20 cm-high succulent herb, dry rock, mountain zone, Alps, Switzerland. *Rhodiola rosea*, tangential section.

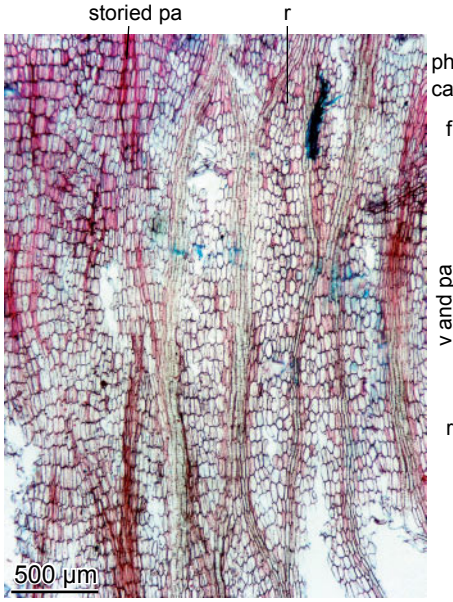



**Fig. 16.** Large rays with thin-walled cells inbetween strips of storied parenchyma and vessels. Rhizome of a succulent herb, meadow, subalpine zone, Rocky Mountains, Colorado, USA. *Rhodiola integrifolia*, tangential section.

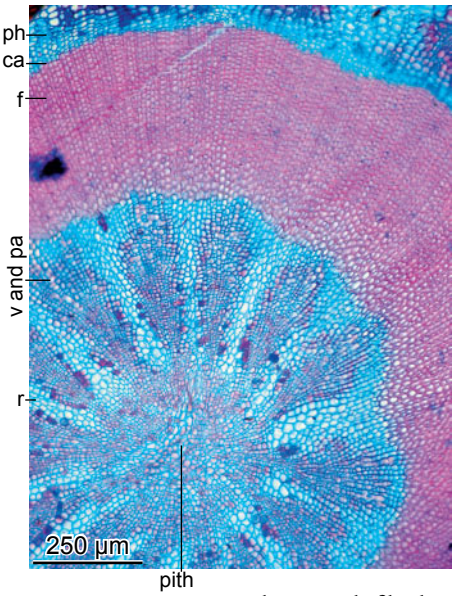



**Fig. 17.** Large rays in the central, fiberless zone. Rays are absent in the fiber zone. Rootstock of a 20 cm-high succulent herb, dry rock in the mountain zone, Little Carpathians, Slovakia. *Jovibarba hirta*, transverse section.

**Characteristics of the phloem and the cortex**

The cortex cells of all succulent plants are extremely large (120-200 µm; **Fig. 18**). Distinct sieve-tube groups occur in all species of the Crassulaceae (**Figs. 19** and **20**). Groups are arranged in tangential rows in the phloem of *Sempervivum arachnoideum* and *S. wulfenii* (**Fig. 21**). Sclereids are absent in all species of the Crassulaceae. Cells filled with dark substances (tannins) are characteristic of most *Aeonium* species and some *Sedum* species (**Fig. 22**). They seem to be absent in *Aichryson*, *Monanthes*, *Greenovia*, *Umbilicus*, *Rhodiola* and *Sempervivum*.

Crystals are frequent and the cortex cells of some species contain small druses (*Sedum, Sempervivum, Monanthes*). Small acicular crystals occur in some *Aeonium* species and crystal sand occurs mainly in *Aeonium* and *Monanthes*. Crystal sand is deposited in idioblasts in the cortex of *Umbilicus* (**Fig. 23**).

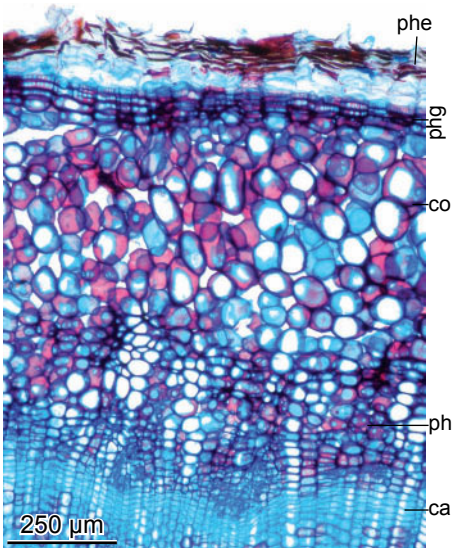



**Fig. 18.** Large parenchyma cells (150 µm) in the cortex of a succulent plant (see also **Fig. 22**). Polar root of a 15 cm-high succulent herb, dry rock, hill zone, Alps, France. *Sedum anopetalum*, transverse section.

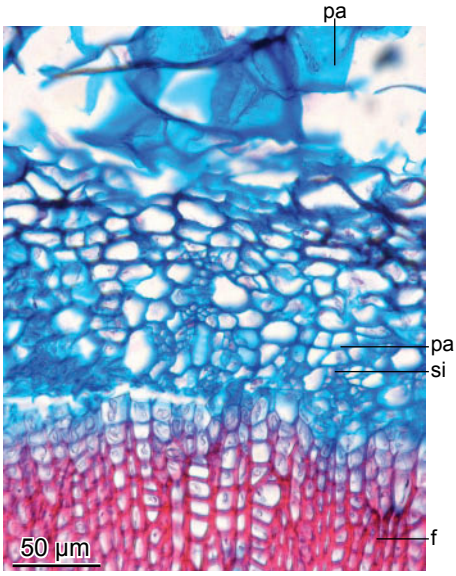



**Fig. 19.** Small groups of small sieve tubes between large parenchyma cells in the phloem. The cortex consists of very large parenchyma cells. Polar root of a 5 cm-high succulent herb, dry rock, subalpine zone, Alps, Switzerland. *Sedum alpestre*, transverse section.

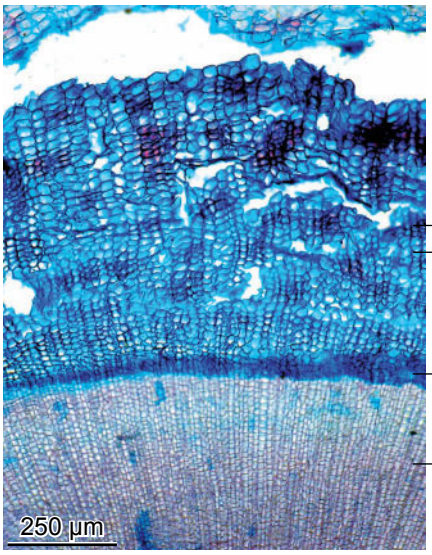



**Fig. 20.** Small groups of small sieve tubes (dark blue) in the phloem. Polar root of a 10 cm-high succulent herb, cultivated on a rock, hill zone, Alps, Switzerland. *Jovibarba arenaria*, transverse section.

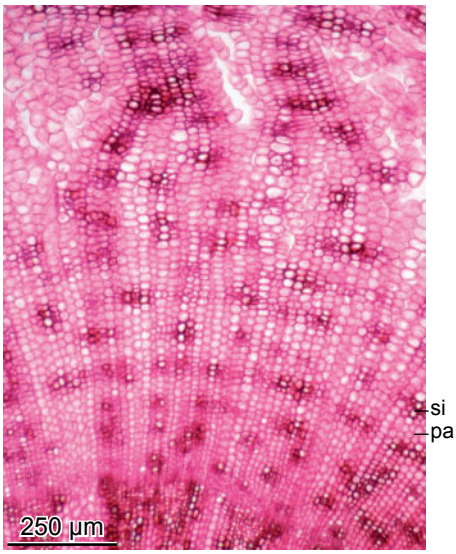



**Fig. 21.** Small groups of small sieve tubes (dark red) are oriented in tangential rows in the phloem. Polar root of a 15 cm- high succulent herb, dry rock, hill zone, Alps, Switzerland. *Sempervivum tectorum*, transverse section.

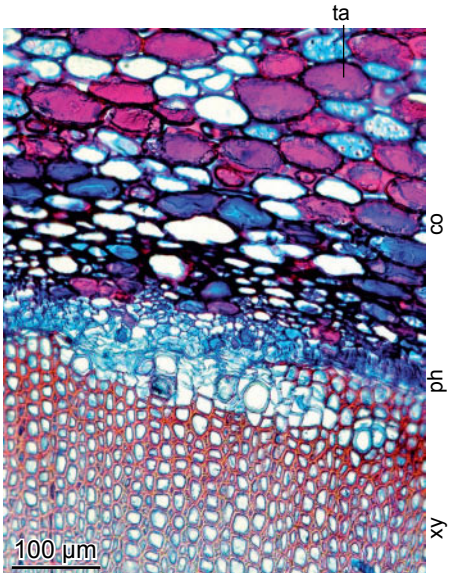



**Fig. 22.** Dark substances, probably tannins, in large parenchyma cells of the cortex. Stem of a small succulent shrub, seasonal dry subtropical climate, dry volcanic rock, succulent zone, Gomera, Canary Islands. *Aeonium decorum*, transverse section.

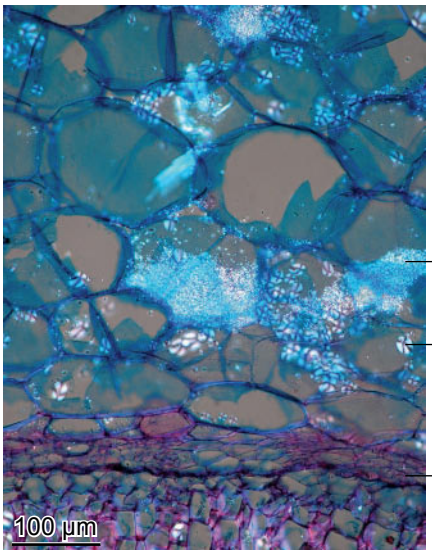



**Fig. 23.** Crystal sand in idioblasts of the cortex. Root collar of a herb, seasonal dry subtropical climate, moist volcanic rock, succulent zone, Gomera, Canary Islands. *Umbilicus horizontalis*, transverse section, polarized light.

**Ecological trends in the xylem**

The temperate zone of Europe and the subtropical climate of the Macaronesian zone is primarily distinguished by the occurrence of different genera. *Sedum*, *Sempervivum*, *Jovibarba* and *Rhodiola* occur in Europe. *Aeonium*, *Aichrysum*, *Greenovia* and *Monanthes* occur in Macaronesia. Interxylary cork exists only in European species. Annual rings are more frequent in Europe than in Macaronesia. Crystals are more frequent in Macaronesian than in European species. There is a slight tendency on a gradient from Europe to Macaronesia. Macaronesian plants to have increasingly larger vessels. Altitudinal gradients do not exist.

**Ecological trends in the phloem and the cortex**

No ecological trends were detected.

**Discussion in relation to revious studies**

The most extensive wood anatomical study of woody species is that of Blesa et al. (1979). The study includes a total of 16 species of the genera *Aeonium*, *Greenovia*, *Aichryson* and *Monanthes* from the Canary Islands. Solereder (1908) characterized the anomalous radial growth of *Sedum populifolium*, Hamet (1925) described 2 species (*Greenovia*, *Echeveria*).

't Hart and Koek-Norman (1989) analyzed 9 woody *Sedum* species and Schweingruber (1990) one *Aeonium* and 3 *Sedum* species.

Most observations of earlier studies could be confirmed e.g. the occurrence imperforate vessel walls, the intervascular axial parenchyma and the absence of rays. The present study differs from the previous studies because all authors concentrated on shrubs and dwarf shrubs. The present study includes also herbaceous growth forms from Europe and the Canary Islands. Therefore it was possible to recognize ecological trends and 5 different anatomical types on the basis of fiber and parenchyma distribution.

**Present features in relation to the number of analyzed specimens**

| IAWA code | | frequency |
|---|---|---|
| **Total number of specimens** | | |
| **(31 species; *Sedium telephium* bulb and annual shoot)** | | **32** |
| 1 | growth rings distinct and recognizable | 16 |
| 2 | growth rings indistinct or absent | 11 |
| 2.1 | only one ring | 5 |
| 4 | semi-ring-porous | 11 |
| 5 | diffuse-porous | 1 |
| 9 | vessels predominantly solitary | 31 |
| 11 | vessels predominantly in clusters | 24 |
| 13 | vessels with simple perforation plates | 29 |
| 20.1 | intervessel pits pseudoscalariform to reticulate | 31 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 18 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 15 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 7 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 23 |
| 58 | dark-stained substances in vessels and/or fibers present (gum, tannins) | 6 |
| 60.1 | fibers absent | 3 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 29 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 2 |
| 68 | fibers thin-walled | 4 |
| 69 | fibers thick-walled | 1 |
| 70 | fibers thin- to thick-walled | 24 |
| 70.1 | intra-annual thick-walled tangential fiber bands | 9 |
| 75 | parenchyma absent or unrecognizable | 1 |
| 79 | parenchyma paratracheal | 13 |
| 79.1 | parenchyma pervasive | 10 |
| 79.2 | parenchyma intervascular, Crassulaceae type | 12 |
| 96 | rays exclusively uniseriate | 1 |
| 97 | ray width predominantly 1-3 cells | 5 |
| 98 | rays commonly 4-10-seriate | 6 |
| 99 | rays commonly >10-seriate | 1 |
| 99.1 | vascular-bundle form remaining | 1 |
| 99.2 | stem lobed | 1 |
| 100.2 | rays not visible in polarized light | 3 |
| 101 | aggregate rays | 0 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 27 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 2 |
| 117 | rayless | 17 |
| 136 | prismatic crystals present | 28 |
| 144 | druses present | 2 |
| R4 | sclereids in phloem and cortex | 4 |
| R6 | sclereids in radial rows | 7 |
| R.6.1 | sclereids in tangential rows | 1 |
| R7 | with prismatic crystals | 1 |
| R8 | with crystal druses | 12 |

# Cucurbitaceae



### Number of species, worldwide and in Europe

The cosmopolitean Cucurbitaceae family includes 118 genera with 825 species. In Europe, there are 8 genera with 14 species. This number includes cultivated species, e.g. *Cucumis* and *Cucurbita*.

**Analyzed species:**
*Bryonia dioeca* Jacq., shoot and tuber
*Bryonia verrucosa* Ait.
*Citrullus colocynthis* (L.) Schrad., shoot and tuber
*Cucurbita maxima* Duch. ex Lam., root collar
*Cucurbita pepo* L., shoot
*Cucumis sativus* L., shoot
*Ecballium elaterinum* (L.) Rich., shoot and tuber

### Analyzed material

The xylem and phloem of 5 genera with 7 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | | 4 |
| Hemicryptophyte with annual, liana-like shoots | 4 | 22 |
| Therophytes with annual, liana-like shoots | 3 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 4 | |
| Mediterranean | 1 | |
| Subtropical | 1 | |
| Arid | 1 | |

*Bryonia dioeca*

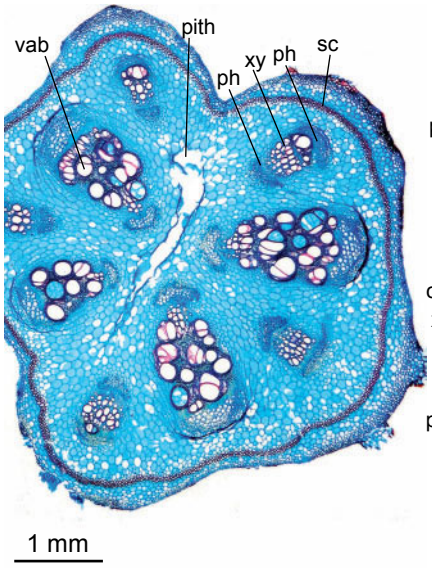
*Cucurbita sativa*

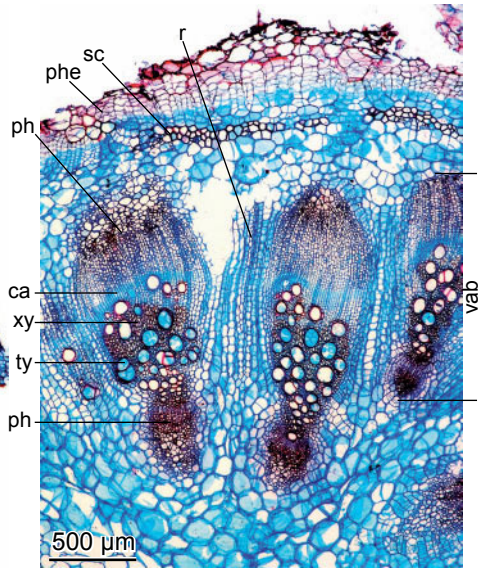
*Citrullus colocynthis*

**Characteristics of the xylem**

The constructions of annual shoots, including those of hemicryptophytes, is consistent. Radially arranged bi-collateral vascular bundles surround the pith (**Figs. 1-3**). Vascular bundles are divided into two parts: the centripetal part consists of a centripetal phloem and a centrifugal metaxylem (**Figs. 4** and **5**) with distinct helical thickenings (**Fig. 6**). A cambium between the xylem and phloem does not exist. The external part represents a vascular bundle with a centripetal xylem, a cambium, and a centrifugal phloem (**Figs. 4** and **5**). Large primary rays separate vascular bundles laterally. Secondary large rays are initiated in the xylem of the vascular bundles (**Fig. 5**). Radial growth between vascular bundles is possible, initiated by an inter-vascular cambium (**Fig. 5** and detailed illustration).

Successive cambia occurring in roots and tubers of perennial species of vascular bundles are arranged in concentric rings in *Bryonia*, *Citrullus* and *Ecballium* (**Fig. 7**). Vessels of most species are arranged solitary (**Figs. 1**, **2** and 7). The diameter of large vessels varies from 150-250 µm. Vessels are short and thick-walled (**Fig. 8**) with simple perforations.




**Left Fig. 1.** Isolated vascular bundles are embedded in parenchyma tissue. The shoot is surrounded by a band of fibers within the cortex. 2 m-long, lying, liana-like annual shoot, therophyte, garden, hill zone, Zürich, Switzerland. *Cucumis sativus*, transverse section.

**Right Fig. 2.** Isolated vascular bundles are embedded in parenchyma tissue. Bundles are separated by large, primary rays. The shoot is surrounded by a band (broken) of fibers within the cortex. The annual shoot has already formed a phellem. 1.5 m-long, lying, liana-like annual shoot, geophyte with a tuber, ruderal site, Mediterranean zone, Estremadura, Spain. *Ecballium elaterinum*, transverse section.

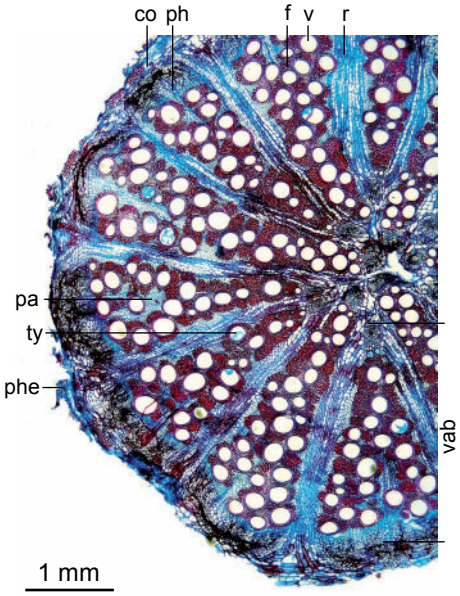



**Fig. 3.** Long vascular bundles between unlinigifed large rays. Vessels are surrounded by lignified paratracheal and unlignified apotracheal parenchyma. A few vessels contain unlignified tylosis. 3 m-long, lying, liana-like annual shoot, geophyte with a tuber, grazed wadi, arid zone, Sahara, Libya. *Citrullus colocynthis*, transverse section.

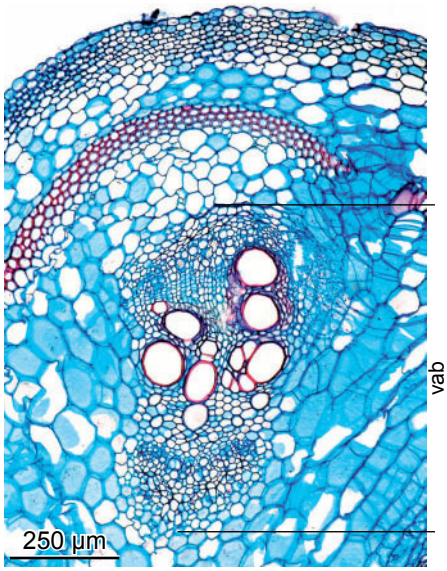



**Fig. 4.** Sector of an annual shoot with a bi-collateral vascular bundle. A cambium occurs only in the external part. 2 m-long, lying, liana-like annual shoot, therophyte, garden, hill zone, Zürich, Switzerland. *Cucumis sativus*, transverse section. See detailed illustration.

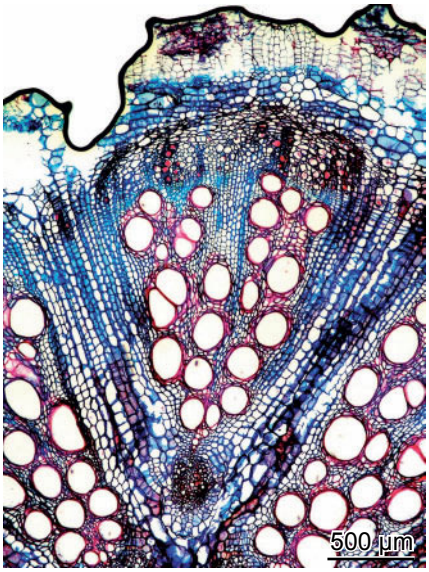



**Fig. 5.** Sector of an annual shoot with a bi-collateral vascular bundle. A cambium occurs only in the external part. 2 m-long annual shoot, geophyte with a tuber, ruderal site, Mediterranean, Santa Pau, Catalonia, Spain. *Bryonia dioeca*, transverse section. See detailed illustration.

Inter-vessel pits are predominantly small and round; they are arranged in opposite position in *Citrullus* (**Fig. 8**) and scalariform in the other species (**Fig. 9**). Small, thin-walled, unlignified tylosis occur in *Cucumis*, *Citrullus* and *Ecballium* (**Figs. 1** and **2**). Fibers are absent in *Cucumis sativus* (**Fig. 4**) and thin- to thick-walled with large pits in the other species. Septate fibers have been observed in *Citrullus* and *Cucumis* (**Fig. 10**).

The axial parenchyma is mostly paratracheal, though it can be locally apotracheal to pervasive, e.g. in the tubers of *Bryonia*, *Citrullus* and *Ecballium* (**Fig. 7**) and it is mostly storied (**Fig. 11**). Rays of all species are very large (>10 cells) and unlignified (**Fig. 12**). Crystals were not found in the material analyzed.

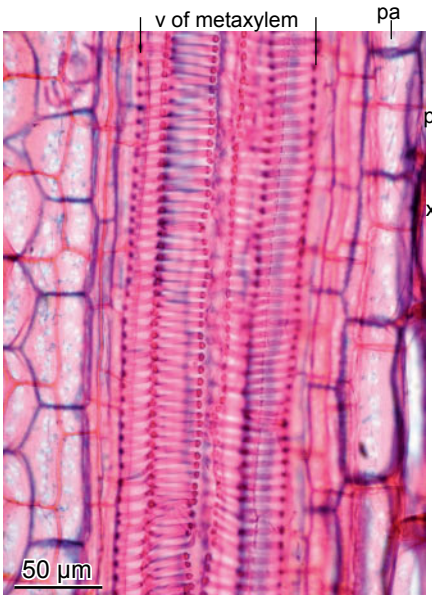



**Fig. 6.** Vessels of a metaxylem (central part of a vascular bundle) with distinct helical thickenings. 3 m-long, lying, liana-like annual shoot, geophyte with a tuber, meadow in a wadi, arid zone, Akkakus Mts., Sahara, Libya. *Citrullus colocynthis*, radial section.

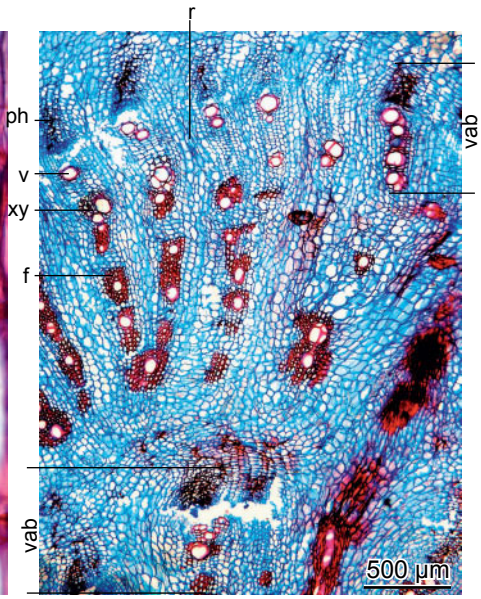



**Fig. 7.** Tuber with concentrically arranged vascular bundles produced by successive cambia. Tuber of a geophyte, ruderal site, Mediterranean zone, Estremadura, Spain. *Ecballium elaterinum*, transverse section. See detailed illustration.

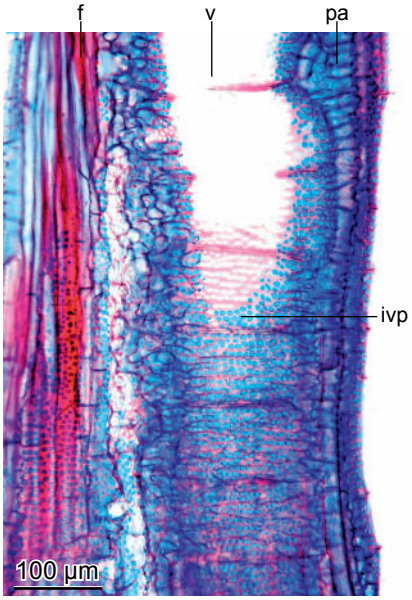
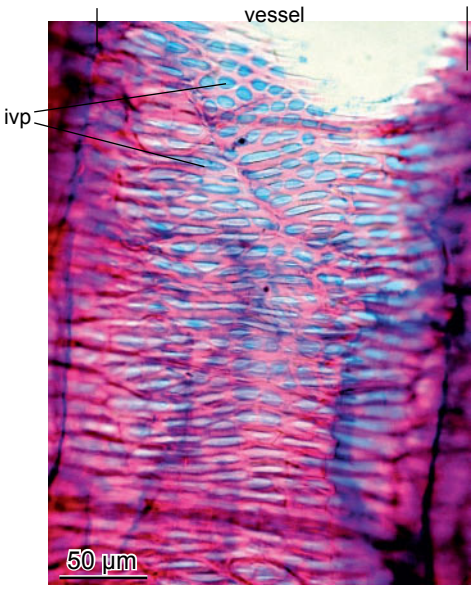


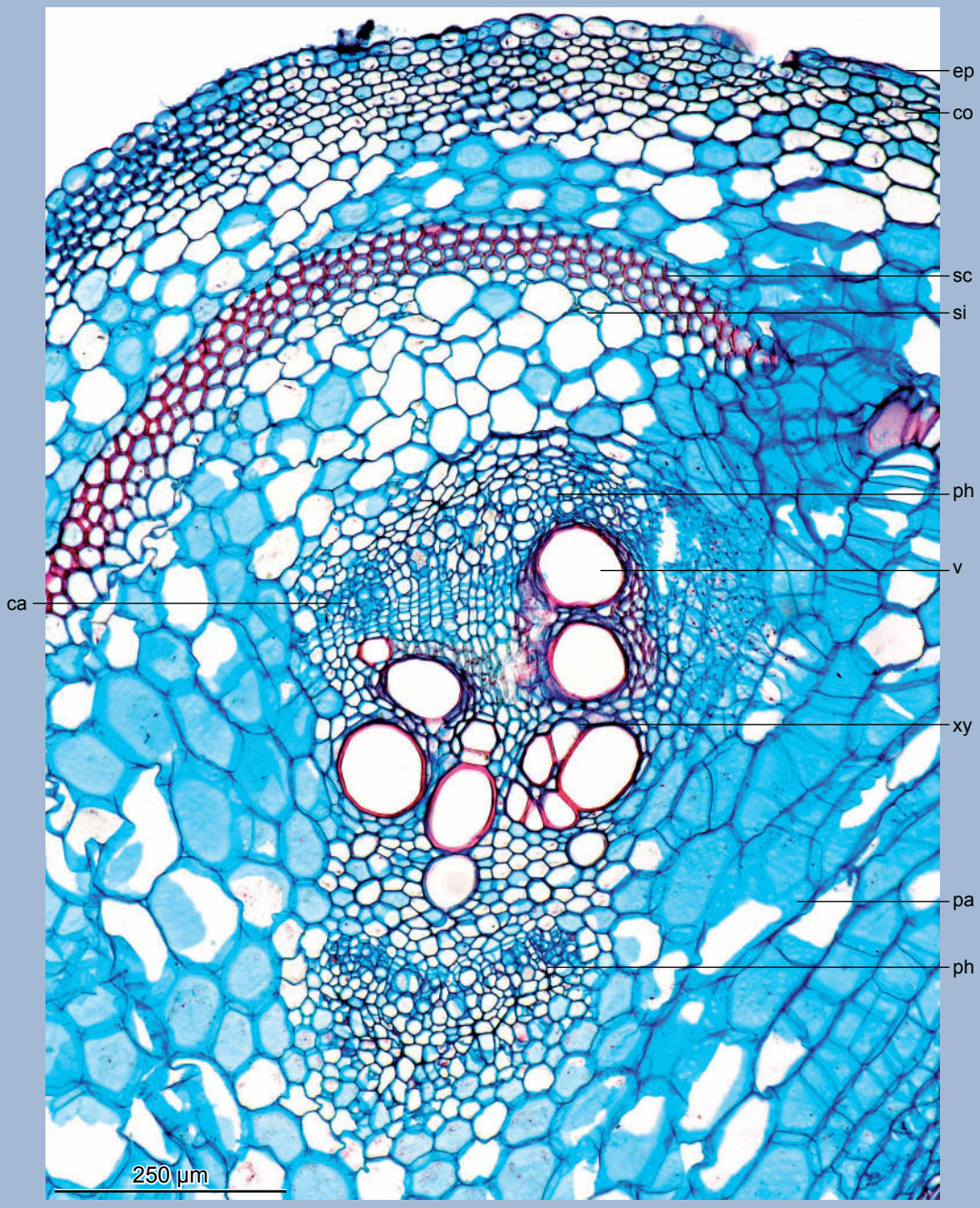

**Fig. 8.** Short vessels with small, round pits in opposite position. 2 m-long, lying, liana-like annual shoot, therophyte, garden, hill zone, Zürich, Switzerland. *Cucumis sativus*, radial section.



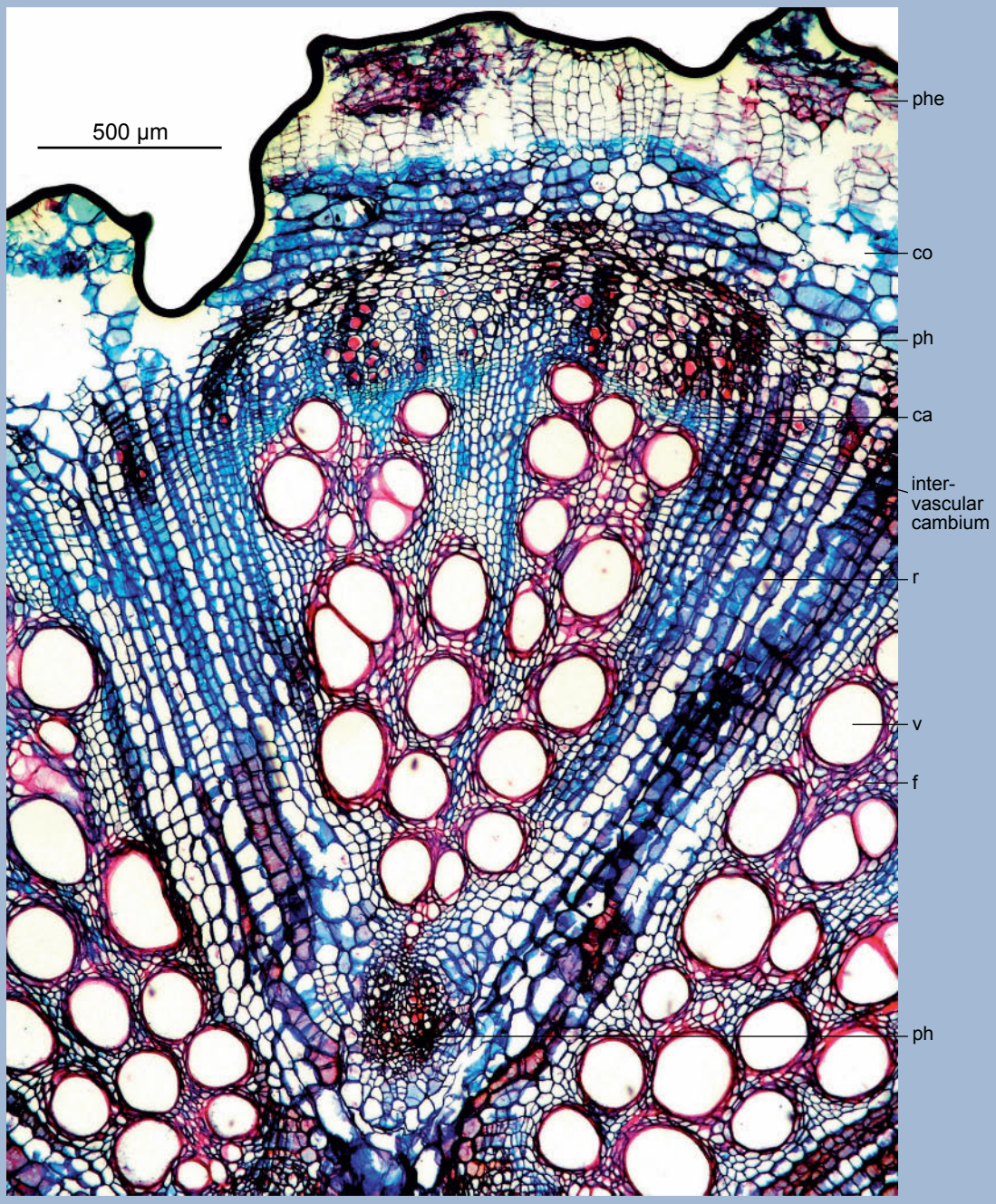
**Left Fig. 9.** Short vessels with scalariform pits. 2 m-long annual shoot, geophyte with a tuber, ruderal site, Mediterranean, Santa Pau, Catalonia, Spain. *Bryonia dioeca*, radial section.

**Right Fig. 10.** Septate fibers of the xylem with fairly large pits. 3 m-long, lying, liana-like annual shoot, geophyte with a tuber, meadow in a wadi, arid zone, Sahara, Libya. *Citrullus colocynthis*, radial section.

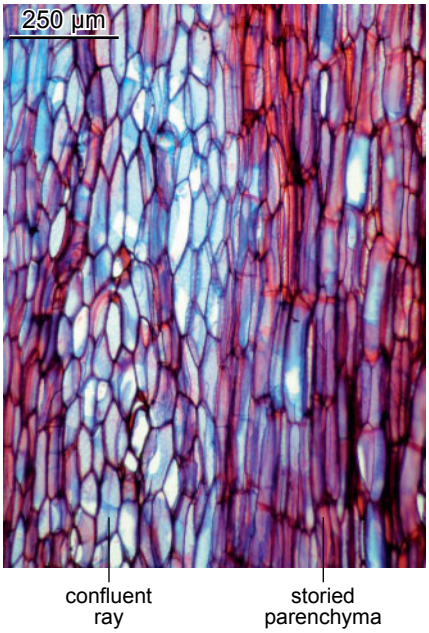
Detailed illustration of **Fig. 4.** Sector of an annual shoot with a bi-collateral vascular bundle. The phloem of the central part is centripetal and that of the external part is centrifugal. A cambium occurs only in the external part. 2 m-long, lying, liana-like annual shoot, therophyte, garden, hill zone, Zürich, Switzerland. *Cucumis sativus*, transverse section.

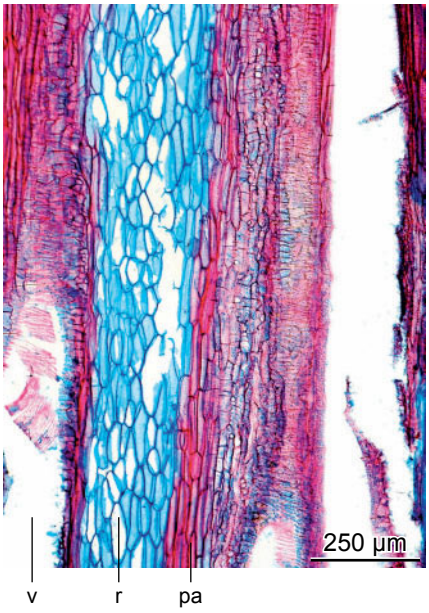


Detailed illustration of **Fig. 5.** Sector of an annual shoot with a bi-collateral vascular bundle. The phloem of the central part is centripetal and that of the external part is centrifugal. A cambium occurs only in the external part. 2 m-long annual shoot, geophyte with a tuber, ruderal site, Mediterranean, Santa Pau, Catalonia, Spain. *Bryonia dioeca*, transverse section.



Detailed illustration of **Fig. 7.** Tuber with concentrically arranged vascular bundles produced by successive cambia. Vascular bundles are arranged in two circles. Tuber of a geophyte, ruderal site, Mediterranean zone, Estremadura, Spain. *Ecballium elaterinum*, transverse section.




**Left Fig. 11.** Irregularly arranged ray cells and storied axial parenchyma cells. 2 m-long annual shoot, geophyte with a tuber, ruderal site, Mediterranean, Santa Pau, Catalonia, Spain. *Bryonia dioeca*, tangential section.

**Right Fig. 12.** Large ray with thin-walled, unlignified walls. 3 m-long, lying, liana-like annual shoot, geophyte with a tuber, grazed meadow in a wadi, arid zone, Sahara, Libya. *Citrullus colocynthis*, tangential section.

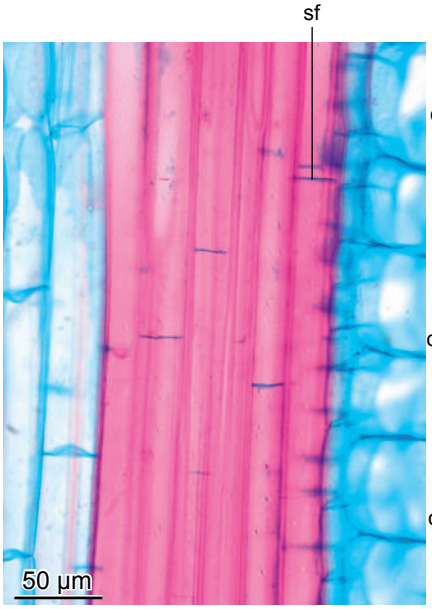


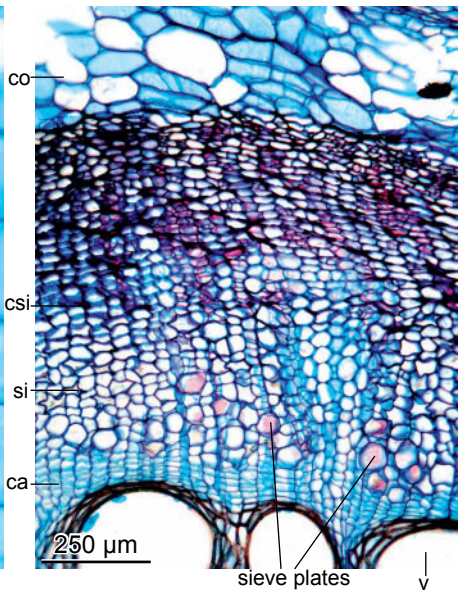
### Characteristics of the phloem and cortex

Outside of the vascular bundles of annual shoots is the cortex. It consists of large, unlignified parenchyma cells. The cortex is divided by a ring of fibers in *Cucumis*, *Cucurbita* and *Ecballium* (**Fig. 4**). Broken fiber-sclerenchyma rings are caused by dilatation (**Fig. 4**). Fibers are often septate (**Fig. 13**). The inner part of the cortex of *Cucumis sativus* contains a few small sieve tubes (**Fig. 4**). Round phloem cells with distinct sieve plates and small rectangular parenchyma cells form the phloem (**Figs. 14** and **15**). Dilatations occur in the bark of all perennial parts (**Fig. 16**). Small crystals are rare, either in irregular or in prismatic or acicular forms (*Ecballium*).

### Discussion in relation to previous studies

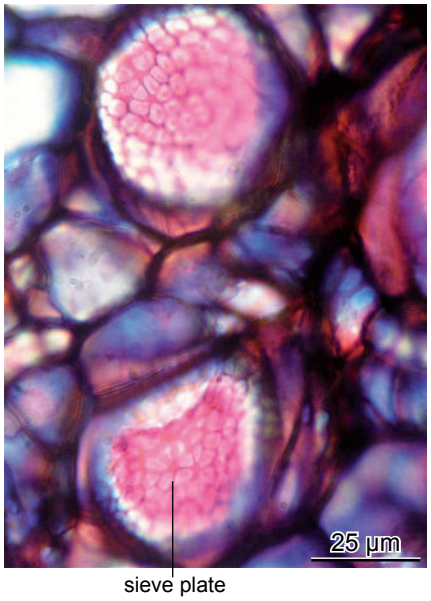
Zimmermann (1922) described shoots of more than 14 species from Eastern Usambara in Tanzania and Carlquist (1991) characterized 4 woody species from tropical and arid regions. Stem cross-sections of a few Cucurbitaceae species, including *Ecballium elaterinum* and *Bryonia dioeca*, are given by Metcalfe and Chalk (1955). An instructive text by Evert (2007) explains a drawing and a photograph of *Cucurbita maxima* and *C. pepo* showing an annual stem with bi-collateral bundles. The occurrence of bi-collateral vascular bundles in annual shoots and collateral bundles in parts produced by successive cambia are unique to the stem construction of all anatomically known Cucurbitaceae species (Carlquist (1991), Evert (2007), Metcalfe and Chalk (1955) and Zimmermann (1922)).

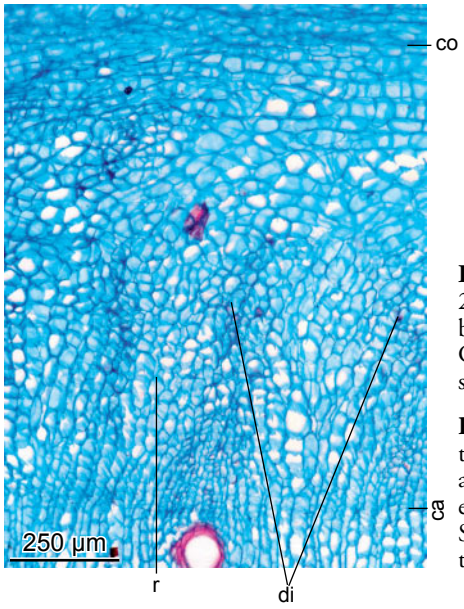



**Left Fig. 13.** Septate fibers of the ring within the cortex (see **Fig. 1**). 2 m-long, lying, liana-like annual shoot, therophyte, garden, hill zone, Zürich, Switzerland. *Cucumis sativus*, radial section.

**Right Fig. 14.** Phloem with round sieve tubes and square and irregular parenchyma cells. Red cell contents highlight sieve plates. 2 m-long, lying, liana-like annual shoot, hemicryptophyte, banana plantation, subtropical climate, Tenerife, Canary Islands. *Bryonia verrucosa*, transverse section.




**Left Fig. 15.** Sieve plates in sieve tubes. 2 m-long annual shoot, geophyte with a tuber, ruderal site, Mediterranean, Santa Pau, Catalonia, Spain. *Bryonia dioeca*, transverse section.

**Right Fig. 16.** Phloem with large dilatations. Bark, 1.5 m-long, lying, liana-like annual shoot, geophyte with a tuber, ruderal site, Mediterranean zone, Estremadura, Spain. *Ecballium elaterinum*, transverse section.

**Present features in relation to the number of analyzed specimens**

| IAWA code | | frequency |
|---|---|---|
| | **Total number of specimens (7 species; *Bryonia dioeca, Citrullus colocynthis and Ecballium elaterinum* shoot and tuber)** | **10** |
| 1 | growth rings distinct and recognizable | 2 |
| 2.1 | only one ring | 8 |
| 9 | vessels predominantly solitary | 10 |
| 13 | vessels with simple perforation plates | 10 |
| 20 | intervessel pits scalariform | 6 |
| 21 | intervessel pits opposite | 7 |
| 39.1 | vessel cell-wall thickness >2 µm | 8 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 3 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 7 |
| 50 | <100 vessels per mm$^2$ in earlywood | 9 |
| 56 | tylosis with thin walls | 6 |
| 60.1 | fibers absent | 4 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 2 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 4 |
| 65 | septate fibers present | 2 |
| 70 | fibers thin- to thick-walled | 6 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 3 |
| 79 | parenchyma paratracheal | 6 |
| 79.1 | parenchyma pervasive | 9 |
| 99 | rays commonly >10-seriate | 10 |
| 99.1 | vascular-bundle form remaining | 4 |
| 99.2 | stem lobed | 0 |
| 100.1 | rays confluent with ground tissue | 4 |
| 100.2 | rays not visible in polarized light | 9 |
| 103 | rays of two distinct sizes (tangential section) | 6 |
| 105 | ray: all cells upright or square | 10 |
| 110 | rays with sheet cells (tangential section) | 2 |
| 120 | storied axial tissue (parenchyma, fibers and vessels in tangential section) | 3 |
| 133.1 | successive cambia, concentrically arranged single vascular bundles | 1 |
| 134 | successive cambia, diffuse = foraminate | 2 |
| 134.1 | conjunctive tissue thin-walled | 3 |
| 135 | interxylary phloem present | 2 |
| R1 | groups of sieve tubes present | 1 |
| R3 | distinct ray dilatations | 9 |
| R4 | sclereids in phloem and cortex | 4 |
| R7 | with prismatic crystals | 1 |
| R10 | phloem not well structured | 10 |
| R11 | with rhaphides | 2 |
| P1 | with medullary phloem or vascular bundles | 10 |

# Droseraceae

### Number of species, worldwide and in Europe

The Droseraceae family has 4 genera with 110 species. *Drosera* and *Aldrovanda* occur worldwide in wet habitats, *Drosophyllum* grows in SW-Europe on dry sites. In Europe there are 3 endemic genera (*Aldrovanda*, *Drosera*, *Drosophyllum*) with 5 species. Representatives of the family Drosearaceae are absent on the Canary Islands and in the Sahara.

### Analyzed material

4 Droseraceae species are analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Semi-woody chamaephytes | 1 | 1 |
| Hemicryptophytes and geophytes | 3 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 13 | |
| Mediterranean | 1 | |

**Analyzed species:**
We describe the transition zone between the main root and the rosette.

*Drosera adelae* F. Muell. Tropical Australia. Material from the Botanical Garden Zürich
*Drosera capensis* L. Temperate zone, South Africa. Material from the Botanical Garden Zürich
*Drosera rotundifolia* L. Bog, mountain zone, Switzerland
*Drosophyllum lusitanicum* (L.) Link. Dry site, Botanical Garden Zürich, Switzerland

*Drosera anglica* (photo: Landolt)

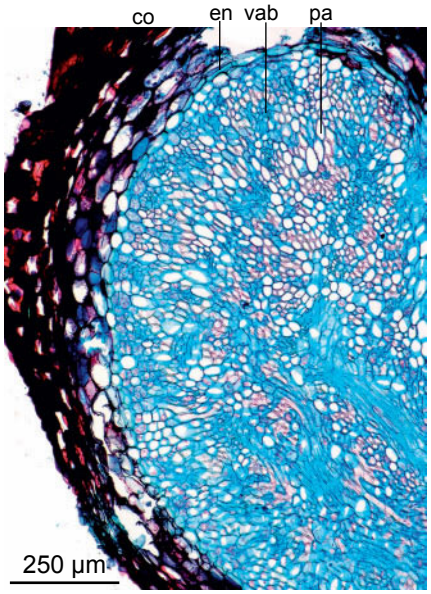
*Drosera rotundifolia*

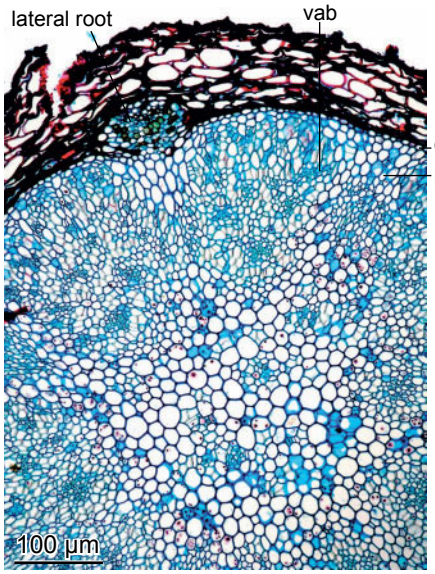
**Characteristics of the xylem**

The family is divided in two different anatomical forms:

1. Genus *Drosera*: Without secondary growth and without annual rings (**Figs. 1**, **2** and **3**). Irregularly formed vascular bundles (**Fig. 3**) occur all over the central cylinder. Vessel diameter varies from 10-20 µm and vessel density from 300-500/mm$^2$ (**Fig. 4**). Small round perforations occur at the radial vessel walls (**Fig. 5**). Inter-vessel pits are partially round (**Fig. 5**) and partially distinct scalariform (metaxylem? **Fig. 6**). Fibers are absent. Parenchyma surrounds vessels and sieve-tube groups (**Figs. 1-3**). Compartimentaliszed leaf bases occur along the shoot basis (**Fig. 7**).

2. Genus *Drosophyllum* differs from *Drosera* as follows: With secondary growth (**Fig. 8**) and indistinct rings, vessels are solitary and vessel density is approximately 200/mm$^2$. Presence of thin- to thick-walled tracheids with large bordered pits (4-5 µm; **Fig. 9**) and oval perforations. Axial parenchyma cannot be differentiated from rays on cross sections. Rays cannot be recognized in tangential and radial sections. Medullary vascular bundles are absent.




**Left Fig. 1.** Irregularly formed and distributed vascular bundles are surrounded by an endodermis and a cortex with large parenchyma cells. Root collar of a 10 cm-high perennial plant with a rosette, wet site, Botanical Garden Zürich, Switzerland. *Drosera adelae*, transverse section.

**Right Fig. 2.** Irregularly formed and distributed vascular bundles are surrounded by an endodermis and a cortex with large parenchyma cells. Root collar of a 10 cm-high perennial plant with a rosette, wet site, Botanical Garden Zürich, Switzerland. *Drosera capensis*, transverse section.

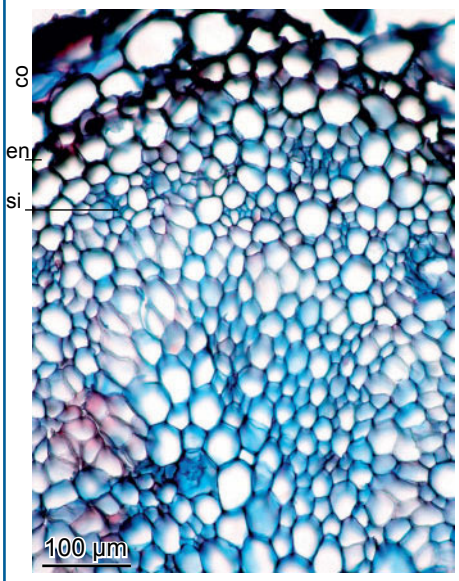



**Fig. 3.** Irregularly formed and distributed vascular bundles are surrounded by an endodermis and a cortex with large parenchyma cells. Root collar of a 10 cm-high plant with a rosette, wet site, mountain zone, Switzerland. *Drosera rotundifolia*, transverse section.

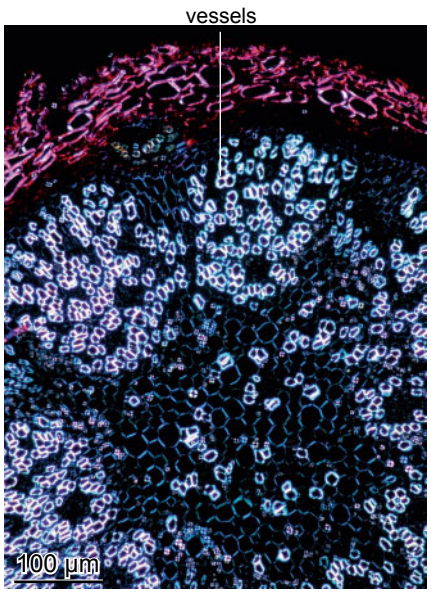



**Fig. 4.** Irregular distribution of vessels (many light circles in the center). Root collar of a 10 cm-high perennial plant with a rosette, wet site, Botanical Garden Zürich, Switzerland. *Drosera capensis*, transverse section, polarized light.

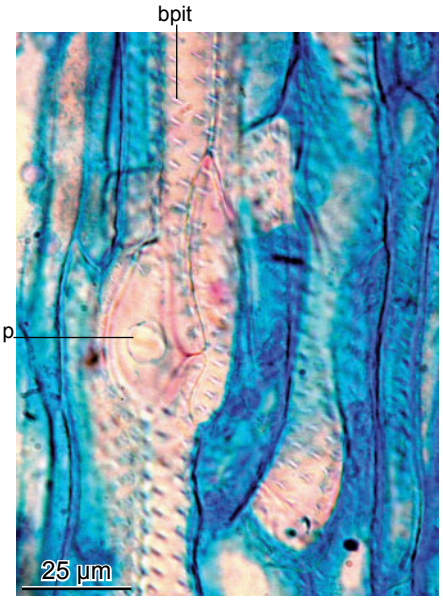



**Fig. 5.** Very small, round perforations and round pits at the radial wall of a vessel. Root collar of a 10 cm-high perennial plant with a rosette, wet site, Botanical Garden Zürich, Switzerland. *Drosera capensis*, radial section.

**Fig. 6.** Helical thickenings in vessels. Root collar of a 10 cm-high perennial plant with a rosette, wet site, Botanical Garden Zürich, Switzerland. *Drosera adelae*, radial section.

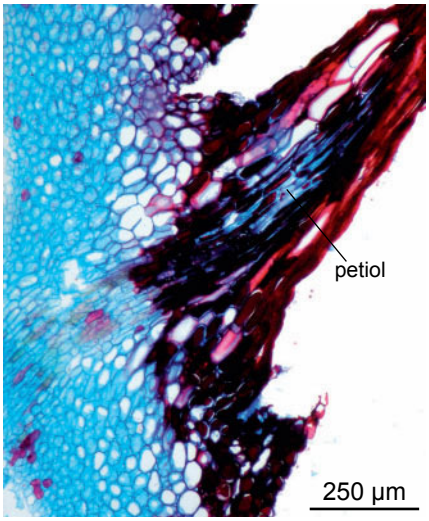



**Fig. 7.** Compartimentalised leaf base. Shoot basis of a 10 cm-high perennial plant with a rosette, wet place, Botanical Garden Zürich, Switzerland. *Drosera capensis*, radial section.

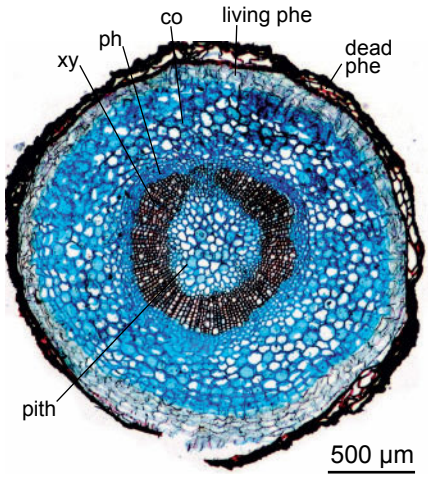
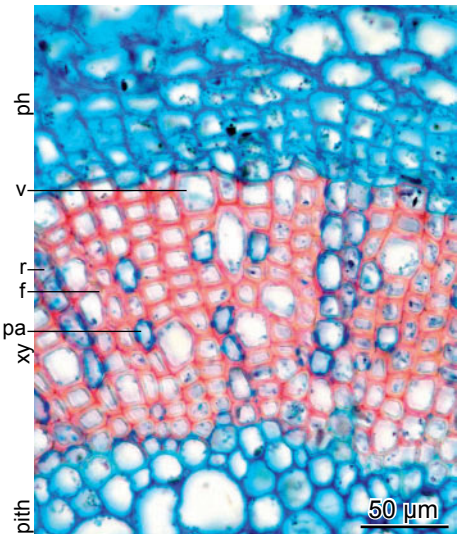
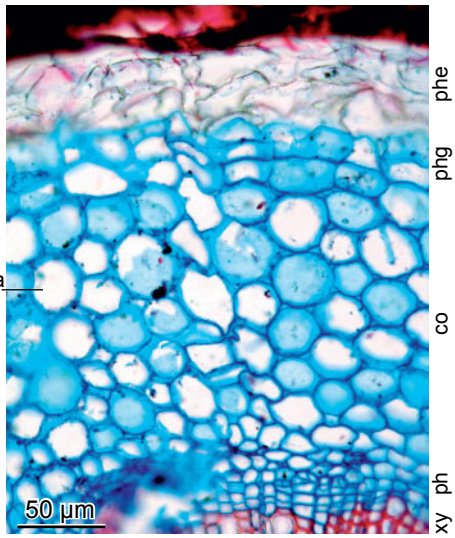



**Fig. 8.** Stem with secondary growth. A small xylem is surrounded by a small phloem, a large cortex and a small phellem. Shoot base of a 10 cm-high perennial plant, dry site, Botanical Garden Zürich, Switzerland. *Drosophyllum lusitanicum*, transverse section.




**Left Fig. 9.** Xylem with small vessels, thin- to thick-walled tracheids and parenchyma cells. Shoot base of a 10 cm-high perennial plant, dry site, Botanical Garden Zürich, Switzerland. *Drosophyllum lusitanicum*, transverse section.

**Right Fig. 10.** Outside a simple-structured phloem is a cortex with round parenchyma cells and a phellem consisting of thin-walled cork cells. Shoot base of a 10 cm-high perennial plant, dry site, Botanical Garden Zürich, Switzerland. *Drosophyllum lusitanicum*, transverse section.

### Characteristics of the phloem and the cortex

The cortex is uniform and consists of round parenchyma cells (**Figs. 2** and **3**). The cortex is separated from the central cylinder by an endodermis (**Figs. 1-3**). A phellem is absent. *Drosophyllum* is differentiated from *Drosera* as follows: The phloem is simply structured. Sieve tubes and parenchyma cells cannot be differentiated on cross-sections. Presence of a phellem (**Fig. 10**)

### Discussion in relation to previous studies

Carlquist (1995) describes the xylem of *Drosophyllum lusitanicum*. Observations on *Drosophyllum* are in accordance with Carlquist (1995). The xylem and phloem of the genus *Drosera* has not been characterized before. The Australian *Drosera* species, which represent a broad range of life forms, remain unstudied.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **4** |
| 2 | growth rings indistinct or absent | 4 |
| 2.2 | without secondary growth | 3 |
| 9 | vessels predominantly solitary | 1 |
| 11 | vessels predominantly in clusters | 3 |
| 13 | vessels with simple perforation plates | 4 |
| 20 | intervessel pits scalariform | 3 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 4 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 4 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 1 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 1 |
| 70 | fibers thin- to thick-walled | 1 |
| 79.1 | parenchyma pervasive | 4 |
| 99.1 | vascular-bundle form remaining | 3 |
| 117 | rayless | 4 |
| R10 | phloem not well structured | 3 |

# Elaeagnaceae



**Number of species, worldwide and in Europe**

The cosmopolitean Elaeagnaceae family includes 3 genera with 50 species. In Europe, only *Hippophae rhamnoides* is endemic. *Elaeagnus angustifolius* and *E. pungens* are partially naturalized. *Shepheria canadensis* is distributed thoughout Western North America.

**Analyzed species:**
*Elaeagnus angustifolia* L.
*Elaeagnus pungens* Thunb.
*Hippophae rhamnoides* L.
*Shepherdia canadensis* Nutt

**Analyzed material**

The xylem and phloem of 3 genera with 4 species has been analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 1 | 1 |
| Nanophanerophytes 0.5-4 m | 3 | 3 |
| **Plants analyzed from different vegetation zones:** | | |
| Boreal | 1 | |
| Mediterranean | 1 | |
| Hill and mountain | 2 | |

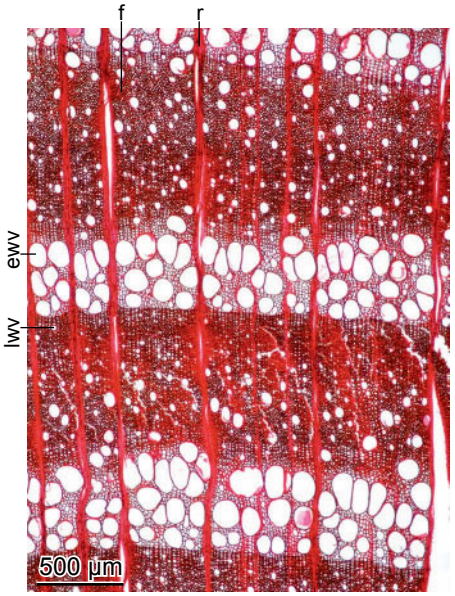
*Hippophae rhamnoides* (photo: Zinnert)

*Hippophae rhamnoides*

*Elaeagnus angustifolia* (photo: Zinnert)

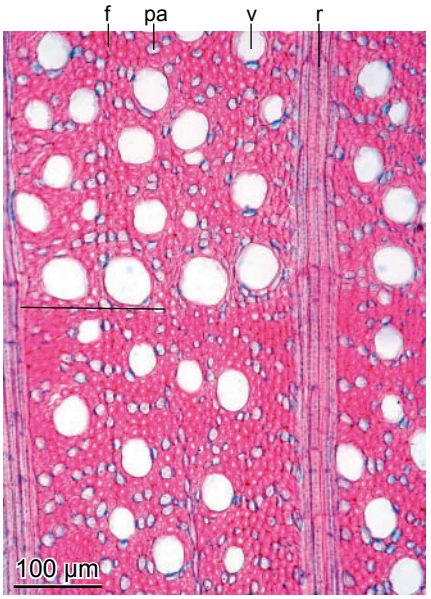
**Characteristics of the xylem**

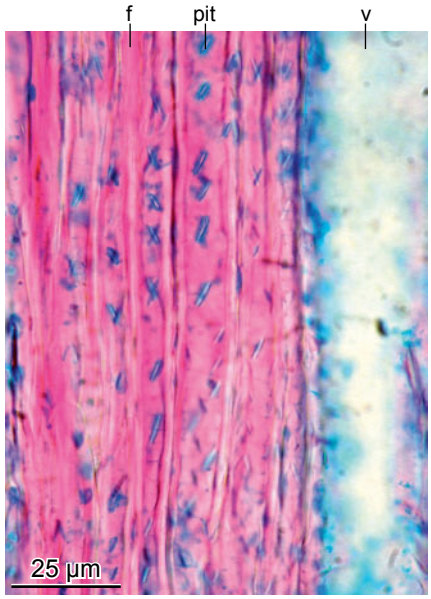
Ring boundaries are distinct in all species (**Figs. 1-3**). Ring-porous are *Elaeagnus angustifolia* (**Fig. 1**) and *Hippophae rhamnoides*, semi-ring- to diffuse-porous *Shepherdia canadensis* (**Fig. 2**) and *Elaeagnus pungens* (**Fig. 3**). Latewood vessels are arranged solitary in all species. (**Figs. 1-3**). Earlywood vessels with a diameter of 100-200 µm are characteristic of *Elaeagnus angustifolia* and *Hippophae rhamnoides* and a diameter of 50-100 µm is characteristic for *Elaeagnus pungens* and *Shepherdia canadensis*. Vessels of all species have simple perforations and helical thickenings. Vessels of *Elaeagnus angustifolia* and *Hippophae rhamnoides* contain thin-walled tylosis. Fibers with large pits with slit-like apertures occur in the radial walls of all species (**Fig. 4**). Fibers are always thick-walled in *Elaeagnus pungens* (**Fig. 3**) and thin- to thick-walled in all other species. The distribution of axial parenchyma is apotracheal (**Fig. 3**). Rays are species-specific: homocellular biseriate and storied in *Hippophae rhamnoides* (**Fig. 5**), biseriate and irregularly distributed in *Shepherdia canadensis*, uniseriate, homocellular with uni-and multiseriate rays in *Elaeagnus pungens*, and almost exclusively large in *Elaeagnus angustifolia* (**Fig. 7**). The occurrence of traumatic gum ducts in *Elaeagnus pungens* is unique (**Fig. 8**).



**Left Fig. 1.** Ring-porous xylem with distinct annual rings. Earlywood vessels are arranged in large bands and latewood vessels are solitary. Stem of a 10 m-high tree, cultivated, Mediterranean, Narbonne, France. *Elaeagnus angustifolia*, transverse section.

**Right Fig. 2.** Semi-ring-porous xylem. Latewood vessels are arranged solitary. Stem of a 1 m-high shrub, dry rock, boreal zone, Alberta, Canada. *Shepherdia canadensis*, transverse section.



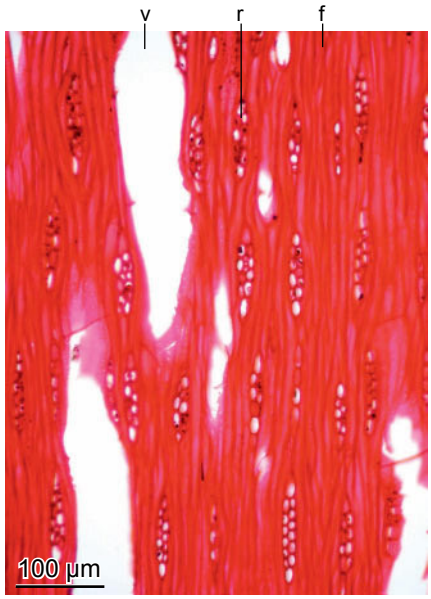




**Fig. 3.** Diffuse-porous xylem with solitary vessels and apotracheal parenchyma. Stem of a 2 m-high shrub, cultivated, hill zone, Locarno, Ticino, Switzerland. *Elaeagnus pungens*, transverse section.

**Fig. 4.** Fiber pits with slit-like apertures. Stem of a 2 m-high shrub, cultivated, hill zone, Locarno, Ticino, Switzerland. *Elaeagnus pungens*, radial section.

**Fig. 5.** Storied biseriate rays. Stem of a 2 m-high tree, cultivated, hill zone, Zürich, Switzerland. *Hippophae rhamnoides*, tangential section.

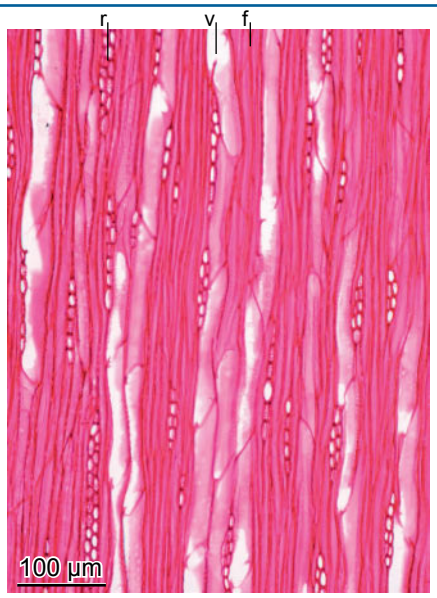



**Fig. 6.** Irregulary arranged biseriate rays. Stem of a 1 m-high shrub, on dry rock, boreal zone, Alberta, Canada. *Shepherdia canadensis*, tangential section.

**Fig. 7.** Rays of distinct sizes: small and very large. Stem of a 2 m-high shrub, cultivated, hill zone, Locarno, Ticino, Switzerland. *Elaeagnus pungens*, tangential section.

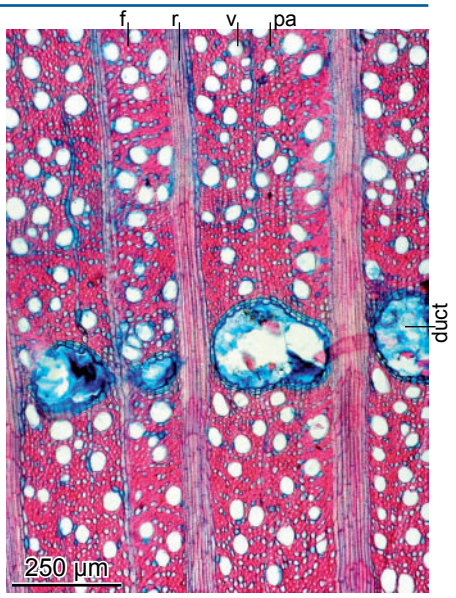
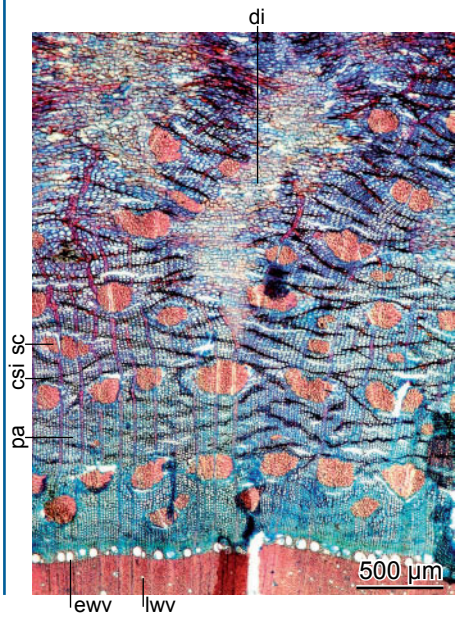
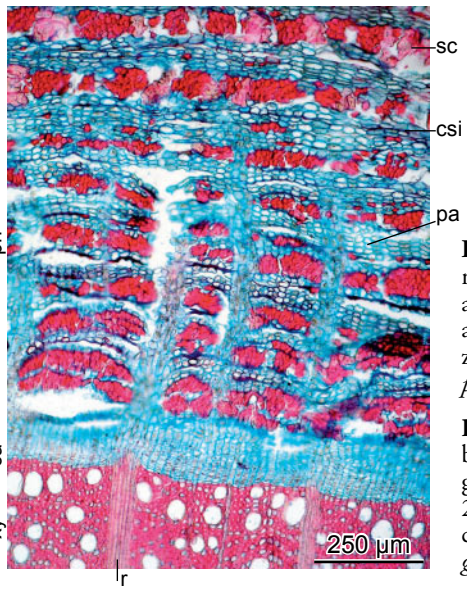



**Fig. 8.** Xylem with traumatic ducts. Ducts are surrounded by small, thin-walled, unlignified excretion cells. Stem of a 2 m-high shrub, cultivated, hill zone, Locarno, Ticino, Switzerland. *Elaeagnus pungens*, transverse section.

### Characteristics of the phloem and the cortex

Tangentially arranged groups of sclerenchyma are characteristic of *Hippophae rhamnoides* (**Fig. 9**) and tangential bands are chracteristic of *Elaeagnus pungens*. (**Fig. 10**). Collapsed sieve-tubes are arranged net-like in *Hippophae rhamnoides* and in tangential layers in *Elaeagnus pungens*.




**Left Fig. 9.** Phloem with tangentially arranged round groups of sclerenchyma cells and net-like collapsed sieve-tubes. Stem of a 0.5 m-high shrub, meadow, subalpine zone, Zermatt, Valais, Switzerland. *Hippophae rhamnoides*, transverse section.

**Right Fig. 10.** Phloem with tangential bands of collapsed sieve-tubes and rectangular groups of sclerenchyma. Stem of a 2 m-high shrub, cultivated, hill zone, Locarno, Ticino, Switzerland. *Elaeagnus pungens*, transverse section.

**Discussion in relation to previous studies**

The xylem of all genera (trees and shrubs) has been characterized before. Gregory (1994) mentioned 27 references. New here are descriptions of the bark of 2 species. The present results are in accordance with previous findings.

The anatomical structure of the xylem is characterized by the presence of simple perforations, helical thickenings, large fiber pits and apotracheal parenchyma. Differentiation between all taxa analyzed is possible based on the distribution of vessels (ring- and diffuse-porous) and on the structure and distribution of rays. Bark structures seem to be species-specific.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **4** |
| 1 | growth rings distinct and recognizable | 4 |
| 3 | ring-porous | 2 |
| 4 | semi-ring-porous | 4 |
| 5 | diffuse-porous | 1 |
| 6 | vessels in intra-annual tangential rows | 2 |
| 9 | vessels predominantly solitary | 4 |
| 13 | vessels with simple perforation plates | 4 |
| 22 | intervessel pits alternate | 4 |
| 31 | vessel-ray pits with large apertures, *Salix/Laurus* type | 1 |
| 36 | helical thickenings present | 4 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 2 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 2 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 4 |
| 56 | tylosis with thin walls | 1 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 2 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 4 |
| 69 | fibers thick-walled | 1 |
| 70 | fibers thin- to thick-walled | 3 |
| 75 | parenchyma absent or unrecognizable | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 3 |
| 97 | ray width predominantly 1-3 cells | 2 |
| 98 | rays commonly 4-10-seriate | 1 |
| 99 | rays commonly >10-seriate | 1 |
| 102 | ray height >1 mm | 1 |
| 104 | ray: all cells procumbent (radial section) | 2 |
| 105 | ray: all cells upright or square | 1 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 120 | storied axial tissue (parenchyma, fibers, and vessels in tangential section) | 1 |
| 127 | intercellular canals | 1 |
| R1 | groups of sieve tubes present | 2 |
| R2 | groups of sieve tubes in tangential rows | 2 |
| R4 | sclereids in phloem and cortex | 2 |
| R6.1 | sclereids in tangential rows | 1 |
| R6.2 | sclereids in tangentially arranged groups, *Rhamnus* type | 1 |
| R7.1 | with acicular crystals | 1 |
| R9 | with crystal sand | 1 |

# Ericaceae



## Number of species, worldwide and in Europe

The cosmopolitan Ericaceae family includes 130 genera with 2700 species. In Europe, there are 24 families with 66 species. Included here are the Pyrolaceae and Empetraceae.

## Analyzed material

The xylem and phloem of 23 genera with 59 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 16 | 20 genera |
| Semi-woody chamaephytes | 1 | |
| Woody chamaephytes | 41 | 20 genera |
| Hemicryptophytes and geophytes | 1 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 9 | |
| Boreal | 12 | |
| Hill and mountain | 29 | |
| Mediterranean | 7 | |
| Subtropical | 2 | |

*Calluna vulgaris* (photo: Lauerer)

*Arbutus andrachne*

**Analyzed species:**

*Andromeda polifolia* L.
*Arbutus andrachne* L.
*Arbutus canariensis* Veill.
*Arbutus unedo* L.
*Arctostaphylos alpina* (L.) Niedenzu
*Arctostaphylos patula* Greene
*Arctostaphylos rubra* Fernald
*Arctostaphylos uva-ursi* (L.) Spreng
*Calluna vulgaris* Hull.
*Cassiope tetragona* D. Don
*Chamaedaphne calyculata* (L.) Moench
*Chimaphila umbellata* (L.) W. Barton
*Corema album* (L.) D. Don
*Daboecia cantabrica* Britten et Rendel
*Empetrum nigrum* L.
*Enkianthus campanulatus* Nichols
*Erica arborea* L.
*Erica carnea* L.
*Erica cinerea* L.
*Erica multiflora* L.
*Erica scoparia* L.
*Erica terminalis* Salisb.
*Erica tetralix* L.
*Erica umbellata* L.
*Erica vagans* L.
*Gaultheria shalon* Pursh
*Kalmia angustifolia* L.
*Ledum decumbens* L.
*Ledum groenlandicum* Retz
*Ledum palustre* L.
*Loiseleria procumbens* Desv.
*Menziesia ferruginea* Sm.
*Phyllodoce coerulea* (L.) Bab.
*Pieris taiwanensis* Hayata
*Pyrola rotundifolia* L.
*Rhododendron adansoni* Pepin
*Rhododendron aureum* Georgi
*Rhododendron caucasicum* Pall.
*Rhododendron dahurica* L.
*Rhododendron ferrugineum* L.
*Rhododendron hirsutum* L.
*Rhododendron lapponicum* L.
*Rhododendron luteum* C.K. Schneid
*Rhododendron macrophyllum* D. Don ex G. Don
*Rhododendron myrtifolium* L.
*Rhododendron parviflorum* Adams
*Rhododendron ponticum* L.
*Rhododendron virginianum* L.
*Rhodothamnus chamaecistus* (L.) Rchb.
*Vaccinium angustifolium* Ait.
*Vaccinium gaultherioides* Bigelow
*Vaccinium maderense* Link.
*Vaccinium myrtillus* L.
*Vaccinium ovalifolium* Sm.
*Vaccinium ovatum* Pursh.
*Vaccinium oxycoccus* L.
*Vaccinium parviflorum* Sm.
*Vaccinium uliginosum* L.
*Vaccinium vitis-idaea* L.

*Erica cinerea*

*Pyrola rotundifolia* (photo: Landolt)

*Kalmia latifolia*

*Vaccinium vitis-idaea*

*Rhododendron hirsutum*

*Ledum palustre*

*Rhododendron virginianum*

*Loiseleuria procumbens*

**Characteristics of the xylem**

All species are diffuse- or semi-ring-porous and have distinct annual rings (**Figs. 1-8**). Vessels are arranged primarily solitary (**Figs. 1-5**), in groups (**Fig. 6**), in radial (**Fig. 7**) or in tangential rows (**Fig. 8**). Ring boundaries are marked by a small zone of flat, often thick-walled fibers (**Figs. 1-8**). The earlywood vessel diameter of dwarf shrubs varies between 15-30 µm and between 30-50 µm in shrubs. Vessel density varies in large shrubs from 50-100/mm$^2$ (**Fig. 1**), from 100-300/mm$^2$ in most dwarf shrubs (**Figs. 2** and **5**), but it can reach 700/mm$^2$ in few species (**Figs. 3** and **4**). The structure of perforations varies: they are simple (**Fig. 9**), scalariform with <10 (**Fig. 10**) or >20 bars (**Fig. 11**). Many species have different types of perforations (**Fig. 10**). Frequent are transitions between intervessel-pits and scalariform perforations (**Fig. 12**). Inter-vessel pits are round and arranged in opposite and alternate position (**Fig. 12**).

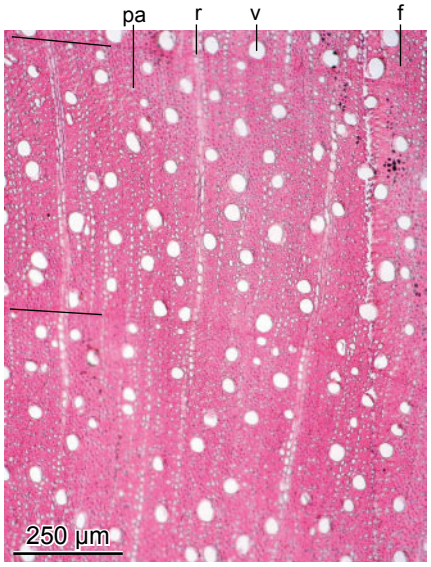



**Fig. 1.** Diffuse-porous xylem with solitary vessels. Stem of a 1 m-high shrub, maccia, Mediterranean zone, Andalusia, Spain. *Erica scoparia*, transverse section.

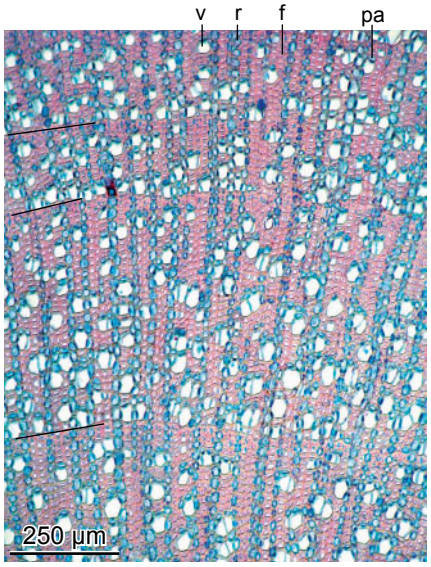



**Fig. 2.** Diffuse-porous xylem with solitary vessels. Parenchyma is primarily paratracheal. Stem of a 20 cm-high dwarf shrub, hill zone, Botanical Garden Bern, Switzerland. *Rhodothamnus chamaecistus*, transverse section.

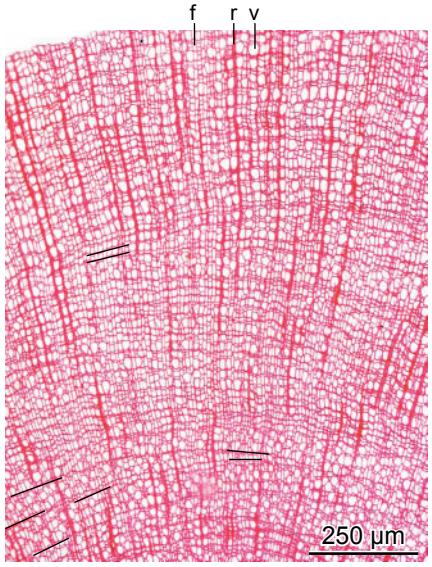



**Fig. 3.** Diffuse-porous xylem with many small and partially wedging annual rings. Fibers are thin-walled. Stem of a 20 cm-high dwarf shrub, on a pingo, subarctic zone, Tuktoyaktuk, Canada. *Ledum groenlandicum*, transverse section.

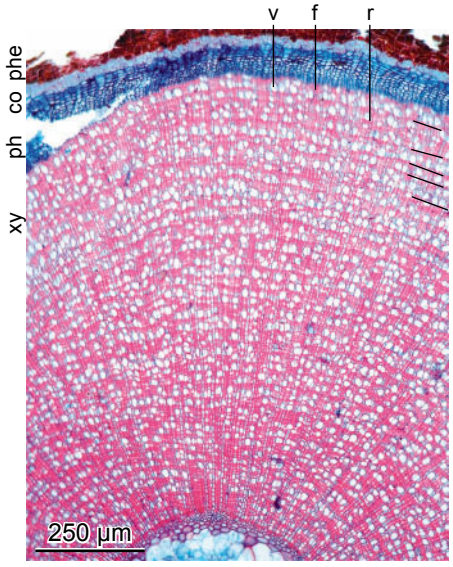



**Fig. 4.** Diffuse-porous xylem with small, solitary vessels and thick-walled fibers. Stem of a 10 cm-high and 50 cm-long chamaephyte, bog, arctic zone, Svalbard, Norway. *Cassiope tetragona*, transverse section.

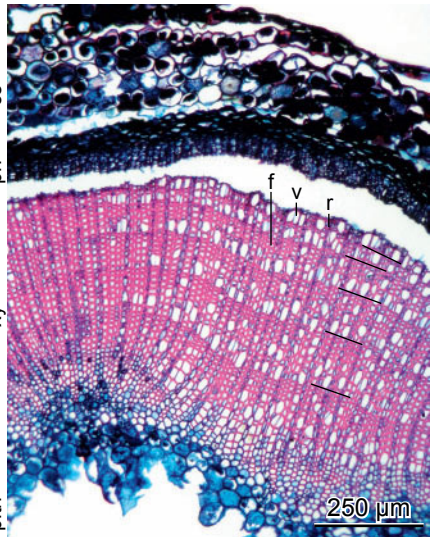



**Fig. 5.** Semi-ring-porous xylem with a few rings. Stem of a 15 cm-high chamaephyte, *Pinus poderosa*-forest, mountain zone, Colorado, USA. *Chimaphila umbellata*, transverse section.

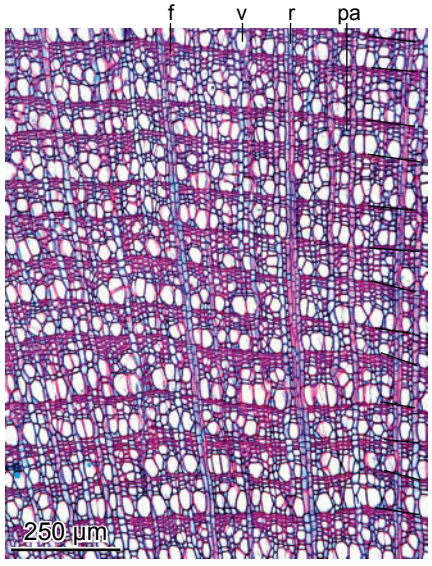
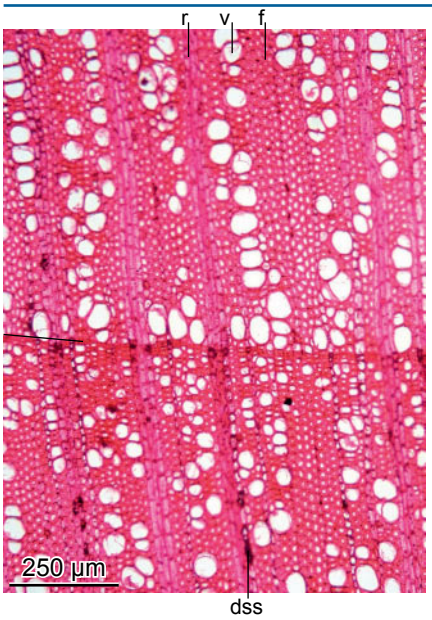
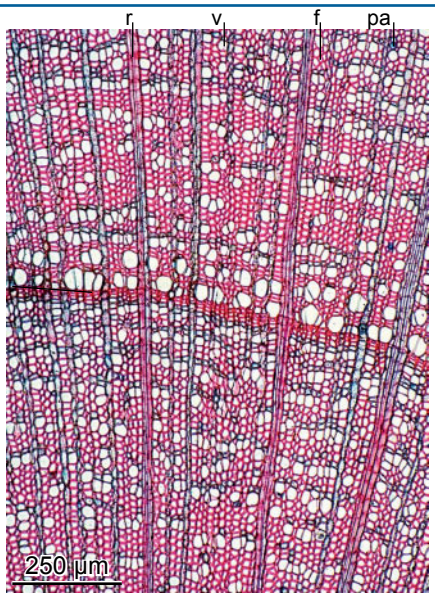


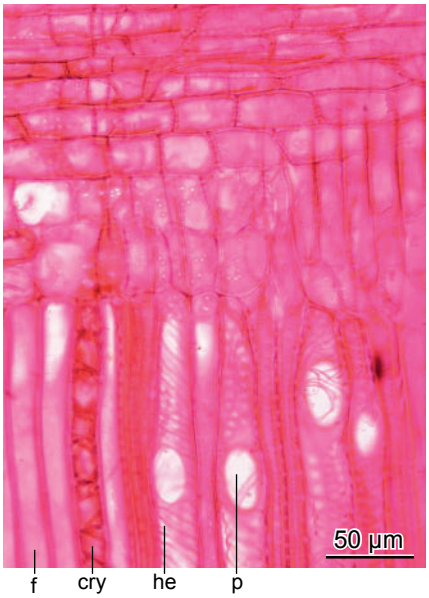

**Fig. 6.** Semi-ring-porous xylem. Ring boundaries are marked by a few rows of thick-walled fibers. Vessels are arranged in radial multiples. Stem of a 10 cm-high, creeping dwarf shrub, bog, arctic zone, Jamal, Russia. *Arctostaphylos alpina*, transverse section.

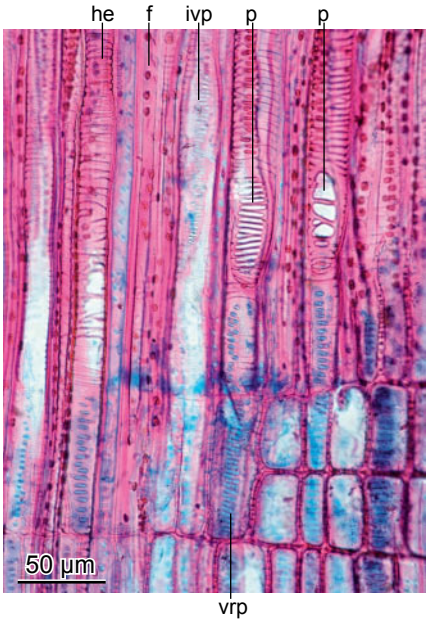



**Left Fig. 7.** Semi-ring-porous xylem. Vessels are arranged in radial mulipels. Stem of a 3 m-high shrub, maccia, Mediterranean zone, Pisa, Italy. *Arbutus unedo*, transverse section.

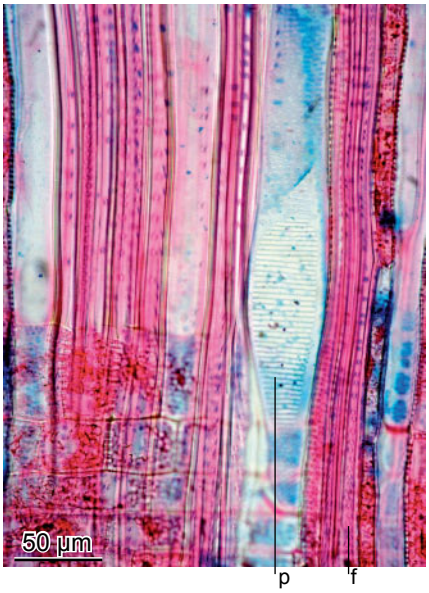
**Right Fig. 8.** Semi-ring-porous xylem with intra-annual tangential rows of vessels. The ring boundary is marked by a few rows of thick-walled fibers. Stem of a 2 m-high shrub, hill zone, Botanical Garden München, Germany. *Enkianthus campanulatus*, transverse section.

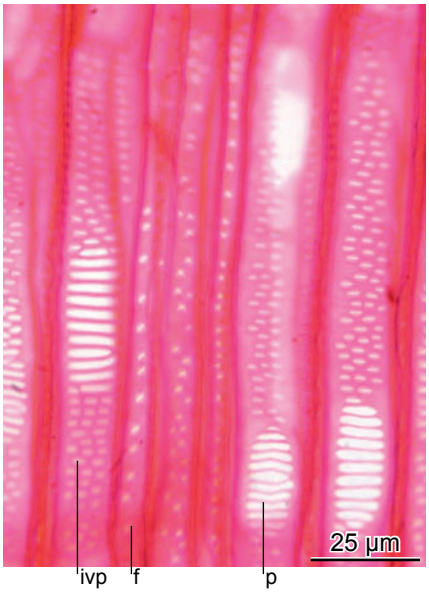



**Left Fig. 9.** Vessels with simple perforations and helical thickenings. Stem of a 3 m-high shrub, maccia, Mediterranean zone, Samos, Greece. *Arbutus andrachne*, radial section.

**Right Fig. 10.** Vessels with helical thickenings and scalariform perforations with 2 and 15 bars. Vessel-ray-pits are horizontally enlarged. Stem of a 1.5 m-high shrub, sea shore, hill zone, New Port, Oregon, USA. *Vaccinium ovatum*, radial section.




**Left Fig. 11.** Vessels with scalariform perforations with >30 bars. Stem of a 2 m-high shrub, hill zone, Botanical Garden München, Germany. *Enkianthus campanulatus*, radial section.

**Right Fig. 12.** Vessels with large pits in alternating and opposite position. There is a continuum between pits and scalariform perforations. Stem of a 20 cm-high dwarf shrub, on a pingo, subarctic zone, Tuktoyaktuk, Canada. *Ledum groenlandicum*, radial section.

Helical thickenings occur in *Chimaphila umbellata*, all *Arctostaphylos* species (**Fig. 9**) and in a few *Vaccinium* species (**Fig. 10**). Ray-vessel-pits are small and round (1-2 µm in diameter; **Fig. 13**) or horizontally enlarged, e.g. in some *Vaccinium* species (**Fig. 10**), in *Loiseleuria procumbens* and in *Arbutus canariensis* (**Fig. 14**). Vessels of a few species contain dark-stained substances. Vessel-wall thickness varies from thick-walled (**Figs. 1**, **2** and **4**) to thin- to thick-walled (**Figs. 5-8** and **15**) and to thin-walled (**Figs. 3** and **16**). Fiber pits have a diameter of 2-4 µm and have slit-like apertures (**Fig. 12**). Septate fibers occur in various genera (**Fig. 14**), but not in *Erica*. Tension wood has not been observed within the family. Parenchyma is frequently absent or not recognizable, but it is often apotracheal diffuse (**Fig. 15**), diffuse in aggregates (**Fig. 16**) or paratracheal (**Figs. 17** and **18**). Rays are uniseriate of different height in many dwarf shrubs (**Figs. 19** and **20**). Many species have rays of two distinct sizes: 2-5-seriate and uniseriate (**Figs. 21** and **22**). Rays are mostly homocellular with square and upright cells (**Fig. 13**). Some *Rhododendron* species with 2-5-seriate rays are heterocellular with 2-5 square and upright marginal cells (**Fig. 23**). Sheet cells occur in a few shrub-like *Vaccinium* and *Gaultheria* species (**Fig. 22**). A few prismatic crystals have been observed only in three *Vaccinium* species. Very special is the occurrence of large, thin-walled, unlignified cell groups in the pith of *Rhododendron caucasicum* and *R. macrophyllum* (**Fig. 24**).

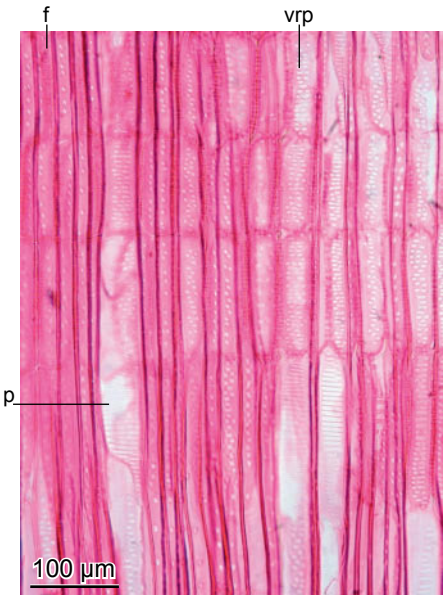



**Fig. 13.** Upright ray-cells with small, round ray-vessel pits. Stem of a 30 cm-high dwarf shrub, bog, boreal zone, Quebec, Canada. *Kalmia angustifolia*, radial section.

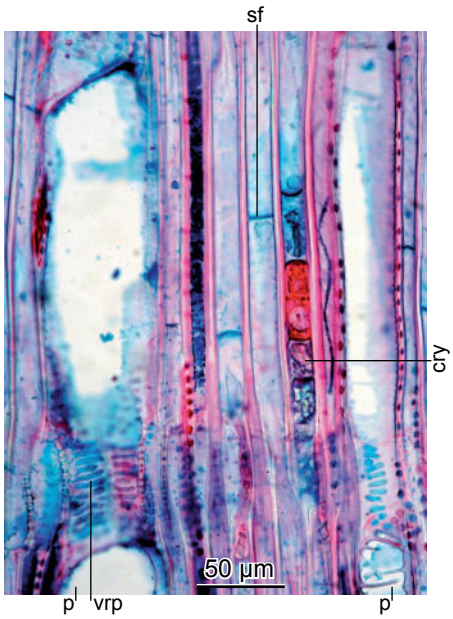



**Fig. 14.** Septate fibers and vessels with horizontally enlarged vessel-ray-pits. Stem of a 2 m-high shrub, thermophile zone, subtropical climate, Gomera, Canary Islands. *Arbutus canariensis*, radial section.

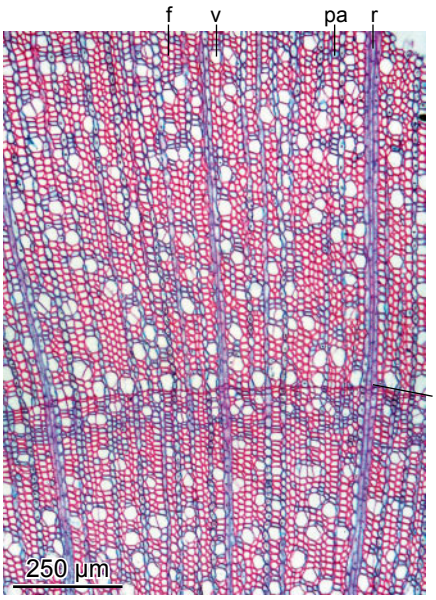
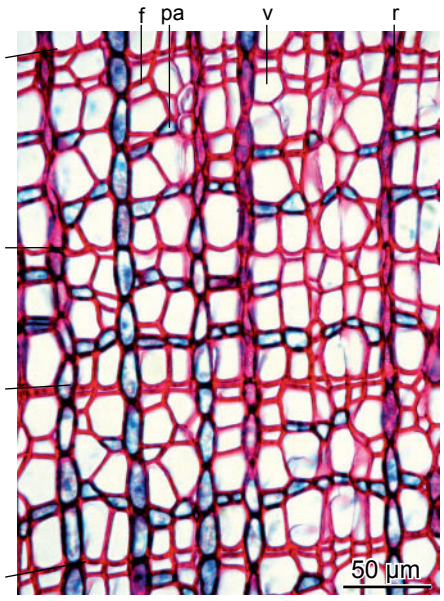
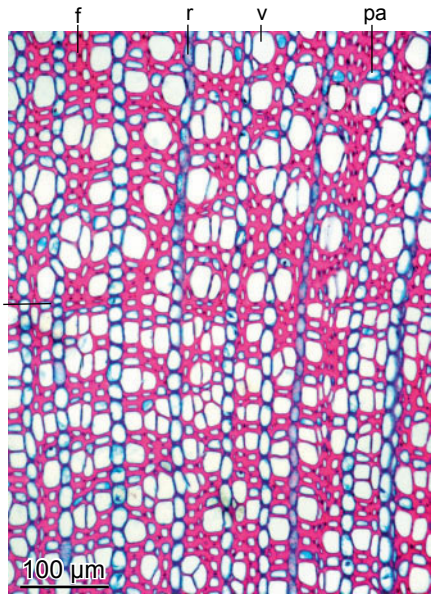


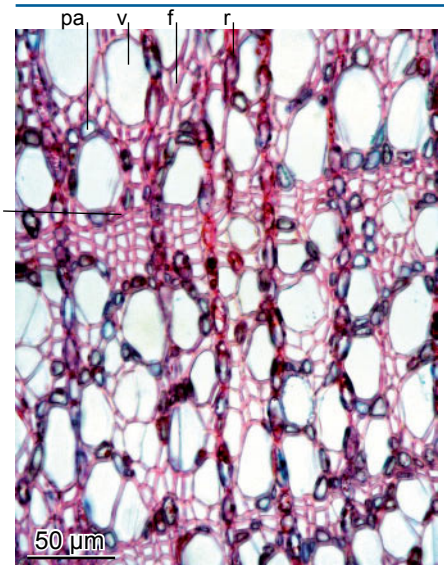

**Fig. 15.** Xylem with apotracheal and paratracheal parenchyma. Stem of a 1 m-high shrub, meadow, subalpine zone, Passalauri, Georgia. *Rhododendron luteum*, transverse section.



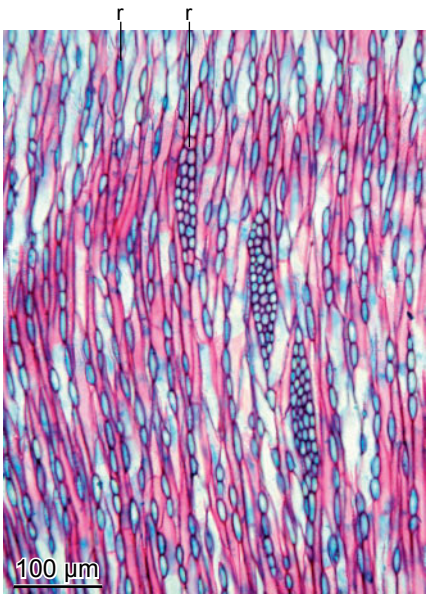

**Left Fig. 16.** Thin-walled xylem with apotracheal parenchyma in aggregates. Ring boundaries are marked by a layer of tangential flat fibers. Stem of a 20 cm-high dwarf shrub, bog, subarctic zone, Jamal, Russia. *Ledum decumbens*, transverse section.

**Right Fig. 17.** Xylem with a few paratracheal parenchyma cells. Fibers are thin-to-thick-walled. Stem of a 1.5 m-high shrub, sea shore, hill zone, Astoria, Oregon, USA. *Gaultheria shalon*, transverse section.



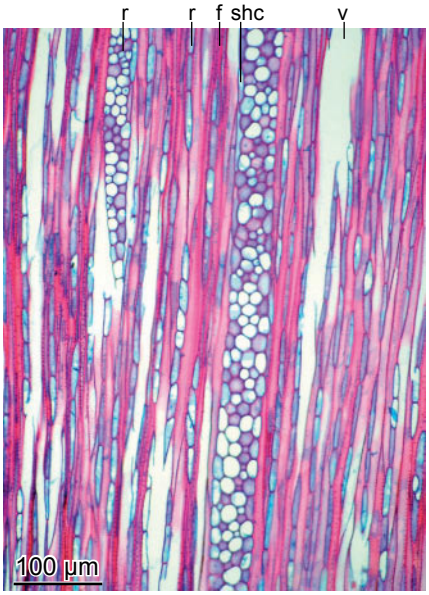
**Left Fig. 18.** Xylem with a few paratracheal parenchyma cells. Stem of a 5 cm-high creeping dwarf shrub, windy crest, alpine zone, Davos, Switzerland. *Loiseleuria procumbens*, transverse section.

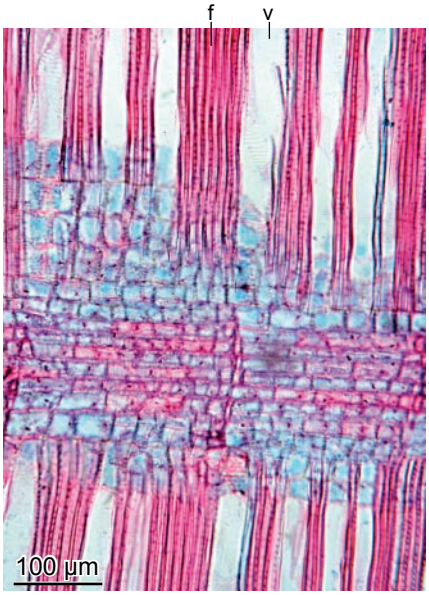
**Right Fig. 19.** Uniseriate rays with a few cells in height. Stem of a 10 cm-high dwarf shrub, bog, boreal zone, Rovaniemi, Finland. *Empetrum nigrum*, tangential section.




**Left Fig. 20.** Uniseriate rays with many cells in height. Stem of a 30 cm-high shrub, bog, boreal zone, Quebec, Canada. *Kalmia angustifolia*, tangential section.

**Right Fig. 21.** Uniseriate and multiseriate rays. Stem of a 30 cm-high shrub, bog, boreal zone, Jakutia, Siberia, Russia. *Rhododendron adansoni*, tangential section.




**Left Fig. 22.** Uniseriate and multiseriate rays. The large rays have sheet cells. Stem of a 1.5 m-high shrub, sea shore, hill zone, Astoria, Oregon, USA. *Gaultheria shalon*, tangential section.

**Right Fig. 23.** Heterocellular ray with many marginal square and upright cells. Stem of a 50 cm-high dwarf shrub, *Alnus virids*-forest, subalpine zone, Tskara, Tskaro-Pass, Georgia. *Rhododendron caucasicum*, radial section.

### Characteristics of the phloem and the cortex

Bark structures are homogeneous within the family. Sieve tubes and parenchyma can not really be differentiated on cross-sections (**Figs. 25-28**). Tangential layers are absent. Ray dilatations are indistinct and occur in a few species only (**Fig. 27**). Sclereids are rare (**Fig. 28**). Prismatic crystals have been found only in *Pieris taiwanensis*. The phellem consists of a belt of one to several layers of rectangular cells (**Figs. 25-27**).

### Characteristic features of taxa

The anatomical structure within the family is fairly homogeneous but vessel density, perforation structure, fiber-wall thickness and ray composition would allow some differentiations. We do not have enough material for a general classification. The following species have unique features within the family:

*Arbutus unedo* and *A. andrachne* (**Fig. 7**): vessels in radial multiples.

*Vaccinium uliginosum*, *Enkianthus campanulatus* (**Fig. 8**): vessels arranged in intra-annual tangential rows.

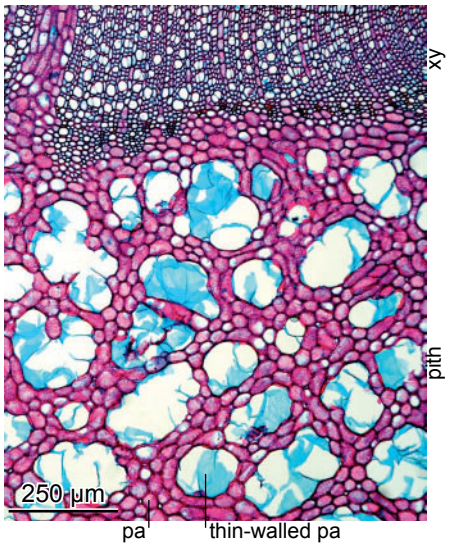
*Arctostaphylos alpina* (**Fig. 6**), *A. rubra*, *A. uva-ursi*: creeping dwarf shrubs, distinctly semi-ring-porous, distinct vessel-free latewood zone.

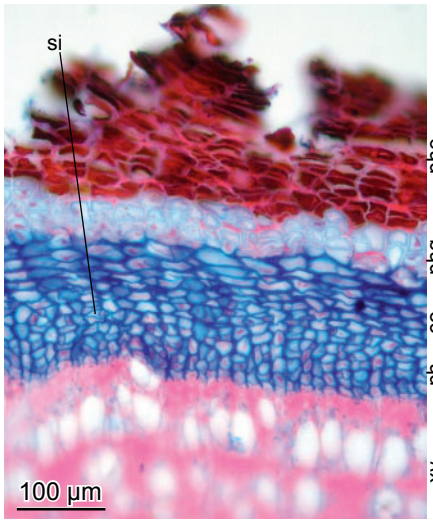
*Cassiope tetragona* (**Fig. 4**): solitary vessel with a diameter less than 20 µm, and with thick-walled fibers.

*Andromeda polifolia*, *Ledum palustre*, *L. groenlandicum* (**Figs. 3** and **16**): very high vessel-density and thin-walled fibers.

*Pyrola rotundifolia* (**Fig. 29**): hemicryptophyte with a few annual rings and a large bark.

*Corema album* (**Fig. 29**): fluted stem




**Left Fig. 24.** Pith with groups of thin-walled, unlignified parenchyma cells. Stem of a shrub, Mediterranean zone, Botanical Garden Santa Barbara, California, USA. *Rhododendron macrophyllum*, transverse section.

**Right Fig. 25.** Uniform phloem consisting of irregularly formed parenchyma and sieve tube cells. The phellem consists of rectangular cork cells. Stem of a 10 cm-high and 50 cm-long chamaephyte, bog, arctic zone, Svalbard, Norway. *Cassiope tetragona*, transverse section.

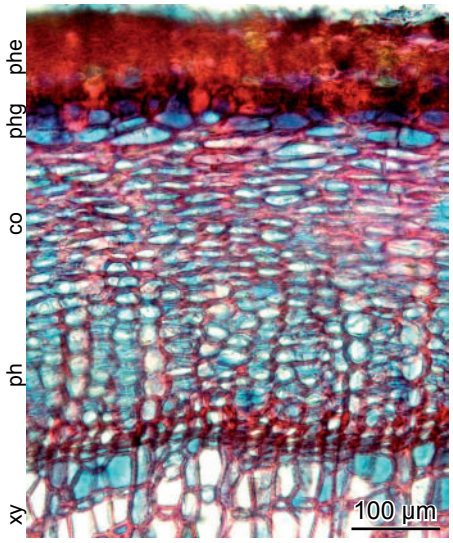



**Fig. 26.** Uniform phloem. Sieve tubes and parenchyma cells cannot be differentiated. Stem of a 10 cm-high dwarf shrub, meadow, alpine zone, Davos, Switzerland. *Vaccinium uliginosum*, transverse section.

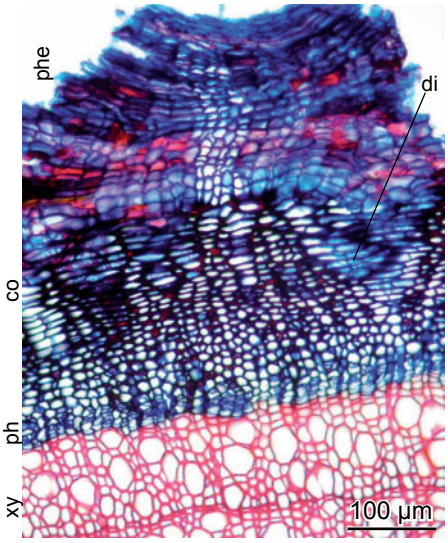



**Fig. 27.** Uniform phloem with dilatations. Sieve tubes and parenchyma cells cannot be differentiated. The phellem is layered. Stem of a 20 cm-high dwarf shrub, on a granite-rock, Val Onsernone, Ticino, Switzerland. *Calluna vulgaris*, transverse section.

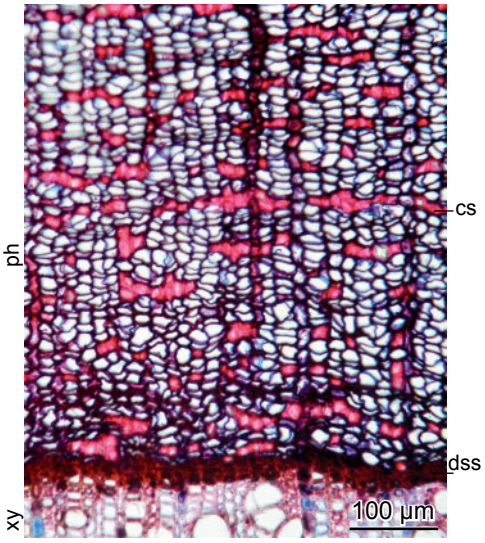
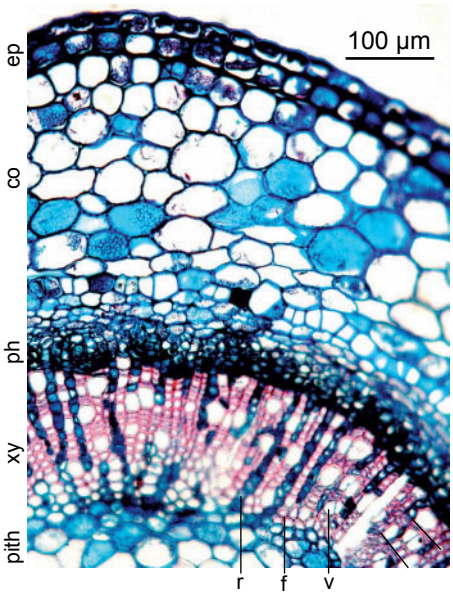



**Fig. 28.** Phloem with short tangential layers of sclerenchyma cells. Stem of a 2 m-high shrub, hill zone, Botanical Garden Tbilisi, Georgia. *Arbutus andrachne*, transverse section.



**Left Fig. 29.** Small uniform phloem and a large cortex which is surrounded by an epidermis. Stem of a 10 cm-high hemicryptophyte, *Larix sibirica*-forest, Ajan Lake, Siberia, Russia. *Pyrola rotundifolia*, transverse section.

**Right Fig. 30.** Fluted stem. Fluting started at the shortest radius after 5 years. The stem counts 16 annual rings. Stem of a 20 cm-high dwarf shrub, dune, Mediterranean, Algarve, Portugal. *Corema album*, transverse section.



### Ecological trends and relations to life forms

The diameter of vessels in dwarf shrubs is smaller (20-30 µm) than those in shrubs (30-50 µm). Very small rays occur only in small dwarf shrubs.

### Discussion in relation to previous studies

Most of the genera have been characterized before by Gregory (1994). Newly described here are the genera *Kalmia*, *Menziesia*, *Pyrola* and *Rhodothamnus*. The present study summarizes and confirms all previous findings. Particular for the family is the diversity of perforation plates and the occurrence of thin-walled groups of parenchyma in the pith of a few *Rhododendron* species (**Fig. 24**).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **59** |
| 1 | growth rings distinct and recognizable | 59 |
| 4 | semi-ring-porous | 16 |
| 5 | diffuse-porous | 46 |
| 6 | vessels in intra-annual tangential rows | 3 |
| 9 | vessels predominantly solitary | 45 |
| 9.1 | vessels in radial multiples of 2-4 common | 3 |
| 10 | vessels in radial multiples of 4 or more common | 2 |
| 11 | vessels predominantly in clusters | 30 |
| 13 | vessels with simple perforation plates | 21 |
| 14 | vessels with scalariform perforation plates | 48 |
| 20 | intervessel pits scalariform | 39 |
| 20.1 | intervessel pits pseudoscalariform to reticulate | 0 |
| 21 | intervessel pits opposite | 39 |
| 22 | intervessel pits alternate | 51 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 9 |
| 36 | helical thickenings present | 11 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 29 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 51 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 8 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 51 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 6 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 5 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 55 |
| 65 | septate fibers present | 6 |
| 68 | fibers thin-walled | 23 |
| 69 | fibers thick-walled | 4 |
| 70 | fibers thin- to thick-walled | 32 |
| 75 | parenchyma absent or unrecognizable | 37 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 14 |
| 79 | parenchyma paratracheal | 12 |
| 89 | parenchyma marginal | 1 |
| 96 | rays uniseriate | 54 |
| 97 | ray width predominantly 1-3 cells | 15 |
| 99.2 | stem lobed | 1 |
| 102 | ray height >1 mm | 30 |
| 105 | ray: all cells upright or square | 50 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 4 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 22 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 4 |
| 110 | rays with sheet cells (tangential section) | 5 |
| 136 | prismatic crystals present | 3 |
| 142 | prismatic crystals in axial chambered cells | 3 |
| R1 | groups of sieve tubes present | 11 |
| R3 | distinct ray dilatations | 11 |
| R4 | sclereids in phloem and cortex | 3 |
| R6.1 | sclereids in tangential rows | 2 |
| R7 | with prismatic crystals | 4 |
| R8 | with crystal druses | 3 |
| R10 | phloem not well structured | 32 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 11 |

# Euphorbiaceae



## Number of species, worldwide and in Europe

The Euphorbia family includes 320 genera with 6100 species. Most of the species grow in the tropics. In Europe, there are 7 genera with 118 species. The majority belongs to the genus *Euphorbia* (105 species). Many species are endemic to the Canary Islands.

## Analyzed material

The xylem and phloem of 7 genera with 48 species are analyzed here. 6 of species are endemic to the Canary Islands.
Bark-slides are missing for 8 of the 48 species.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 13 | 5 and many from the tropics |
| Succulent plants | 3 | 1 |
| Semi-woody chamaephytes | 5 | |
| Woody chamaephytes | 4 | |
| Hemicryptophytes and geophytes | 16 | 2 |
| Therophytes | 7 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 1 | |
| Hill and mountain | 23 | |
| Mediterranean | 10 | |
| Arid | 6 | |
| Subtropical | 8 | |

**Analyzed species:** (species with * are described also by other authors)
*Andrachne colchica* Mill. Arg.
*Euphorbia acanthothamnos* Heldr. et Start *
*Euphorbia albomarginata* Torr. et A. Gray
*Euphorbia amygdaloides* L.
*Euphorbia aphylla* Brouss. Ex. Willd.
*Euphorbia armena* Prokh.
*Euphorbia atropurpurea* W. et B.
*Euphorbia balsamifera* Ait.
*Euphorbia calyptra* Cosson et DR.
*Euphorbia canariensis* L.
*Euphorbia corollata* L.
*Euphorbia chamaesyce* L.
*Euphorbia characias* L.
*Euphorbia collina* Sublis
*Euphorbia cyparissias* L.
*Euphorbia dendroides* L. *
*Euphorbia dulcis* L.
*Euphorbia echinus* Hook et Coss. *
*Euphorbia esula* L.
*Euphorbia graminifolia* Vill.
*Euphorbia hadramautica* Baker
*Euphorbia helioscopia* L.
*Euphorbia larica* Boiss.
*Euphorbia lathyris* L.
*Euphorbia leptocaula* Boiss.
*Euphorbia maculata* L.
*Euphorbia mellifera* Ait. *
*Euphorbia nicaeensis* All.
*Euphorbia paralias* L.
*Euphorbia piscatoria* Link. *
*Euphorbia platyphyllos* L.
*Euphorbia prostrata* Aiton
*Euphorbia pulcherrima* Willd. *
*Euphorbia regis-jubaea* Webb et Berth.
*Euphorbia rigida* M. Bieb.
*Euphorbia schimperi* C. Presl.
*Euphorbia seguieriana* Neck
*Euphorbia squamaria* Loisel. *
*Euphorbia verrucosa* L.
*Euphorbia villosa* Waldst. et Kit.
*Euphorbia virgata* Waldst.
*Jathropha dhofarica* R.-Sem.
*Leptopus colchicus* Pojark
*Mercurialis annua* L.
*Mercurialis ovata* Stern et Hoppe
*Mercurialis perennis* L.
*Ricinus communis* L. *
*Securinega suffruticosa Rehd.* *

*Euphorbia balsamifera*

*Euphorbia maculata*

*Euphorbia cyparissias*

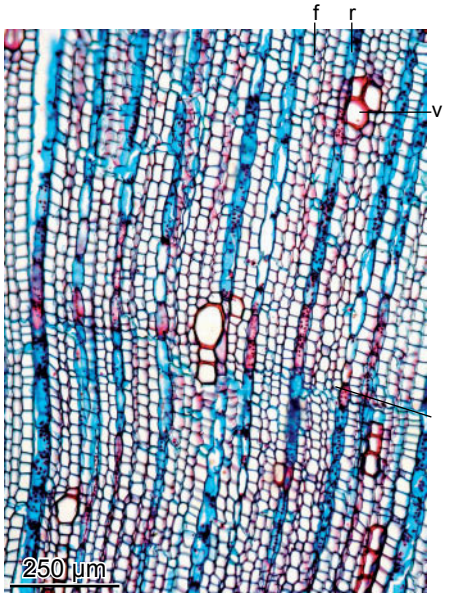
*Euphorbia esula*

*Euphorbia atropurpurea*

*Euphorbia canariensis*

**Characteristics of the xylem**

In the present material, 6 species have only one ring (**Figs. 1** and **7**). Annual rings occur in 26 perennial species present in all vegetation zones. Ring boundaries appear in 9 diffuse-porous (**Fig. 2**) and 15 semi-ring-porous species (**Fig. 3**). Only *Securinega suffruticosa* is ring-porous (**Fig. 4**). Rings are indistinct or absent in 12 species (**Figs. 5** and **6**). Vessels are arranged mostly in uni- or multiseriate radial multiples (short: 19 species, long: 23 species; **Figs. 6-8**) and are in groups (2 species; **Figs. 9** and **12**). Vessels are arranged solitary in 6 species but are ocasionally in dendritic patterns or tangential rows (**Figs. 10** and **11**). Vessel diameter is between 30-50 µm in 25 species or 50-100 µm in 23 species. Very small vessels with a diameter <20 µm are an exception (*Euphorbia dulcis*). Vessels with a diameter between 100-200 µm occur in large plants such as *Ricinus communis*, *Jatropha dhofarica* and *Euphorbia larica*. Vessels contain almost exclusively simple perforations (**Figs. 13-15**). A few small vessels with scalariform perforations have been found in *Mercurialis annua*. Inter-vessel pits are predominantly small and round (**Fig. 13**) but are slightly laterally enlarged in 13 species (**Fig. 14**). Vessel-ray pits are horizontally enlarged in a few *Euphorbia* species (**Figs. 15** and **16**). *Jatropha dhofarica*, *Ricinus communis* and *Securinega suffruticosa* produce small, thin-walled, unlignified tylosis (**Fig. 17**). Dark-staining substances occur only around wounds.




**Left Fig. 1.** Annual herb with a single ring. Root collar of a 20 cm-high therophyte, dry site, hill zone, Switzerland. *Euphorbia helioscopia*, transverse section.

**Right Fig. 2.** Growth zone marked by small vessels in the latewood and larger vessels in the earlywood. A few rows of fibers are flattened at the end of growth ring boundaries. Stem of a 2 m-high shrub, thermophile zone, Canary Islands, Spain. *Euphorbia balsamifera*, transverse section.

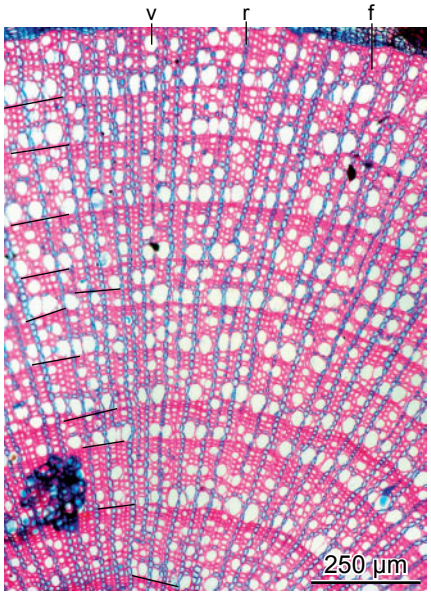



**Fig. 3.** Distinct rings of a semi-ring-porous wood. Root collar of a 20 cm-high dwarf shrub, hill zone, Botanical Garden Tbilisi, Georgia. *Leptopus colchicus*, transverse section.

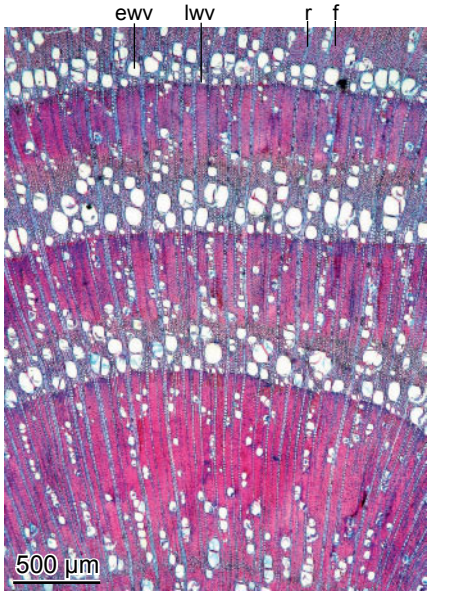



**Fig. 4.** Distinct rings of a ring-porous wood. Stem of a 2 m-high shrub, hill zone, Botanical Garden Zürich, Switzerland. *Securinega suffruticosa*, transverse section.

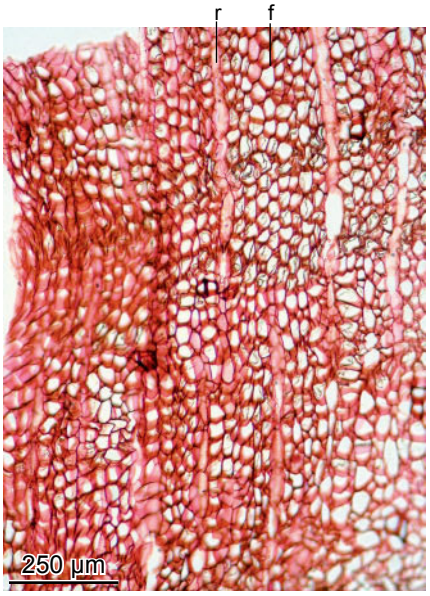
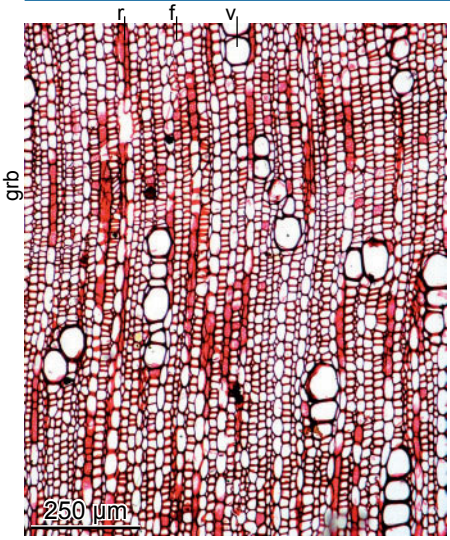
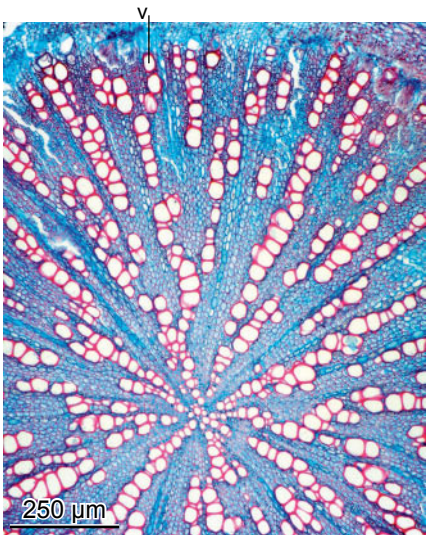


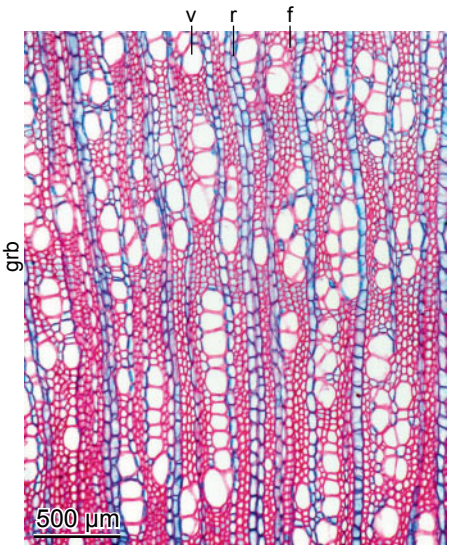

**Fig. 5.** Xylem without annual rings. Fibers and vessels have almost the same diameter. Stem base of 40 cm-high succulent plant, arid zone, Sahara, Algeria. *Euphorbia echinus*, transverse section.

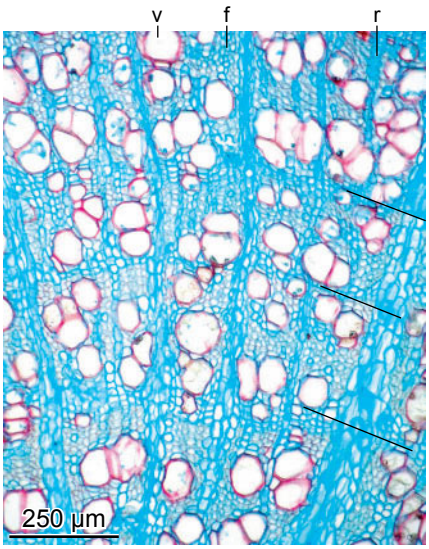



**Left Fig. 6.** Xylem with indistinct rings. Growth zones are indicated by a slight reduction of vessel diameter in the latewood and a zone of slightly flattened fibers. Stem of a 2 m-high shrub, subtropical climate, Canary Islands. *Euphorbia mellifera*, transverse section.

**Right Fig. 7.** A single ring with long radial rows of vessels in an annual herb. Root collar of a 2 cm-high prostrate therophyte, Mediterranean zone, Provence, France. *Euphorbia maculata*, transverse section.



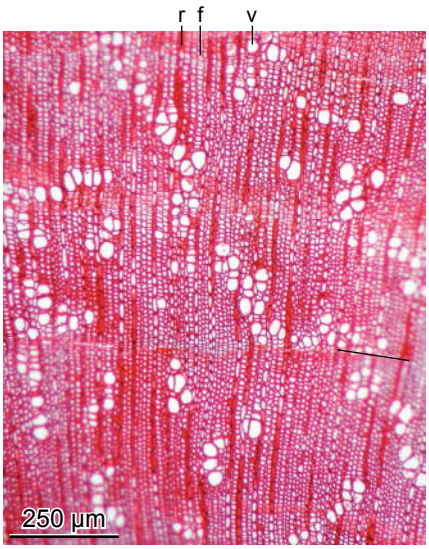
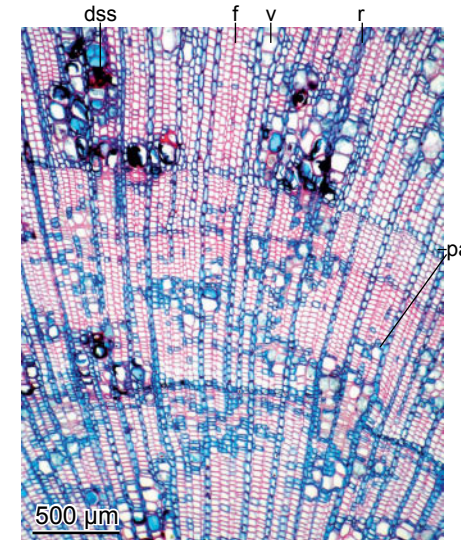




**Fig. 8.** Xylem without distinct rings. Vessels are arranged in long radial multiples, which are arranged in indistinct tangential bands. Stem base of a 50 cm-high dwarf shrub, arid zone, Sahara, Libya. *Euphorbia calyptra*, transverse section.

**Fig. 9.** Vessels are arranged in groups embedded in an unlignified fiber tissue (blue). Root collar of a 20 cm-high chamaephyte, Mediterranean zone, Provence, France. *Euphorbia nicaeensis*, transverse section.

**Fig. 10.** Vessels in dendritic groups embedded in a lignified fiber tissue. Root collar of a 20 cm-high chamaephyte, Mediterranean zone, Samos, Greece. *Euphorbia acanthothamnus*, transverse section.



**Left Fig. 11.** Vessels occur in dendritic groups and are embedded in a thin-walled lignified fiber tissue. Vessels are partially filled with dark-staining substances. Parenchyma is apotracheal and paratracheal (blue cells). Stem of a 1.5 m-high succulent, subtropical climate, Canary Islands. *Euphorbia aphylla*, transverse section.

**Right Fig. 12.** Vessels in irregular groups surrounded by fibers. The pervasive parenchyma forms large zones of a thin-walled tissue. Root collar of a 20 cm-high hemicryptophyte, dry site, alpine zone, Switzerland. *Euphorbia cyparissias*, transverse section.

The radial walls of fibers of most species are perforated by very small round pits (<2 µm) with slit-like apertures. Large fiber pits occur only in *Andrachne colchica* and *Leptopus colchicus* (**Fig. 18**). Septate fibers have been found only in *Euphorbia paralias*, *Mercurialis perennis* and *Andrachne colchica* (**Fig. 18**). Fibers are mostly thin-walled (26 species) or thin- to thick-walled (16 species). They are thick-walled only in *Euphorbia leptocaula*. Tension wood has been found in 26 species (**Figs. 19** and **20**). Axial parenchyma is apotracheal in 19 species and vasicentric paratracheal in 15 species (**Fig. 21**). A few species have pervasive parenchyma (**Figs. 12** and **22**), sometimes only in the center of the stem (**Fig. 42**). It is marginal in 11 species (**Fig. 23**). Different types of parenchyma occur within single individuals (**Figs. 22** and **42**).

Rays are rarely absent, e.g. in *Mercurialis perennis* and *Euphorbia chamaesyce*. 10 species have uniseriate rays (**Figs. 24** and **25**), 31 species have rays with 1-3 cells (**Fig. 26** and **27**) and 6 have rays >3 cells wide (**Fig. 28**). Vascular bundles remain in *Mercurialis ovata* (**Fig. 29**). The majority of rays are homocellular, consisting of square or upright cells (**Fig. 33**). Heterocellular rays with a few procumbent and many upright cells occur mainly in shrub-like *Euphorbia* species (**Fig. 30**). Rays are confluent with the axial fiber tissue in *Mercurialis annua*. 6 species have rays with horizontal canals (**Figs. 31** and **32**). Crystals are rare. Prismatic crystals occur in ray cells of *Securinega suffruticosa* (**Fig. 33**) and crystal druses occur in ray cells of *Jatropha dhofarica*.

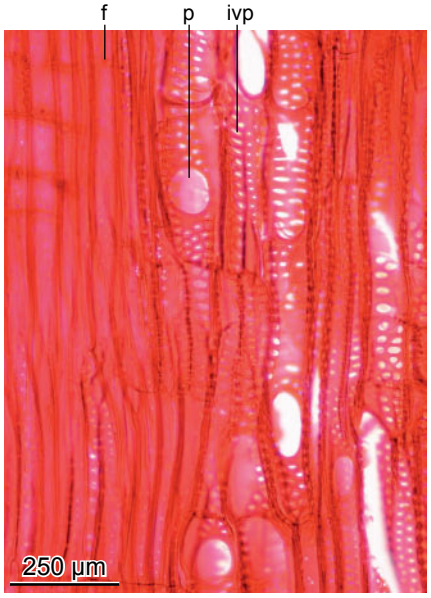



**Fig. 13.** Vessels with simple perforations. Intervessel pits are mostly round. Root collar of a 20 cm-high chamaephyte, Mediterranean zone, Samos, Greece. *Euphorbia acanthothamnos*, radial section.

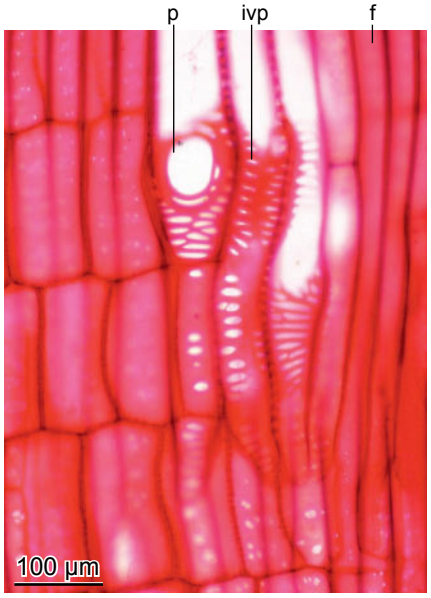



**Fig. 14.** Vessels with simple perforations. Intervessel pits are round to slightly scalariform. Stem of a 4 m-high shrub, thermophile zone, Canary Islands. *Euphorbia mellifera*, radial section.

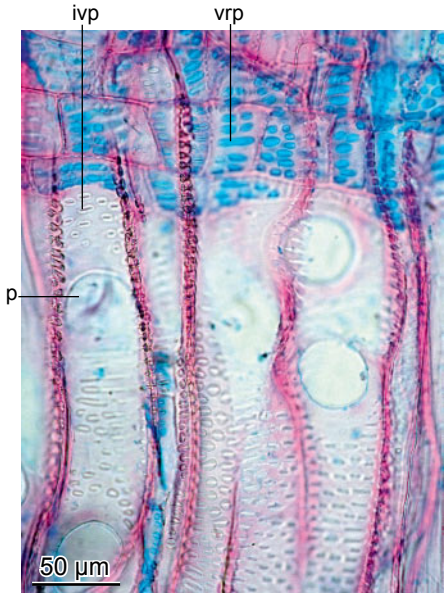
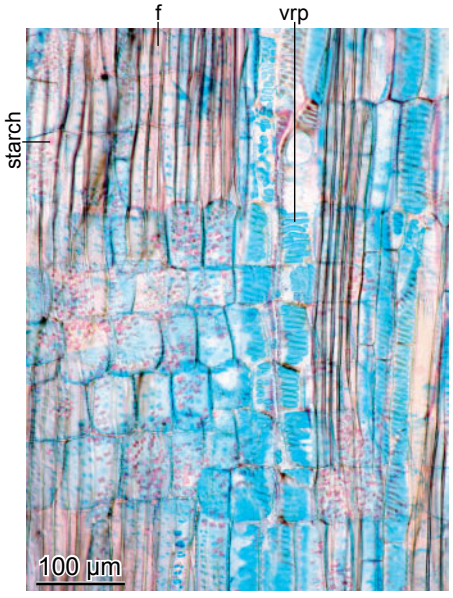
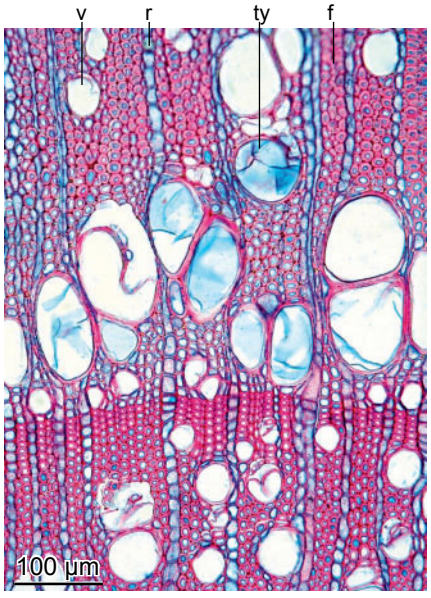


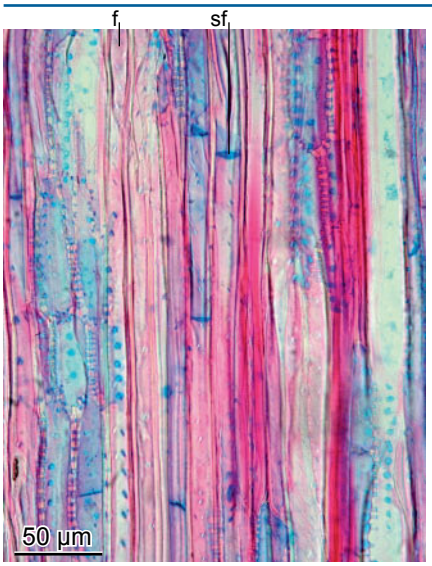

**Fig. 15.** Vessels with simple perforations. Vessel-ray pits are horizontally enlarged. Stem of a 50 cm-high dwarf shrub, arid zone, Sahara, Libya. *Euphorbia calyptra*, radial section.

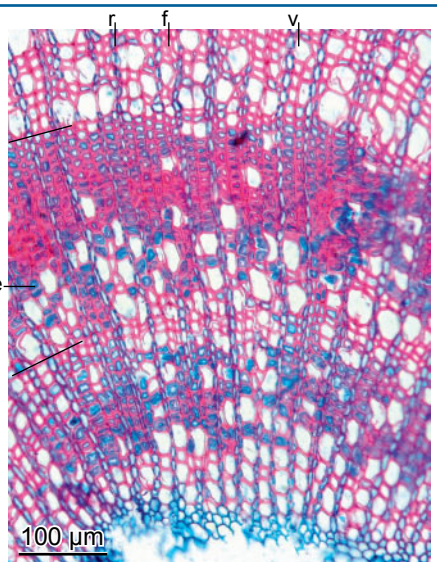



**Left Fig. 16.** Homocellular ray with square and upright cells and with distinctly horizontally enlarged intervessel pits. Stem of a 2 m-high shrub, thermophile zone, Canary Islands. *Euphorbia atropurpurea*, radial section.




**Right Fig. 17.** Thin-walled, unlignified tylosis in earlywood vessels. Stem of a 2 m-high shrub, hill zone, Botanical Garden Zürich, Switzerland. *Securinega suffruticosa*, transverse section.




**Left Fig. 18.** Xylem with septate fibers. The transverse walls are unlignified (blue). Stem base of a 30 cm-high dwarf shrub, hill zone, Botanical Garden Tbilisi, Georgia. *Andrachne colchica*, radial section.

**Right Fig. 19.** Tension wood zones of various intensity. Stem base of a 30 cm-high dwarf shrub, hill zone, Botanical Garden Tbilisi, Georgia. *Andrachne colchica*, transverse section.

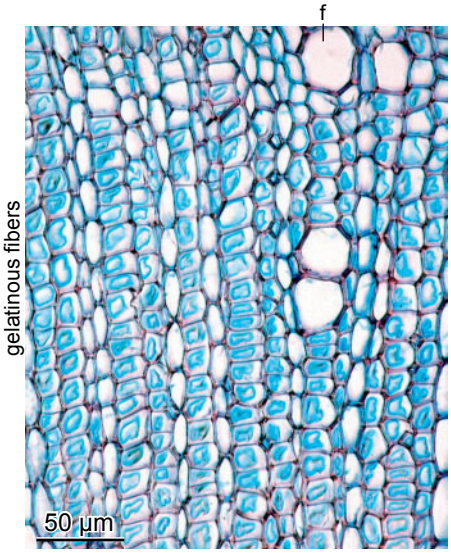



**Fig. 20.** Gelationous fibers (tension wood). Root collar of a 20 cm-high hemicryptophyte, dry site, hill zone, Switzerland. *Euphorbia helioscopia*, transverse section.

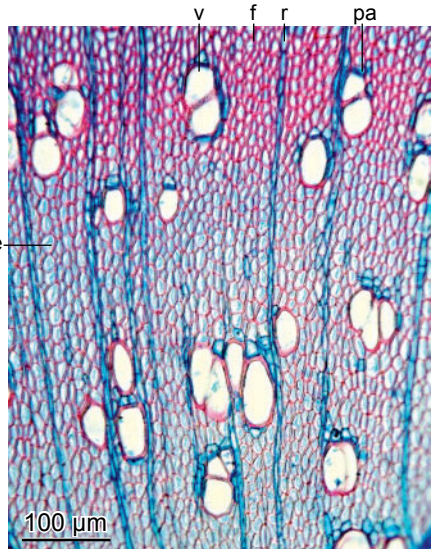



**Fig. 21.** Paratracheal parenchyma. Root collar of a 20 cm-high hemicryptophyte, dry site, Mediterranean zone, Provence, France. *Euphorbia graminifolia*, transverse section.

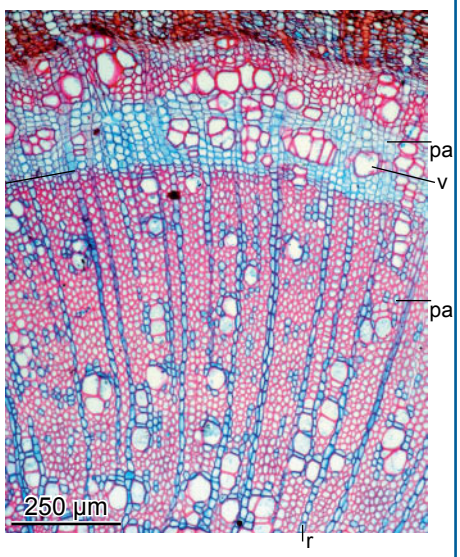
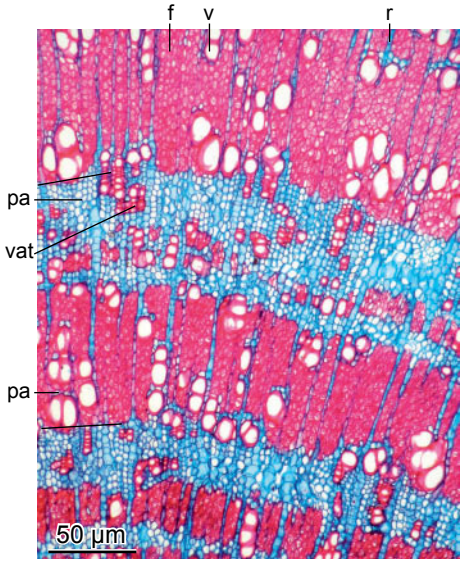
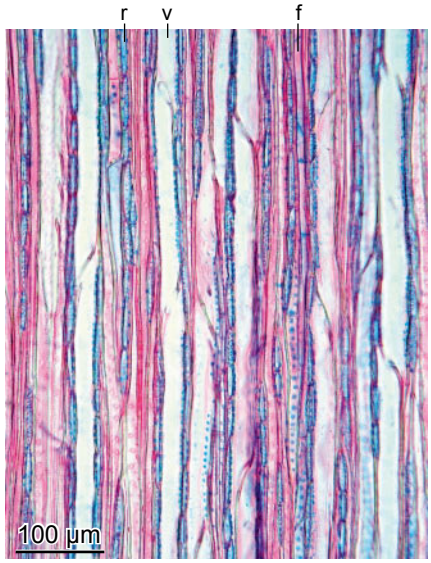


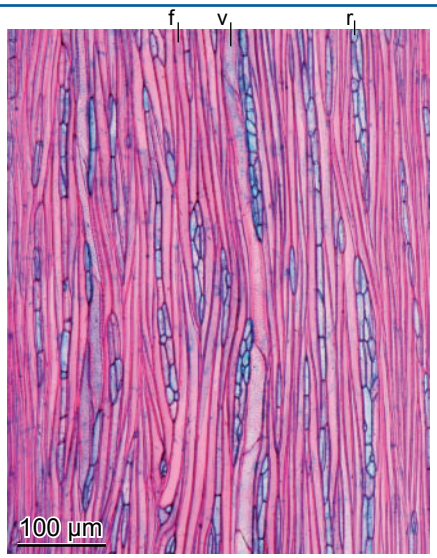

**Fig. 22.** Apotracheal, paratracheal and pervasive parenchyma (blue cells). Root collar of a 20 cm-high chamaephyte, hill zone, Botanical Garden Tbilisi, Georgia. *Euphorbia villosa*, transverse section.



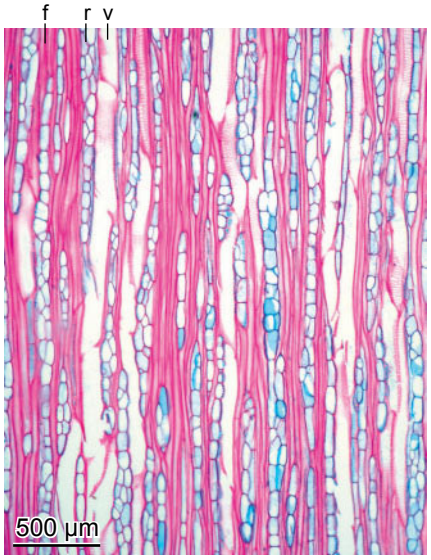

**Left Fig. 23.** Paratracheal parenchyma in zones with lignified fibers and pervasive parenchyma in terminal bands. Stem base of a 20 cm-high chamaephyte, dry site, hill zone, Valais, Switzerland. *Euphorbia seguieriana*, transverse section.

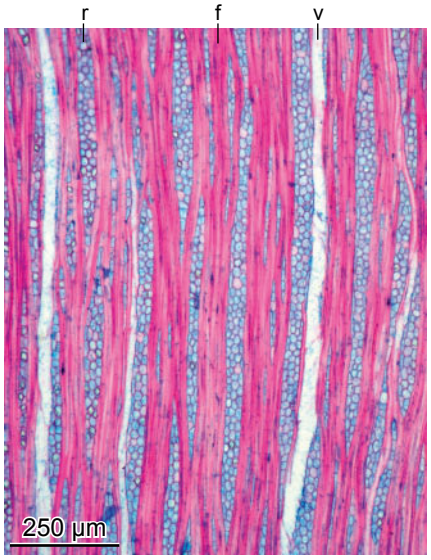
**Right Fig. 24.** Uniseriate homocellular rays consisting of slender cells. Stem base of a 30 cm-high dwarf shrub, hill zone, Botanical Garden Tbilisi, Georgia. *Andrachne colchica*, tangential section.




**Left Fig. 25.** Uniseriate homocellular rays consisting of distinctly axially elongated cells. Stem of a 2 m-high shrub, subtropical climate, Madeira, Portugal. *Euphorbia piscatoria*, tangential section.

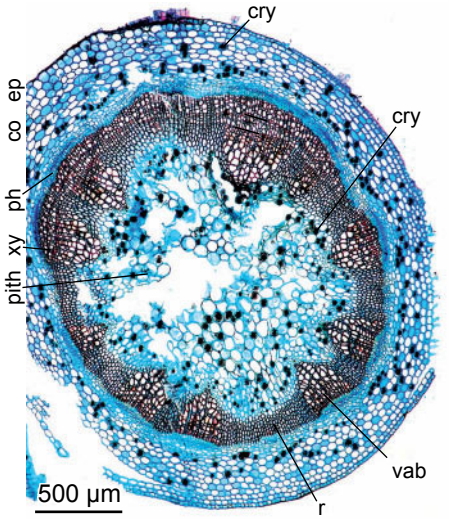
**Right Fig. 26.** Uniseriate homocellular rays consisting of distinctly axially elongated cells and biseriate rays consisting of slightly elongated cells. Root collar of a 20 cm-high therophyte, dry site, hill zone, Switzerland. *Euphorbia lathyris*, tangential section.

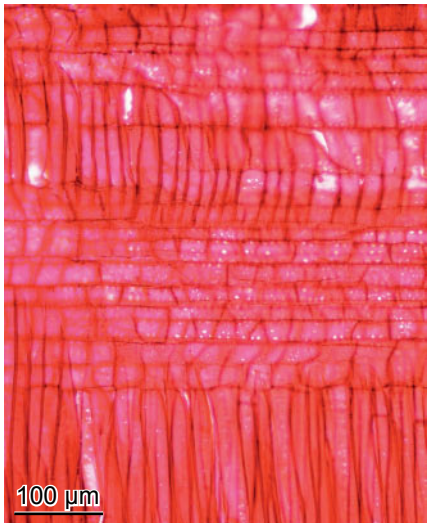



**Left Fig. 27.** Uni- and biseriate rays consisting of roundish cells. Stem base of 50 cm-high dwarf shrub, arid zone, Sahara, Libya. *Euphorbia calyptra*, tangential section.

**Right Fig. 28.** Homocellular rays, 2-4 cells wide, consisting of small roundish cells. Uniseriate rays consist of axially elongated cells. Stem of a 2 m-high shrub, hill zone, Botanical Garden Zürich, Switzerland. *Securinega suffruticosa*, tangential section.



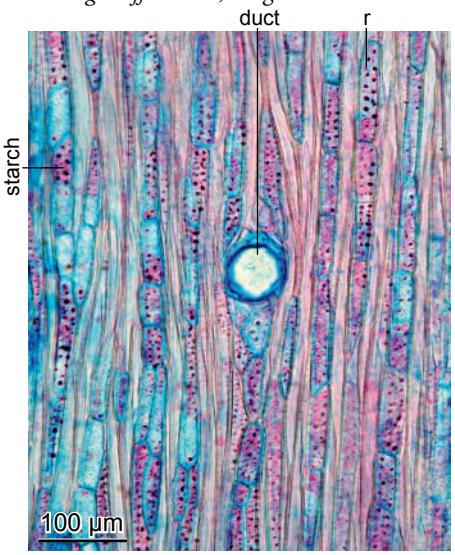
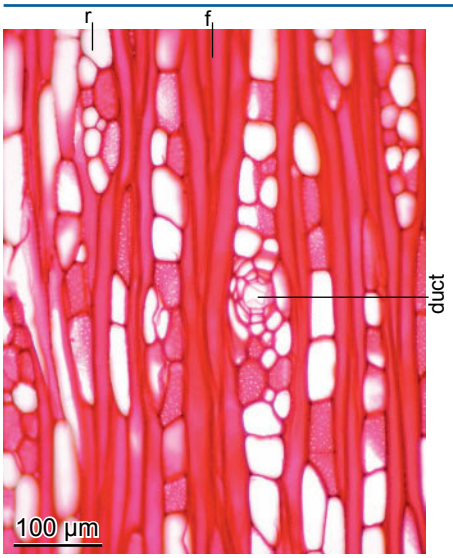




**Fig. 29.** Very large rays between vascular bundles in a three-year-old rhizome. Crystal druses occur in the cortex and the pith. Rhizome of a 20 cm-high hemicryptophyte, hill zone, Burgenland, Austria. *Mercurialis ovata*, transverse section.

**Fig. 30.** Heterocellular ray with a few procumbent and many upright cells. Stem base of a 2 m-high hemicryptophyte/shrub, arid zone, Oman. *Ricinus communis*, radial section.

**Fig. 31.** Radial canal in a ray. The canal is surrounded by thin-walled, unlignified cells. Stem of a 1.5 m-high shrub, subtropical climate, Salallah, Oman. *Euphorbia schimperi*, tangential section.



**Left Fig. 32.** Radial canal in a ray. The canal is surrounded by cells with normally-thick walls. In the center are thin-walled cells (excretion cells). Stem of a 2 m-high shrub, thermophile zone, Tenerife, Canary Islands. *Euphorbia pulcherrima*, tangential section.

**Right Fig. 33.** Prismatic crystals in ray cells. Stem of a 2 m-high shrub, hill zone, Botanical Garden Zürich, Switzerland. *Securinega frutiosa*, radial section.



### Characteristic features of taxa

A few species have an unusual anatomy: *Securinega suffruticosa* is ring-porous and has no ducts in the cortex. *Andrachne colchica* and *Leptopus colchicus* are semi-ring-porous, with many regularly dispersed vessels and absent ducts in the cortex. Shrub-like *Euphorbia* species are characterized by a thin-walled fiber tissue and a few fairly large vessels in radial multiples, e.g. *Euphorbia atropurpurea*, *E. balsamifera*, and *E. regis-jubaea*. We believe that many species have species-specific structures, but we hesitate to declare all the recognized differences because there exists a large intra-specific variability. The intra-specific variability along an elevation gradient is demonstrated by *Euphorbia cyparissias* (**Figs. 41-44**).

### Characteristics of the phloem and the cortex

The phloem and cortex is often simply structured and sieve-cell groups can hardly be distinguished from parenchyma cells (30 of 40 species analyzed; **Figs. 34** and **35**). Small groups of sieve-tubes are arranged in tangential rows in a few shrub-like species of the Canary Islands (*Euphorbia atropurpurea*, *E. balsamifera*, *E. canariensis*). Sclereids are fairly rare and occur in the genera *Euphorbia* and *Mercurialis*. They occur isolated, in groups (**Fig. 36**), in radial rows of 3 shrub-like *Euphorbia* species (**Figs. 37** and **38**) and in tangential rows of *Ricinus communis* (**Fig. 39**). Crystals are absent in the genus *Euphorbia*. *Securinega suffruticosa* has large prismatic crystals. Crystal druses occur in the genera *Mercurialis* (**Fig. 29**), *Jatropha* and *Ricinus* (**Fig. 40**). Laticifers are a dominant feature in most *Euphorbia* species, but they are absent in all other genera analyzed (**Figs. 34**, **37-40**).

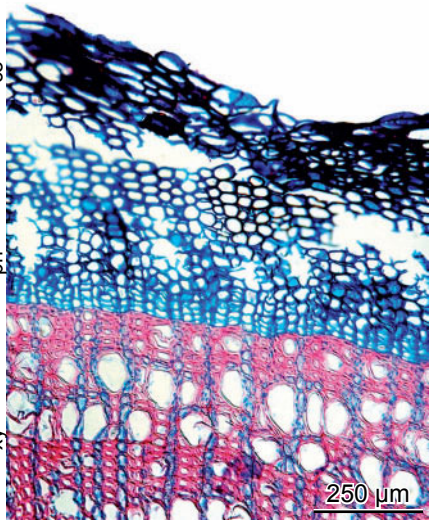



**Fig. 34.** Phloem and cortex with a uniform structure . Stem base of a 30 cm-high dwarf shrub, hill zone, Botanical Garden Tbilisi, Georgia. *Andrachne colchica*, transverse section.

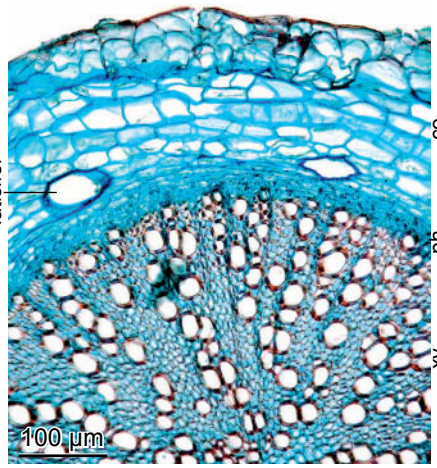



**Fig. 35.** Cortex with very large laticifers. Root collar of a 3 cm-high prostrate therophyte, ruderal site, Mediterranean zone, Provence, France. *Euphorbia chamaesyce*, transverse section.

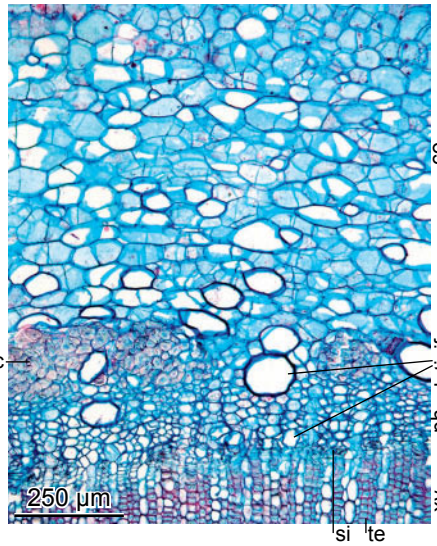
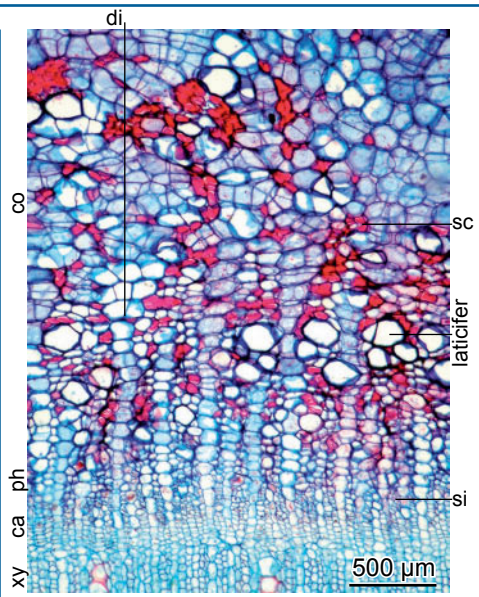
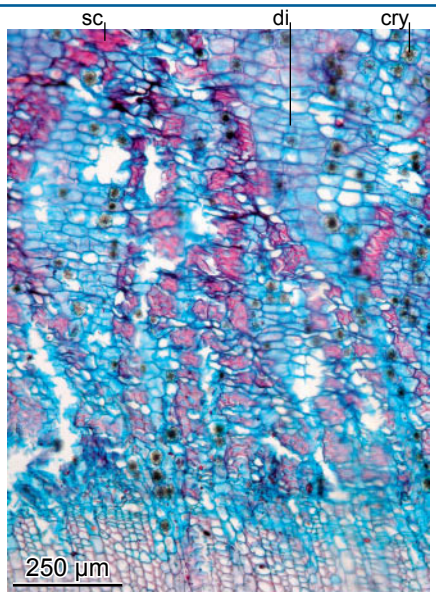


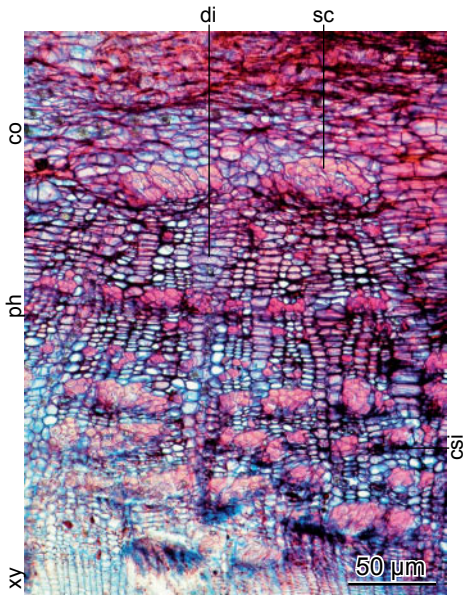

**Fig. 36.** Phloem and cortex with many laciitifers. Groups of sclerenchymatic cells are outside of the phloem. Stem of a 1.5 m-high succulent, subtropical climate, Canary Islands. *Euphorbia aphylla*, transverse section.

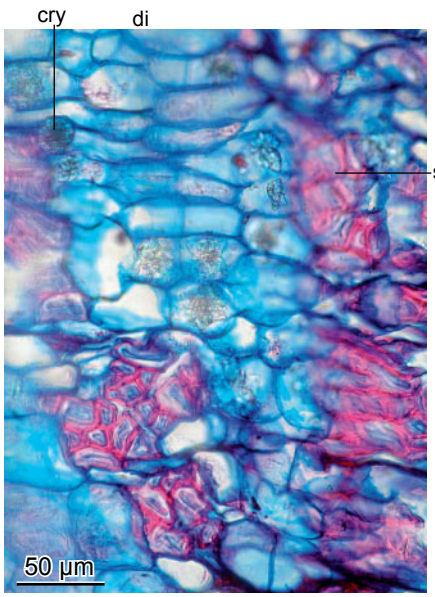



**Left Fig. 37.** Phloem and cortex with many lacitifers and radially arranged small groups of sclereids. Stem of a 2 m-high shrub, thermophile zone, Tenerife, Canary Islands. *Euphorbia canariensis*, transverse section.

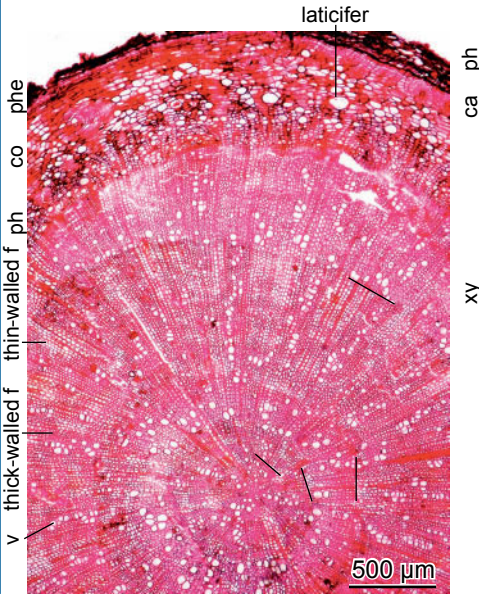
**Right Fig. 38.** Phloem and cortex with radially arranged groups of sclereids and distinct dilatations. Stem of a 2 m-high shrub, subtropical climate, Salallah, Oman. *Jatropha dhofarica*, transverse section.

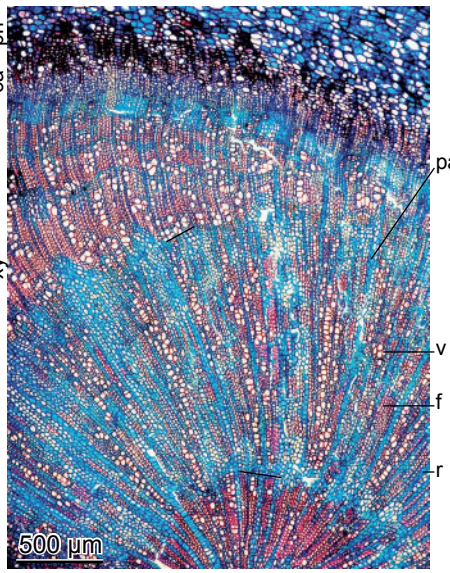



**Left Fig. 39.** Phloem with tangentially arranged groups of sclereids. Stem base of a 2 m-high hemicryptophyte/shrub, arid zone, Oman. *Ricinus communis*, transverse section.

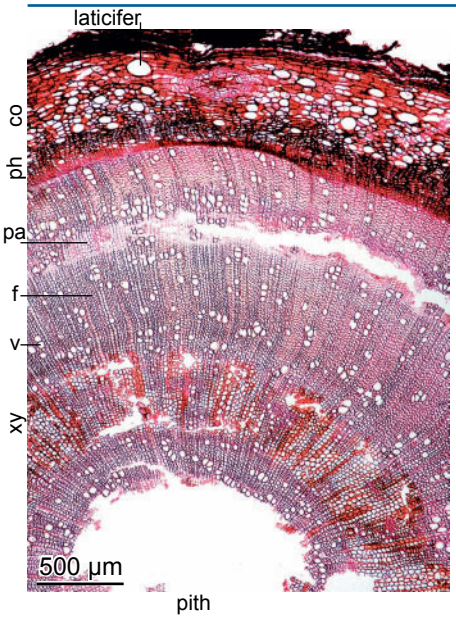
**Right Fig. 40.** Crystal druses in dilated ray cells of the phloem. Stem of a 2 m-high shrub, subtropical climate, Salallah, Oman. *Jatropha dhofarica*, transverse section.

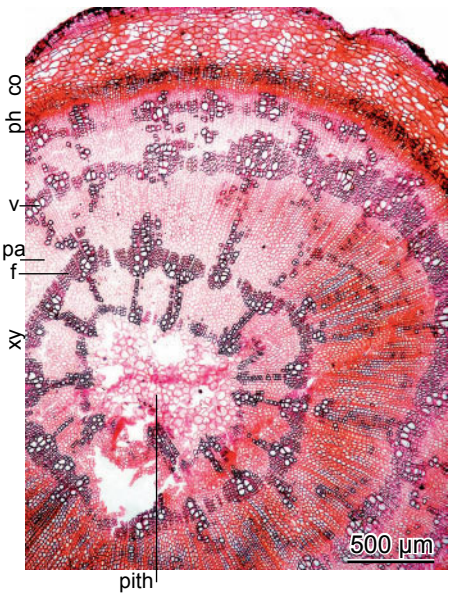



**Left Fig. 41.** Xylem with a dominance of fibers. Vessels are arranged mostly in short radial multiples. Rhizome of a 25 cm-high hemicryptophyte, dry ruderal site, Mediterranean, Cairo (200 m a.s.l.), Liguria, Italy. *Euphorbia cyparissias*, transverse section.

**Right Fig. 42.** Xylem with various amounts of parenchyma and fibers. Vessels are arranged mostly in long radial multiples. Rhizome of a 50 cm-high hemicryptophyte, plantation, hill zone, Blaufelden (400 m a.s.l.), Bavaria, Germany. *Euphorbia cyparissias*, transverse section.




**Left Fig. 43.** Xylem dominanted by fibers. Vessels are arranged mostly in short radial multiples. Parenchyma appears in marginal bands. Rhizome of a 25 cm-high hemicryptophyte, very dry site, hill zone, Ausserberg (700 m a.s.l.), Valais, Switzerland. *Euphorbia cyparissias*, transverse section.

**Right Fig. 44.** Xylem dominated by parenchyma. Vessels are arranged mostly in groups and fibers and appear in tangential bands. Rhizome of a 25 cm-high hemicryptophyte, dry site, alpine zone, Gornergrat (2900 m a.s.l.), Valais, Switzerland. *Euphorbia cyparissias*, transverse section.



**Ecological trends and relations to life forms**

Generally, ecological trends are difficult to detect because life and growth forms, plant size, and age greatly vary and the ecological range of the species analyzed is limited. Variability within species is demonstrated on *Euphorbia cyparissias* along an altitudinal gradient (200-2500 m a.s.l.). Taxonomic differences seem to dominate the anatomical variability.

**Discussion in relation to previous studies**

Woody species have been described intensively. Gregory (1994) mentioned approximately 180 articles. Hayden and Hayden (2000) concentrated on species of the subfamily Acalyphoidea. Further references are given by Westra and Koek-Noormann (2004) and by Mennega (2005) primarily on tropical woody species. 5 shrub-like *Euphorbia* species of the Canary Islands have been characterized by Carlquist (1970). Schweingruber (1990) characterized 6 *Euphorbia* species and *Ricinus communis* from Italy, Spain and Madeira. Benkova and Schweingruber (2005) described *Securinega suffruticosa* from eastern Siberia, Neumann et al. (2001) described 4 species from the Sahara/Sahel (*Chrozophora brocchiana*, *Euphorbia echinus*, *Securinega virosa*, *Ricinus communis*) and Jagiella and Kürschner (1987) described *Euphorbia cuneata* from Saudi Arabia. Only 8 of the species described here have been characterized before.

Xylem anatomy of Euphorbiaceae is extremely heterogeneous. By respecting therophytes, hemicryptophytes, and chamaephytes, the anatomical structure is much more diverse than it has been mentioned before. Radial multiples, fibers with gelatinous fibers (tension wood), apotracheal parenchyma, small rays, and the presence of radial laticifers seem to be characteristic of many species of the family (Mennega 2005). That partially corresponds with our findings. As shown above, vessels can be almost entirely absent, or occur in high density, parenchyma can be paratracheal or even pervasive and rays absent. Crystals are extremely rare in the present material.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **48** |
| 1 | growth rings distinct and recognizable | 26 |
| 2 | growth rings absent | 13 |
| 2.1 | only one ring | 10 |
| 3 | ring-porous | 1 |
| 4 | semi-ring-porous | 15 |
| 5 | diffuse-porous | 9 |
| 6 | vessels in intra-annual tangential rows | 1 |
| 7 | vessels in diagonal and/or radial patterns | 1 |
| 9 | vessels predominantly solitary | 11 |
| 9.1 | vessels in radial multiples of 2-4 common | 19 |
| 10 | vessels in radial multiples of 4 or more common | 23 |
| 11 | vessels predominantly in clusters | 9 |
| 13 | vessels with simple perforation plates | 48 |
| 14 | vessels with scalariform perforation plates | 1 |
| 20 | intervessel pits scalariform | 13 |
| 21 | intervessel pits opposite | 1 |
| 22 | intervessel pits alternate | 42 |
| 31 | vessel-ray pits with large apertures, *Salix*/*Laurus* type | 2 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae ype | 7 |
| 39.1 | vessel cell-wall thickness >2 µm | 13 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 2 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 24 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 21 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 4 |
| 50 | <100 vessels per $mm^2$ in earlywood | 16 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 31 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 1 |
| 56 | tylosis with thin walls | 3 |
| 58 | dark staining substances in vessels and/or fibers (gum, tannins) | 2 |
| 60.1 | fibers absent | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 44 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 3 |
| 65 | septate fibers present | 2 |
| 68 | fibers thin-walled | 26 |
| 69 | fibers thick-walled | 1 |
| 70 | fibers thin- to thick-walled | 16 |
| 70.2 | tension wood present | 25 |
| 75 | parenchyma absent or unrecognizable | 17 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 19 |
| 79 | parenchyma paratracheal | 15 |
| 79.1 | parenchyma pervasive | 5 |
| 89 | parenchyma marginal | 11 |
| 96 | rays uniseriate | 10 |
| 97 | ray width predominantly 1-3 cells | 31 |
| 98 | rays commonly 4-10-seriate | 6 |
| 99 | rays commonly >10-seriate | 1 |
| 99.1 | vascular-bundle form remaining | 2 |
| 100.1 | rays confluent with ground tissue | 1 |
| 100.2 | rays not visible in polarized light | 11 |
| 104 | ray: all cells procumbent (radial section) | 1 |
| 105 | ray: all cells upright or square | 36 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 8 |
| 117 | rayless | 3 |
| 130 | with radial canals | 6 |
| 133 | successive cambia, Caryophyllacea type | 1 |
| 136 | prismatic crystals present | 1 |
| 144 | druses present | 1 |
| R1 | groups of sieve tubes present | 14 |
| R2 | groups of sieve tubes in tangential rows | 3 |
| R3 | distinct ray dilatations | 14 |
| R4 | sclereids in phloem and cortex | 8 |
| R6 | sclereids in radial rows | 5 |
| R6.1 | sclereids in tangential rows | 4 |
| R7 | with prismatic crystals | 1 |
| R8 | with crystal druses | 5 |
| R9 | with crystal sand | 1 |
| R10 | phloem not well structured | 19 |
| R12 | with laticifers, oil ducts or mucilage ducts | 26 |
| R13 | tannins in parenchyma cells | 3 |

# Fabaceae



### Number of species, worldwide and in Europe

The Fabaceae family has an almost cosmopolitan distribution and includes approximately 620 genera with 18000 species. Most tree species grow in the tropics. In Europe there are 74 genera with 802 species. Some few species but no genera are endemic on the Canary Islands.

### Analyzed material

The xylem and phloem of 55 genera with 211 species are analyzed here. The material is composed of 6 species of the subfamily Mimosoideae (*Acacia*), 5 species of the Caesalpinioideae and 200 species of the Faboideae.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 16 | >600 |
| Liana | 3 | <5 |
| Nanophanerophytes 0.5-4 m | 48 | ca. 20 |
| Semi-woody chamaephytes | 12 | <5 |
| Woody chamaephytes | 37 | ca. 20 |
| Hemicryptophytes and geophytes | 81 | <5 |
| Therophytes | 15 | <5 |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and supalpine | 21 | |
| Boreal | 14 | |
| Hill and mountain | 94 | |
| Mediterranean | 54 | |
| Arid | 12 | |
| Suptropical | 16 | |

*Laburnum anagyroides* (photo: B. Schulze)

**Analyzed species:**

*Acacia dealbata* Link
*Acacia greggii* A. Grey
*Acacia mearnsi* De Wild
*Acacia raddiana* Savi
*Acacia senegal* (L.) Willd.
*Acacia tortilis* (Forssk.) Hayne
*Adenocarpus decorticans* Boiss.
*Adenocarpus telonensis* DC
*Adenocarpus viscosus* Webb et Bert
*Amorpha fruticosa* L.
*Anagyris foetida* L.
*Anthyllis cytisoides* L.
*Anthyllis terniflora* (Lag.) Pau
*Anthyllis tetraphylla* L.
*Anthyllis vulneraria* L.
*Astragalus alpinus* L.
*Astragalus armatus* Lam.
*Astragalus campestre* L.
*Astragalus cruckshansii* Griesb.
*Astragalus depressus* L.
*Astragalus exscapus* L.
*Astragalus frigidus* (L.) A. Grey
*Astragalus fruticosus* Ledeb
*Astragalus glyciphyllos* L.
*Astragalus lentiginosus* Douglas
*Astragalus leontinus* Wulfen
*Astragalus massiliensis* (Miller) Lam.
*Astragalus microcephalus* Willd.
*Astragalus monspessulanus* L.
*Astragalus penduliflorus* Lam.
*Astragalus praelongus* Sheld
*Astragalus sempervirens* Lam.
*Astragalus stella* Guan.
*Astragalus subulatus* M.B.
*Calicotome spinosa* (L.) Link
*Calicotome villosa* (Poiret) Link
*Calliandra eriophyllum* Benth.
*Caragana arborescens* L.
*Caragana jubata* (Pall.) Poir
*Caragana pygmaea* Bondreva
*Caragana ussuriensis* (Regel) Pojark
*Cassia holosericea* Fresen.
*Cassia obovata* Collad.
*Ceratonia siliqua* L.
*Cercis siliquastrum* L.
*Chamaecytisus hirsutus* L.
*Chamaecytisus proliferus* Link.
*Chamaecytisus purpureus* (Scop.) Link
*Chamaecytisus ratisbonensis* Rothm
*Chamaecytisus supinus* (L.) Link
*Colutea arborescens* L.
*Colutea atlanica* Browicz
*Coronilla coronata* L.
*Coronilla juncea* L.
*Coronilla minima* L.
*Coronilla vaginalis* L.
*Coronilla valentina* L.
*Crotalaria saharae* Coss.
*Cytisophyllum sessilifolium* (L.) O. Lang
*Cytisus austriacus* L.
*Cytisus maderensis* Masf.
*Cytisus nigricans* L.
*Cytisus patens* L.
*Cytisus pseudodecumbens* Spach
*Cytisus scoparius* Link

*Cytisus striatus* Roth.
*Cytisus tener* Jacq.
*Dalea lanata* Michaux
*Desmodium glutinosum* Schindl.
*Desmodium illinoense* A. Grey
*Dorycnium pentaphyllum* Scop.
*Dorycnium germanicum* Gams.
*Dorycnium graecum* (L.) Ser.
*Dorycnium herbaceum* Vill.
*Dorycnium hirsutum* (L.) Ser.
*Dorycnium intermedium* Ledeb
*Dorycnium suffruticosum* Vill.
*Echinospartium boissieri* Rothm.
*Erinacea anthyllis* Link.
*Genista aethnensis* DC
*Genista anglica* L.
*Genista candicans* L.
*Genista cinerea* (Vill.) DC
*Genista germanica* L.
*Genista hispanica* L.
*Genista pilosa* L.
*Genista pulchella* Vis.
*Genista purgans* DC
*Genista radiata* (L.) Spach
*Genista saggitalis* L.
*Genista spartioides* Spach
*Genista sphacellata* Spach
*Genista tinctoria* L.
*Genista triacanthos* Brot.
*Genista umbellata* Poiret
*Gleditsia triacanthos* L.
*Hedysarum arcticum* B. Fedtsch
*Hedysarum gmelinii* Ledeb
*Hedysarum hedysaroides* Schinz et Thell.
*Hedysarum zundukii* Peschkova
*Hippocrepis comosa* L.
*Hippocrepis emerus* (L.) Lassen
*Hippocrepis glauca* Ten.
*Laburnum alpinum* L.
*Laburnum anagyroides* Med.
*Lathyrus heterophyllus* L.
*Lathyrus niger* (L.) Bern.
*Lathyrus occidentalis* Fritsch
*Lathyrus sylvestris* L.
*Lathyrus venetus* Wohlf.
*Lathyrus vernus* Bernh.
*Lespedeza hirta* Hornem.
*Lespedeza virginiana* Britton
*Lotus aragonensis* Bramwell
*Lotus campylocladus* Webb et Berth.
*Lotus corniculatus* L.
*Lotus creticus* L.
*Lotus glaucus* Ait.
*Lotus maritimus* L.
*Lotus mascaensis* Burch
*Lotus sesslilifolius* DC
*Lupinus albicaulis* Hook
*Lupinus argenteus* Pursh.
*Lupinus obtusifolius* Heller
*Lupinus tassilicus* Mair
*Lygos monosperma* (L.) Heywood
*Lygos retam* Heywood
*Medicago arborea* L.
*Medicago falcata* L.
*Medicago lupulina* L.
*Medicago minima* L.
*Medicago rididula* L.
*Medicago sativa* L.
*Melilotus albus* Medik.
*Melilotus indica* (L.) All.
*Onobrychis arenaria* DC
*Onobrychis caput-galli* (L.) Lam.
*Onobrychis montana* DC
*Onobrychis viciifolia* Scop.
*Ononis angustissima* Lam.
*Ononis aragonensis* Asso
*Ononis cristata* Miller
*Ononis fruticosa* L.
*Ononis minutissima* L.
*Ononis mitissima* L.
*Ononis natrix* L.
*Ononis repens* L.
*Ononis rotundifolia* L.
*Ononis serrata* Forst.
*Ononis speciosa* Lag.
*Ononis spinosa* L.
*Ononis tridentata* L.
*Oxytropis campestre* (L.) DC
*Oxytropis coerulea* Turcz
*Oxytropis helvetica* Scheele
*Oxytropis jaquinii* Bunge
*Oxytropis pilosa* (L.) DC
*Oxytropis popoviana* Peschkova
*Oxytropis tragacanthoides* Fisch ex DC
*Oxytropis triphylla* DC
*Petteria ramentecea* C. Presl
*Phaseolus angustissimus* A. Grey
*Phaseolus coccineus* L.
*Psoralea bituminosa* L.
*Pueraria hirsuta* Kurz
*Robinia neo-mexicana* A. Grey
*Robinia pseudoacacia* L.
*Securigera varia* (L.) Lassen
*Senna armata* Irwin et Barneby
*Spartium junceum* L.
*Spartocytisus filipes* Webb et Berth
*Spartocytisus supranubicus* Santos
*Sophora japonica* L.
*Staurocanthus boivinii* Samp.
*Teline nervosa* Hans. et Sund.
*Teline canariensis* Webb et Berth.
*Teline maderensis* Masf.
*Teline monspessulana* K. Koch
*Tephrosia leptostachya* DC
*Thermopsis divaricarpa* Nelson
*Trifolium alpinum* L.
*Trifolium ambiguum* M Bieb
*Trifolium angustifolium* Lam.
*Trifolium arvense* L.
*Trifolium aureum* Pollich
*Trifolium badium* Schreber
*Trifolium dasyphyllum* Torrey
*Trifolium incarnatum* L.
*Trifolium maciletum* Greene
*Trifolium medium* L.
*Trifolium montanum* L.
*Trifolium nanum* Torrey
*Trifolium pallescens* Schreber
*Trifolium pratense* L.
*Trifolium repens* L.
*Trifolium rubens* L.
*Trifolium saxatile* All.
*Trifolium thalii* Vill.
*Ulex baeticus* Boiss.
*Ulex europaeus* L.
*Ulex minor* Roth
*Ulex parviflorus* Pourret
*Vicia hirsuta* S.F. Gray
*Vicia onobrychioides* L.
*Vicia pannonica* Crantz
*Vicia pisiformis* L.
*Vicia sativa* L.
*Vicia sepium* L.
*Vicia sylvatica* L.
*Vicia villosa* Roth
*Wisteria sinensis* Sweet

*Ononis natrix*

*Genista tinctoria* (photo: Landolt)

*Melilotus albus*

*Astragalus exscapus* (photo: Landolt)

*Lathyrus vernus*

*Vicia sepium*

*Anthyllis vulneraria*

*Onobrychis sativa* (photo: Landolt)

*Hippocrepis comosa*

*Lupinus tassilicus*

*Hedysarum hedysaroides*

*Acacia tortuosa*

*Cytisus scoparius*

*Acacia raddiana*

## Characteristics of the xylem

### Characteristic features of subfamilies, genera and species

The only common xylem anatomical feature within the family of Fabaceae are the simple perforations.

### Fabioideae

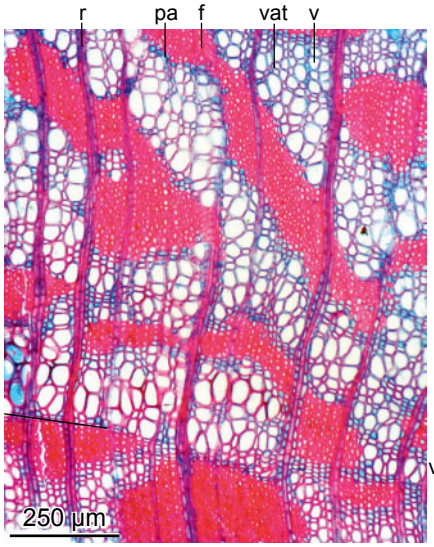
All species analyzed have vestured intervessel pits and fibers with small intervessel pits and oblique slit-like apertures. Fiber pits are small (<3 µm) with simple to minute borders.

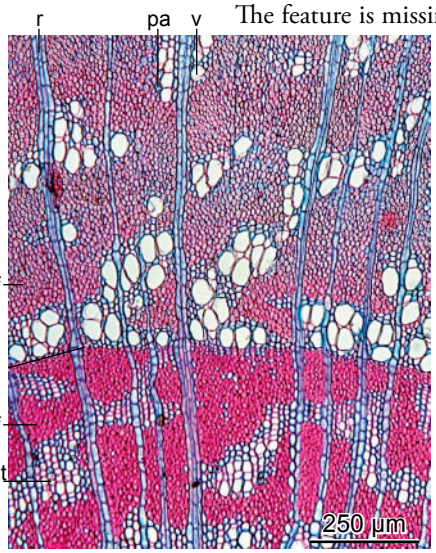
A pure anatomical grouping within the whole family is not possible. Therefore we decided to summarize those with dendritic vessel patterns (anatomical based subgroup 1), all *Astragalus* and *Oxytropis* species (anatomical and taxonomic based subgroup 2) and all chameaphytes, hemicrytophytes and therophytes exclusively species in subgroups 1 and 2 (life form-based subgroup).

#### *Subgroup 1. Species with dendritic and diagonal vessel patterns*

The group includes the following genera and a few species of some genera: *Adenocarpus*, *Anagyris foetida*, *Anthyllis cytisoides*, *A. terniflora*, *Calicotome*, *Caragana*, *Chamacytistus proliferus*, *Colutea*, *Coronilla juncea*, *C. minima*, *C. valentina*, *Crotalaria saharae*, *Cytisophyllum*, *Cytisus*, *Dorycnium*, *Echinospartium*, *Erinacea*, *Genista*, *Hippocrepis emerus*, *Laburnum*, *Lotus corniculatus*, *Lygos*, *Ononis speciosa*, *Petteria*, *Senna*, *Spartium*, *Spartocytisus*, *Staurocanthus*, *Teline*, *Ulex*.

Vessels in dendritic patterns are a constant feature in shrubs and dwarf shrubs, however, transitions to diagonal patterns are frequent in individuals with small rings (**Figs. 1-3**). Exclusively diagonal to radial patterns occur in *Dorycnium* (**Fig. 4**) and *Crotolaria saharae* (small shrub; **Fig. 5**). The only hemicryptophyte with a dendritic-like vessel pattern is *Lotus corniculatus* (**Fig. 6**). The feature is missing in the shrubs *Amorpha fruticosa* (**Fig. 7**),




**Left Fig. 1.** Dendritic vessel pattern in the the earlywood of a semi-ring-porous wood. Xylem of a 2 m-high shrub, *Adenocarpus* bush. Subalpine belt, subtropical zone, Tenerife, Canary Islands. *Adenocarpus viscosus*, transverse section.

**Right Fig. 2.** Dendritic vessel pattern in the latewood, diagonal vessel pattern in the earlywood of a semi-ring-porous wood. Xylem of a 1 m-high shrub, maccia, Mediterranean zone, Provence, France. *Cytisophyllum sessilifolium*, transverse section.

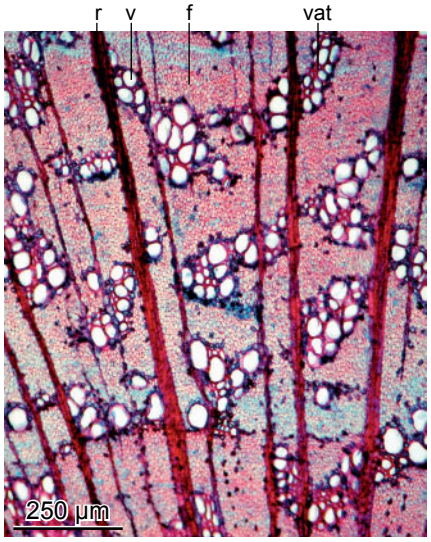



**Fig. 3.** Diagonal to reticulate vessel pattern in a semi-ring-porous wood. Xylem of a 40 cm-high dwarf shrub, maccia, Mediterranean zone, Provence, France. *Cytisus pseudodecumbens*, transverse section.

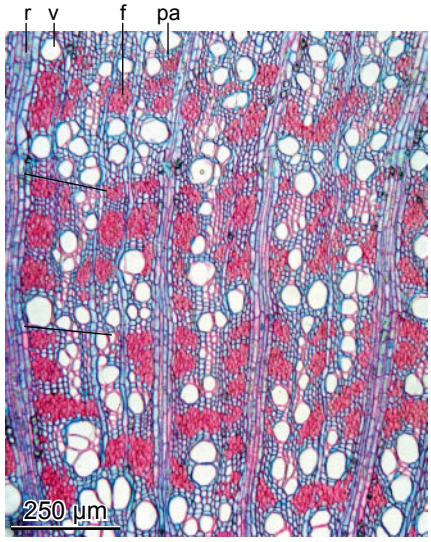



**Fig. 4.** Radial to diagonal vessel pattern in a semi-ring- to ring-porous wood. Xylem of a 40 cm-high dwarf shrub, garigue, Mediterranean zone, Alicante, Spain. *Dorycnium pentaphyllum*, transverse section.

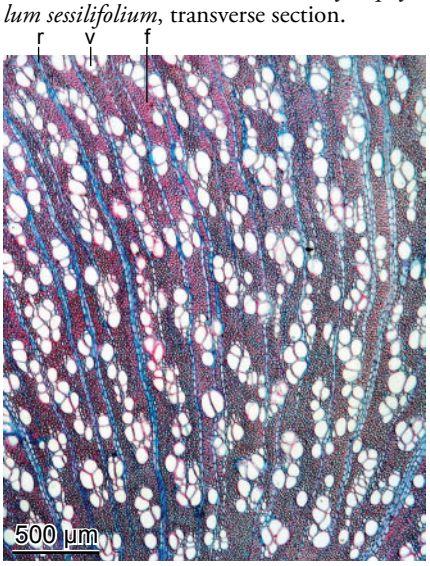


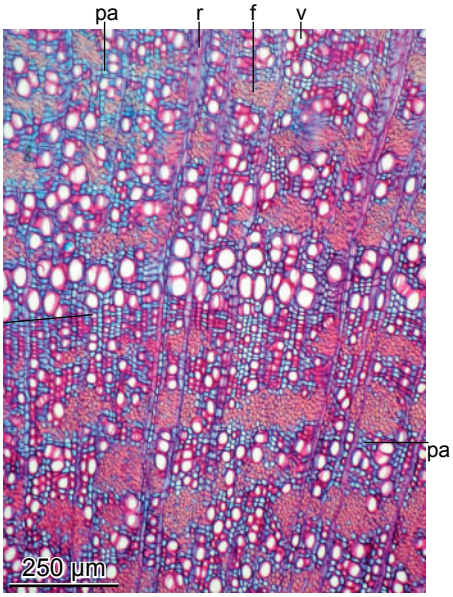

**Fig. 5.** Radial to diagonal vessel pattern in a wood without annual rings. Xylem of a 40 cm-high dwarf shrub, sand desert, arid zone, Libya. *Crotalaria saharae*, transverse section.

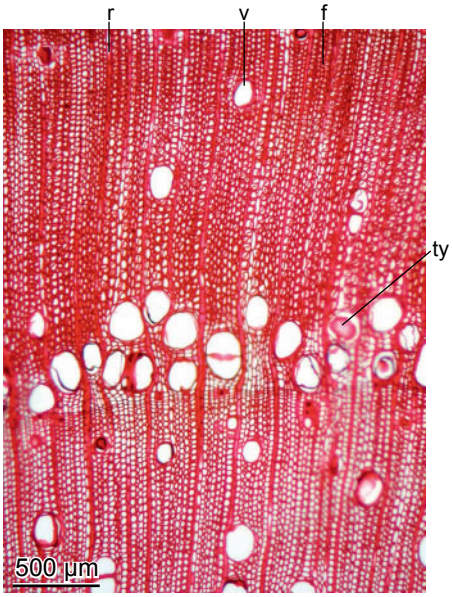
*Calliandra*, *Lygos retam* and *Medicago arborea*.

Common anatomical features in this group are:
- Fibers are mostly thick-walled.
- Some few prismatic crystals occur in rays of a very few species (*Anthyllis terniflora*, *Coronilla minima* and *C. valentina*).
- Ray cells are always fairly thick-walled and do not disappear in polarized light.

Within this group exist differences:
- A few species are ring porous (**Figs. 7-9**)
- Most species are semi-ring-porous (**Figs. 1-4** and **6**).
- Helical thickenings occur almost constantly in this subfamily (**Fig. 10**). They are missing only in the genera *Anthyllis* and *Coronilla*.
- Marginal parenchyma is a constant feature in this subfamily (**Fig. 11**). It is missing only in the genera *Calycotome* and *Petteria*.
- Ray width is variable. Rays of a few species vary between 1-3 cells (**Fig. 12**). Most species have rays with 2-4 or 3-6 cells (**Fig. 13**) in width. Rays are larger than 8-seriate in a few species (**Fig 14**). Rays are mostly homocellular, consisting either of square and upright procumbent cells. Heterogeneity is rare. Sheet cells occur in various genera, however, they are never very distinct.
- Storied structures are fairly common, however, this feature does not seem to be a genus-characteristic feature (**Figs. 14** and **15**).

We do not have enough slides with bark for a definite classification. Groups of sclereids of most species are arranged in tangential layers (**Figs. 16** and **17**) or in *Dorycnium* in radial groups (**Fig. 18**).




**Left Fig. 6.** Dendritic vessel/parenchyma pattern in a semi-ring-porous wood. Fibers occur in patches and vessels are surrounded by parenchyma cells. Xylem of a 20 cm-high hemicryptophyte, dry meadow, hill zone, Valais, Switzerland. *Lotus corniculatus*, transverse section.

**Right Fig. 7.** Xylem of a ring-porous wood with few vessels (<100/mm$^2$). 1 m-high shrub, cultivated, hill zone, Switzerland. *Amorpha fruticosa*, transverse section.

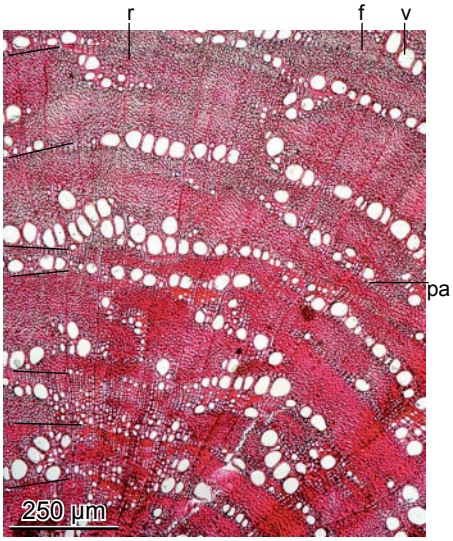



**Fig. 8.** Xylem of a ring-porous wood with dendritic vessel patterns in the latewood. 1 m-high shrub, meadow, mountain zone, Altai Mountains, Russia. *Caragana jubata*, transverse section.

**Fig. 9.** Xylem of a ring-porous wood with dendritic vessel patterns in the latewood. 3 m-high shrub, *Ostrya carpinifolia* forest, hill zone, Switzerland. *Laburnum anagyroides*, transverse section.

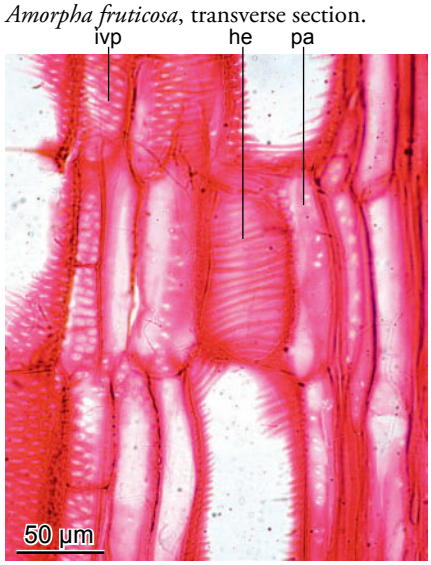



**Fig. 10.** Helical thickenings in vessels. Stem of a 1.5 m-high shrub, hedge, thermophile zone, subtropical zone, Tenerife, Canary Islands. *Chamaecytisus proliferus*, radial section.

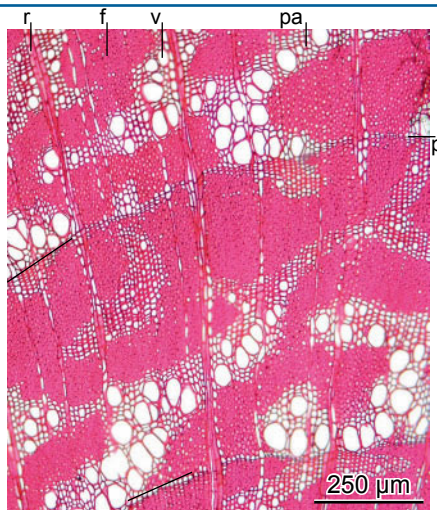



**Fig. 11.** 1-3 rows of marginal parenchyma cells in the latewood. Stem of a 60 cm-high dwarf shrub, abanonned meadow, montane zone, Trentino, Italy. *Genista radiata*, transverse section.

**Fig. 12.** 1-3-seriate homocellular rays. Vessels are storied. Stem of a 80 cm-high shrub, hedge, thermophile zone, subtropical zone, Madeira, Portugal. *Cytisus tener*, tangential section.

**Fig. 13.** 5-7-seriate rays with unlignified cell walls. Stem of a 50 cm-high dwarf shrub, dry meadow, montaine zone, Kaukasus, Georgia. *Dorycnium graecum*, tangential section.

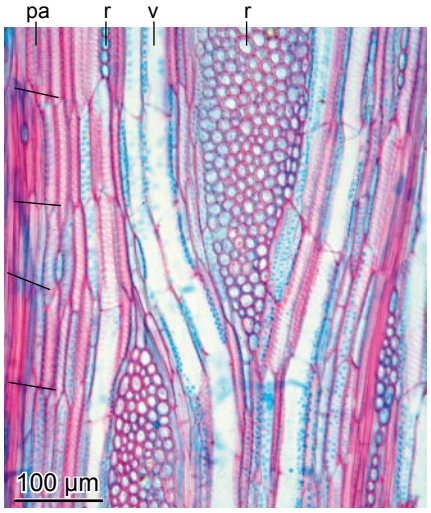



**Fig. 14.** 1 to >10-seriate homocellular rays with lignified cell walls and storied parenchyma. Stem of a 80 cm-high shrub, meadow, subalpine zone, Provence, France. *Genista cinerea*, tangential section.

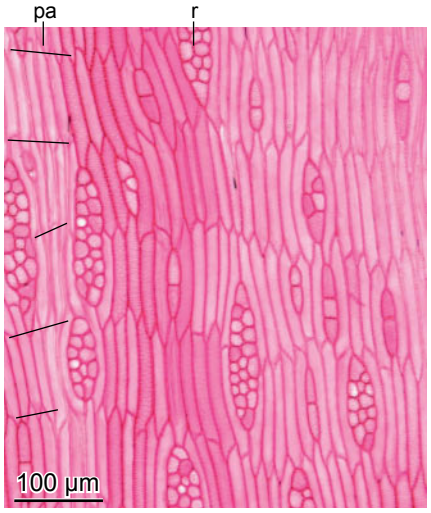



**Fig. 15.** Storied parenchyma and 1-3-seriate homocellular rays. Stem of a 80 cm-high shrub, maccia, montain zone, Andalusia, Spain. *Adenocarpus decorticans*, tangential section.

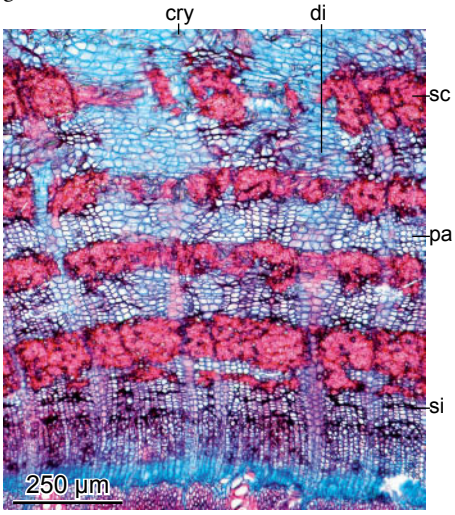
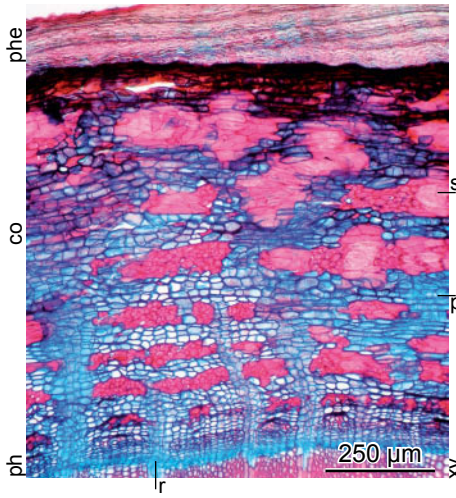
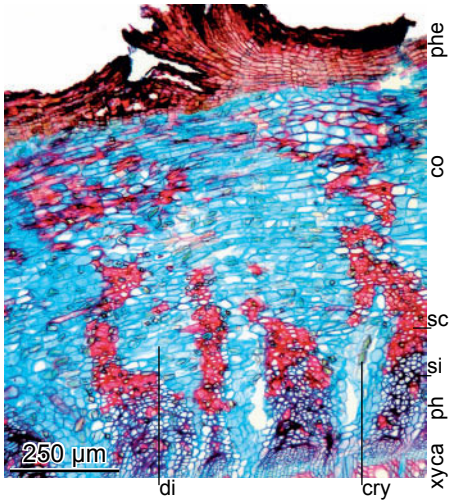



**Fig. 16.** Phloem with tangential bands of thick-walled sclerenchyma cells. Stem of a 80 cm-high shrub, garigue, Mediterranean, Almeria, Spain. *Anthyllis cytisoides*, transverse section.




**Left Fig. 17.** Phloem with radially interrupted, tangential bands of thick-walled sclerenchyma cells. Stem of a 80 cm-high shrub, meadow, Mediterranean, Provence, France. *Cytisophyllum sessilifolium*, transverse section.

**Right Fig. 18.** Phloem with irregular radial groups of thick-walled sclerenchyma cells. Stem of a 40 cm-high dwarf shrub, dry meadow, Mediterranean, Provence, France. *Dorycnium pentaphyllum*, transverse section.

***Subgroup 2. Astragalus and Oxytropis***

All species with annual rings are semi-ring-porous (**Figs. 19-21**) or ring-porous. Ring-porosity occurs only in the genus *Astragalus* (**Fig. 22**). Vessels of all species are thick-walled (**Figs. 26** and **30**). Most species have round intervessel pits, arranged in alternating and rarely in opposite position (**Fig. 23**) and pits with horizontally enlarged apertures (variable degree of scalariform pits; **Fig. 24**). Transitions between alternating and horizontally enlarged pits are frequent. Exclusively round pits have been found in *Astraglus armatus*, *A. leontinus* and *A. massiliensis*.

Vessels stay mostly solitary or in small irregular groups (**Figs. 19-22**, **26** and **27**). Earlywood vessel diameter varies between 30-80 µm. Vessel diameter does do not exceed 50 µm in *Astragalus armatus*, *A. campestre*, *A. depressus*, *A. exscapus*, *A. fruticosus* and *A. stella*.

An axial parenchymatisation occurs in all species. It varies form a distinct apotrachal (diffuse in aggregates; **Fig. 25**) to a confluent paratracheal (**Fig. 26**) and a pervasive parenchyma (**Fig. 27**).

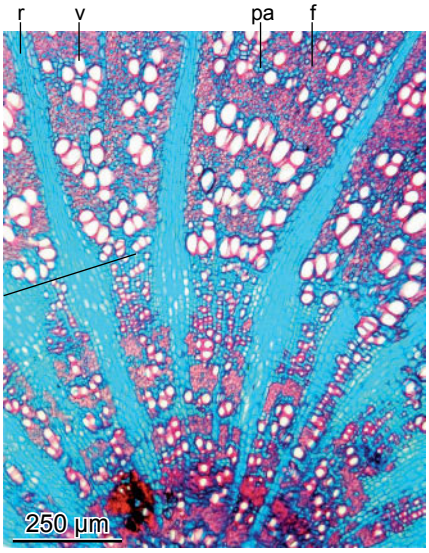



**Fig. 19.** Distinctly semi-ring-porous wood with two rings. Parenchyma cells in the latewood zone and the rays are unlignified. Root collar of a 20 cm-high hemicryptophyte, dry meadow, hill zone, Valais, Switzerland. *Oxytropis pilosa*, transverse section.

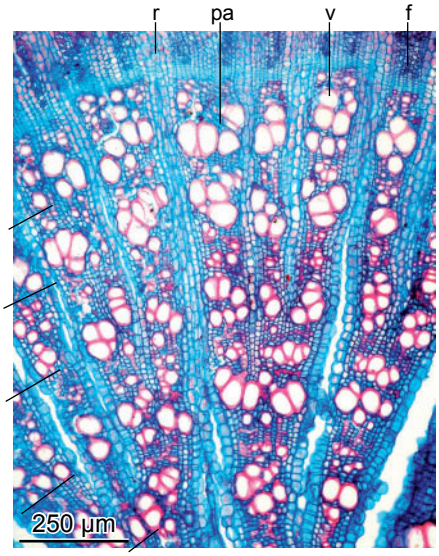



**Fig. 20.** Distinctly semi-ring-porous wood with six rings. Parenchyma cells in the rays are unlignified. Root collar of a 20 cm-high hemicryptophyte, dry meadow, steppe, mountain zone, Colorado, USA. *Astragalus lentiginosus*, transverse section.

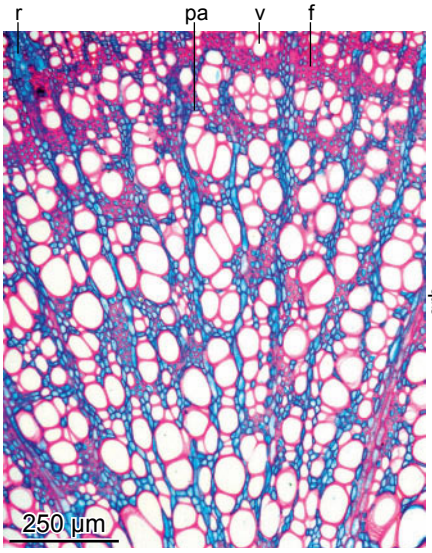



**Fig. 21.** Indistinct rings with a slight tendency to semi-ring-porosisty. Root collar of a 5 cm-high hemicryptophyte, dry meadow, steppe, mountain zone, Colorado, USA. *Astragalus praelongus*, transverse section.

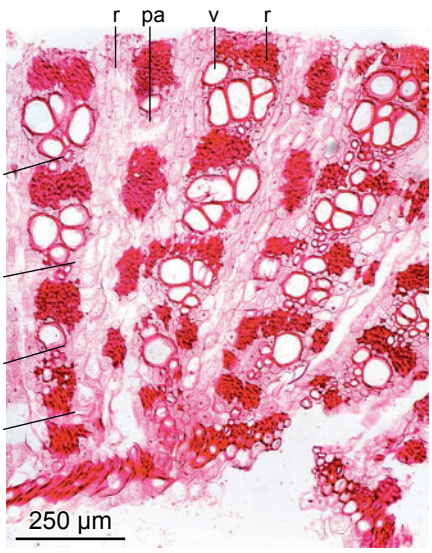



**Fig. 22.** Ring-porous wood with thick-walled fiber groups located in a thin-walled parenchymatic tissue. Root collar of a 40 cm-high hemicryptophyte, wet meadow, subalpine zone, Valais, Switzerland. *Astragalus frigidus*, transverse section.

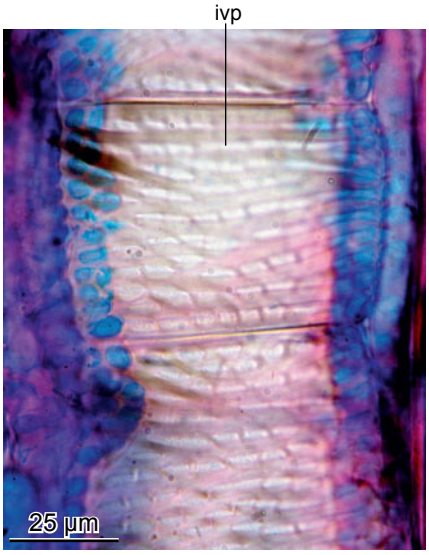



**Fig. 23.** Vessel with opposite arranged intervessel pits. Pits have a tendency to scalariformity. Root collar of a 5 cm-high hemicryptophyte, dry meadow, steppe, mountain zone, Colorado, USA. *Astragalus praelongus*, radial section.

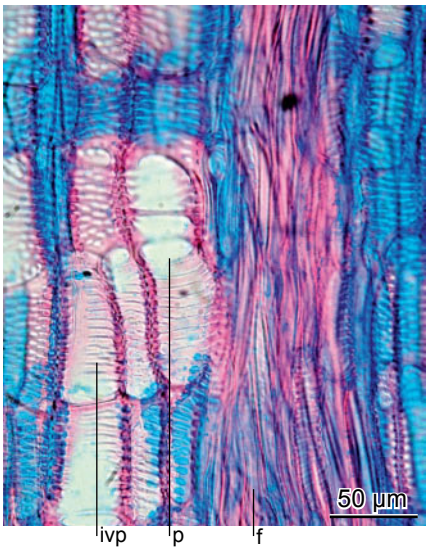



**Fig. 24.** Vessels with simple perforations. Scalariform and round intervessel pits arranged in alternate position. Root collar of a 20 cm-high hemicryptophyte, dry meadow, hill zone, Valais, Switzerland. *Oxytropis pilosa*, radial section.

Part of the parenchymatisation are the thin-walled, unlignified rays (**Fig. 28**). Marginal parenchyma exists but it is not a constant feature. The distribution of parenchyma corresponds with the occurrence with fibers and fiber groups. Fibers dominate the transverse section (**Fig. 29**), are rare (**Fig. 30**) or are absent (**Fig. 27**).

Most of the species are homocellular. Ray cells are mostly procumbent and square in *Astragalus* (**Fig. 31**) and predominatly square and upright in *Oxytropis*. Ray width varies from 1-2-seriate to 3-5-seriate (**Fig. 32**) to >10-seriate (**Fig. 33**). Rays with sheet cells are rare (**Fig. 34**). Ray height exceeds 1 mm in species with large rays (**Fig. 33**). Many species have storied axial elements (**Fig. 33**). Crystals are absent.

The arrangement of sclereids in the phloem characterizes species. Sclereids are arranged in irregular radial strips (**Figs. 35** and **36**) or in more or less dense tangential bands (**Fig. 37**).

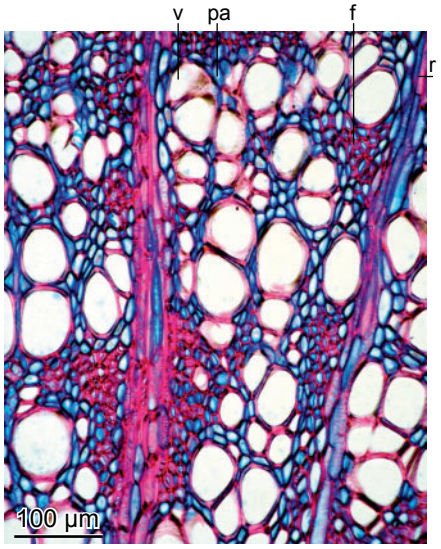



**Fig. 25.** Apotracheal and paratracheal parenchyma. Root collar of a 5 cm-high hemicryptophyte, dry meadow, steppe, mountain zone, Colorado, USA. *Astragalus praelongus*, transverse section.

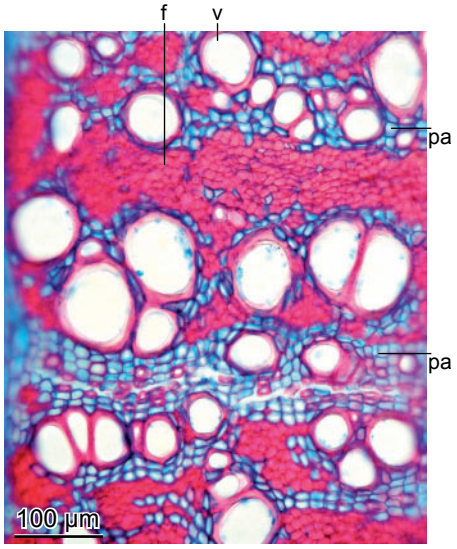



**Fig. 26.** Paratracheal confluent parenchyma in the latewood. Some few apotracheal parenchyma cells are embedded in a thick-walled fiber tissue. Root collar of a 5 cm-high hemicryptophyte, dry meadow, steppe, mountain zone, Colorado, USA. *Astragalus praelongus*, transverse section.

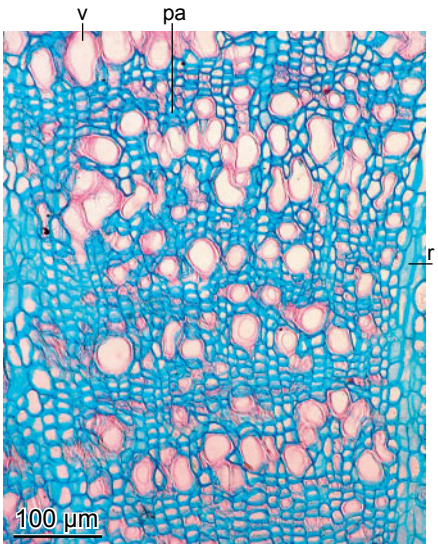



**Fig. 27.** Thick-walled fibers are surrounded by a pervasive parenchyma. Root collar of a 20 cm-high hemicryptophyte, dry meadow, steppe, mountain zone, Colorado, USA. *Astragalus lentiginosus*, transverse section.

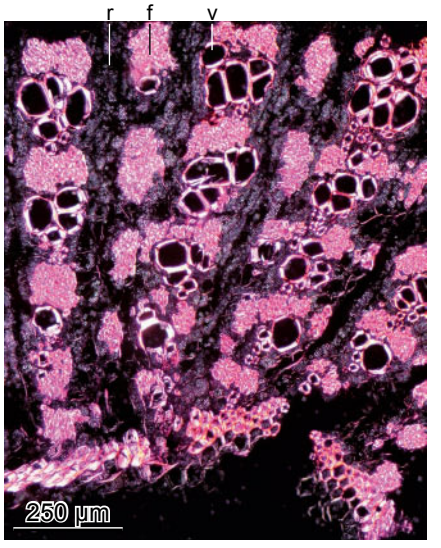



**Fig. 28.** Ring-porous wood. Unlignified parenchyma in the rays and the latewood (dark parts), and groups of thick-walled fibers (red). Root collar of a 40 cm-high hemicryptophyte, wet meadow, subalpine zone, Valais, Switzerland. *Astragalus frigidus*, transverse section, polarized light.

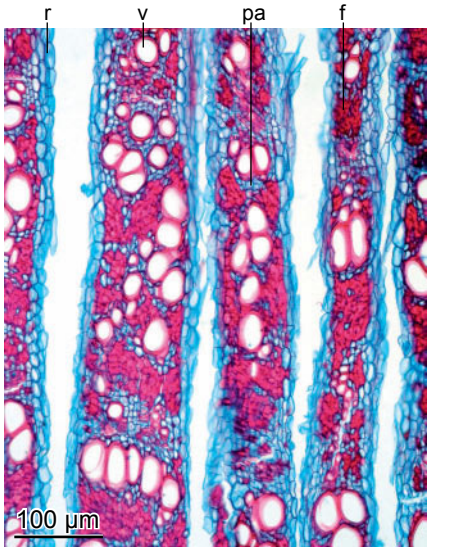



**Fig. 29.** The axial tissue is dominated by fibers. Rays are unlignified and extremely thin-walled. Root collar of a 20 cm-high hemicryptophyte, dry meadow, cold steppe, boreal zone, Lake Baikal, boreal zone, Russia. *Astragalus cruckshansii*, transverse section.

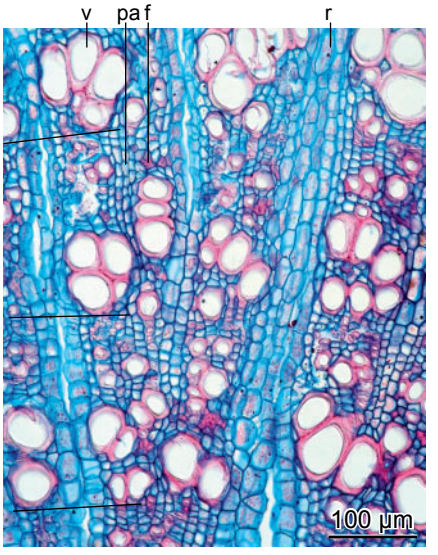



**Fig. 30.** A few fibers occur in the parenchyma-dominated axial tissue. Vessels are thick-walled. Root collar of a 20 cm-high hemicryptophyte, dry meadow, steppe, mountain zone, Colorado, USA. *Astragalus lentiginosus*, transverse section.

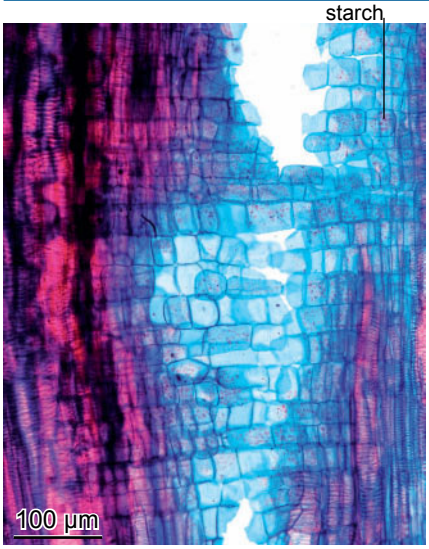



**Fig. 31.** Homocellular ray with square and upright, thin-walled, unlignified cells. Root collar of a 20 cm-high hemicryptophyte, dry meadow, steppe, mountain zone, Colorado, USA. *Astragalus lentiginosus*, radial section.

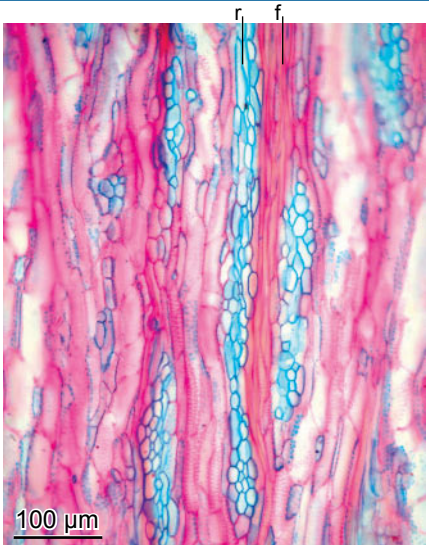
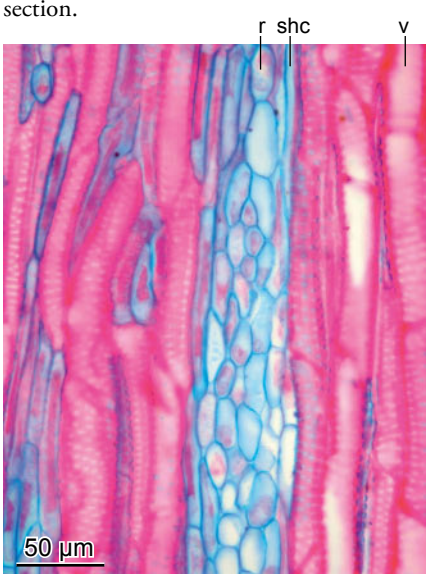
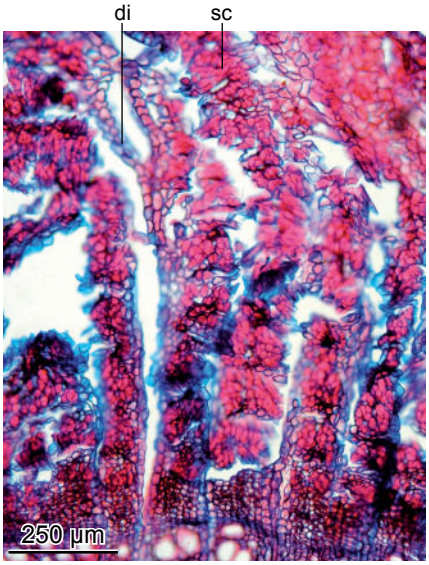



**Fig. 32.** 2-4-seriate, unlignified rays. Root collar of a 5 cm-high therophyte, dry meadow, steppe, Mediterranean, Andalusia, Spain. *Astragalus stella*, tangential section.

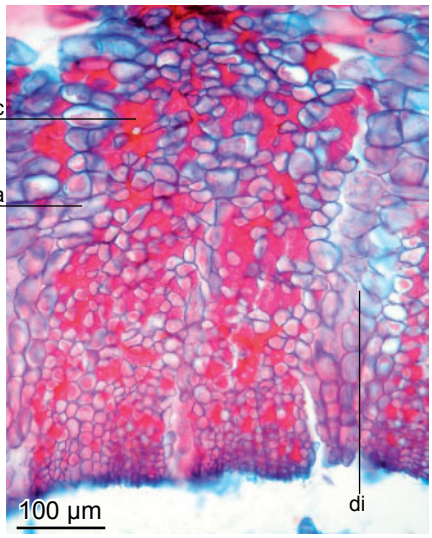
**Fig. 33.** Rays with more than 10 cells in width. Axial cell elements are storied. Stem of a 40 cm-high chamaephyte, dry meadow, hill zone, Borjomi, Georgia. *Astragalus subulatus*, tangential section.

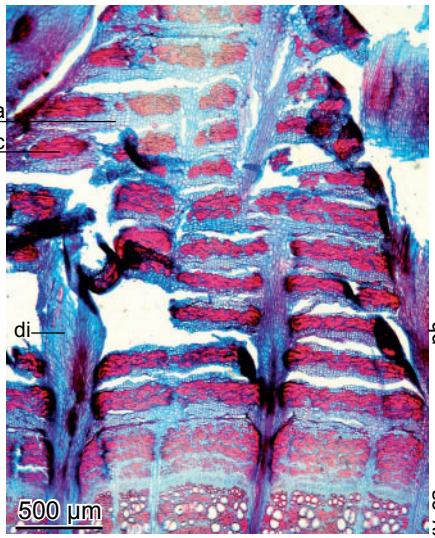



**Left Fig. 34.** Unlignified ray with distinct sheet cells. Root collar of a 5 cm-high hemicryptophyte, dry meadow, steppe, mountain zone, Colorado, USA. *Astragalus praelongus*, tangential section.

**Right Fig. 35.** Phloem with radial strips of thick-walled fibers. Fiber groups are slightly tangentially oriented. Root collar of a 20 cm-high hemicryptophyte, cold steppe, boreal zone, Lake Baikal, Russia. *Oxytropis tragacanthoides*, transverse section.



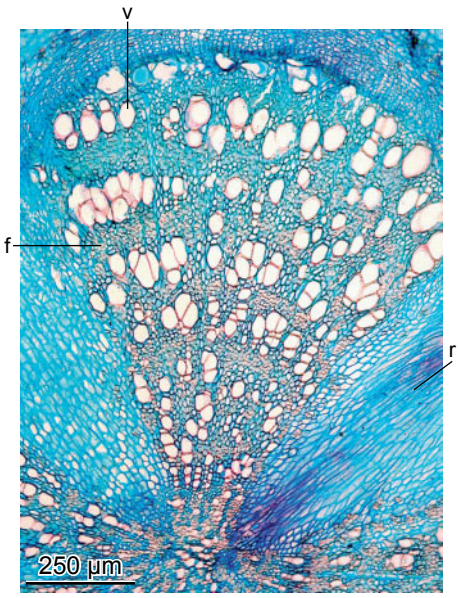



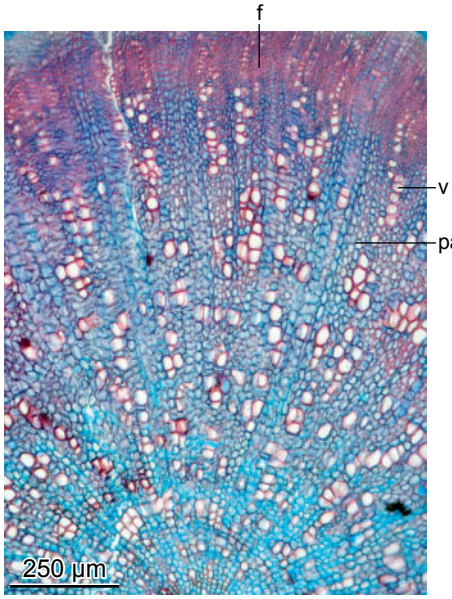

**Left Fig. 36.** Phloem with radial patches of thick-walled fibers. Root collar of a 5 cm-high hemicryptophyte, dry meadow, steppe, mountain zone, Colorado, USA. *Astragalus praelongus*, transverse section.

**Right Fig. 37.** Phloem with tangentially arranged blocks of fibers and tangential zones of parenchyma and phloem cells. Stem of a 40 cm-high chamaephyte, dry meadow, hill zone, Borjomi, Georgia. *Astragalus microcephalus*, transverse section.

***Subgroup 3. Chamaephytes, hemicrytophytes and therophytes, excluding species in the subgroups 1 and 2.***
Described are 11 chamaephytes, 58 hemicryptophytes and 15 therophytes. Since we do not have more slides from species from single genera or ecological units we have to accept that the group is taxonomically and anatomically heterogenic. The following paragraph will give an impression of the possible structural variability. A few species were also placed in subgroup 1.

Therophytes have only one ring (**Figs. 38** and **39**). Rings are absent in a few species of arid regions (**Figs. 40**, **41** and **49**). The majority of the chamaephytes and hemicryptophytes in all vegetation zones have distinct or recognizable rings (**Figs. 42-47**) and (**Figs. 50**, **51** and **58**). Ring-porous is only *Coronilla vaginalis* (**Fig. 43**). Most species are semi-ring-porous to various degrees (**Figs. 44-47**). Vessels are grouped in radial multiples of different length (**Figs. 47-49**) or in tangential to radial patterns (**Figs. 50**, **51**, **56**, **59**). All species have simple perforations (**Fig. 52**). Intervessel pits are small and round (**Fig. 53**) or scalariform in different intensities (**Fig. 52**). Vessels are thick-walled in most species (**Fig. 54**). Helical thickenings and tylosis are absent. Dark staining substances occur occasionally but they are not a species-characteristic feature (**Figs. 44**, **46**). Very small vessels (<20 µm) occur in a few *Trifolium* species. Fibers are




**Left Fig. 38.** Annual plant (therophyte) with one ring. Vessels are arranged in tangential layers. Root collar of a 50 cm-high therophyte, vineyard, hill zone, Vienna, Austria. *Vicia sativa*, transverse section.

**Right Fig. 39.** Annual plant (therophyte) with one ring. Vessels are arranged in radial multiples. Root collar of a 25 cm-high therophyte, (seeded in autumn, grown in spring), meadow, cultivated, hill zone, Birmensdorf, Switzerland. *Trifolium incarnatum*, transverse section.

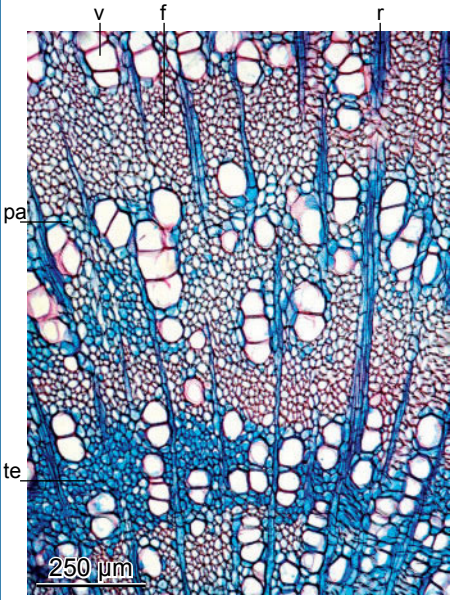



**Fig. 40.** Plant without annual rings. Vessels are arranged in radial multiples and in tangential layers. Root collar of a 25 cm-high hemicryptophyte, sandy plain, arid zone, Fezzan, Libya. *Lupinus tassilicus*, transverse section.

**Fig. 41.** Plant without annual rings. Vessels are arranged in radial and diagonal multiples. Root collar of a 25 cm-high chamaephyte, sandy plain, arid zone, Fezzan, Libya. *Crotalaria saharae*, transverse section. The species is also placed in subgroup 1.

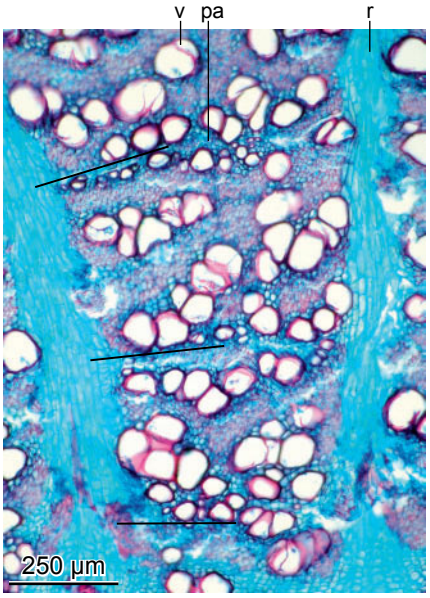
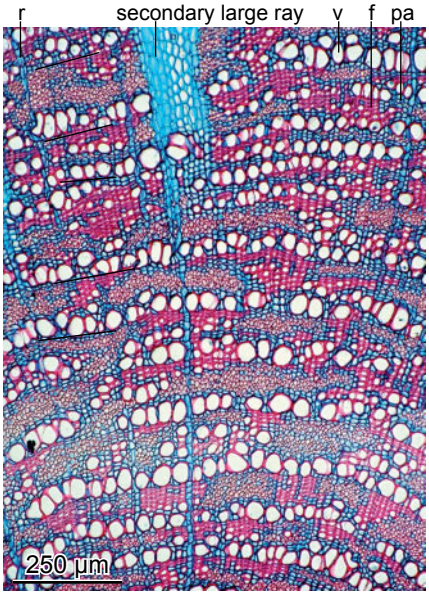


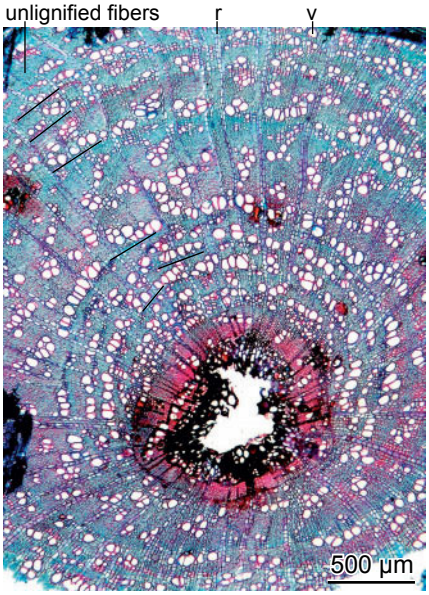

**Fig. 42.** Ring-porous hemicryptophyte with indistinct rings. Root collar of a 40 cm-high hemicryptophyte, moist forest, hill zone, Idahoe, USA. *Lupinus albicaulis*, transverse section.

mostly thick-walled and frequently contain tension wood (**Fig. 44**). Vessel diameter of the majority varies from 30-80 µm and the number of vessels from 100-200/mm$^2$. The distribution of axial parenchyma cells can be apotracheal (diffuse in aggregates) (**Figs. 55** and **56**) or paratracheal, e.g. in tangential intra-annual (**Fig. 57**) or marginal bands (**Figs. 58** and **59**).

Ray width varies from uni-seriate (**Fig. 60**), to 1-2 (**Fig. 61**), 2-4 (**Figs. 62** and **63**), 4-10 (**Figs. 64** and **65**) and up to >10-seriate (**Figs. 66** and **67**). Only *Desmodium illionense* has rays with two distinct sizes (**Fig. 68**). Rays of many species are not lignified (**Figs. 66** and **67**). Rays of most species are homocellular, consisting of square and upright cells (**Fig. 69**). Prismatic crystals occur in more than half of the species analyzed (**Fig. 70**).

There is a large variability in the anatomy of phloem and cortex structures. Collapsed sieve cells in tangential bands (**Figs. 71** and **72**) or radial strips (**Fig. 73**) are not frequent. Ray dilatations occur in the majority of species (**Figs. 72-76**). Sclereids occur in small groups (**Figs. 74** and **75**), in irregular radial groups (**Fig. 76**) in tangential belts (**Fig. 77**) or in tangential bands (**Figs. 78** and **79**). Prismatic crystals occur in the majority of species (**Fig. 79**).




**Left Fig. 43.** Ring-porous to semi-ring-porous xylem of a long-living dwarf shrub. Root collar of a 15 cm-high chamaephyte, dry meadow, hill zone, Valais, Switzerland. *Coronilla vaginalis*, transverse section.

**Right Fig. 44.** Semi-ring-porous wood with diagonal vessel distribution in the latewood. Blue zones represent tension wood. Root collar of a 20 cm-high hemicryptophyte, dry *Pinus ponderosa* forest, mountain zone, Colorado, USA. *Thermopsis divaricarpa*, transverse section.

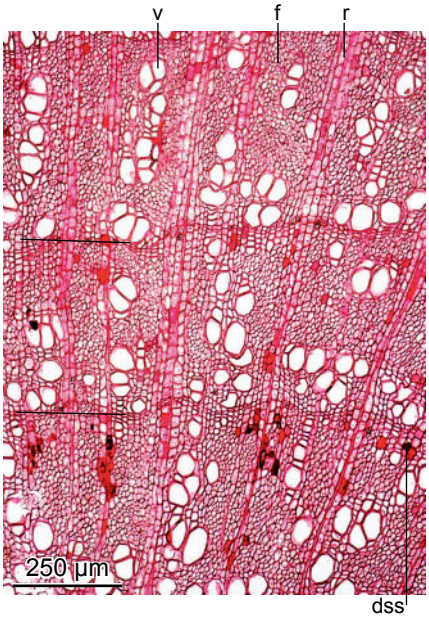



**Fig. 45.** Semi-ring-porous wood with vessels in short radial multiples. Root collar of a 40 cm-high hemicryptophyte, meadow, hill zone, Illinois, USA. *Lespedeza hirta*, transverse section.

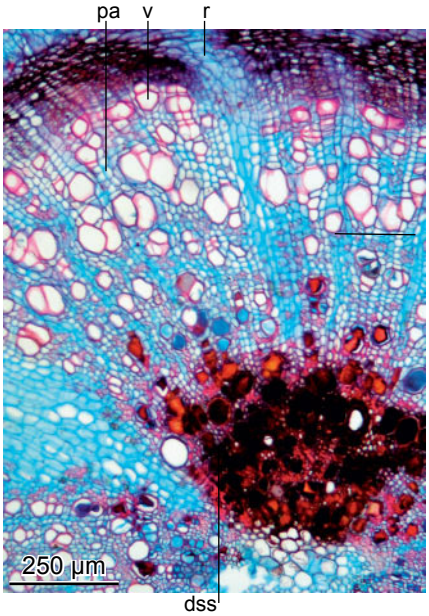



**Fig. 46.** Semi-ring-porous xylem with indistinct rings. Part of the central tissue is filled with dark substances. Root collar of a 40 cm-high hemicryptophyte, meadow, hill zone, Birmensdorf, Switzerland. *Vicia sepium*, transverse section.

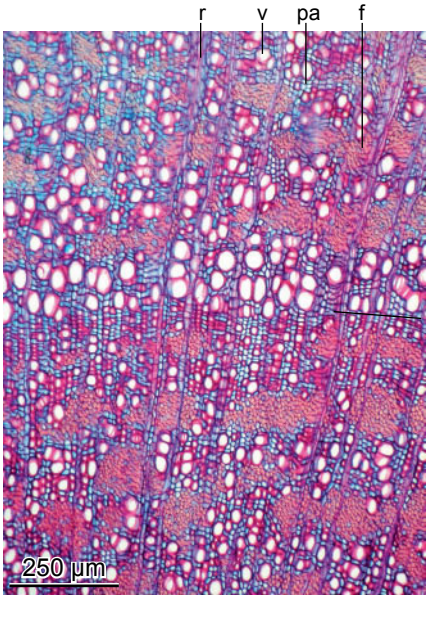
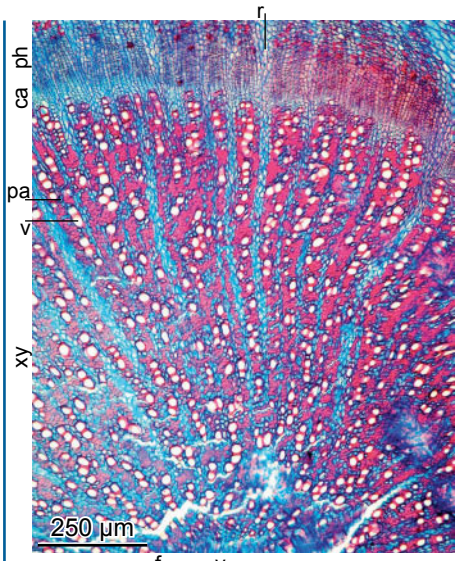
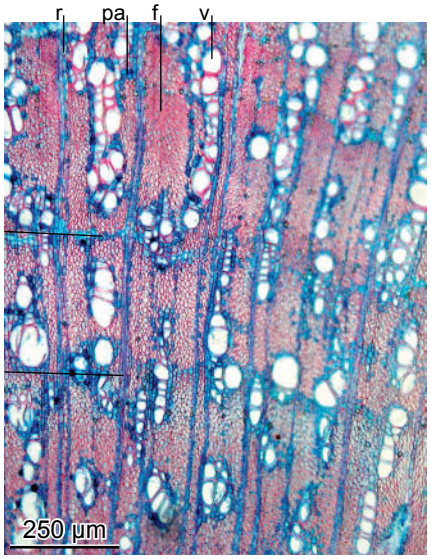


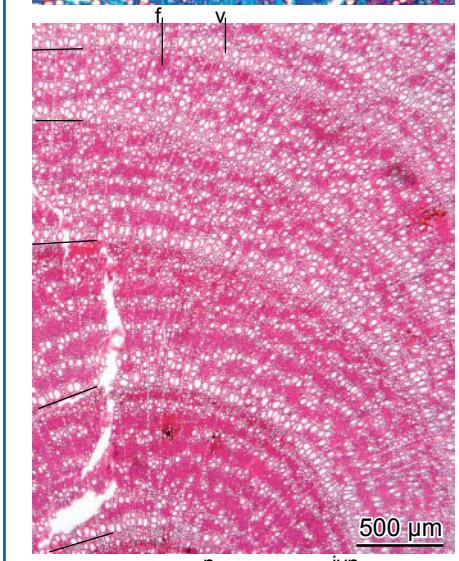

**Fig. 47.** Semi-ring-porous xylem. Fibers are arranged in patches within a parenchymatic tissue. Root collar of a 15 cm-high hemicryptophyte, dry meadow, hill zone, Briançon, France. *Lotus corniculatus*, transverse section. The species is also placed in subgroup 1.

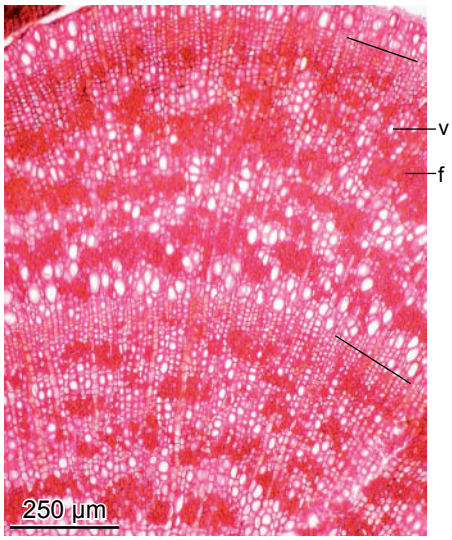



**Left Fig. 48.** Plant with one ring (therophyte). Vessels are arranged in radial multiples. Root collar of a 20 cm-high hemicryptophyte, dry meadow, Mediterranean zone, Provence, France. *Medicago rididula*, transverse section.

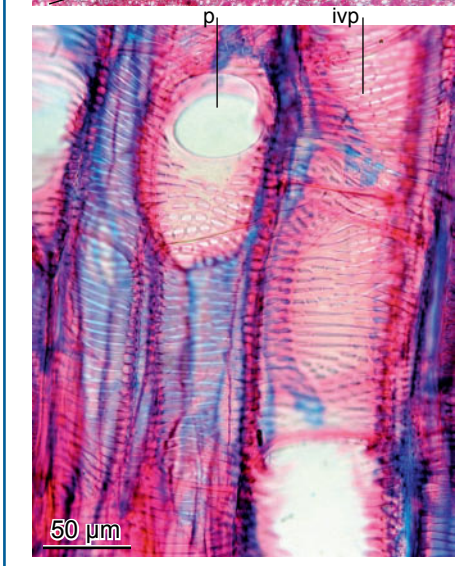
**Right Fig. 49.** Vessels are arranged in radial multiples. Parenchyma is arranged paratracheal vasicentric and in tangential layers. Root collar of a 25 cm-high hemicryptophyte, sandy plain, arid zone, Fezzan, Libya. *Tephrosia leptostachya*, transverse section.




**Left Fig. 50.** Vessels in the latewood are arranged in tangential and slightly diagonal patterns. Root collar of a 20 cm-high hemicryptophyte, meadow, subalpine zone, Grisons, Switzerland. *Hippocrepis comosa*, transverse section.

**Right Fig. 51.** Vessels and fiber groups in the latewood are arranged in diagonal patterns. Root collar of a 25 cm-high hemicryptophyte, meadow, mountain zone, Grisons, Switzerland. *Anthyllis vulneraria*, transverse section.



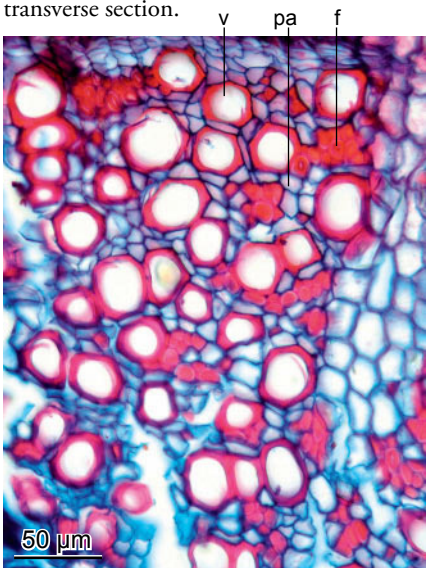
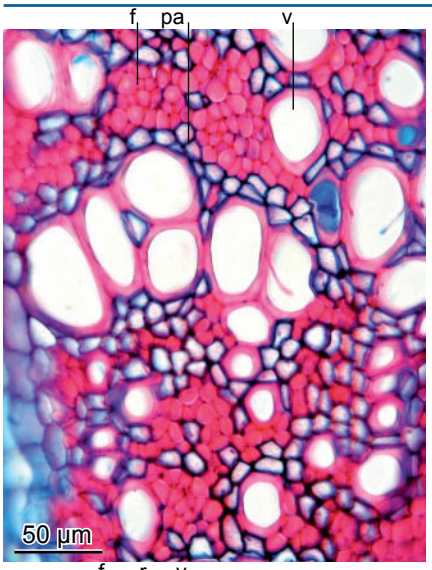
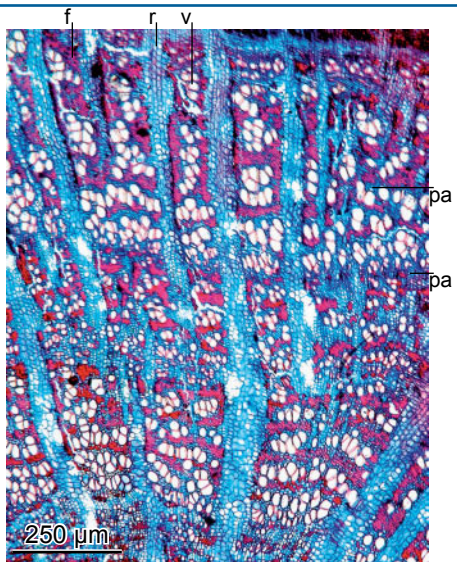



**Fig. 52.** Vessels with simple perforations and sclaraiform and round intervessel pits in opposite position. Root collar of a 25 cm-high hemicryptophyte, cold steppe, boreal zone, Lake Baikal, Russia. *Hedysarum gmelinii*, radial section.

**Fig. 53.** Vessels with small round intervessel pits in alternate position. Rhizome of a 60 cm-high hemicryptophyte, dry meadow, Mediterranean, Provence, France. *Lathyrus sylvestris*, radial section.

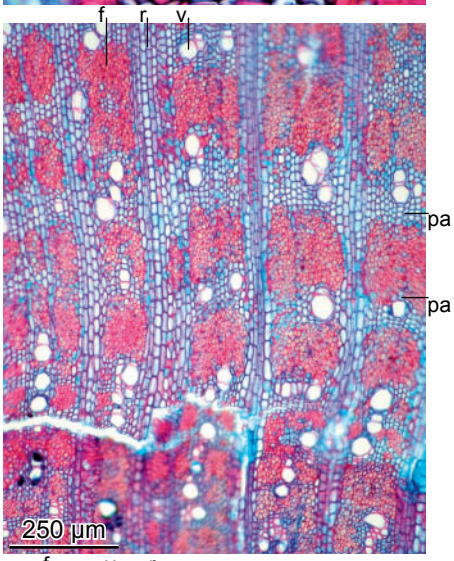
**Fig. 54.** Thick-walled solitary vessels surrounded by pervasive parenchyma cells and thick-walled fibers. Root collar of a 20 cm-high hemicryptophyte, meadow, mountain zone, Grisons, Switzerland. *Trifolium pratense*, transverse section.

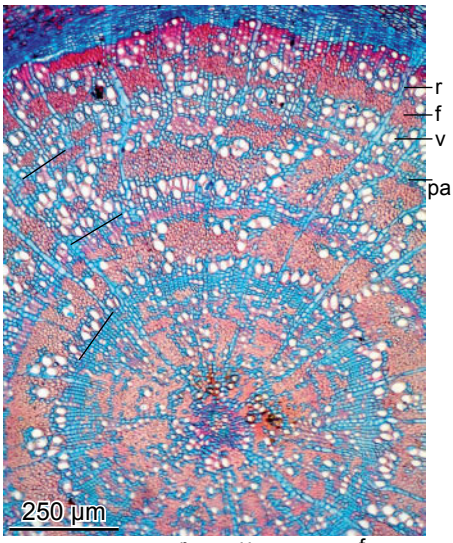



**Left Fig. 55.** Thick-walled vessel groups. Parenchyma is apotracheal and paratracheal. Root collar of a 20 cm-high hemicryptophyte, wet meadow, subalpine zone, Kaukasus, Georgia. *Trifolium ambiguum*, transverse section.

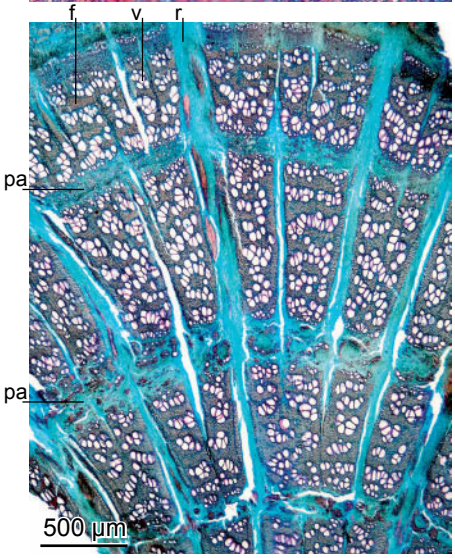
**Right Fig. 56.** Vessels and fibers are arranged in tangential layers and are surrounded by paratracheal and marginal parenchyma. The large rays are not lignified. Root collar of a 40 cm-high hemicryptophyte, meadow, mountain zone, Grisons, Switzerland. *Onobrychis viciifolia*, transverse section.

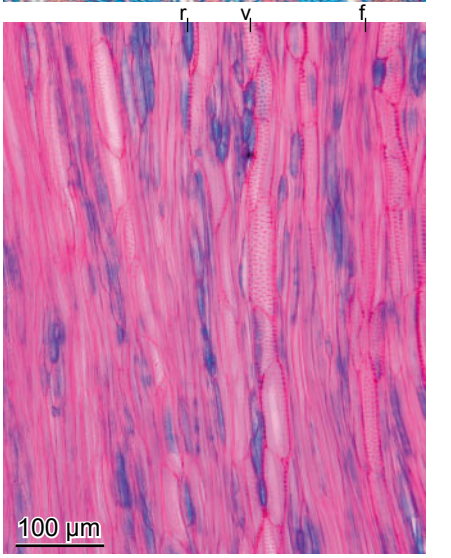



**Left Fig. 57.** Fibers and parenchyma cells (vasicentric paratracheal confluent) are arranged in tangential layers. Vessel density varies from 30-50/mm$^2$. Root collar of a 25 cm-high hemicryptophyte, meadow, subtropical zone, Gran Canaria, Canary Islands. *Ononis angustissima*, transverse section.

**Right Fig. 58.** Fibers and vessels are arranged in tangential layers. Parenchyma is vasicentric paratracheal and marginal. Root collar of a 5 cm-high hemicryptophyte, meadow, Mediterranean, Provence, France. *Ononis minutissima*, transverse section.



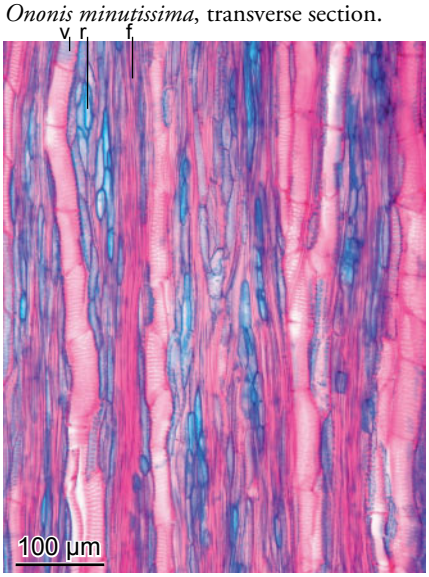
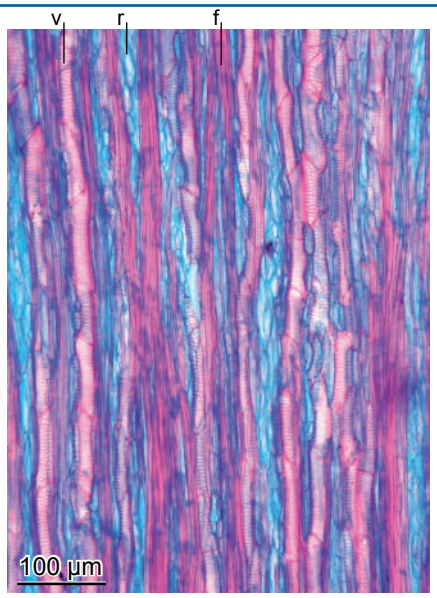
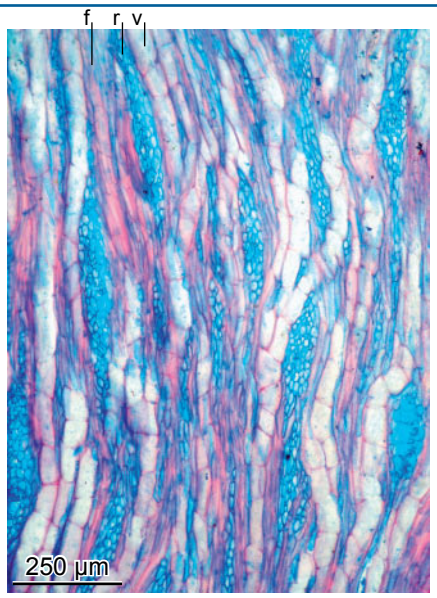




**Fig. 59.** Xylem with distinct marginal parenchymtic layers. Rays are not lignified. Root collar of a 20 cm-high hemicryptophyte, meadow, subalpine zone, Washington, USA. *Lupinus obtusifolius*, transverse section.

**Fig. 60.** Uni-seriate rays with unlignified cells. Root collar of a 25 cm-high therophyte, meadow, hill zone, Birmensdorf, Switzerland. *Trifolium incarnatum*, tangential section.

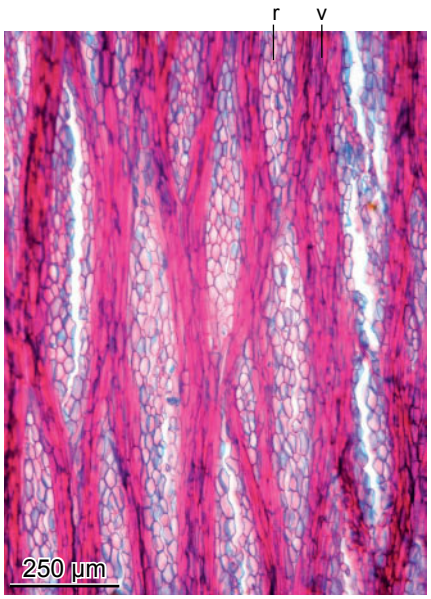
**Fig. 61.** Uni- and biseriate rays with unlignified cells. Root collar of a 20 cm-high hemicryptophyte, dry meadow, hill zone, Valais, Switzerland. *Medicago minima*, tangential section.



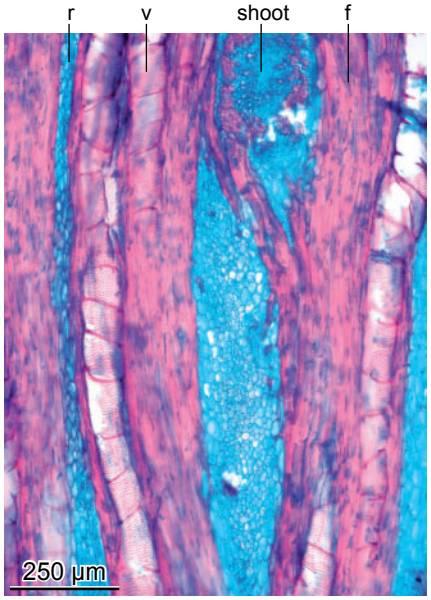

**Left Fig. 62.** 2-4-seriate rays with unlignified cells. Root collar of a 25 cm-high hemicryptophyte, dry meadow, Mediterranean zone, Provence, France. *Medicago rididula*, tangential section.

**Right Fig. 63.** Irregularly formed, 3-5-seriate rays with unlignified cells. Root collar of a 50 cm-high hemicryptophyte, vineyard, hill zone, Vienna, Austria. *Vicia pannonica*, tangential section.



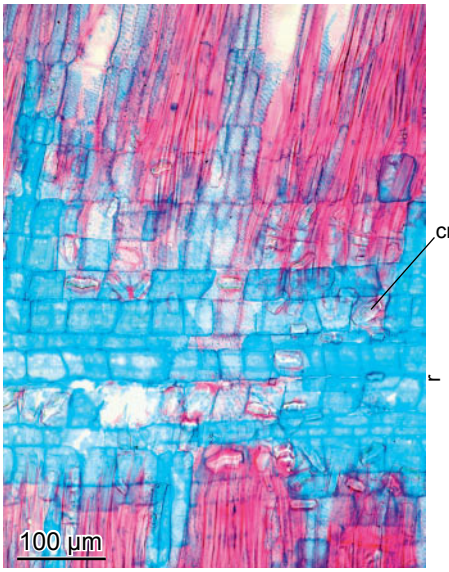
**Left Fig. 64.** Slender 4-7-seriate rays, partially with sheet cells. Root collar of a 5 cm-high hemicryptophyte, steppe, mountain zone, Colorado, USA. *Trifolium dasyphyllum*, tangential section.

**Right Fig. 65.** Elliptic 4-8-seriate rays. Root collar of a 5 cm-high hemicryptophyte, meadow, subalpine zone, Colorado, USA. *Trifolium nanum*, tangential section.



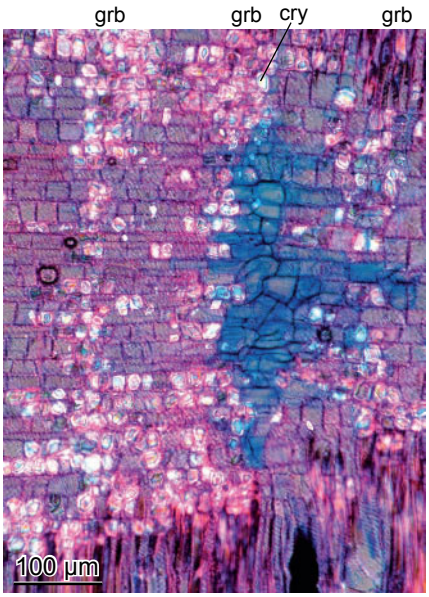
**Left Fig. 66.** >10-seriate rays with unlignified cells. Rhizome of a 20 cm-high hemicryptophyte, moist forest, hill zone, Idaho, USA. *Lupinus albicaulis*, tangential section.

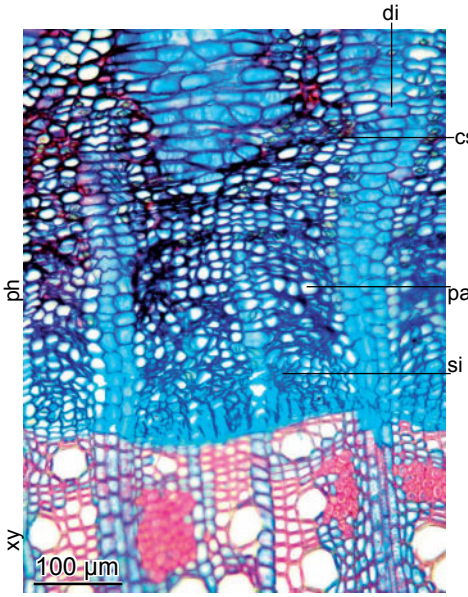
**Right Fig. 67.** >10-seriate rays with unlignified cells, partially with lateral layers of sheet cells. Root collar of a 15 cmhigh hemicryptophyte, meadow, arctic zone, Yamal Penninsula, Russia. *Hedysarum arcticum*, tangential section.




**Left Fig. 68.** Ray dimorphism: uni- and multi-seriate rays. Root collar of a 40 cm-high hemicryptophyte, meadow, hill zone, Michigan, USA. *Desmodium illionense*, tangential section.

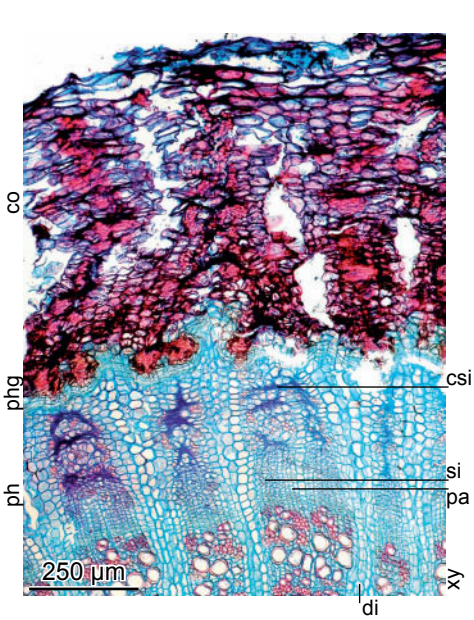
**Right Fig. 69.** Mainly homocellular ray with square and upright cells. Some cells contain prismatic crystals. Root collar of a 20 cm-high hemicryptophyte, subtropical zone, on volcanic rock, Gran Canaria, Canary Islands. *Lotus aragonensis*, radial section.

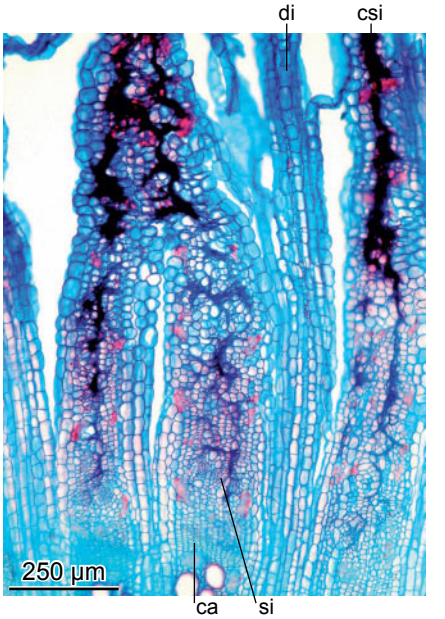



**Left Fig. 70.** Ray cells containing prismatic crystals. Heterocellular ray with a few procumbent and many square and upright cells. Root collar of a 20 cm-high hemicryptophyte, meadow, subtropical zone, Gran Canaria, Canary Islands. *Ononis angustissima*, radial section.

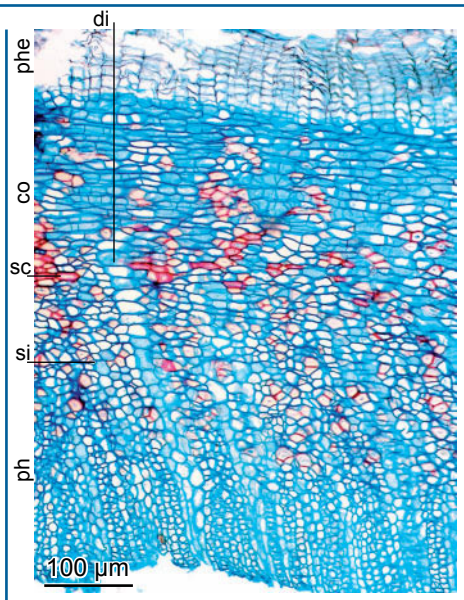
**Right Fig. 71.** Phloem with irregular zones of collapsed sieves tubes. Sclereids occur in older external parts near ray dilatations. Root collar of a 50 cm-high dwarf shrub, dry oak forest, hill zone, Trento, Italy. *Hippocrepis emerus*, transverse section.

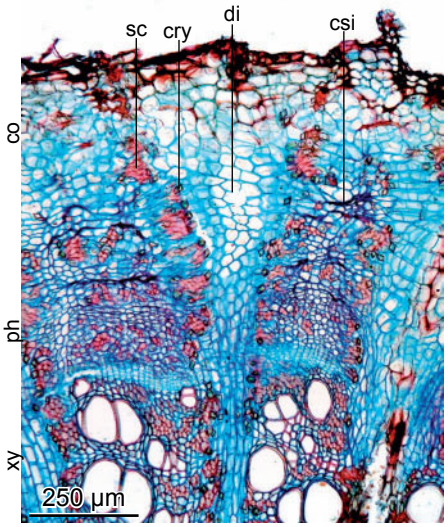



**Left Fig. 72.** Young phloem (blue) with tangential layers of collapsed sieve-tubes and older phloem (red) with sclereids. Ray dilatations are distinct in the young phloem. Root collar of a 40 cm-high hemicryptophyte, meadow, mountain zone, Briançon, France. *Trifolium rubens*, transverse section.

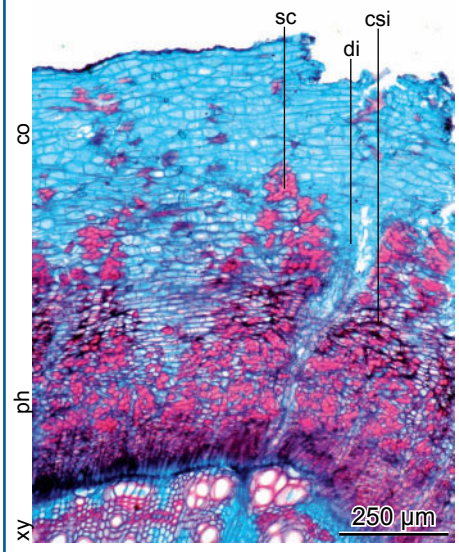
**Right Fig. 73.** Phloem with irregular radial zones of collapsed sieve-tubes (dark blue). Root collar of a 25 cm-high hemicryptophyte, meadow, arctic zone, Yamal Peninsula, Russia. *Hedysarum arcticum*, transverse section.

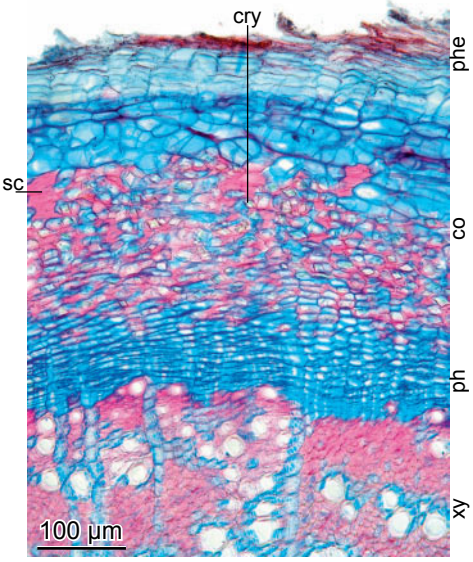



**Left Fig. 74.** Phloem and cortex with a few isolated sclereids (red). Root collar of a 25 cm-high chamaephyte, sandy plain, arid zone, Fezzan, Libya. *Crotalaria saharae*, transverse section.

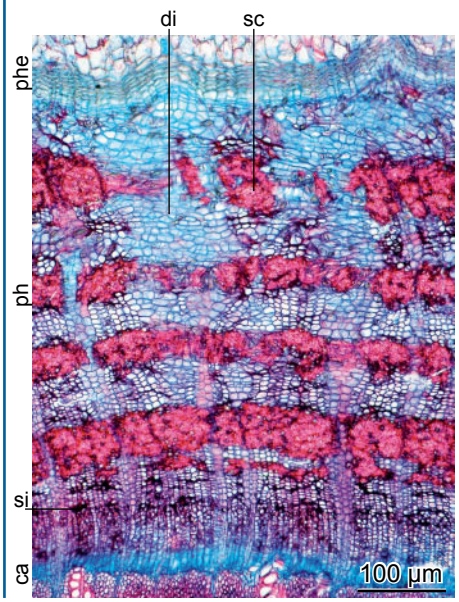
**Right Fig. 75.** Phloem and cortex with small groups of sclereids (red) between ray dilatations. Root collar of a 25 cm-high hemicryptophyte, meadow, Mediterranean zone, Provence, France. *Lathyrus sylvestris*, transverse section.

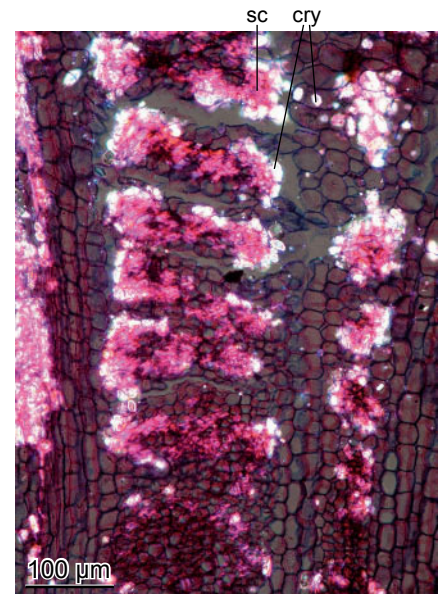



**Left Fig. 76.** Phloem with a dense sclerenchymatic zone which wedges out towards the cortex. Root collar of a 5 cm-high hemicryptophyte, coastal rock, subtropical zone, Tenerife, Canary Islands. *Lotus glaucus*, transverse section.

**Right Fig. 77.** Belt of small groups of sclereids in the older phloem. Root collar of a 5 cm-high hemicryptophyte, dry oak forest, Mediterranean, Provence, France. *Ononis minutissima*, transverse section.




**Left Fig. 78.** Tangential layers of sclereids and parenchyma/sieve-tubes. Root collar of a 40 cm-high dwarf shrub, garigue, Mediterranean, Andalusia, Spain. *Anthyllis cytisoides*, transverse section.

**Right Fig. 79.** Tangentially oriented groups of sclereids are surrounded by prismatic crystals (white). Root collar of a 20 cm-high hemicryptophyte, cold steppe, boreal zone, Laike Baikal, Russia. *Hedysarum zundukii*, transverse section, polarized light.

***Subgroup 4. Perennial Lianas***

Characteristic for perennial lianas is the coccurence of solitary large vessels (>200 µm), combined with grouped small vessels (**Fig. 80**). Both *Pueraria hirsuta* and *Wisteria sinensis* have large bands of included phloem (**Figs. 81** and **82**). Crystals are fequent in both species, tylosis occur in *Wisteria sinensis* (**Fig. 82**). Annual lianas, e.g. *Phaseolus angustissimus,* and a few long climbing hemicrypotophytes, e.g *Lathyrus heterophyllus*, *Vicia sativa*, *Vicia sepium*, have larger vessels than the majority of the 20-40 cm-high not-winding species.

***Subgroup 5. Mimosoideae (Acacia)***

The present collection of trees is limited and therefore it is impossible to discuss the anatomy seriously. We refer to the vast literature referenced by Gregory 1994. A few large vessels embedded in a tissue with thick-walled fibers and paratracheal parenchyma are characteristic for the few species collected in arid land of the desert in the Northwestern USA and the Sahara (**Figs. 83** and **84**). The anatomy of the bark is described in the figure legend of **Fig. 85**.

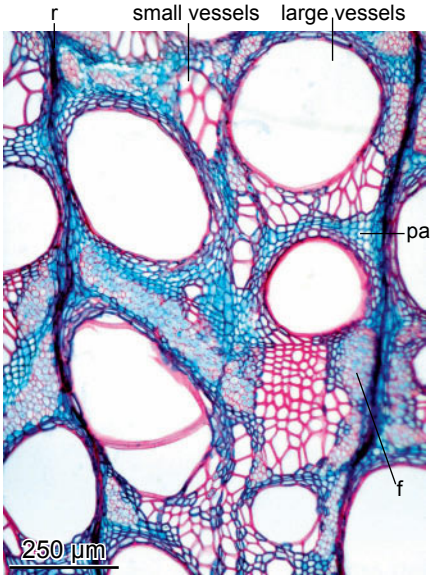



**Fig. 80.** Vessel dimorphism: very large solitary vessels and groups of small vessles. Stem of a 15 m-long shoot, subtropical zone, cultivated, Botanical Garden Batumi, Georgia. *Pueraria hirsuta*, transverse section.

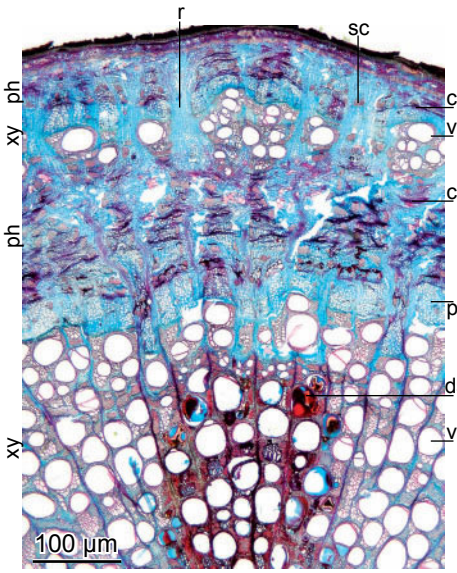



**Fig. 81.** Phloem zone between two parts of xylem (included phloem). Stem of a 15 m-long shoot, cultivated, subtropical zone, Botanical Garden Batumi, Georgia. *Pueraria hirsuta*, transverse section.

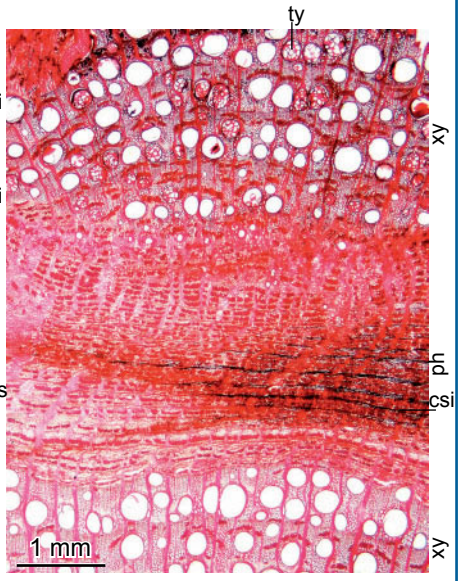



**Fig. 82.** Phloem zone between two parts of xylem (included phloem). Stem of a 15 m-long shoot, cultivated, hill zone, Bern, Switerland. *Wisteria sinensis*, transverse section.

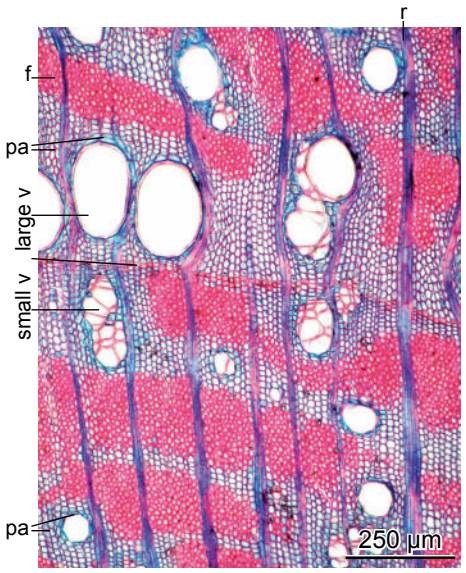



**Fig. 83.** A few large vessels are surrounded by thick-walled fibers and confluent parenchyma. Stem of a 3 m-high tree, shrub desert, arid zone, Tucson, Arizona, USA. *Acacia greggii*, transverse section.

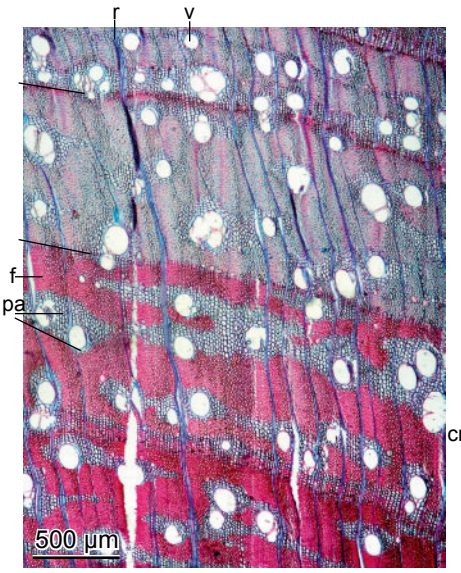



**Fig. 84.** A few large vessels are surrounded by thick-walled fibers and confluent parenchyma. Stem of a 6 m-high tree, sand desert, arid zone, Fezzan, Libya. *Acacia raddiana*, transverse section.

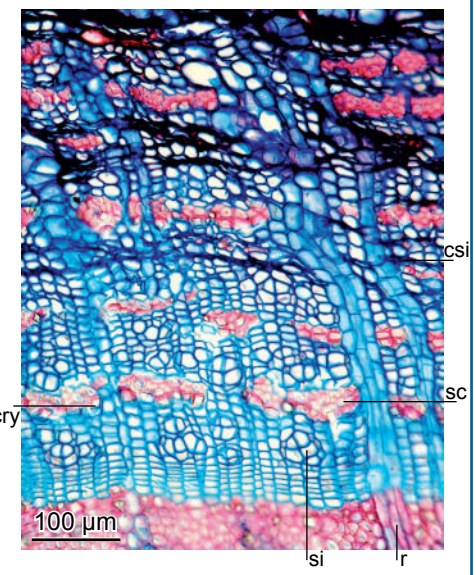



**Fig. 85.** Groups of sieve-tubes and sclereids are embedded in a parenchymatic tissue. Sieve-tubes collaps after a few years. Stem of a 6 m-high tree, sand desert, arid zone, Fezzan, Libya. *Acacia raddiana*, transverse section.

**Ecological trends and relations to life forms**

The recognition of ecological trends fails because the collected and analyzed material is heterogeneous in relation to different life forms occurring in different vegetation zones. The present life forms are not representative for all vegetations zones, e.g the selection for the subalpine and mountain zone is dominated by hemicryptophytes (81 and 68%), and the Mediterranean zone by shrubs and dwarf shrubs (50 and 22%). Serious ecological comparisons will be possible only on the basis of more material, representative for the vegetation zones.

**Discussion in relation to previous studies**

The wood anatomy of Fabaceae trees is well known. INSIDE WOOD mentions 682 species and Gregory 1994 over 300 articles. Comparable with our study are 16 species from 13 genera with 16 species. The major wood anatomical atlases describe the following number of species:

Benkova and Schweingruber (2004): 17 species. Trees, shrubs and dwarf shrubs from Russia.

Edlmann et al. (1994): 9 species. Trees and shrubs growing in Italy.

Fahn et al. (1986): 14 species. Trees and shrubs from Isreal.

Greguss (1945): 19 species. Trees and shrubs from Europe.

Holdheide (1951): 2 species. Bark of trees (*Laburnum*, *Robinia*) growing in Central Europe.

Jaquiot et al. (1973): 7 species. Trees growing in France.

Neumann et al. (2001): 31 species. Trees and shrubs from the Sahel and the Sahara. The material is dominted by 14 *Acacia* species.

Schweingruber (1990): 68 species. Trees, shrubs and dwarf shrubs from Western Europe. Descriptions in various details.

The results of our study principally agree with all previous descriptions of trees and shrubs. The present descriptions of the xylem of 120 herbs (therophytes and hemicryptophytes) clearly show, that the anatomical variability is much larger than it has been suggested before.

New is the description of the bark of 107 species. A detailed comparison with all previous studies would go far beyond the principal goal of the present study. We intend to give an overview of the anatomical variability within the family in relation to life forms and a few taxonomic subgroups and not a characterization of species.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **211** |
| 1 | growth rings distinct and recognizable | 184 |
| 2 | growth rings absent | 18 |
| 2.1 | only one ring | 6 |
| 3 | ring-porous | 28 |
| 4 | semi-ring-porous | 162 |
| 5 | diffuse-porous | 8 |
| 6 | vessels in intra-annual tangential rows | 32 |
| 7 | vessels in diagonal and/or radial patterns | 42 |
| 8 | vessels in dendritic patterns | 51 |
| 9 | vessels predominantly solitary | 62 |
| 9.1 | vessels in radial multiples of 2-4 common | 36 |
| 10 | vessels in radial multiples of 4 or more common | 11 |
| 11 | vessels predominantly in clusters | 147 |
| 13 | vessels with simple perforation plates | 205 |
| 20 | intervessel pits scalariform | 48 |
| 21 | intervessel pits opposite | 8 |
| 22 | intervessel pits alternate | 189 |
| 29 | vestured pits | 135 |
| 36 | helical thickenings present | 62 |
| 39.1 | vessel cell-wall thickness >2 µm | 78 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 6 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 109 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 87 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 26 |
| 50 | <100 vessels per mm$^2$ in earlywood | 17 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 184 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 1 |
| 56 | tylosis with thin walls | 4 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 56 |
| 59 | vessels absent or indistinguishable from fibers | 3 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 1 |
| 60.1 | fibers absent | 3 |
| 61 | fiber-pits small and simple to minutely bordered (<3 µm = libriform fibers) | 203 |
| 65 | septate fibers present | 2 |
| 67 | thick- and thin walled fiber bands, *Acer* type | 0 |
| 68 | fibers thin-walled | 1 |
| 69 | fibers thick-walled | 168 |
| 70 | fibers thin- to thick-walled | 20 |
| 70.1 | intra-annual thick-walled tangential fiber bands | 2 |
| 70.2 | tension wood present | 17 |
| 75 | parenchyma absent or unrecognizable | 6 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 29 |
| 79 | parenchyma paratracheal | 190 |
| 79.1 | parenchyma pervasive | 34 |
| 86 | axial parenchyma in narrow bands or lines, *Quercus* type | 12 |
| 89 | parenchyma marginal | 85 |
| 89.2 | ring shake, *Saxifraga* type | 7 |
| 96 | rays uniseriate | 3 |
| 97 | ray width predominantly 1-3 cells | 101 |
| 98 | rays commonly 4-10-seriate | 113 |
| 99 | rays commonly >10-seriate | 19 |
| 99.1 | vascular bundle form remaining | 6 |
| 100.1 | rays confluent with ground tissue | 1 |
| 100.2 | rays not visible in polarized light | 82 |
| 103 | rays of two distinct sizes (tangential section) | 21 |
| 102 | ray height >1 mm | 3 |
| 104 | ray: all cells procumbent (radial section) | 85 |
| 105 | ray: all cells upright or square | 73 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 21 |
| 107 | ray: heterocellular with 2-4 upright cell rows (rad. section) | 13 |
| 108 | ray: heterocellular with >4 cell upright rows (rad. section) | 19 |
| 110 | rays with sheet cells (tangential section) | 24 |
| 120 | storied axial tissue (parenchyma, fibers, vessels in tangential section) | 61 |
| 133 | successive cambia, Caryophyllaceae type | 1 |
| 135 | interxylary phloem present | 1 |
| 136 | prismatic crystals present | 58 |
| 142 | prismatic crystals in axial chambered cells | 7 |
| R1 | groups of sieve tubes present | 41 |
| R2 | groups of sieve tubes in tangential rows | 10 |
| R2.1 | groups of sieve tubes in radial rows | 34 |
| R3 | distinct ray dilatations | 110 |
| R4 | sclereids in phloem and cortex | 122 |
| R6 | sclereids in radial rows | 29 |
| R6.1 | sclereids in tangential rows | 74 |
| R7 | with prismatic crystals | 66 |
| R7.1 | with acicular crystals | 1 |
| R8 | with crystal druses | 2 |
| R10 | phloem not well structured | 5 |
| R12 | with laticifers, oil ducts or mucilage ducts | 2 |
| R14 | cortex with aerenchyma | 1 |

# Fagaceae

### Number of species, worldwide and in Europe

The Fagaceae family includes 9 genera with 900 species. The species are distributed in the temperate and tropical northern hemisphere. *Quercus* is represented by 450 species. In Europe, there are 3 genera (*Castanea*, *Fagus* and *Quercus*).

### Analyzed material

The xylem and phloem of 3 genera with 22 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 21 | numerous |
| Nanophanerophytes 0.5-4 m | 1 | ? |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 8 | |
| Mediterranean | 14 | |

**Analyzed species:**

*Castanea sativa* Mill.
*Fagus grandifolia* Erh.
*Fagus orientalis* Lipsky
*Fagus sylvatica* L.
*Quercus alba* L.
*Quercus alnifolia* Poech *
*Quercus cerris* L.
*Quercus coccifera* L.*
*Quercus congesta* C. Presl
*Quercus faginea* Lam.
*Quercus frainetto* Brot.
*Quercus fruticosa* Brot.
*Quercus ilex* L.*
*Quercus infectoria* Olivier
*Quercus petraea* Liebl.
*Quercus ponticum* K. Koch
*Quercus pubescens* Will.
*Quercus pyrenaica* Willd, syn. *tozza*
*Quercus robur* L.
*Quercus rubra* L.
*Quercus suber* L.*
*Quercus trojana* Webb.

*evergreen species of the subgenus *sclerophyllodris*

*Castanea sativa*

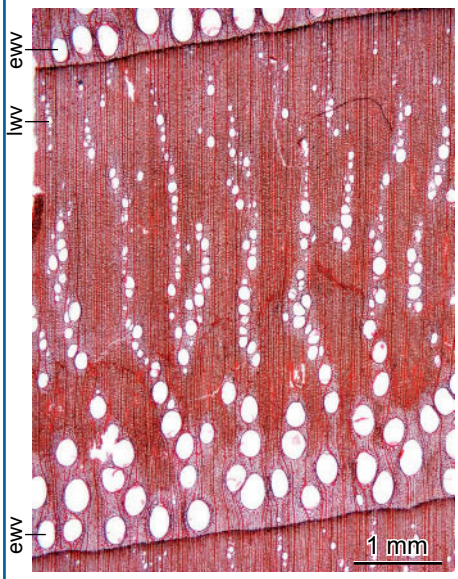
*Quercus robur* (photo: Zinnert)

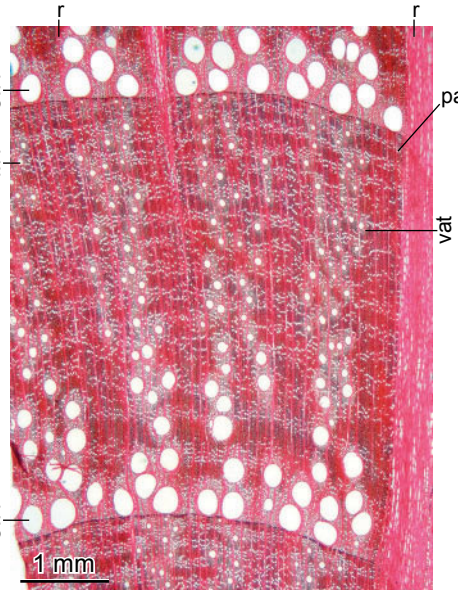
*Fagus sylvatica* (photo: Zinnert)

**Characteristics of the xylem**

Ring boundaries are distinct in most species (**Figs. 1-4** and **6**) except in the *Quercus* species of the subgenera *sclerophyllodris* (**Fig. 5**). All *Fagus* species are semi-ring-porous (**Fig. 6**). *Castanea* (**Fig. 1**) and all *Quercus* species are ring-porous (**Figs. 2-4**) except those of the subgenera *sclerophyllodris* (**Fig. 5**), which are diffuse-porous. Latewood vessels are arranged solitary and in small groups in *Fagus* (**Fig. 6**), or are arranged in radial, diagonal or dendritic patterns as in *Castanea* and *Quercus* (**Figs. 1-4**). Earlywood-vessel diameter between 50-90 µm is characteristic for *Fagus* and 100-200 µm for *Quercus*. Vessels of *Castanea* and *Quercus* have exclusively simple perforations, while those of *Fagus* are a combination of simple and scalariform (**Fig. 7**). Vessel pits are arranged opposite in *Fagus* but alternate in *Quercus* and *Castanea*. Ray-vessel pits are enlarged in all species analyzed. Their form varies between round, upright and prostrate oval (**Figs. 8** and **9**). Vessels of all species contain thin-walled tylosis (**Fig. 10**).

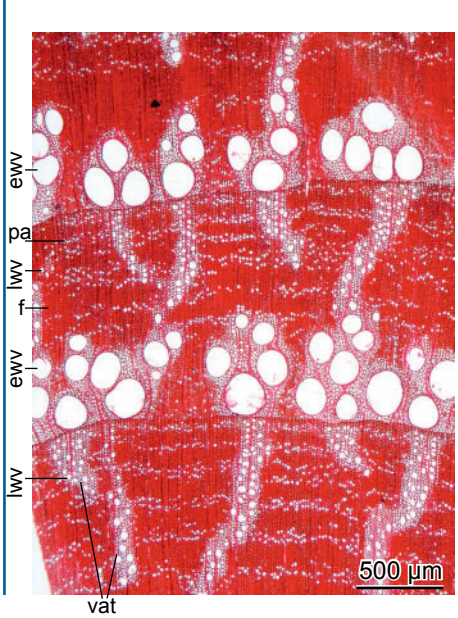
Fibers are thick- and thin- to thick-walled. The diameter of fiber pits with slit-like apertures varies between 2-4 µm (**Figs. 8** and **11**). Latewood vessels of *Quercus* and *Castanea* are often surrounded by tracheids (**Figs. 1-3**). All species produce tension wood (**Figs. 10** and **12**). The distribution of axial parenchyma is apotracheal, diffuse in aggregates (**Figs. 13** and **14**). Rays of all species are homocellular, but their width is genera-specific: Uniseriate in *Castanea sativa* (**Fig. 15**), biseriate to multiseriate in *Fagus* (**Fig. 16**) and uni- and multiseriate in *Quercus* (**Fig. 17**). Prismatic crystals occur in *Fagus* and *Quercus*.

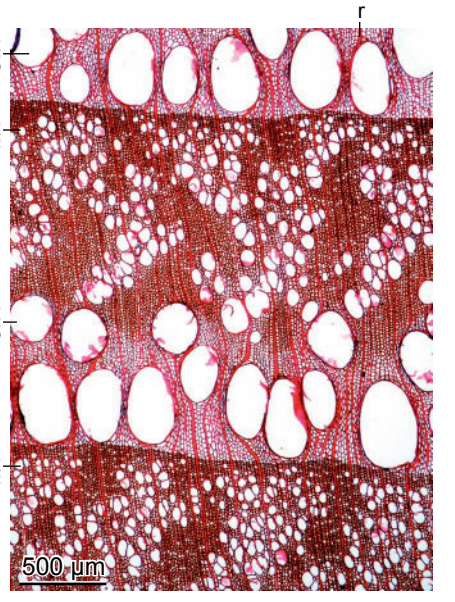



**Left Fig. 1.** Ring-porous xylem with distinct annual ring boundaries. Latewood vessels are arranged in diagonal to radial strips. Vessel size continuously decreases from earlywood to latewood. Stem of a young 15 m-high tree, Chestnut forest, hill zone, Locarno, Ticino, Switzerland. *Castanea sativa*, transverse section.

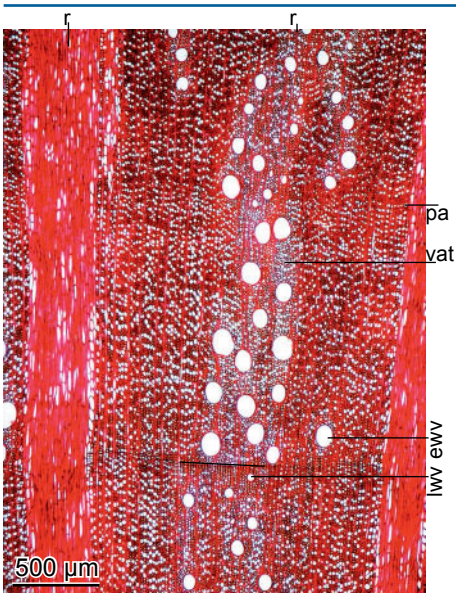
**Right Fig. 2.** Ring-porous xylem with distinct annual ring boundaries. Latewood vessels are arranged in diagonal to radial strips. Vessel size continuously decreases from earlywood to latewood. Parenchyma cells form intra-annual tangential bands. Stem of a young 15 m-high tree, *Quercus cerris* forest, Mediterranean, Tuscany, Italy. *Quercus cerris*, transverse section.

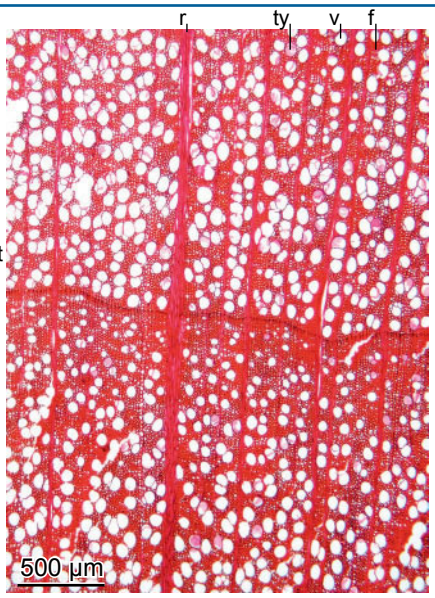



**Left Fig. 3.** Ring-porous xylem with distinct annual ring boundaries. Latewood vessels are arranged in diagonal strips. Vessel size abruptly decreases from earlywood to latewood. Vessels are surrounded by thin-walled tracheids. Parenchyma cells form intra-annual tangential bands. Stem of a 15 m-high tree, beech forest, hill zone, Zürich, Switzerland. *Quercus robur*, transverse section.

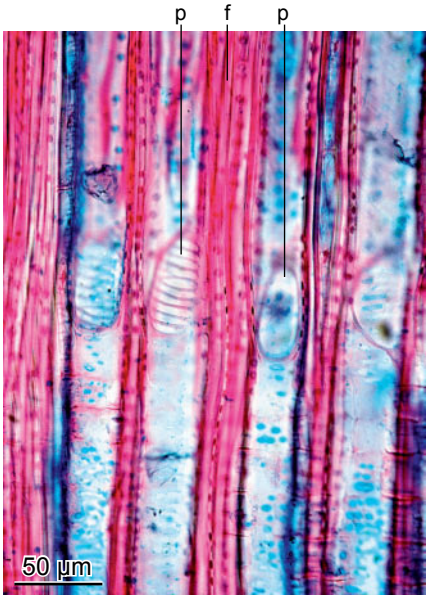
**Right Fig. 4.** Ring-porous xylem with distinct annual ring boundaries. Latewood vessels are arranged in dendritic patterns. Stem of an old, 20 m-high tree, Chestnut forest, hill zone, Locarno, Ticino, Switzerland. *Castanea sativa*, transverse section.

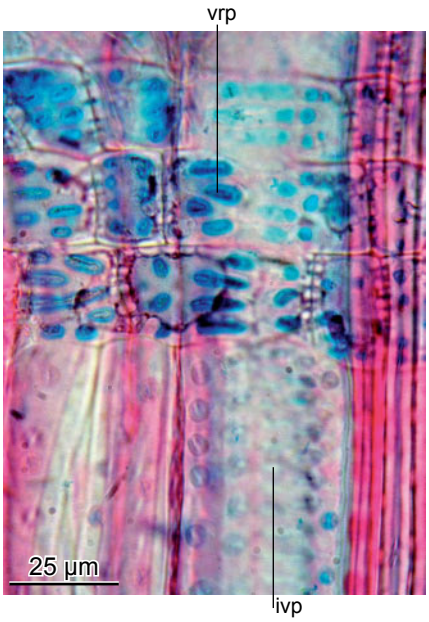



**Left Fig. 5.** Indistinct annual rings. Solitary vessels are arranged in radial patterns between vessel-free zones and very large rays. Stem of a 10 m-high tree, cork oak plantation, Mediterranean, Algarve, Portugal. *Quercus suber*, transverse section.

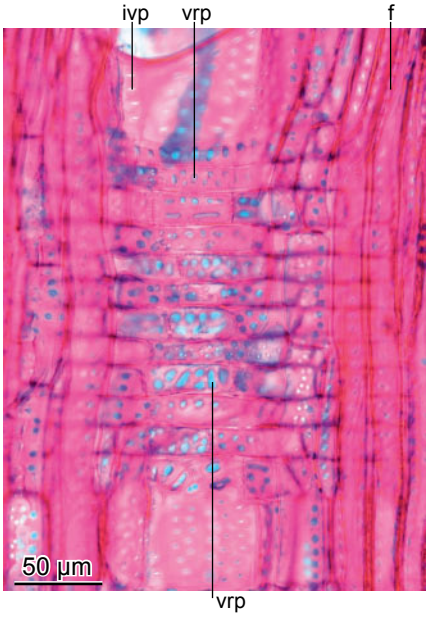
**Right Fig. 6.** Semi-ring-porous xylem with a distinct annual ring boundary. Vessels are arranged solitary or in small groups. Stem of a 20 m-high tree, beech forest, hill zone, Zürich, Switzerland. *Fagus sylvatica*, transverse section.

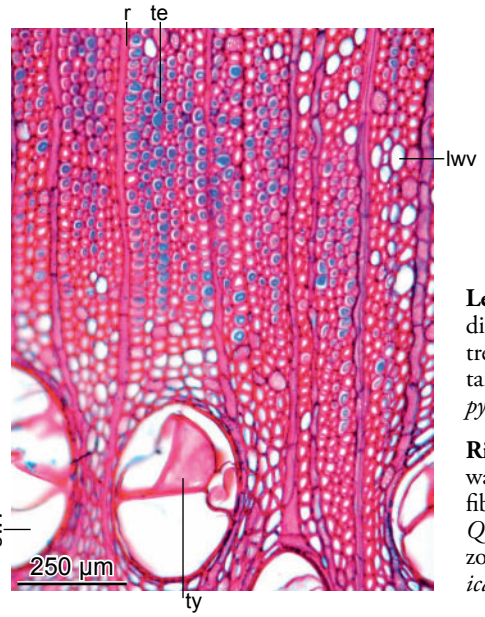



**Left Fig. 7.** Vessels with simple and scalariform perforations. Stem of a 15 m-high tree, beech forest, mountain zone, Goderzi Pass, Georgia. *Fagus orientalis*, radial section.

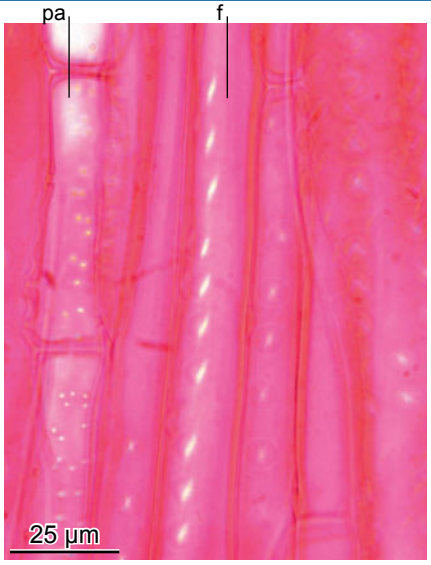
**Right Fig. 8.** Horizontally enlarged vessel-ray-pits. Stem of a 15 m-high tree, beech forest, mountain zone, Goderzi Pass, Georgia. *Fagus orientalis*, radial section.

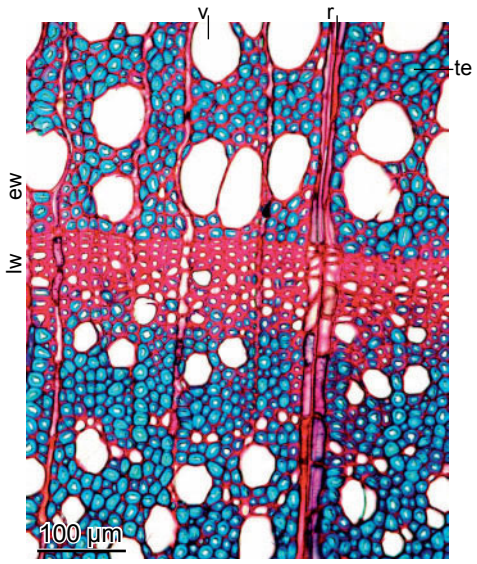



**Left Fig. 9.** Enlarged vessel-ray-pits with different forms. Stem of a young, 6 m-high tree, *Quercus pyrenaica* afforestation, mountain zone, Estremadura, Spain. *Quercus pyrenaica*, radial section.

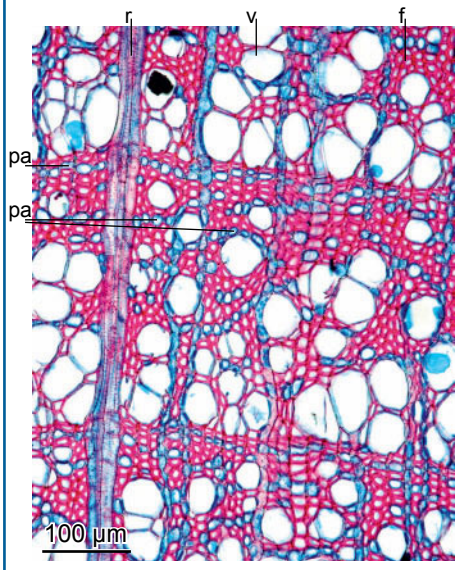
**Right Fig. 10.** Earlywood vessels with thin-walled tylosis and latewood with gelatinous fibers. Stem of a young, 6 m-high tree, *Quercus pyrenaica* afforestation, mountain zone, Estremadura, Spain. *Quercus pyrenaica*, transverse section.

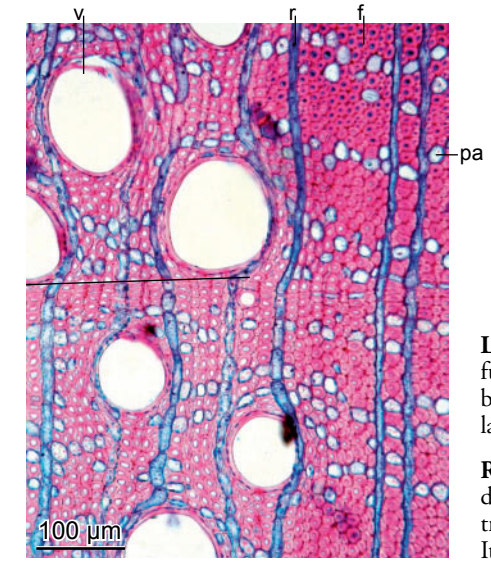



**Left Fig. 11.** Parenchyma with small simple pits, and fibers with large bordered pits with slit-like apertures. Stem of a 15 m-high tree, beech forest, hill zone, Winterthur, Switzerland. *Quercus rubra*, radial section.

**Right Fig. 12.** Earlywood and latewood with tension wood. The most recent latewood zone lacks tension wood. Stem of a 12 m-high tree, beech forest, hill zone, Zürich, Switzerland. *Fagus sylvatica*, transverse section.




**Left Fig. 13.** Apotracheal parenchyma, diffuse in aggregates. Stem of a 6 m-high tree, beech forest, hill zone, Fricktal, Switzerland. *Fagus sylvatica*, transverse section.

**Right Fig. 14.** Apotracheal parenchyma, diffuse in aggregates. Stem of a 5 m-high tree, macchia, Mediterranean, Tuscany, Italy. *Quercus ilex*, transverse section.

**Fig. 15.** Uniseriate homocellular rays. Stem of an old, 20 m-high tree, Chestnut forest, hill zone, Locarno, Ticino, Switzerland. *Castanea sativa*, tangential section.

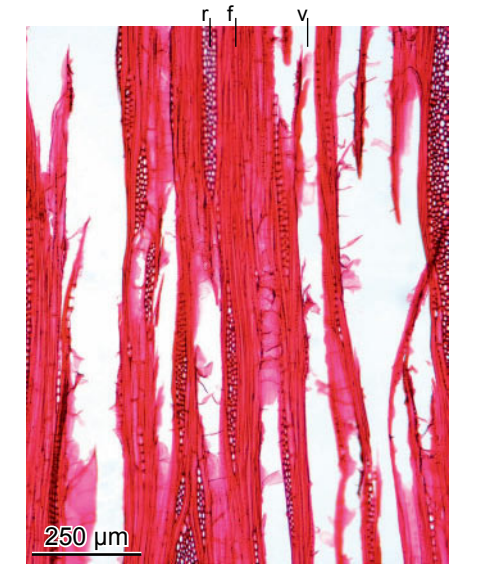



**Fig. 16.** Rays with 2 to many cells width. Stem of a 15 m-high tree, beech forest, mountain zone, New Hampshire, USA. *Fagus grandifolia*, tangential section.

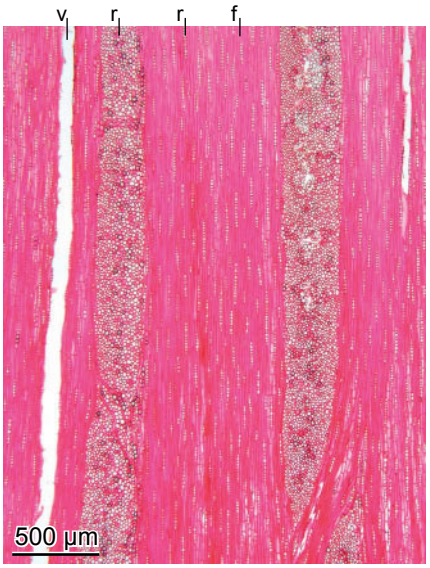



**Fig. 17.** Uniseriate and multiseriate rays. Stem of a young, 15 m-high tree, *Quercus cerris* forest, Mediterranean, Tuscany, Italy. *Quercus cerris*, tangential section.

**Characteristics of the phloem and the cortex**

Tangentially arranged groups of sclerenchyma are characteristic of *Castanea* (**Figs. 18-20**) and *Quercus* (**Fig. 19**). The bands are often discontinuous or rudimentary (**Fig. 20**) and replaced by large sclerenchyma groups (**Fig. 19**). Rays are often intensively sclerotized (**Figs. 20** and **21**). *Fagus* contains a dense belt of sclerenchyma (**Fig. 21**). Sieve-tubes and parenchyma cells normally collapse in older parts and appear as dark bands (**Figs. 21** and **22**).

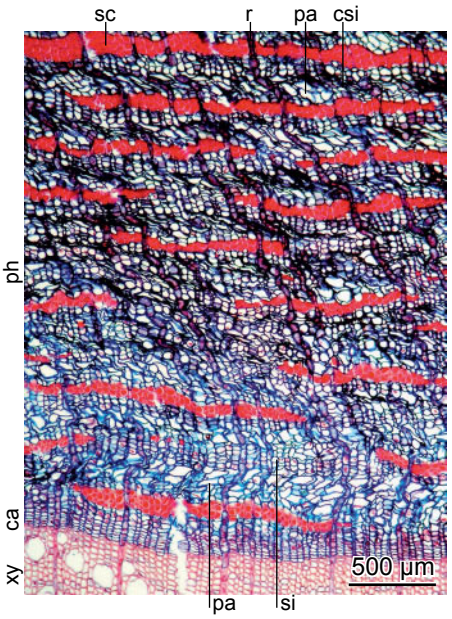



**Fig. 18.** Phloem with tangential bands of sclerenchyma, collapsed sieve-tubes and bent rays. Stem of an old, 20 m-high tree, Chestnut forest, hill zone, Locarno, Ticino, Switzerland. *Castanea sativa*, transverse section.

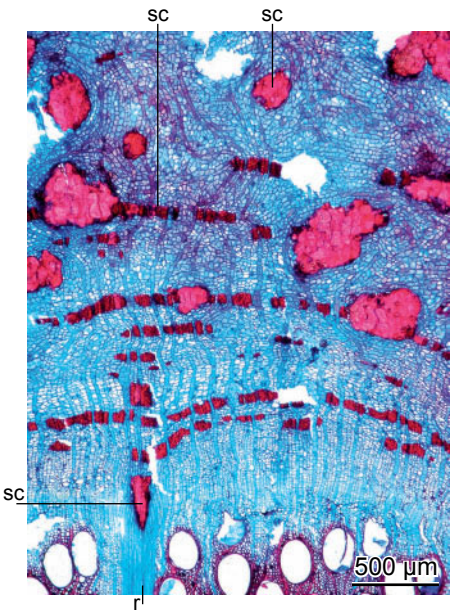



**Fig. 19.** Phloem with large irregular groups of sclerenchyma and a few short tangential bands. The center of the large ray is sclerotized at the initial zone. Stem of a young, 6 m-high tree, *Quercus pyrenaica* afforestation, mountain zone, Estremadura, Spain. *Quercus pyrenaica*, transverse section.

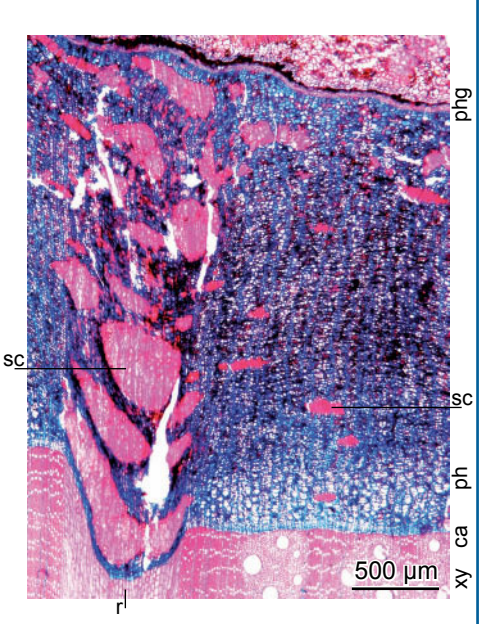
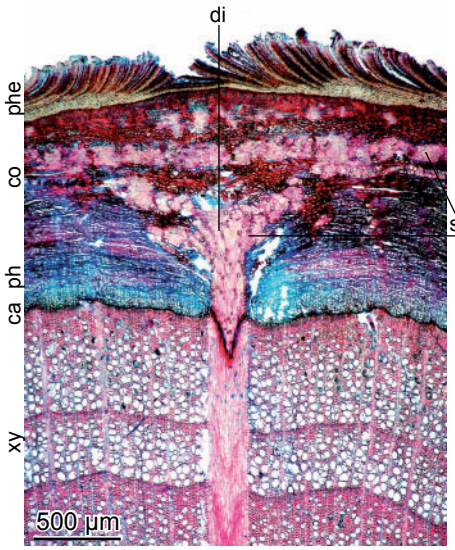
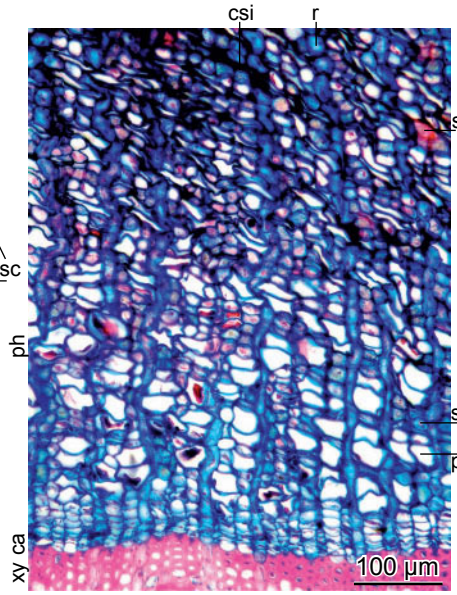



**Fig. 20.** Phloem with large irregular groups of sclerenchyma in the large ray and a few short rudimentary tangential bands in the zone with uniseriate rays. Stem of a 5 m-high tree, macchia, Mediterranean, Tuscany, Italy. *Quercus ilex*, transverse section.




**Left Fig. 21.** Phloem with a large, sclerotized ray dilatation and a dense tangential band of sclerenchyma between the phloem and the cortex. Older sieve-tubes are collapsed. The phellem consists of several broken layers. Stem of a 15 m-high tree, beech forest, mountain zone, Goderzi Pass, Georgia. *Fagus orientalis*, transverse section.

**Right Fig. 22.** Cambial zone. The young phloem consists of large parenchyma cells and smaller sieve-tubes. Both cell types are collapsed in the older phloem. Stem of a 5 m-high tree, macchia, Mediterranean, Tuscany, Italy. *Quercus ilex*, transverse section.

**Discussion in relation to previous studies**

Since most species represent valuable timbers, the xylem has been described many times. Gregory (1994) mentioned more than 200 references. Holdheide (1951) described the bark of *Castanea sativa*, *Fagus sylvatica*, *Quercus petraea* and *Q. robur*. New to this study are descriptions of the bark of 3 *Quercus* and 1 *Fagus* species. The present results are in accordance with previous findings.

Characteristic of the family is the presence of enlarged intervessel pits. All other features are taxa-specific and allow the determination of genera or even groups of species.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **22** |
| 1 | growth rings distinct and recognizable | 18 |
| 2 | growth rings absent | 4 |
| 3 | ring-porous | 15 |
| 4 | semi-ring-porous | 3 |
| 7 | vessels in diagonal and/or radial patterns | 19 |
| 8 | vessels in dendritic patterns | 18 |
| 9 | vessels predominantly solitary | 12 |
| 11 | vessels predominantly in clusters | 3 |
| 13 | vessels with simple perforation plates | 22 |
| 14 | vessels with scalariform perforation plates | 3 |
| 21 | intervessel pits opposite | 3 |
| 22 | intervessel pits alternate | 19 |
| 31 | vessel-ray pits with large apertures, *Salix/Laurus* type | 22 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 3 |
| 39.1 | vessel cell-wall thickness >2 µm | 4 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 3 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 19 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 22 |
| 56 | tylosis with thin walls | 18 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 13 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 14 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 18 |
| 69 | fibers thick-walled | 21 |
| 70 | fibers thin- to thick-walled | 12 |
| 70.2 | tension wood present | 18 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 22 |
| 79 | parenchyma paratracheal | 19 |
| 86 | axial parenchyma in narrow bands or lines, *Quercus* type | 18 |
| 96 | rays uniseriate | 19 |
| 98 | rays commonly 4-10-seriate | 3 |
| 99 | rays commonly >10-seriate | 21 |
| 103 | rays of two distinct sizes (tangential section) | 21 |
| 102 | ray height > 1mm | 10 |
| 104 | ray: all cells procumbent (radial section) | 22 |
| 136 | prismatic crystals present | 21 |
| R1 | groups of sieve tubes present | 6 |
| R2 | groups of sieve tubes in tangential rows | 3 |
| R2.1 | groups of sieve tubes in radial rows | 0 |
| R3 | distinct ray dilatations | 8 |
| R4 | sclereids in phloem and cortex | 3 |
| R6.1 | sclereids in tangential rows | 7 |
| R6.2 | sclereids in tangential arranged groups, *Rhamnus* type | 1 |
| R7 | with prismatic crystals | 3 |
| R8 | with crystal druses | 2 |
| R15 | oil in rays | 6 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 3 |

# Gentianaceae



### Number of species, worldwide and in Europe

The Gentianaceae family includes 88 genera with 1500 species. They are distributed worldwide, but mainly in the temperate zone of the Northern hemisphere. In Europe, there are 9 genera with 72 species, whereas on the Canary Islands there is only one species.

### Analyzed material

The xylem and phloem of 26 Gentianaceae species has been analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 1 | |
| Woody chamaephytes | | 19 |
| Hemicryptophytes and geophytes | 13 | 5 |
| Therophytes | 8 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 16 | |
| Hill and mountain | 9 | |
| Subtropical | 1 | |

**Analyzed species:**

*Blackstonia perfoliata* Huds.
*Centaurium erythraea* Rafn.
*Gentiana acaulis* L.
*Gentiana asclepiadea* L.
*Gentiana bavarica* L.
*Gentiana campestris* L.
*Gentiana ciliata* L.
*Gentiana clusii* Perrier
*Gentiana cruciata* L.
*Gentiana germanica* Willd.
*Gentiana insubrica* Kunz
*Gentiana lutea* L.
*Gentiana nana* Wulfen
*Gentiana nivalis* L.
*Gentiana orbicularis* Schur
*Gentiana pneumonanthe* L.
*Gentiana punctata* L.
*Gentiana purpurea* L.
*Gentiana ramosa* Hegetschw.
*Gentiana tenella* Rottb.
*Gentiana utriculosa* L.
*Gentiana verna* L.
*Ixanthus viscosus* Grieseb.
*Lomatogonium carinthiacum* (Wulfen) Rchb.
*Swertia perennis* L.
*Swertia radiata* Kunze

*Swertia perennis*

*Ixanthus viscosus*

*Gentiana lutea*

*Centaurium erythraea*

*Gentiana acaulis*

**Characteristics of the xylem**

Distinct annual ring boundaries in perennial plants can be recognized only in a few species, e.g. *Gentiana asclepiadea* (**Fig. 1**) and *Ixanthus viscosus* (**Fig. 2**). They can also be observed sporadically in *Gentiana acaulis* (**Fig. 3**). One ring is characteristic for annual plants (**Figs. 4** and **5**). Plants which germinate in fall and flower in the following years have two rings, e.g. *Centaurium erythraea* (**Fig. 6**).

Radial vessel diameter is normally below 20 µm. Vessels are mostly solitary, e.g. in *Gentiana tenella*, *G. acaulis* (**Fig. 3**). They are in radial multiples, e.g. in *Gentiana nivalis* (**Fig. 4**), *G. asclepiadea* (**Fig. 1**), and *G. germanica* (**Fig. 10**). Vessel density normally exceeds 200/mm$^2$. Only *Ixanthus* has much fewer vessels (**Fig. 2**). A few species have thick-walled vessels: e.g. *Gentiana cruciata* (**Fig. 7**). Perforations are simple in all species. Earlywood inter-vessel pitting is mostly scalariform (**Fig. 8**), but in *Blackstonia*, round pits are in alternating position. Axial paren-

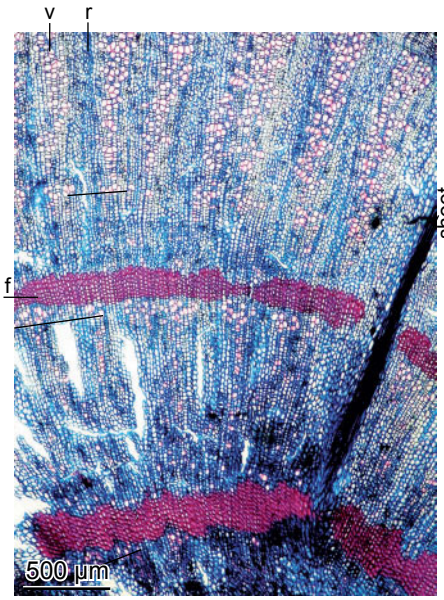



**Fig. 1.** Recognizable rings in a semi-ring-porous xylem. Tangential fiber bands embedded in unlignified parenchymatic tissue characterize the last two rings. The outermost ring made up of long radial vessel strips between ray-like parenchymatic zones. Rhizome of a 40 cm-high perennial herb, moist meadow, mountain zone, Alps, Switzerland. *Gentiana asclepiadea*, transverse section.

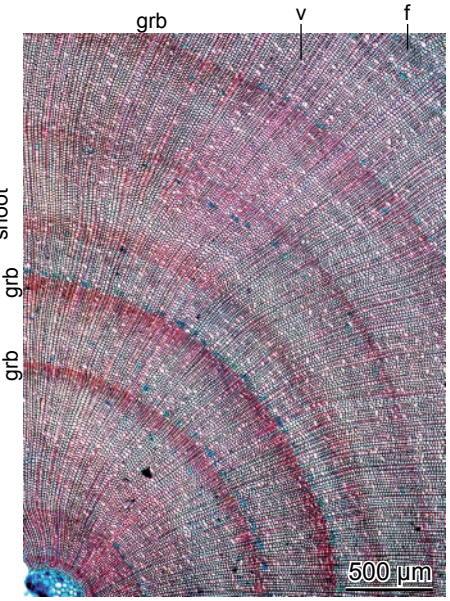



**Fig. 2.** Distinct rings in a diffuse-porous xylem. Ring boundaries are marked by tangential bands of thick-walled fibers in the latewood. The vessels are extremely small (<20 µm). Suppressed 40 cm-high dwarf shrub, laurel forests, subtropical climate, Gomera, Canary Islands. *Ixanthus viscosus*, transverse section.

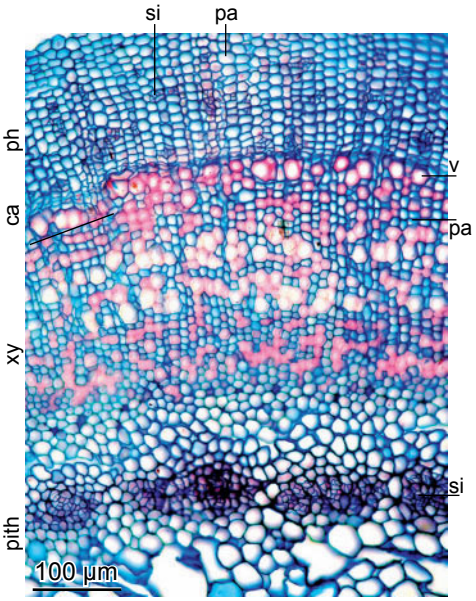
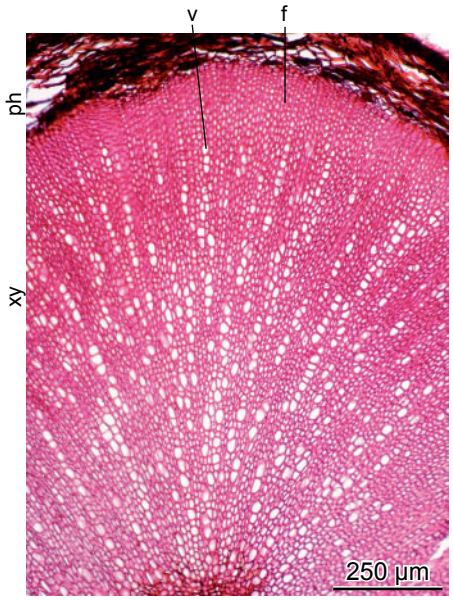



**Fig. 3.** Indistinct rings. The periphery of the pith and the phloem are characterized by sieve-tube groups. Rhizome of a prostrate perennial herb, subalpine zone, Alps, Switzerland. *Gentiana acaulis*, transverse section.



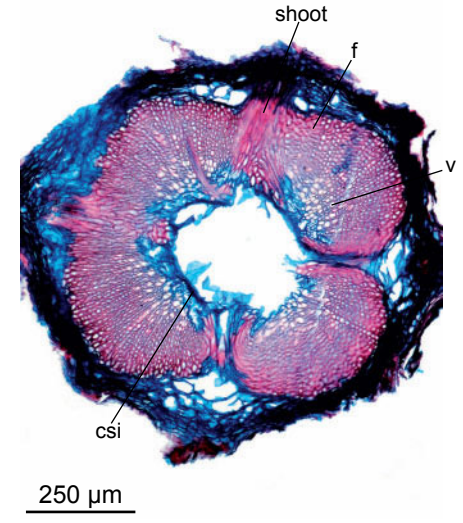




**Fig. 4.** One ring in a xylem with vessels in radial multiples. The latewood is without vessels. 10 cm-high annual plant, subalpine zone, Alps, Switzerland. *Gentiana germanica*, transverse section.

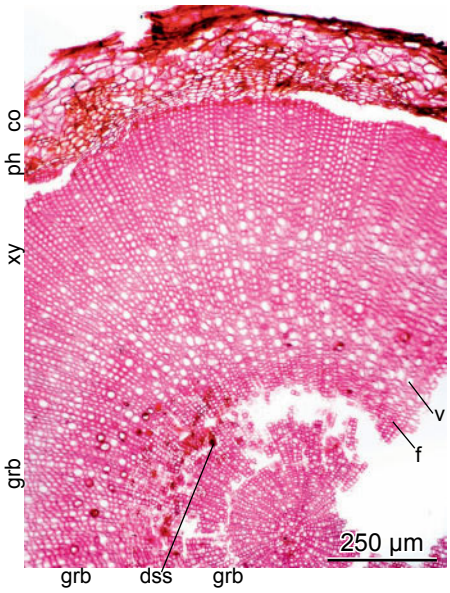
**Fig. 5.** One ring. Vessels are present in the earlywood and absent in the latewood. 5 cm-high annual plant, alpine meadow, Alps, Austria. *Lomatogonium carinthiacum*, transverse section.

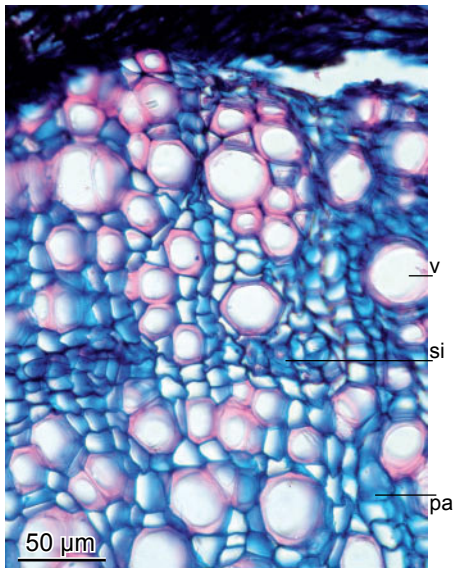
chyma is mostly not recognizable (*Gentiana germanica*, **Fig. 4;** *Centaurium erythraea*, **Fig. 6**) or it is pervasive (*Gentiana acaulis*, **Fig. 3**).

The composition of the ground tissue allows to classify the Gentianaceae into two groups: It is fibrous in *Blackstonia perfoliata* (**Fig. 9**), *Centaurium erythrea*, the *Gentiana germanica* group (**Fig. 10**), *G. nivalis*, *G. tenella* and *Lomatogonium carinthiacum* (**Fig. 5**). In all other species (*Gentiana* and *Swertia*) the vessels are embedded in pervasive parenchyma.

Rays are mostly absent (**Fig. 11**). They occur only in *Ixanthus viscosus*. A special feature is the presence of sieve-tube groups (inter-xylary phloem) in *Ixanthus viscosus* (**Fig. 12**), *Gentiana asclepiadea* (**Fig. 13**), *G. lutea* (**Fig. 14**), *G. punctata*, *G. purpurea* and *G. cruciata* (**Fig. 7**).

The presence of sclerotic parenchymatic groups embedded in a thin-walled parenchymatic tissue in *Gentiana asclepiadea* is an exception in the family of Gentianaceae (**Fig. 12**).




**Left Fig. 6.** Indistinct rings in diffuse-porous xylem with very small vessels (<20 µm). The plant germinated in fall and developed further in the following year. The wide second ring is divided. After formation of an earlywood zone with many vessels, the summer drought triggered a zone with a few vessels The late summer rains then triggered a second earlywood zone before death. 30 cm-high hemicryptophyte, meadow, submediterranean zone, Alps, Italy. *Centaurium erythraea*, transverse section.

**Right Fig. 7**. Thick-walled vessels and sieve tube groups surrounded by a pervasive parenchyma. Rhizome of a 15 cm-high plant, dry meadow, hill zone, Alps, France. *Gentiana cruciata*, transverse section.

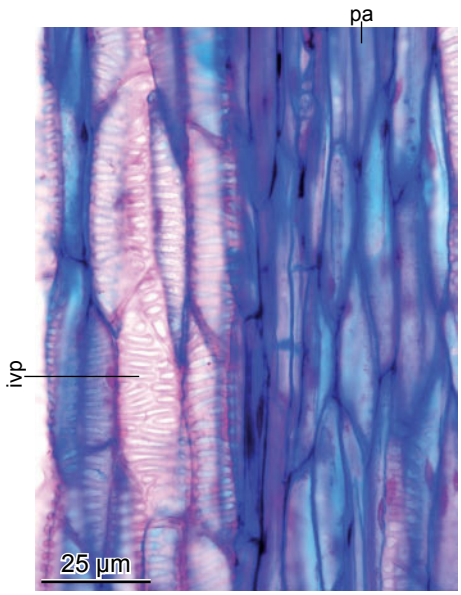



**Fig. 8.** Scalariform inter-vessel pits. 70 cm-high dwarf shrub, laurel forests, subtropical climate, Gomera, Canary Islands. *Ixanthus viscosus*, radial section.

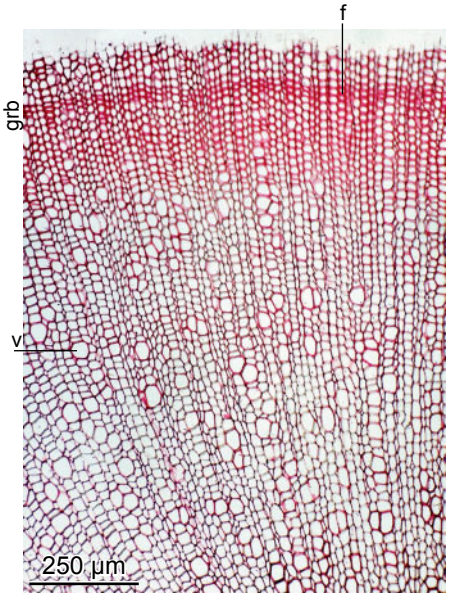



**Fig. 9.** Vessels between a radially-oriented fibrous tissue. Fibers and parenchyma cannot be distinguished. 30 cm-high biannual plant, meadow, submediterranean zone, Alps, Italy. *Blackstonia perfoliata*, transverse section.

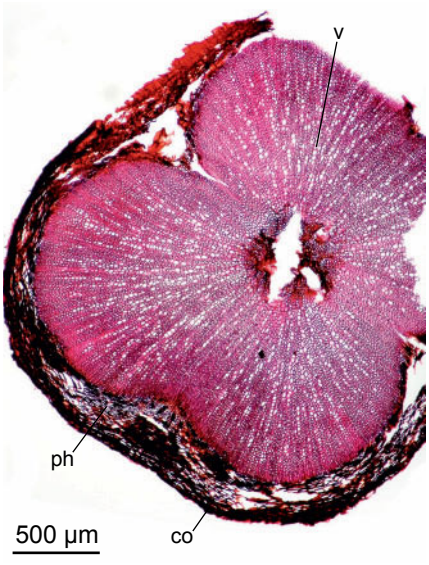
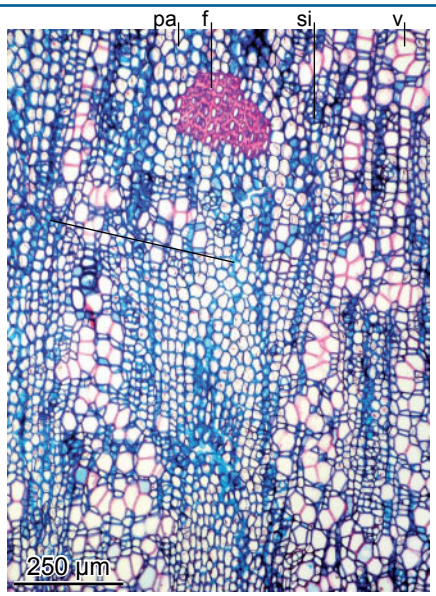
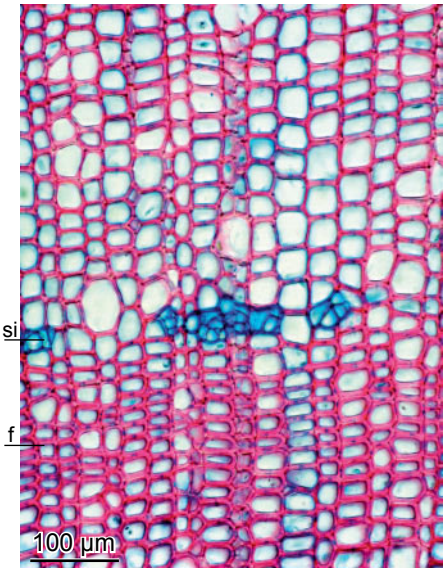


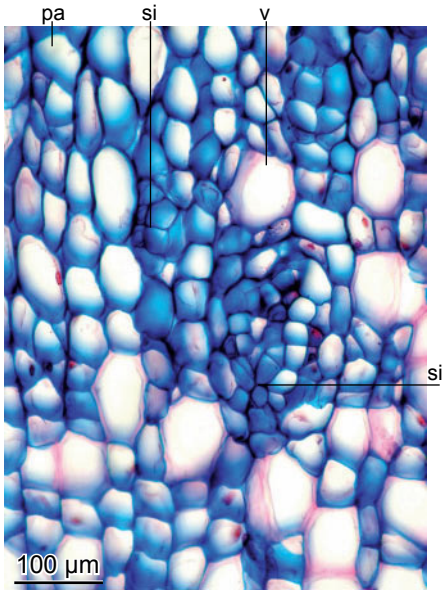

**Fig. 10.** Radially-oriented multiple vessels between fibrous tissue in a lobed stem. Fibers and parenchyma cannot be distinguished. 10 cm-high annual plant, subalpine zone, Alps, Switzerland. *Gentiana germanica*, transverse section.




**Left Fig. 11.** Rayless tissue. The tissue consists mainly of libriform fibers with minutely bordered pits. 30 cm-high biannual plant, meadow, submediterranean zone, Alps, Italy. *Blackstonia perfoliata*, tangential section.

**Right Fig. 12.** Rayless tissue. The tissue consists of vessels, unlignified fibers and parenchyma cells. Special is the presence of groups of sclerenchymatic cells in a tissue of predominantly unlignified parenchyma cells. Rhizome of a 40 cm-high perennial herb, moist meadow, mountain zone, Alps, Switzerland. *Gentiana asclepiadea*, transverse section.




**Left Fig. 13.** Groups of sieve tubes (intraxylary phloem) in a tissue of radially oriented lignified fibers. Rays cannot be distinguished from fibers in the transverse section. 70 cm-high dwarf shrub, laurel forest, subtropical climate, Gomera, Canary Islands. *Ixanthus viscosus*, transverse section.

**Right Fig. 14.** Groups of sieve tubes (intra-xylary phloem) between thin-walled, unlignified fibers and vessels. Rhizome of a 40 cm-high perennial herb, moist meadow, mountain zone, Alps, Switzerland. *Gentiana asclepiadea*, transverse section.

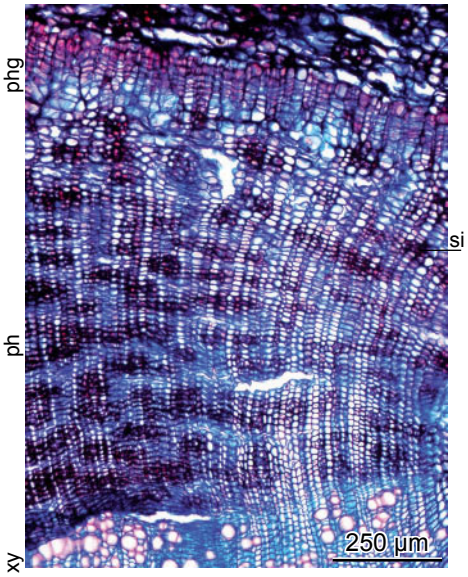
### Characteristics of the phloem, the cortex and the pith

Sieve-tube groups, often arranged in tangential rows, are characteristic of the phloem of many *Gentiana* species and *Swertia perennis* (**Fig. 15**). A special feature in *Gentiana asclepiadea* and *G. cruciata* (**Fig. 16**) is the presence of very tiny acicular crystals (small needle-like crystals; **Fig. 17**).

Groups of sieve tubes (medullary phloem), e.g. in *Gentiana acaulis*, *G. punctata* (**Figs. 3** and **19**) and *Ixanthus viscosus* (**Fig. 18**) occur at the periphery of the pith of some *Gentiana* species, *Swertia perennis* and *Swertia radiata*. They are absent in the *Gentiana germanica* group in *G. nivalis*, *G. utriculosa*, *Lomatogonium carinthiacum*, *Blackstonia perfoliata* and *Centaurium erythrea*.

### Ecological trends in the xylem

No ecological groups could be found. Differences are, at least in some cases, related to taxonomic units, e.g. for *Ixanthus*, *Blackstonia* and *Centaurium*, *Gentiana* section Gentianae: *Gentiana lutea*, *G. punctata* and *Gentiana* section Pneumonanthe: *Gentiana asclepiadea*.



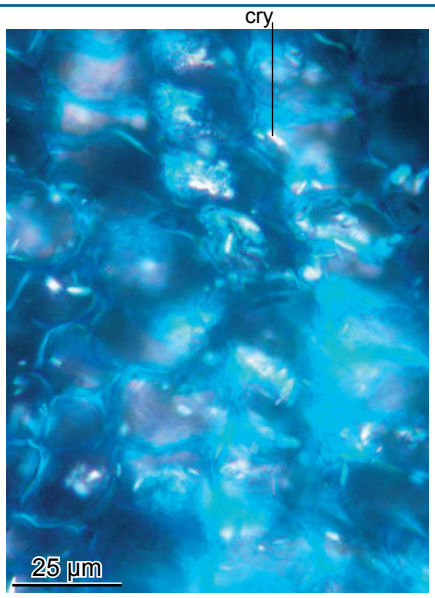
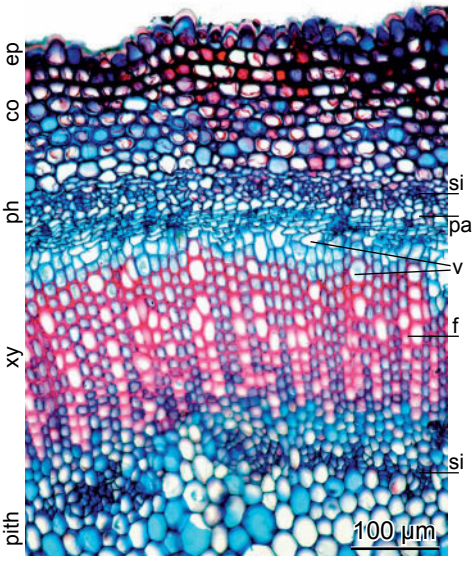
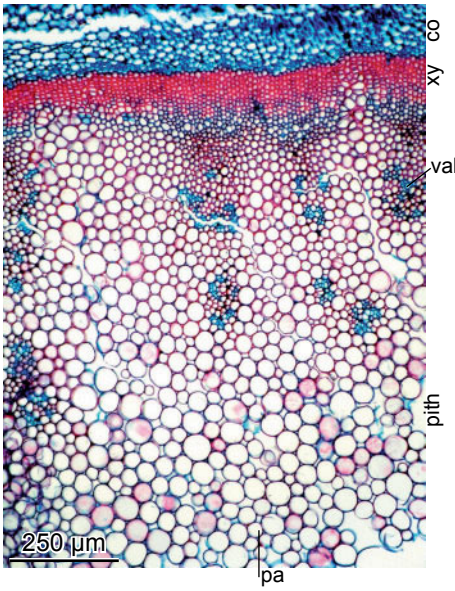




**Fig. 16.** Groups of sieve tubes in the radially-oriented parenchymatic tissue of the phloem. Rhizome of a 20 cm-high perennial plant, dry meadow, mountain zone, Alps, France. *Gentiana cruciata*, transverse section.

**Fig. 17.** Acicular crystals (small needle-like crystals) in the phloem. Rhizome of a 20 cm-high perennial plant, dry meadow, mountain zone, Alps, France. *Gentiana cruciata*, transverse section, polarized light.




**Left Fig. 18.** Tangential rows of sieve-cell groups at the periphery of the pith (medullary phloem) and in the phloem. Long shoot of a 70 cm-high dwarf shrub, laurel forests, subtropical climate, Gomera, Canary Islands. *Ixanthus viscosus*, transverse section.

**Right Fig. 19.** Vascular bundles at the periphery of the pith (medullary phloem). Annual shoot of a 50 cm-high flowering perennial plant, meadow, Jura mountains, France. *Gentiana punctata*, transverse section.

**Discussion in relation to previous studies**

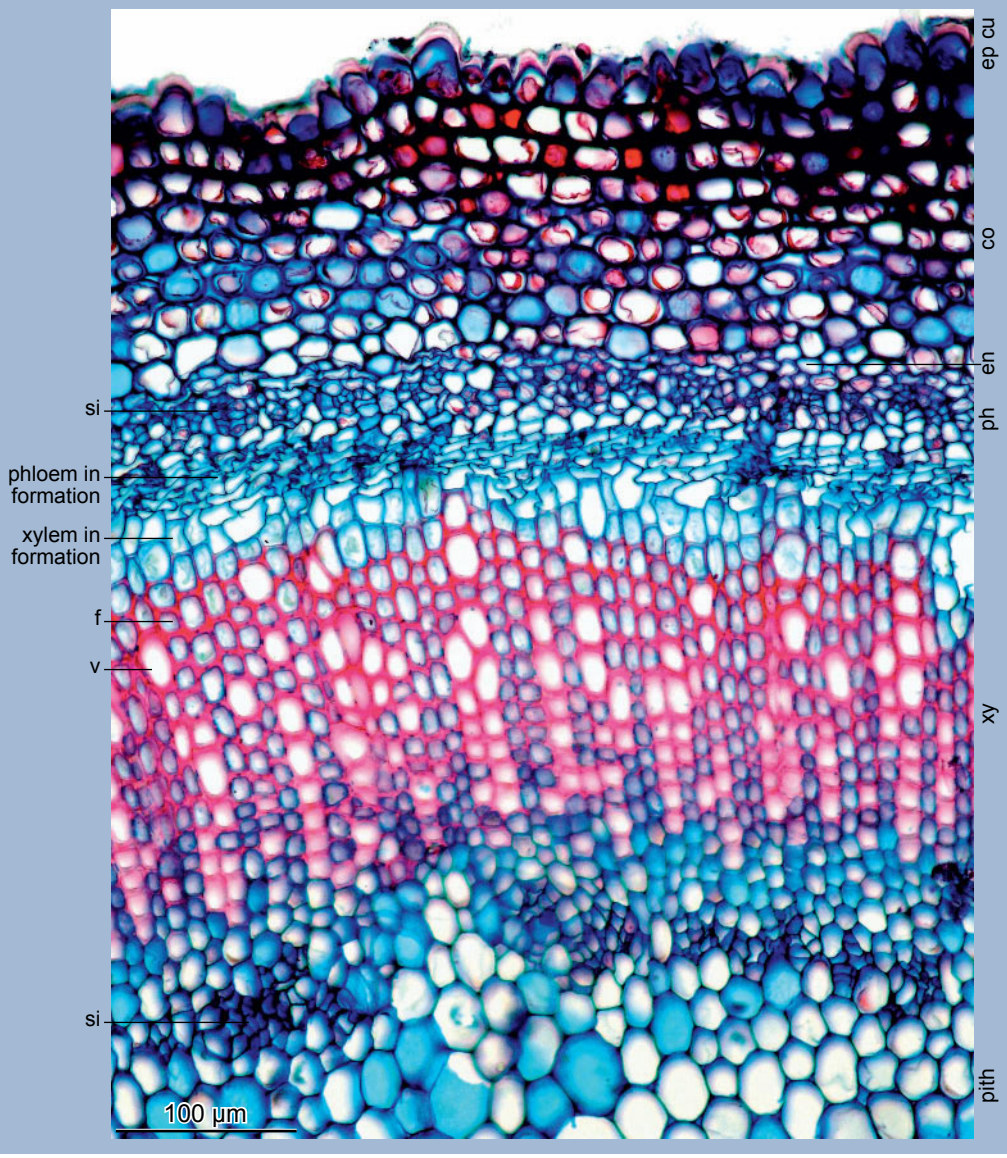
Detailed studies of 19 woody Gentianaceae species were performed by Carlquist (1984) and by Carlquist and Grant (2005). The xylem and phloem of Gentianaceae of a few herbaceous species is briefly described in Metcalfe and Chalk (1957; *Blackstonia*, *Centaurium*, *Swertia*). Jansen and Smets (1998) studied vestured pits in woody Gentianaceae.

All observations on *Ixanthus* correspond with those from Carlquist (1984). Metcalfe and Chalk (1957) recognized medullary phloem as a family-typical feature. The present study differs from the previous studies because earlier authors concentrated on the xylem of shrubs and dwarf shrubs. The present study concentrates on herbaceous species. Interxylary phloem as well as medullary phloem occurs frequently but is not always present. Two groups could be separated: The first is characterized by a fibrous xylem and the second by pervasive parenchyma.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **25** |
| 1 | growth rings distinct and recognizable | 11 |
| 2 | growth rings indistinct or absent | 1 |
| 2.1 | only one ring | 14 |
| 4 | semi-ring-porous | 3 |
| 5 | diffuses-porous | 4 |
| 9 | vessels predominantly solitary | 18 |
| 9.1 | vessels in radial multiples of 2-4 common | 3 |
| 10 | vessels in radial multiples of 4 or more common | 8 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 23 |
| 20 | intervessel pits scalariform | 5 |
| 39.1 | vessel cell-wall thickness >2 µm | 2 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 14 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 11 |
| 50.1 | 100-200 vessels per mm² in earlywood | 24 |
| 50.2 | 200-1000 vessels per mm² in earlywood | 1 |
| 59 | vessels absent or indistinguishable from fibers | 1 |
| 60.1 | fibers absent | 9 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 11 |
| 68 | fibers thin-walled | 2 |
| 69 | fibers thick-walled | 8 |
| 70 | fibers thin- to thick-walled | 7 |
| 75 | parenchyma absent or unrecognizable | 13 |
| 79 | parenchyma paratracheal | 1 |
| 79.1 | parenchyma pervasive | 12 |
| 97 | rays width predominantly 1-3 cells | 1 |
| 105 | ray: all cells upright or square | 1 |
| 117 | rayless | 25 |
| 120 | storied axial tissue (parenchyma, fibers, vessels in tangential section) | 4 |
| 135 | interxylary phloem present | 4 |
| R1 | groups of sieve tubes present | 21 |
| R2 | groups of sieve tubes in tangential rows | 10 |
| R9 | with crystal sand | 1 |
| R10 | phloem not well structured | 8 |
| R11 | with rhaphides | 1 |
| R14 | cortex with aerenchyma | 1 |
| P1 | with medullary phloem or vascular bundles | 25 |

Detailed illustration of Fig. 18: *Ixanthus viscosus*, transverse section.



# Geraniaceae



### Number of species, worldwide and in Europe

The Geraniaceae family includes 7 genera with 750 species. Major genera are *Geranium* (300 species), *Pelargonium* (250 species) and *Erodium* (75 species). Species are wide-spread, especially in temperate and subtropical climate regions. In Europe there are 3 genera with 104 species. The majority belongs to *Geranium* (39 species) and *Erodium* (34 species).

### Analyzed material

The xylem and phloem of 20 Geraniaceae species has been analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Woody chamaephytes | 1 | 12 |
| Hemicryptophytes and geophytes | 9 | |
| Therophytes | 10 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 2 | |
| Hill and mountain | 16 | |
| Subtropical | 2 | |

**Analyzed species:**

*Erodium ciconium* (L.) Hér.
*Erodium cicutarium* (L.) Hér.
*Erodium laciniatum* (Cav.) Willd.
*Erodium pilosum* (Thill.) Jord.
*Geranium caespitosum* James
*Geranium canariense* Reut.
*Geranium columbinum* L.
*Geranium dissectum* L.
*Geranium divaricatum* Ehrh.
*Geranium molle* L.
*Geranium nodosum* L.
*Geranium phaeum* L.
*Geranium pratense* L.
*Geranium pusillum* L.
*Geranium pyrenaicum* Burm.
*Geranium richardsonii* Fisch *et* Tautv.
*Geranium robertianum* L.
*Geranium rotundifolium* L.
*Geranium sanguineum* L.
*Geranium sylvaticum* L.

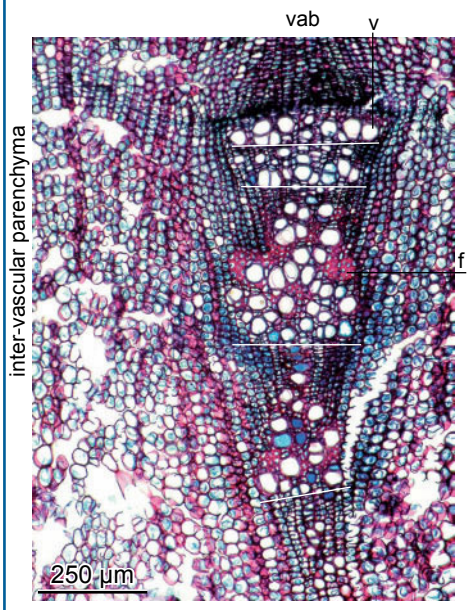
*Geranium sylvaticum*

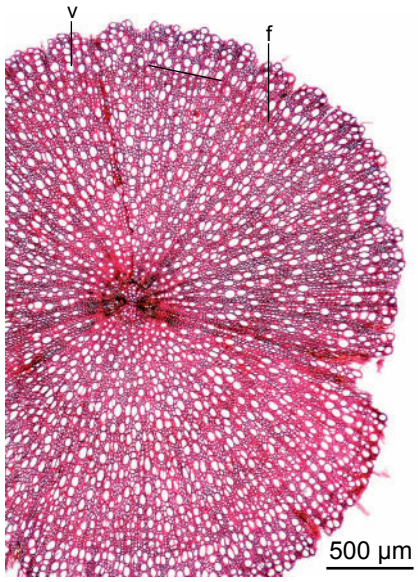
*Geranium nodosum*

*Erodium cicutarium* (photo: Stützel)

**Characteristics of the xylem**

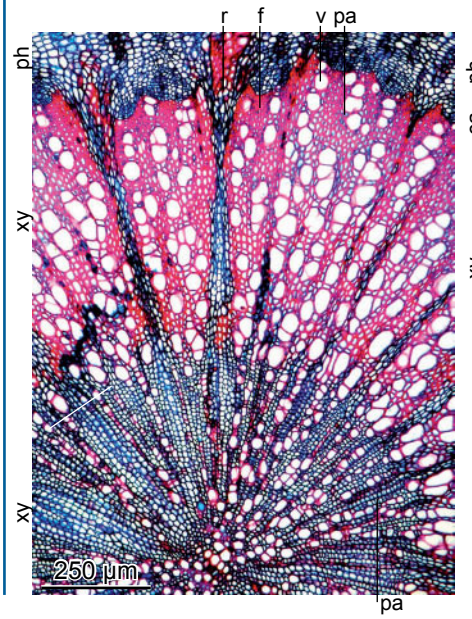
Annual rings occur in the present material in all perennial species of all vegetation zones. Ring boundaries of most perennial species are defined by semi-ring porosity (**Fig. 1**) or diffuse porosity (**Fig. 2**). Two rings occur in taproots in species of the temperate zone, which germinate in autumn and bloom in the next spring (**Figs. 2** and **3**). Only one ring is formed in annual plants (**Figs. 4**, **9** and **10**). Vessels are solitary (**Fig. 9**) or more often in short radial multiples with 2-4 vessels (**Figs. 2** and **10**) or in longer multiples (**Fig. 4**). Earlywood vessel diameter of the majority of species varies between 30-50 µm. Diameter exceeds 100 µm in *Erodium laciniatum*. Vessel density varies mostly between 200-300/mm$^2$. It is sometimes lower in species with isolated vascular bundles as e.g. *Geranium phaeum* (**Fig. 12**). Vessels contain exclusively simple perforations (**Figs. 5** and **6**). Inter-vessel pits are predominantly small and round (**Fig. 6**). A few species have scalariform inter-vessel pits, e.g. *Erodium pilosum*, *Geranium caespitosum*, and *G. richardsonii* (**Fig. 5**). Vestured pits are probably absent. Thin-walled tylosis (**Fig. 7**) are quite common in the genus *Geranium* but have not been observed in the genus *Erodium*. Dark-stained substances occur in older rings of *Geranium sanguineum* (**Fig. 8**) and *G. richardsonii*. Vessel walls are mostly thin, except in *Geranium pratense* and *Erodium pilosum* where they are thick-walled (**Fig. 9**). The radial walls of fibers are perforated by very small slit-like or round pits (<2 µm) in all species (**Fig. 6**). Fibers are mostly thin- or thin- to thick-walled. They are thick-walled in the polar root of the tiny annual herb *Geranium pusillum* (**Fig. 9**) and the rhizomes of *Geranium pratense* and *G. sanguineum* (**Fig. 8**).

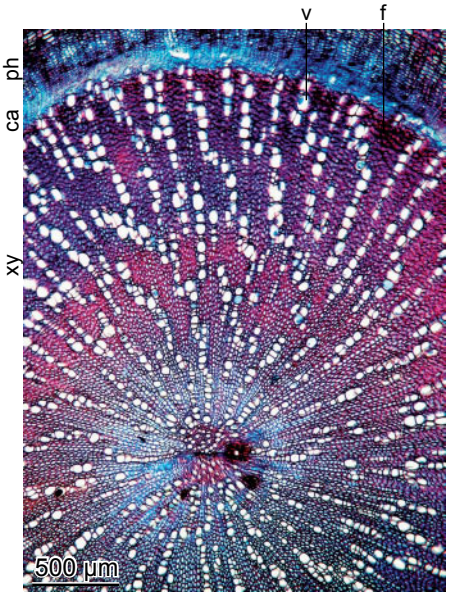



**Left Fig. 1.** Distinct rings in a semi-ring-porous xylem with isolated vascular bundles. Between the bundles is an intervascular parenchyma, which can be interpreted as a very large ray. Rhizome of a 30 cm-high hemicryptophyte, meadow, mountain zone, Colorado, USA. *Geranium caespitosum*, transverse section.

**Right Fig. 2.** Two distinct rings in a semi-ring-porous xylem. The herb germinates in the autumn of the previous year, blooms in the following spring and dies in early summer. Most vessels stay solitary. 30 cm-high biannual herb, vineyard, hill zone, Valtellina, Italy. *Geranium molle*, transverse section.




**Left Fig. 3.** Two distinct rings in a semi-ring-porous xylem. The tissue formed in autumn of the previous year is composed of vessels with a pervasive parenchyma. The xylem, formed in spring of the following year contains radially grouped vessels with a scanty parenchyma. 30 cm-high biannual herb, vineyard, hill zone, Provence, France. *Geranium columbinum*, transverse section.

**Right Fig. 4.** Vessels are arranged in long radial multiples. Root collar of a10 cm-high annual plant, vineyard, thermophile zone, Gran Canaria, Canary Islands. *Erodium laciniatum*, transverse section.

The distribution of axial parenchyma is often difficult to determine, especially on slides stained only with safranin. There is a predominance of scanty paratracheal parenchyma (**Fig. 9**). Pervasive parenchyma occurs in a few species just at the beginning of xylem formation (**Fig. 9**) or it occupies the whole xylem (**Fig. 10**) or occurs mainly in the earlywood in rhizomes of a few *Geranium* species (**Fig. 8**). Rays are very diverse. Rays are absent in 10 of the 20 species analyzed. *Geranium columbinum* (**Figs. 3** and **11**) and *Erodium ciconium* have rays 3-4 cells in width with thin-walled, unlignified cell walls. Rays in all species with isolated vascular bundles are very large and can be interpreted as intervascular parenchyma (**Figs. 1**, **12** and **13**). Ray cells are square or upright. The vascular bundle form is found in 9 of the 20 species analyzed. Crystal druses exist in a few species e.g. *Erodium cicutarium* and *Geranium sylvaticum*. The rhaphide-like crystals in *Geranium divaricatum* are rather special (**Fig. 7**).

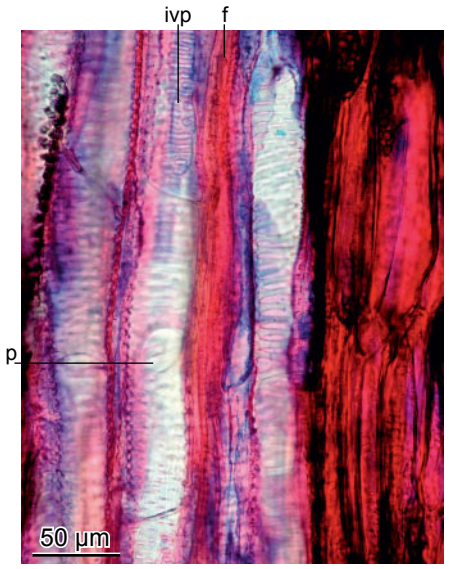



**Fig. 5.** Vessels with simple perforations and scalariform inter-vessel pits. Rhizome of a 30 m-high hemicryptophyte, meadow, mountain zone, Colorado, USA. *Geranium caespitosum*, radial section.

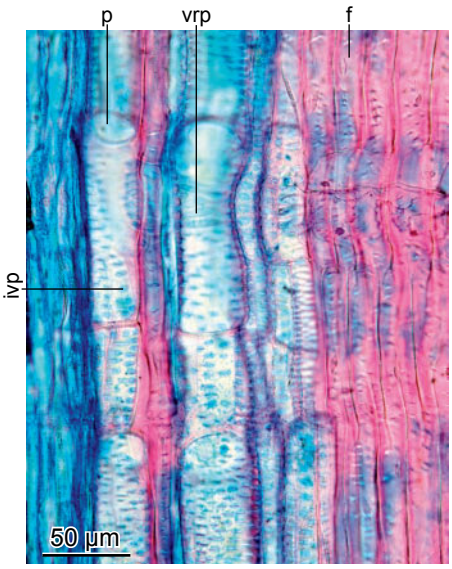



**Fig. 6.** Vessels with simple perforations and small round inter-vessel pits. Small slit-like pits are characteristic of fibers. Rhizome of a 50 cm-high hemicryptophyte, meadow, mountain zone, Savoy, France. *Geranium phaeum*, radial section.

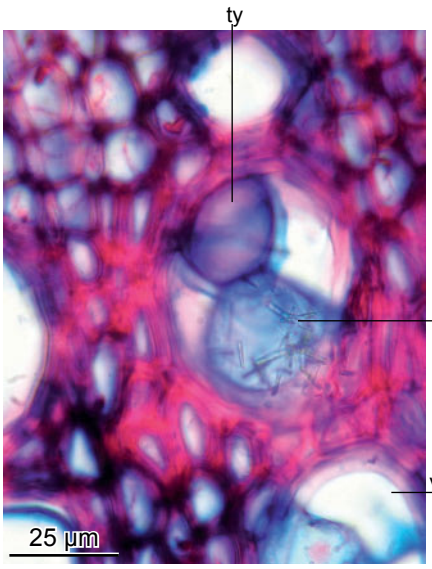



**Fig. 7.** Thin-walled tylosis and rhaphide-like crystals with blunt ends. Root collar of a 10 cm-high annual herb, meadow, mountain zone, Grisons, Switzerland. *Geranium divaricatum*, transverse section.

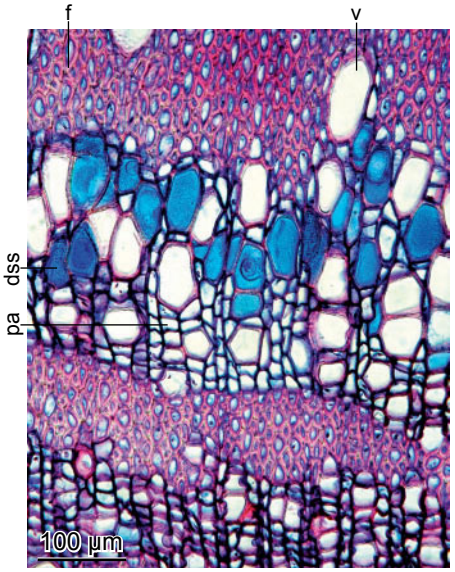



**Fig. 8.** Dark-stained substances in earlywood vessels. The earlywood consists of vessels and pervasive parenchyma, the latewood mainly of thick-walled fibers. Rhizome of a hemicryptophytic herb, garden, hill zone, Bavaria, Germany. *Geranium sanguineum*, transverse section.

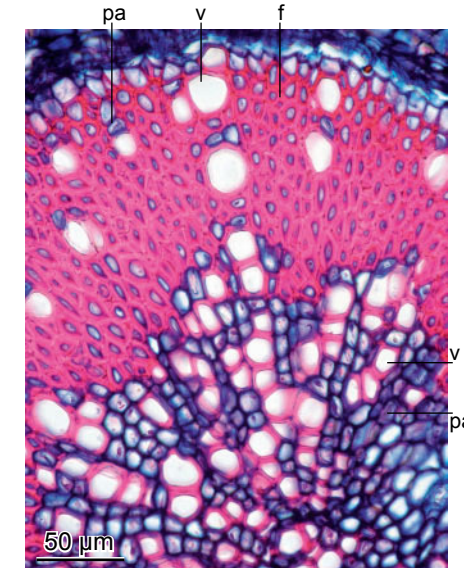



**Fig. 9.** Vessels in the center of the root (earlywood) are surrounded by pervasive parenchyma. Thick-walled fibers with scanty parenchyma are characteristic of the second part of the ring. Root collar of an annual herb, vineyard, hill zone, Alps, France. *Geranium pusillum*, transverse section.

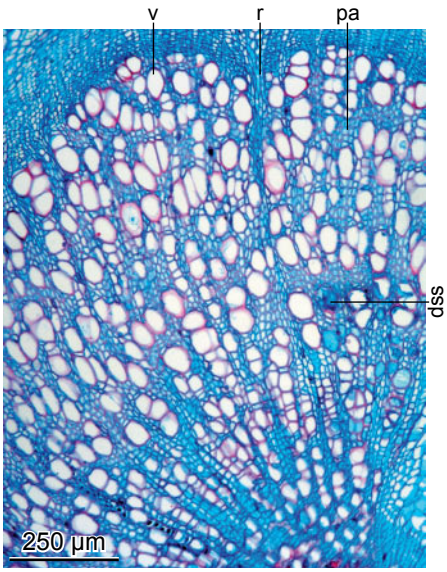



**Fig. 10.** Vessels with lignified walls are surrounded by pervasive parenchyma. Fibers are absent. Root collar of a 30 cm-high biannual herb, vineyard, hill zone, Provence, France. *Geranium columbinum*, transverse section.

### Taxa characteristic features

Only plants with rhizomes of the genus *Geranium* reach ages of 4-8 years. The age of all species with taproots in both genera varies betwenn 1-3 years. The occurrence of isolated vascular bundles is concentrated in species with rhizomes of the genus *Geranium* (**Figs. 1**, **12** and **13**), but they also occur in species with taproots such as *Geranium robertianum* and *G. pyrenaicum*. They are absent in *Erodium*. The presence of rhaphide-like crystals in *Geranium divaricatum* and groups of sclereids in the cortex of *Geranium sanguineum* are rather special. Since we normally do not have several slides of single species, it is difficult to judge whether the presence or absence of tylosis, scalariform inter-vessel pits and crystal druses is species-characteristic. *Erodium* and *Geranium* have no genus specific features.

**Fig. 11.** Ray 5-7 cells in width. Ray cells are unlignified and have similar forms to those of axial parenchyma cells. Root collar of a 30 cm-high biannual herb, vineyard, hill zone, Provence, France. *Geranium columbinum*, tangential section.

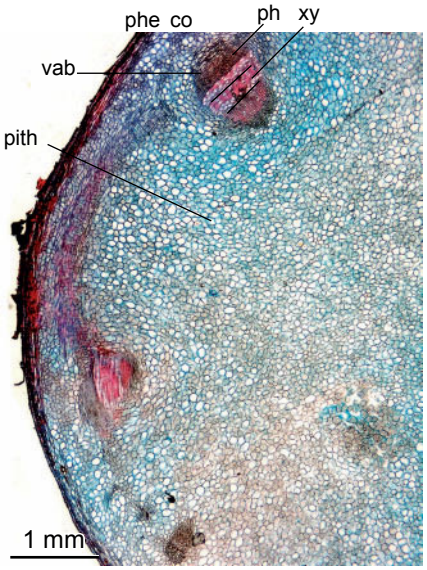



**Fig. 12.** A few isolated vascular bundles at the periphery of a very large pith. Three rings can be identified in the xylem. Rhizome of a 50 cm-high hemicryptophyte, meadow, mountain zone, Savoy, France. *Geranium phaeum*, radial section.

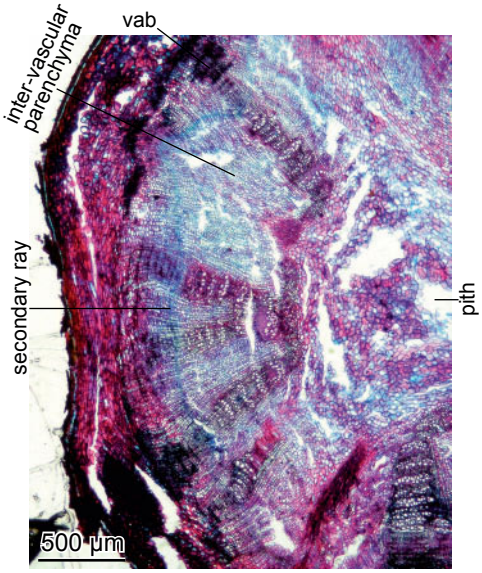



**Fig. 13.** Very large rays between radially oriented vascular bundles. 10 rings can be identified in the xylem. Rhizome of a 50 cm-high hemicryptophyte, meadow, mountain zone, Colorado, USA. *Geranium richardsonii*, transverse section.

### Ecological trends and relations to life forms

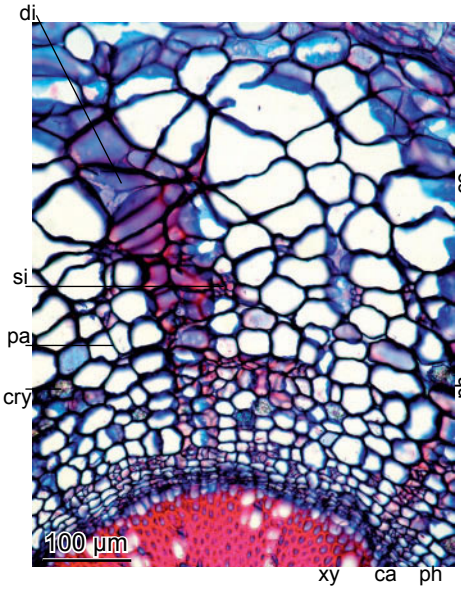
Since most of the analyzed species grow in the hill zone, no ecological trends can be identified. Differences exist between taproots and rhizomes. The latter are dominated by intervascular parenchyma (**Figs. 1**, **12** and **13**).

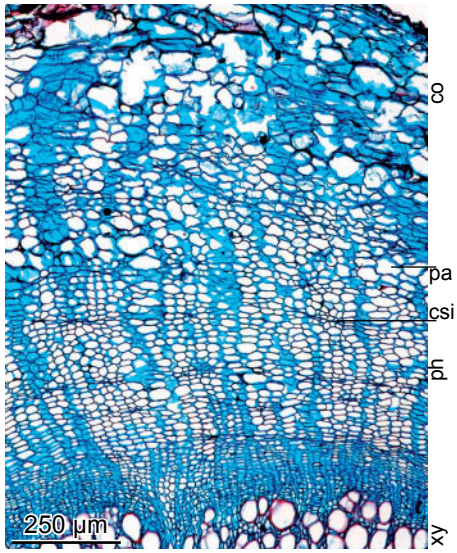
### Characteristics of the phloem and the cortex

Common to all species in both genera is the thick bark with small cells in the phloem and large cells in the cortex (dilatation; **Figs. 14**, **15** and **17**). Small groups of sieve tubes are embedded in more-or-less distinct and radially arranged parenchyma cells (**Fig. 14**). The former are often compressed and form tangential rows with dark zones (**Figs. 15** and **16**). The only species with small groups of sclereids in the cortex is *Geranium sanguineum*. 5 out of 20 species in both genera contain crystal druses in parenchymatic cells. The presence of bacteria-like crystals in the xylem and phloem (rhaphides with blunt points) of *Geranium divaricatum* (**Fig. 7**) are very special. Dilatations are mainly found as enlarged parenchyma cells in the cortex (**Figs. 14**, **15** and **17**). Ray dilations are indistinct (**Fig. 14**).

### Discussion in relation to previous studies

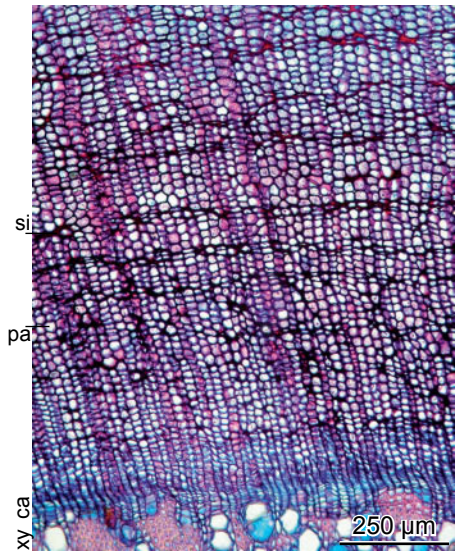
Van der Walt et al. (1987) characterized the xylem of 12 *Pelargonium* species growing in South Africa and discuss vessel characteristics in relation to annual rainfall. Carlquist (1985) described two woody species from South America. All descriptions in the present study are new.

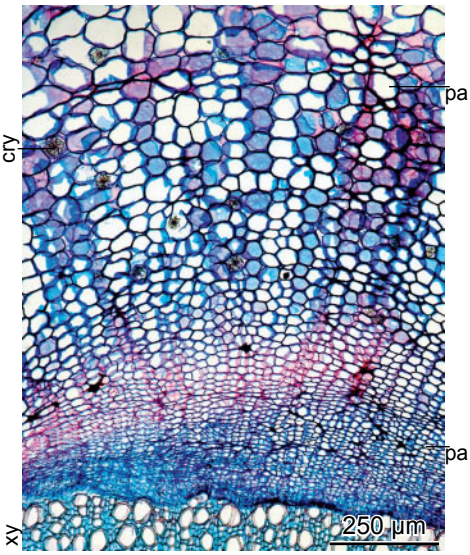



**Left Fig. 14.** The phloem consists of small, radially-oriented parenchyma cells and groups of very small sieve tubes. The parenchymatic cortex cells are dilated and therefore much larger. Root collar of an annual herb, vineyard, hill zone, Alps, France. *Geranium pusillum*, transverse section.

**Right Fig. 15.** Large phloem consisting of radially-oriented, unlignified parenchyma cells and small, often collapsed sieve tubes. Root collar of a 20 cm-high annual plant, ruderal site, hill zone, Ticino, Switzerland. *Geranium rotundifolium*, transverse section.




**Left Fig. 16.** Large phloem consisting of radially-oriented, unlignified parenchyma cells and tangential layers of collapsed sieve tubes (dark rows). Rhizome of a hemicryptophytic herb, cultivated, hill zone, Bavaria, Germany. *Geranium sanguineum*, transverse section.

**Right Fig. 17.** Large phloem consisting of radially-oriented, unlignified parenchyma cells. A few crystal druses are in cortex cells. Rhizome of a hemicryptophytic herb, meadow, mountain zone, Uri, Switzerland. *Geranium sylvaticum*, transverse section.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **20** |
| 1 | growth rings distinct and recognizable | 9 |
| 2 | growth rings indistinct or absent | 1 |
| 2.1 | only one ring | 10 |
| 4 | semi-ring-porous | 5 |
| 5 | diffuse-porous | 4 |
| 9 | vessels predominantly solitary | 7 |
| 9.1 | vessels in radial multiples of 2-4 common | 9 |
| 10 | vessels in radial multiples of 4 or more common | 8 |
| 11 | vessels predominantly in clusters | 3 |
| 13 | vessels with simple perforation plates | 20 |
| 20 | intervessel pits scalariform | 1 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 1 |
| 39.1 | vessel cell-wall thickness >2 µm | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 18 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 4 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 1 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 19 |
| 56 | tylosis with thin walls common | 7 |
| 58 | dark-stained substances in vessels and/or fibers (gum, tannins) | 2 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 20 |
| 68 | fibers thin-walled | 1 |
| 69 | fibers thick-walled | 3 |
| 70 | fibers thin- to thick-walled | 16 |
| 75 | parenchyma absent or unrecognizable | 9 |
| 79 | parenchyma paratracheal | 9 |
| 79.1 | parenchyma pervasive | 3 |
| 89 | parenchyma marginal | 1 |
| 98 | rays commonly 4-10-seriate | 4 |
| 99 | rays commonly >10-seriate | 8 |
| 99.1 | vascular-bundle form remaining | 9 |
| 100.1 | rays confluent with ground tissue | 1 |
| 100.2 | rays not visible in polarized light | 2 |
| 105 | ray: all cells upright or square | 7 |
| 117 | rayless | 10 |
| 144 | druses present | 4 |
| R1 | groups of sieve tubes present | 15 |
| R2 | groups of sieve tubes in tangential rows | 10 |
| R3 | distinct ray dilatations | 3 |
| R4 | sclereids in phloem and cortex | 1 |
| R8 | with crystal druses | 5 |
| R10 | phloem not well structured | 4 |
| R11 | with rhaphides | 1 |

# Grossulariaceae



**Number of species, worldwide and in Europe**

The Grossulariaceae family occurs mainly in the Northern hemisphere. It includes one genus (*Ribes*) with 150 species. In Western Europe there is one genus with 9 species. Macaronesia has no endemic species.

**Analyzed material**

Analyzed are the xylem of 15 and the phloem from 7 *Ribes* species.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 15 | ca. 20 |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 3 | |
| Boreal | 10 | |
| Hill and mountain | 2 | |

**Analyzed species:**

*Ribes acicularis* (Sith) Spach
*Ribes alpinum* L.
*Ribes bracteosum* S. Watson
*Ribes dikuscha* Fisch ex Truc.
*Ribes glandulosum* Ait.
*Ribes hudsonianum* Richards
*Ribes lacustre* Poir.
*Ribes laxiflorum* Pursh
*Ribes nigrum* L.
*Ribes pauciflorum* Turcz. ex Pojarh.
*Ribes petraeaum* Wulfen
*Ribes procumbens* Pall.
*Ribes rubrum* L.
*Ribes triste* Pall.
*Ribes uva-crispa* L.

*Ribes nigrum*

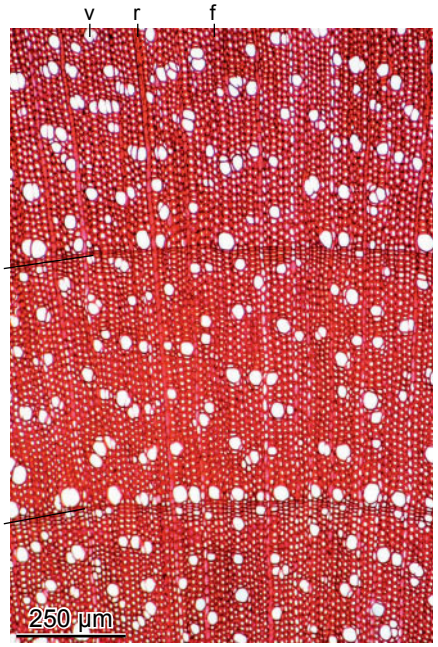
*Ribes uva-crispa* (photo: Zinnert)

*Ribes rubrum*

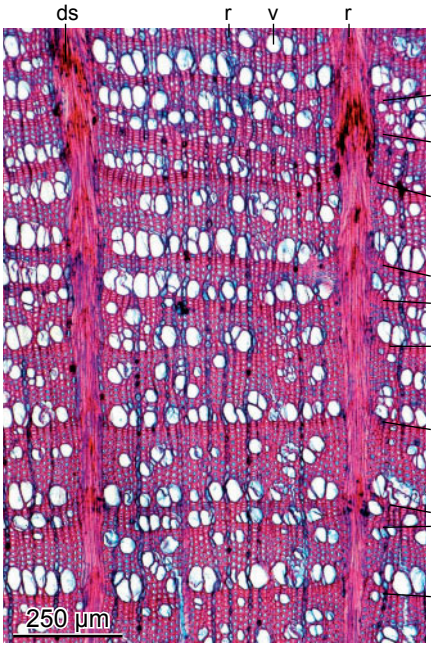
### Characteristics of the xylem

Annual rings occur in the present material in all analyzed species (**Figs. 1-5**). Ring distinctness is always indicated by flat radial latewood fibers (**Fig. 3**). The wood is diffuse-porous or semi-ring-porous. Site conditions seem to determine the size and the distribution of vessels (**Figs. 1** and **2**). Earlywood vessel diameter varies from 30-60 µm and vessel density from 300-500/mm$^2$.

Two types of vessel arrangement have been observed: Most species have distinct intra-annual tangential rows of vessels, e.g. *Ribes acicularis* and *R. triste* (**Fig. 4**) while few have a more or less uniform vessel distribution, e.g. *Ribes alpinum* from one site (**Fig. 1**) and *Ribes nigrum* (**Fig. 5**).




**Left Fig. 1.** Diffuse-porous xylem with 2 distinct annual ring boundaries. Vessels are solitary or in small groups. Vessel density is relatively low. Fibers are fairly thick-walled. Stem of a 1 m-high shrub, beech forest, mountain zone, Alps, Switzerland. *Ribes alpinum*, transverse section.




**Right Fig. 2.** Semi-ring-porous xylem with 12 distinct annual ring boundaries. Vessels are solitary or in small groups. Fibers are fairly thick-walled. Stem of a 1 m-high shrub, *Quercus pubescens* forest, mountain zone, Jura mountains, France. *Ribes alpinum*, transverse section.

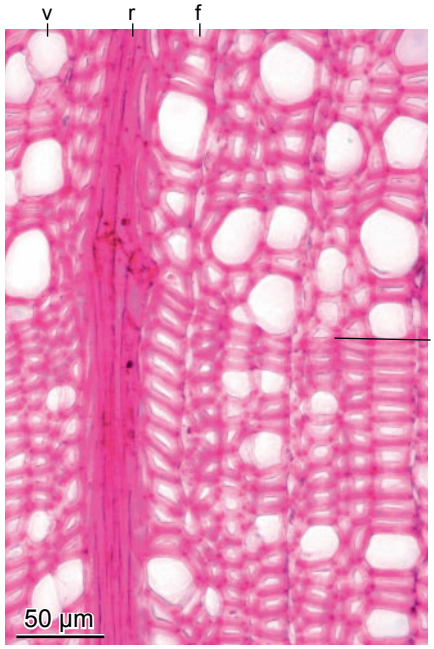



**Fig. 3.** The ring boundary is marked by a few rows of tangential flat fibers and thickened large rays. Stem of a 1 m-high shrub, Botanical Garden Jakutsk, Siberia, Russia. *Ribes triste*, transverse section.

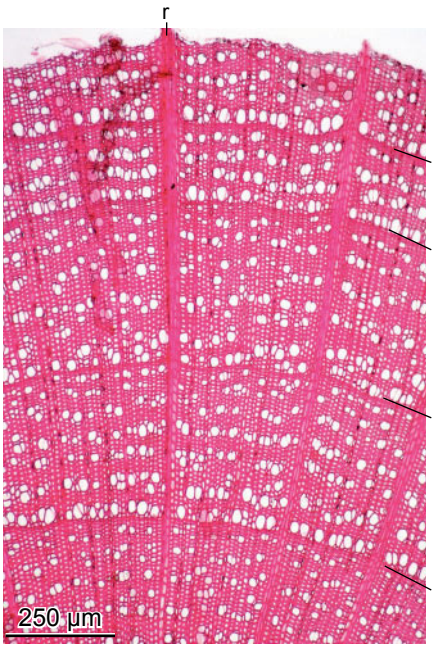



**Fig. 4.** Diffuse and semi-ring-porous xylem with 4 distinct annual ring boundaries. Vessels are arranged in tangential rows. Large rays dilate from the pith to the periphery. Stem of a 1 m-high shrub, pine forest, boreal zone, Siberia, Russia. *Ribes acicularis*, transverse section.

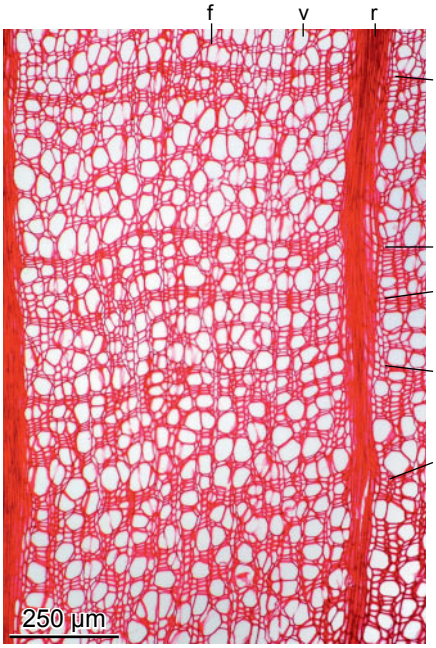
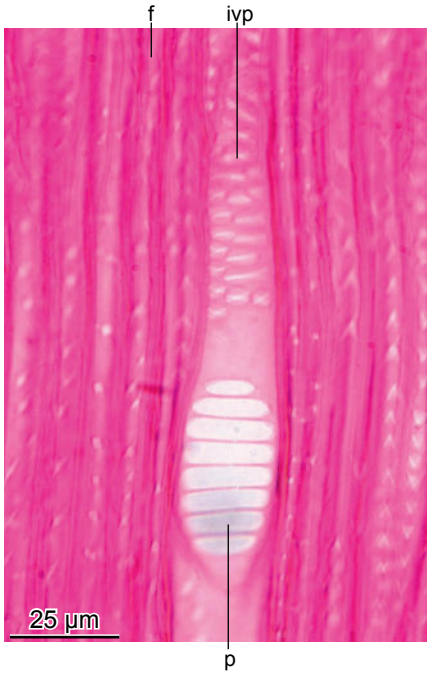



**Fig. 5.** Diffuse-porous xylem with 5 annual ring boundaries. Vessels are regularly distributed. Vessel density is relatively high (500/mm$^2$) Large rays are enlarged at ring boundaries. Stem of a 1.5 m-high shrub, garden, Bern, Switzerland. *Ribes nigrum*, transverse section.

Vessels contain exclusively scalariform perforations, the number of bars can vary from 6-20 bars (**Figs. 6** and **7**). Intervessel pits are small, round in opposite or alternate position or often slit-like in the vicinity of scalariform perforations (**Figs. 6** and **7**). Fiber-walls vary from thin- to thick-walled, but most species are thick-walled (**Figs. 1** and **2**). In the present material only *Ribes nigrum* has thin-walled fibers (**Fig. 5**). Fiber pits are distinctly bordered (**Fig. 6**). Septate fibers occur only in *Ribes alpinum* and *R. acicularis* (**Fig. 8**).

Axial parenchyma is difficult to recognize as it is very rare or apotracheal-diffuse. Rays have two distinct sizes: uniseriate with upright cells and multiseriate rays (**Fig. 2**) with some square and upright marginal cells. The width of large rays varies from 3 to 5 to >10 cells (**Figs. 9** and **10**). Large rays can be slightly thicker at the ring boundaries than in the intra-annual zones (**Figs. 3** and **5**).



**Left Fig. 6.** Scalariform perforation with 7 bars. Pith apertures are slit-like above the perforation. Fiber pits are large and distinctly bordered with slit-like apertures (3-4 µm). Stem of a 1 m-high shrub, spruce forest, boreal zone, Canada. *Ribes glandulosum*, radial section.

**Right Fig. 7.** Scalariform perforation with 15 bars. Pith apertures are slit-like and round above the perforation. Stem of a 1 m-high shrub, beech forest, mountain zone, Alps, Switzerland. *Ribes alpinum*, radial section.

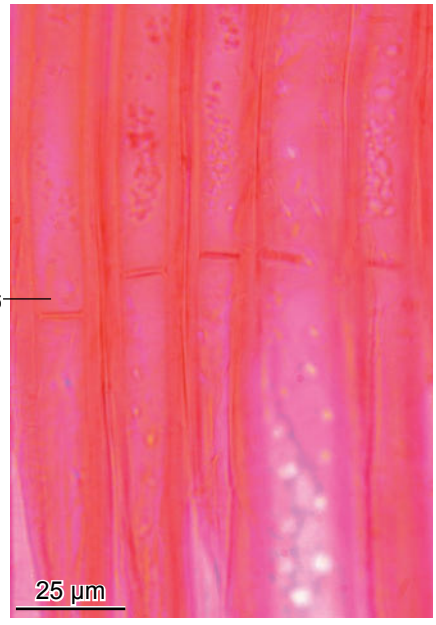



**Fig. 8.** Septate fibers. Stem of a 1 m-high shrub, beech forest, mountain zone, Alps, Switzerland. *Ribes alpinum*, radial section.

Fig. 9. Rays of two different sizes: Uniseriate and multiseriate (3-4 cells) rays. Stem of a 1 m-high shrub, Botanical Garden Jakustk, Siberia, Russia. *Ribes pauciflorum*, tangential section.

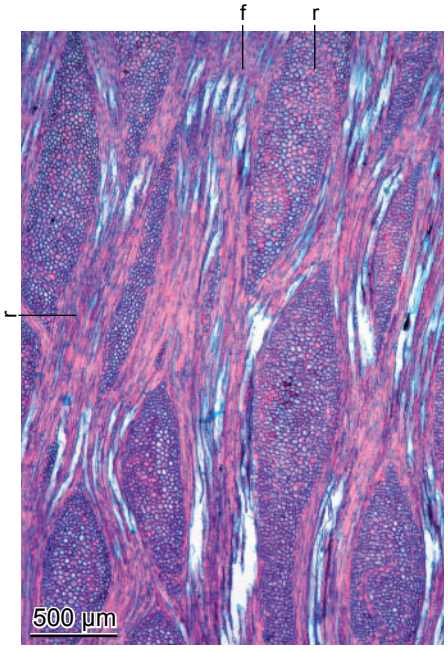
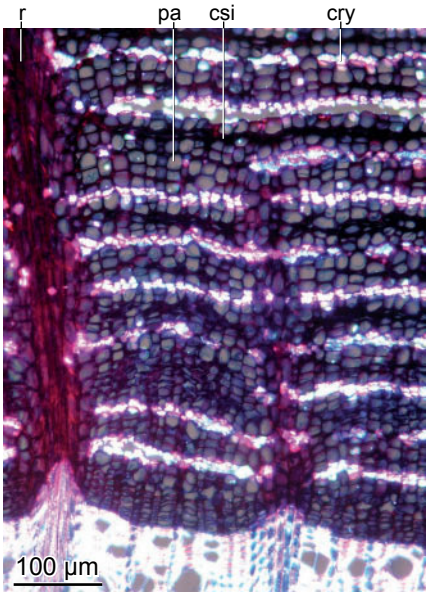
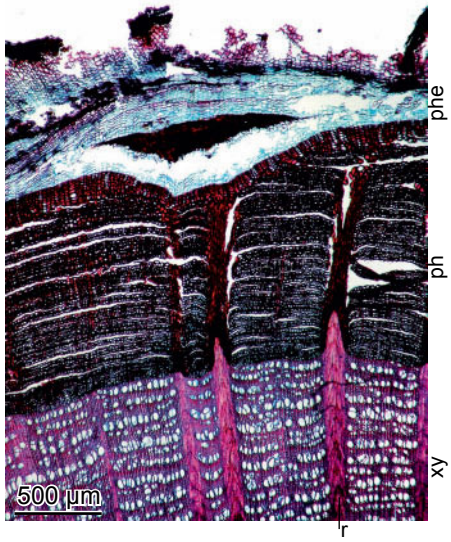



**Fig. 10.** Rays of two different sizes: Uniseriate and multiseriate (>10 cells) rays. Stem of a 50 cm-high shrub, *Tsuga mertensiana* forest, subalpine zone, Diamond lake, Oregon, USA. *Ribes laxiflorum*, tangential section.

### Family characteristics of the phloem and the cortex

The phloem is tangentially layered. Collapsed sieve tubes (dark-stained) and parenchyma alternate. Crystals (prismatic or druses) typically split the parenchyma zones (**Fig. 11**). Many species have a well-developped phellem (**Fig. 12**).




**Right Fig. 11.** Phloem with large, alternating parenchyma cells and collapsed sieve tubes (dark lines). Tangential crystal bands are in the middle of the parenchyma zones. Stem of a 1 m-high shrub, hedge, mountain zone, Engadin, Alps, Switzerland. *Ribes petraeum*, transverse section.

**Left Fig. 12.** Distinct phellem outside of a large tangentially layered phloem. Xylem rays penetrate the phloem (Keilwuchs). Stem of a 1 m-high shrub, *Quercus pubescens* forest, mountain zone, Jura mountains, France. *Ribes alpinum*, transverse section.

### Ecological trends in the xylem, phloem and the cortex

Trends along altitudinal gradients have not been detected. Drought stress influences vessel distribution, e.g. diffuse-porous to semi-ring-porous (**Figs. 1** and **2**). Mechanical stress may trigger the formation of thick fiber cell walls and large rays (**Fig. 10**).

### Discussion in relation to previous studies

The xylem of the genus *Ribes* is described in many wood anatomical atlases. Greguss (1954), Grosser (1977) and Schweingruber (1990) described the European species, whereas Benkova and Schweingruber (2004) described the Eurasian species. For further references see Gregory (1994). The results of the present study agree with all previous observations.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **15** |
| 1 | growth rings distinct and recognizable | 15 |
| 4 | semi-ring-porous | 13 |
| 5 | diffuse-porous | 1 |
| 6 | vessels in intra-annual tangential rows | 10 |
| 9 | vessels predominantly solitary | 11 |
| 11 | vessels predominantly in clusters | 15 |
| 14 | vessels with scalariform perforation plates | 15 |
| 20 | intervessel pits scalariform | 9 |
| 21 | intervessel pits opposite. | 2 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 15 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 2 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 15 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 2 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 13 |
| 65 | septate fibers present | 4 |
| 68 | fibers thin-walled | 1 |
| 69 | fibers thick-walled | 3 |
| 70 | fibers thin- to thick-walled | 11 |
| 75 | parenchyma absent or unrecognizable | 15 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 3 |
| 102 | ray height >1 mm | 15 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 11 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 3 |
| R2.1 | groups of sieve tubes in radial rows | 7 |
| R7 | with prismatic crystals | 2 |
| R8 | with crystal druses | 5 |

# Haloragaceae



**Number of species, worldwide and in Europe**

The cosmopolitan Haloragaceae family includes 8 genera with 145 species. In Europe occur 3 native submerse species.

**Analyzed species:**
*Myriophyllum alternifolium* DC.
*Myriophyllum spicatum* L.

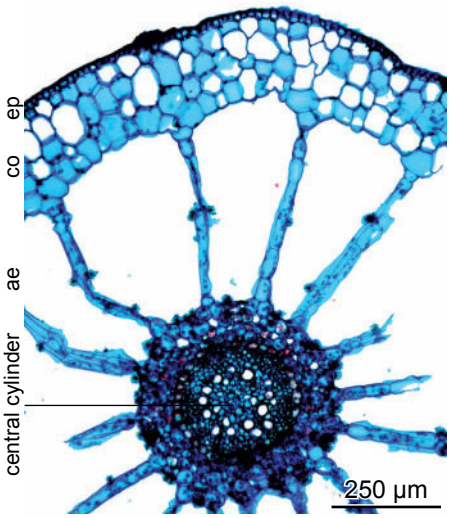
**Analyzed material**

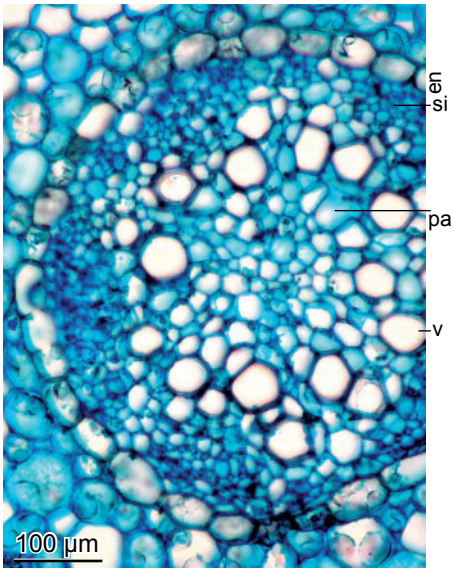
Two submerse species (helophytes) from Central Europe are analyzed here.

*Myriophyllum spicatum* (photo: Landolt)

### Characteristics of the stem

Secondary growth is absent. The stem consists of a central vascular cylinder and a peripheral cortex (**Fig. 1**). The cylinder consists of a xylem with a few solitary vessels (**Fig. 2**) with simple perforations and annular thickenings (**Figs. 3** and **4**). They are embedded in a parenchymatic tissue with many living cells (**Fig. 3**). Fibers and rays are absent. Isolated groups of phloem are arranged in a circle (**Fig. 2**). The cylinder and the cortex are demarcated by a one-cell-wide, thin-walled endodermis (**Fig. 2**). The three-part cortex is characterized by parenchyma cells: A compact belt of round cells with intercellulars, a middle aerenchymatic part and an external belt of large thin-walled angular cells. Crystal druses occur in the aerenchymatic part (**Fig. 5**). The epidermis has no stomata (**Fig. 1**). A phellem is absent (**Fig. 1**). The structure is adapted to submerse conditions.




**Left Fig. 1.** A central cylinder is surrounded by a large aerenchymatic cortex. Stem of a submerse plant, cultivated in a pond, hill zone, Botanical Garden Regensurg, Germany. *Myriophyllum spicatum*, transverse section.

**Right Fig. 2.** An endodermis surrounds the vascular cylinder. The xylem of the cylinder consists of vessels and parenchyma cells. Phloem strand forms groups around the endodermis. Stem of a submerse plant, cultivated in a pond, hill zone, Botanical Garden Regensurg, Germany. *Myriophyllum spicatum*, transverse section.

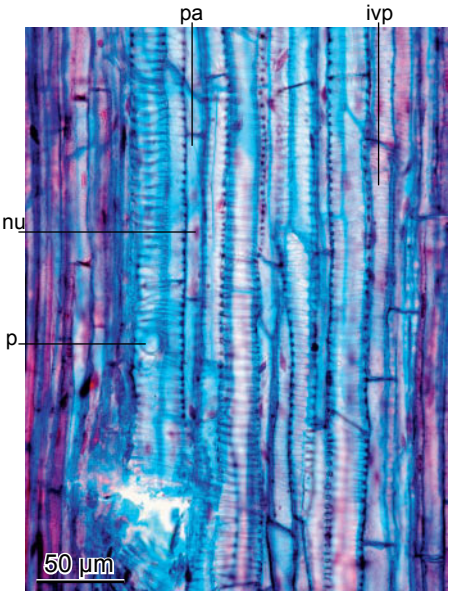



**Fig. 3.** Vessels with simple perforations and annular thickenings stay between living parenchyma cells (with nuclei). Stem of a submerse plant, cultivated in a pond, hill zone, Botanical Garden Bern, Switzerland. *Myriophyllum alternifolium*, radial section.

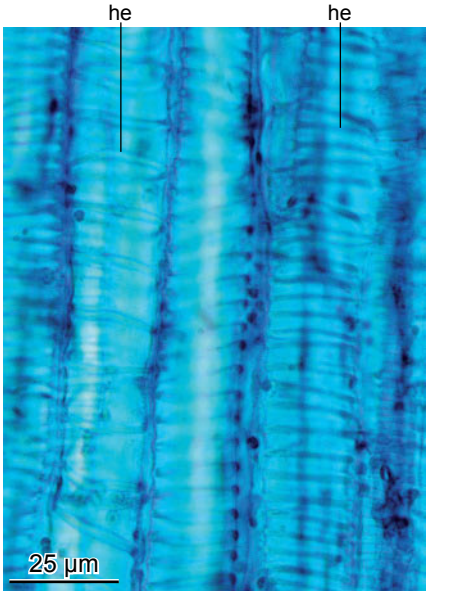



**Fig. 4.** Annular and spiral-like vessel-wall thickenings. Stem of a submerse plant, cultivated in a pond, hill zone, Botanical Garden Regensurg, Germany. *Myriophyllum spicatum*, radial section.

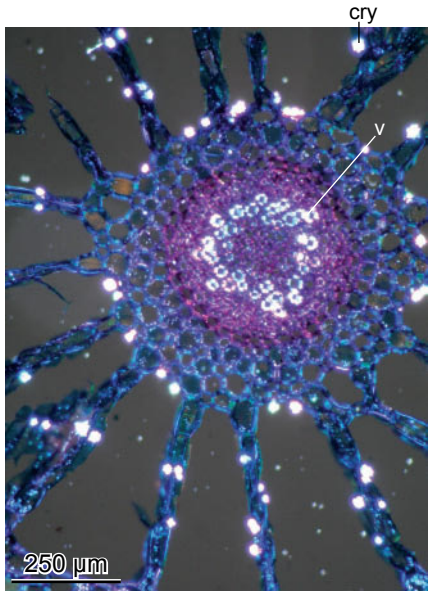



**Fig. 5.** Crystal druses in the aerenchymatic part of the cortex. Stem of a submerse plant, cultivated in a pond, hill zone, Botanical Garden Bern, Switzerland. *Myriophyllum alternifolium*, transverse section, polarized light.

**Discussion in relation to previous studies**

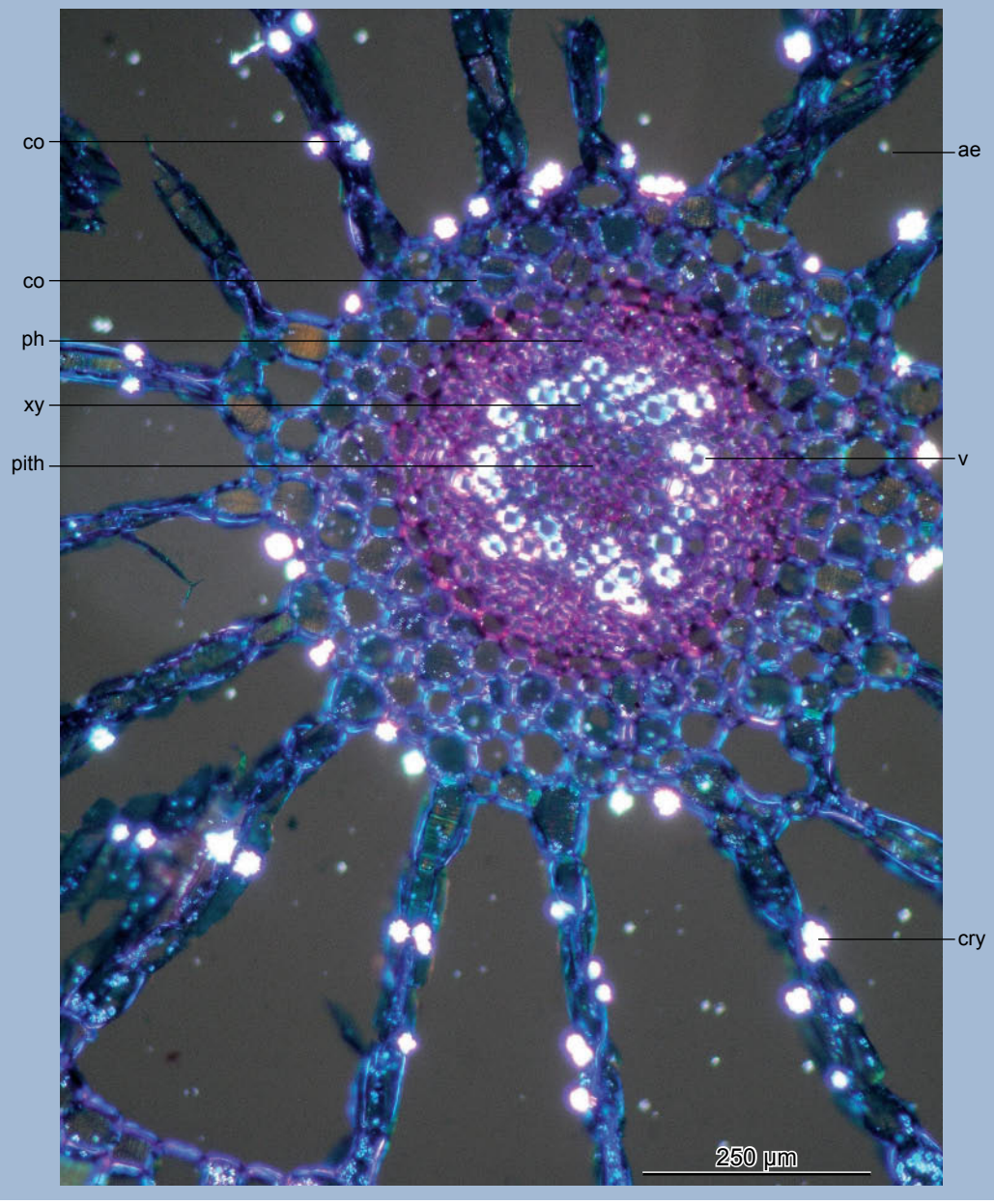
Metcalfe and Chalk (1957) give a limited description of *Myriophyllum* in the frame of other genera of the Haloragaceae. The present study characterizes the stem of two *Myriophyllum* species. The anatomical spectrum of the family is therefore not fully respected.

Wayne et al. (1964) studied the intra-annual development of the shoot apex.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **2** |
| 1 | growth rings distinct and recognizable | 1 |
| 2 | growth rings indistinct or absent | 2 |
| 2.1 | only one ring | 2 |
| 2.2 | without secondary growth | 2 |
| 9 | vessels predominantly solitary | 1 |
| 13 | vessels with simple perforation plates | 1 |
| 20 | intervessel pits scalariform | 1 |
| 22 | intervessel pits alternate | 1 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 1 |
| 60.1 | fibers absent | 2 |
| 98 | rays commonly 4-10-seriate | 1 |
| 117 | rayless | 1 |
| 127 | intercellular canals | 2 |
| R2.1 | groups of sieve tubes in radial rows | 1 |
| R14 | cortex with aerenchyma | 1 |

Detailed illustration of **Fig. 5**: *Myriophyllum alternifolium*, transverse section, polarized light.



# Hamamelidaceae and Altingiaceae



### Number of species, worldwide and in Europe

The Hamamelidaceae family includes 25 genera with 80 species. Species occur from tropical to temperate regions. No species of the family Hamamelidaceae are found in Europe. Here we include one species of Atingiaceace: *Liquidambar styraciflua* is often planted as an ornamental tree along road sides in Europe.

### Analyzed material

The xylem and phloem of 7 genera of Hamamelidaceae and one Altingiaceae have been analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 2 | 2 |
| Nanophanerophytes 0.5-4 m | 6 | ca. 10 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 8 | |

The material was collected in the Botanical Gardens of Basel and of Zürich, Switzerland.

**Analyzed species:**
*Corylopsis pauciflora* Sieb. *et* Zucc.
*Distylium racemosum* Sieb. *et* Zucc.
*Fothergilla gardeni* Murr.
*Fortunearia sinensis* Rehd. *et* Wils.
*Hamamelis virginiana* L.
*Liquidambar styraciflua* L. (Altingiaceae)
*Parrotia persica* C.A. Mey
*Sycopsis sinensis* Oliv.

*Parrotia persica*

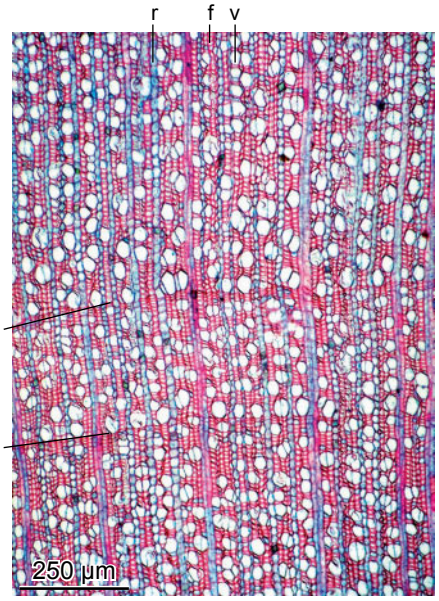
*Hamamelis virginiana* (photo: Zinnert)

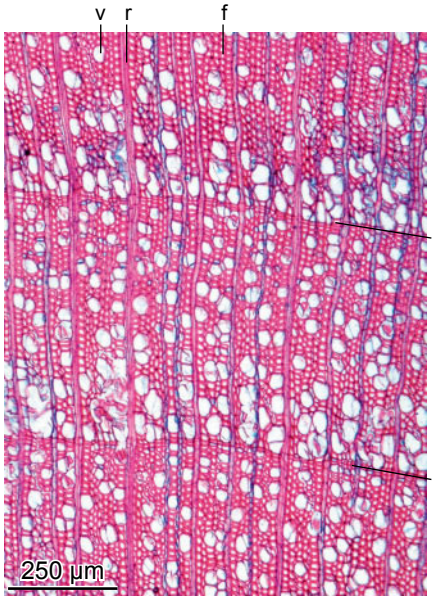
*Liquidambar styraciflua*

*Corylopsis pauciflora* (photo: Zinnert)

**Characteristics of the xylem**

The anatomical structure of the analyzed species is quite uniform. Annual rings occur in all species (**Fig. 1**), but they are indistinct in *Sycopsis sinensis*. Ring boundaries of most species are defined by a small band of radial, flat fiber cells (**Fig. 1**) or by a slight semi-ring porosity (**Fig. 2**). All species are diffuse-porous (**Fig. 1**) or indistinctly semi-ring-porous (**Fig. 2**). All species have solitary vessels with a slightly angular outline (**Figs. 1**, **2**, **5** and **7**), a diameter of 30-50 µm and scalariform perforations with >10 bars (**Fig. 3**). Vessel density varies from 300-500/mm$^2$. Intervessel pits are predominantly small and round. Vessel-ray pits are mostly horizontal (gash-like) or round (**Figs. 3** and **4**). The radial walls of fibers are perforated by round pits with a diameter of 2-5 µm (**Fig. 4**). Fibers are mostly thin- or thin- to thick-walled (**Figs. 5** and **7**). All species produce tension wood (**Fig. 6**). The axial parenchyma is mostly apotracheal (**Figs. 5** and **7**) or arranged in tangential uni- and biseriate bands (*Parrotia persica*, *Sycopsis sinensis* and *Distylium racemosum*; **Fig. 7**). It is rare or difficult to detect in *Fortunearia sinensis*. Most species have rays 1-3 cells in width (**Figs. 8** and **9**). The rays of *Hamamelis virginiana* are exclusively uniserate (**Fig. 8**). Heterocellular rays with 1 row of upright cells are characteristic for all species (**Fig. 9** and **10**) except for *Hamamelis virginiana* where there are 2-4 square (**Fig. 10**) or upright cells. All species contain prismatic crystals in the rays and fibers.




**Left Fig. 1.** Diffuse-porous wood with distinct rings. Ring boundaries are defined by a few rows of radial, flat fiber cells. Stem of a 1.5 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Basel, Switzerland. *Corylopsis pauciflora*, transverse section.

**Right Fig. 2.** Diffuse-porous to slightly semi-ring-porous wood with distinct rings. The ring boundary is usually defined by the difference of vessel sizes between the latewood and the earlywood. Stem of a 4 m-high tree, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Liquidambar styraciflua*, transverse section.

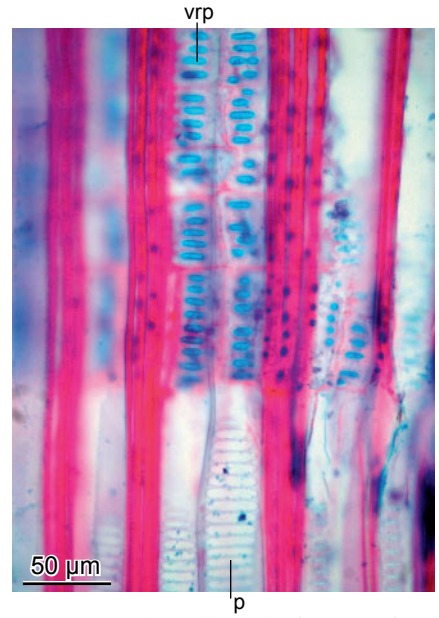



**Fig. 3.** Vessels with scalariform perforations and horizontal vessel-ray pits. Stem of a 1.5 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Fothergilla gardeni*, radial section.

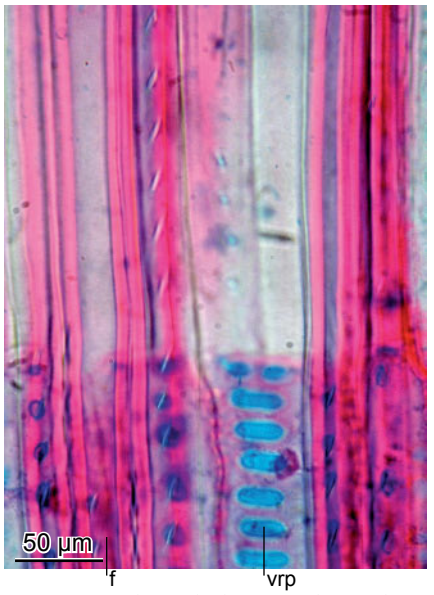



**Fig. 4.** Vessels with horizontal vessel-ray pits and fibers with large, round pits with slit-like apertures. Stem of a 1.5 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Fothergilla gardeni*, radial section.

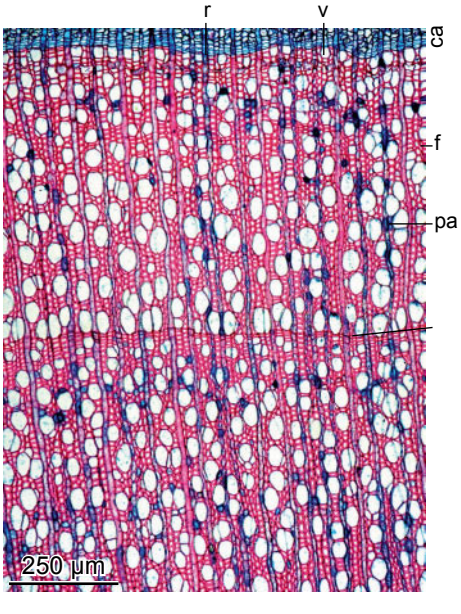
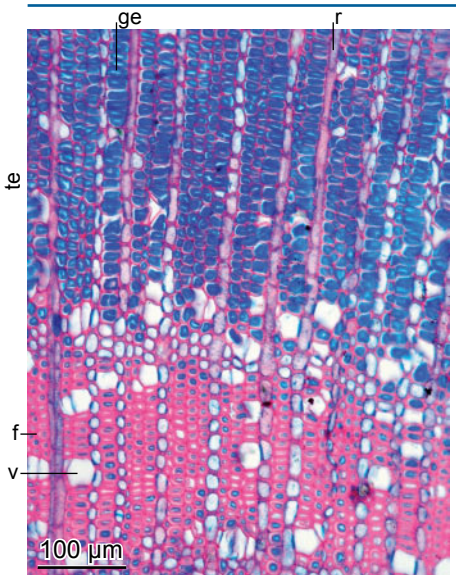
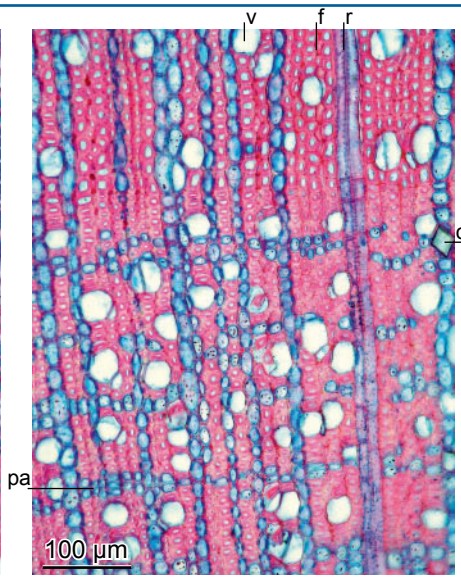



**Fig. 5.** Diffuse-porous to slightly semi-ring-porous wood with thin- to thick-walled fibers and apotracheal parenchyma. Stem of a 2 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Hamamelis virginiana*, transverse section.




**Left Fig. 6.** Tension wood in earlywood fibers. Stem of a 1.5 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Sycopsis sinensis*, transverse section.

**Right Fig. 7.** Diffuse-porous wood with an indistinct ring boundary and tangential rows of parenchyma cells. Stem of a 1.5 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Sycopsis sinensis*, transverse section.

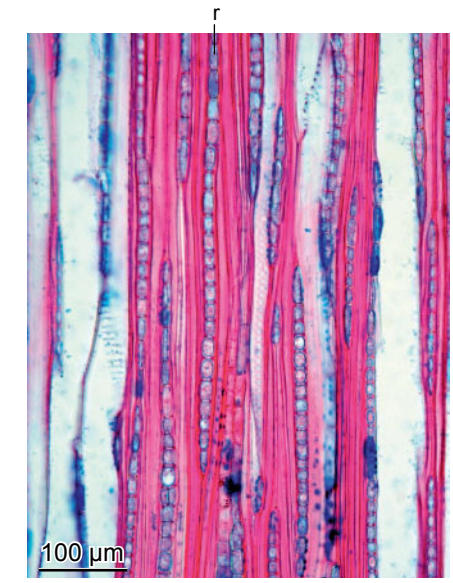



**Fig. 8.** Uniseriate rays with at least one upright marginal cell. Stem of a 2 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Hamamelis virginiana*, tangential section.

**Fig. 9.** Heterocellular, biseriate rays with at least one upright marginal cell. Stem of a 4 m-high tree, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Liquidambar styraciflua*, tangential section.

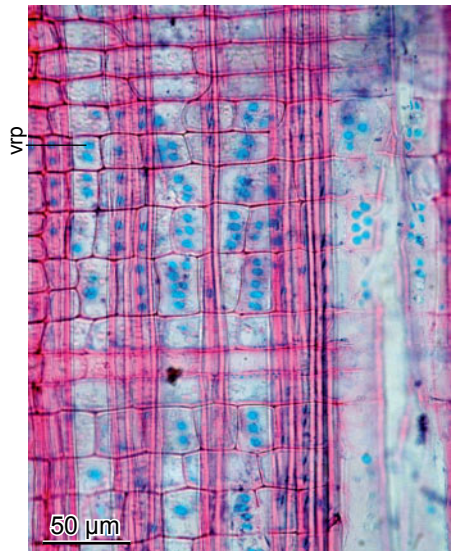



**Fig. 10.** Vessels with round vessel-ray pits in a ray with square marginal cells. Stem of a 4 m-tall tree, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Liquidambar styraciflua*, radial section.

### Characteristic features of taxa

The occurrence and distribution of an axial parenchyma seems to be species-specific. Parenchyma rarely occurs in *Fortunearia sinensis*. Small tangential bands are characteristic of *Distylium racemosum*, *Parrotia persica* and *Sycopsis sinensis* (**Figs. 7** and **13**). Of all analyzed species, ducts in the pith occur only in *Liquidambar styraciflua* (**Fig. 11**). Ducts are absent in all other species (**Fig. 12**).

### Ecological trends and relations to life forms

All the species analyzed are shrubs growing in seasonal, temperate climatic regions. Ecological trends are absent.

### Characteristics of the phloem and the cortex

All species are characterized by the presence of a sclerenchyma belt in the cortex (**Fig. 13**). Single sclerenchyma groups in different quantities occur in the phloem of all species (**Figs. 14** and **15**). Tangential sclerechyma belts can be found in the phloem of *Liquidambar styraciflua* (**Fig. 16**) and *Sycopsis sinensis*. Prismatic crystals of different sizes occur in all species. The occurrence of crystal druses in the multiple-layered phellem is specific to *Liquidambar styraciflua* (**Figs. 16** and **17**).

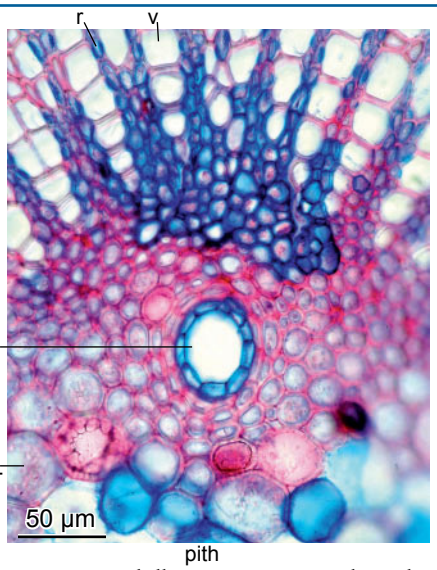



**Fig. 11.** Medullary secretory canal in the pith located at the initial part of a vascular bundle. Long shoot of a 4 m-high tree, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Liquidambar styraciflua*, transverse section.

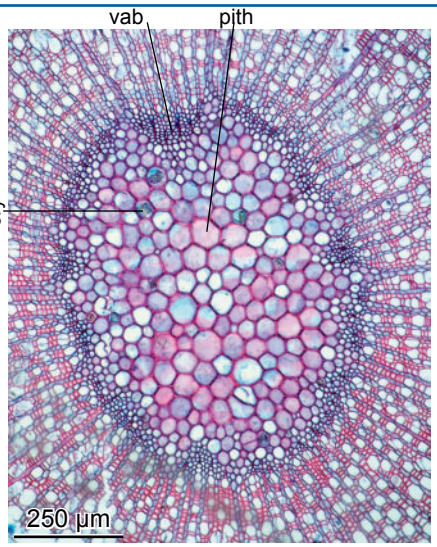



**Fig. 12.** Pith of a diffuse-porous wood. Medullary canals are absent. Long shoot of a 2 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Basel, Switzerland. *Corylopsis pauciflora*, transverse section.

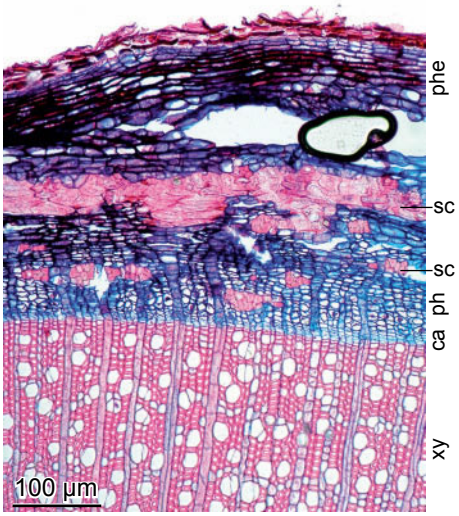
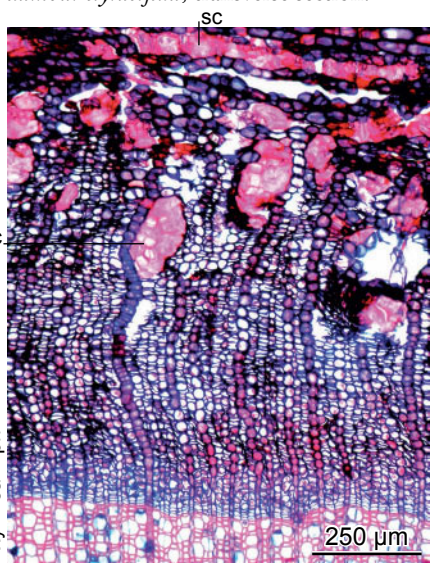
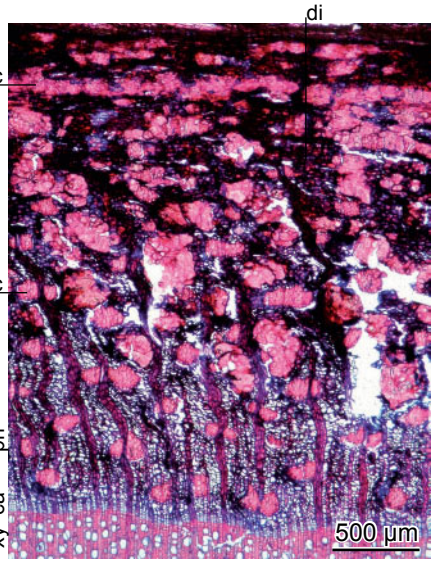


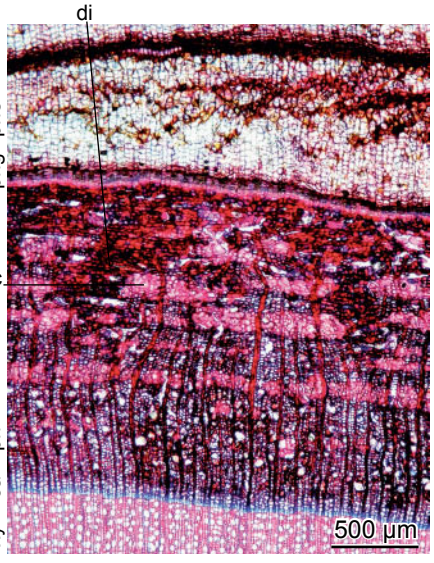

**Fig. 13.** Bark with distinct ray dilatations, a tangential band of sclerenchyma in the cortex and groups of sclerenchyma in the phloem. Long shoot of a 2 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Distylium racemosum*, transverse section.

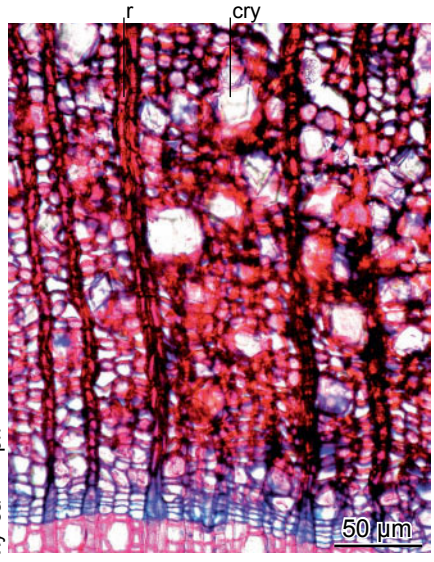



**Left Fig. 14.** Bark with a tangential band of sclerenchyma in the cortex and groups of sclerenchyma in the phloem. Stem of a 1.5 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Fothergilla gardeni*, transverse section.

**Right Fig. 15.** Bark with ray dilatations, a tangential band of sclerenchyma in the cortex and many groups of sclerenchyma in the phloem. Stem of a 3 m-high shrub, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Fortunearia sinensis*, transverse section.




**Left Fig. 16.** Bark with distinct ray dilatations, tangential bands of sclerenchyma in the older phloem and groups of sclerenchyma in the younger phloem. A large phellem is present outside the cortex. Stem of a 4 m-high tree, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Liquidambar styraciflua*, transverse section.

**Right Fig. 17.** Phloem with prismatic crystals and crystal druses. Stem of a 4 m-high tree, cultivated, hill zone, temperate climate, Botanical Garden Zürich, Switzerland. *Liquidambar styraciflua*, transverse section.

**Discussion in relation to previous studies**

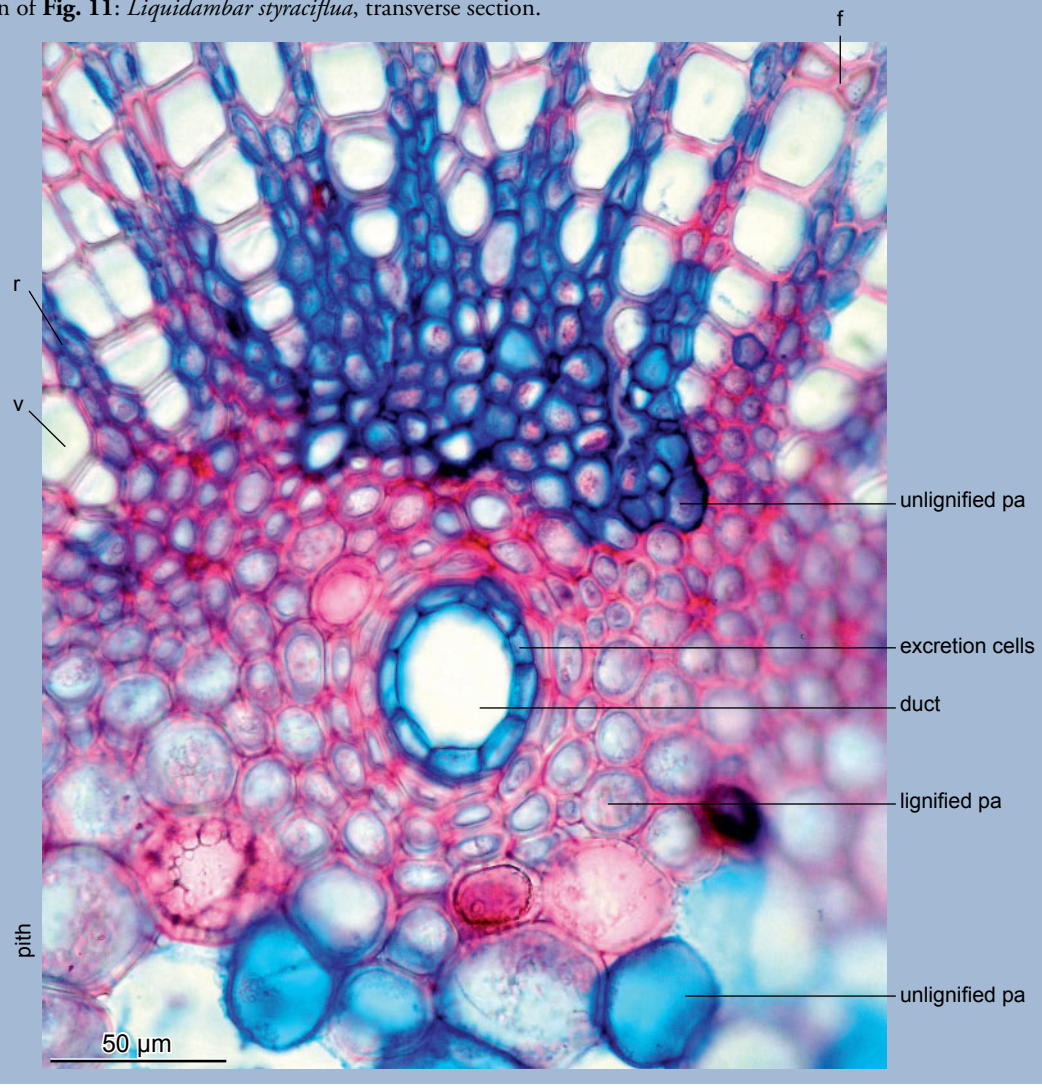
The comparative studies were made by Huang (1986) and Cheng et al. (1992) on the basis of 9 Chinese genera. *Liquidambar*, *Hamamelis*, *Distylium* and *Parrotia* have been described extensively. See Gregory (1994) for further references.

The results of the present study agree with all previous observations. In particular it confirms Huangs statement that *Liquidambar formosa* belongs to a different family (Altingiacaea).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **8** |
| 1 | growth rings distinct and recognizable | 8 |
| 5 | diffuse-porous | 8 |
| 9 | vessels predominantly solitary | 8 |
| 14 | vessels with scalariform perforation plates | 8 |
| 20 | intervessel pits scalariform | 8 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 8 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 8 |
| 50.2 | 200-1000 vessels per mm² in earlywood | 8 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 8 |
| 70 | fibers thin- to thick-walled | 8 |
| 70.2 | tension wood present | 8 |
| 75 | parenchyma absent or unrecognizable | 2 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 7 |
| 79 | parenchyma paratracheal | 1 |
| 96 | rays uniseriate | 2 |
| 97 | ray width predominantly 1-3 cells | 7 |
| 104 | ray: all cells procumbent (radial section) | 1 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 6 |
| 136 | prismatic crystals present | 7 |
| R1 | groups of sieve tubes present | 8 |
| R3 | distinct ray dilatations | 4 |
| R4 | sclereids in phloem and cortex | 5 |
| R6.1 | sclereids in tangential rows | 4 |
| R7 | with prismatic crystals | 8 |
| R8 | with crystal druses | 1 |
| P2 | with laticifers or intercellular canals | 1 |

Detailed illustration of **Fig. 11**: *Liquidambar styraciflua*, transverse section.



# Juglandaceae



**Number of species, worldwide and in Europe**

The Juglandaceae family includes 8 genera with 60 species. Species are distributed in the temperate and tropical climat of the northern hemisphere. Only *Juglans regia* is endemic to Europe and SW-Asia.

**Analyzed species:**
*Juglans regia* L.

**Analyzed material**

The xylem and phloem of 1 genera with 1 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 1 | many |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 1 | |

*Juglans regia* (photo: Lauerer)

*Juglans regia* (photo: Zinnert)

*Juglans regia* (photo: Zinnert)

### Characteristics of the xylem

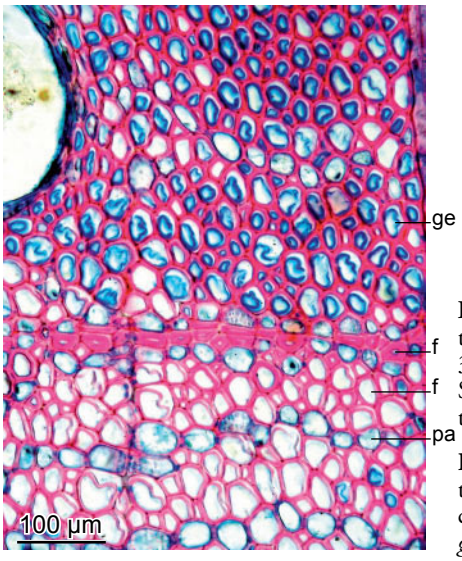
Annual rings are distinct. Ring boundaries, are represented by a marginal, uniseriate band of thick-walled fibers (**Figs. 1** and **2**). Vessels are arranged solitary or in short radial multiples (**Fig. 1**). The earlywood vessel diameter varies from 100-200 µm and vessel density varies from 10-30/mm$^2$. Vessels contain exclusively simple perforations. Inter-vessel pits are predominantly large and round and are arranged in alternating position. Vessels in the heartwood contain tylosis. Tension wood is frequent (**Fig. 2**). Radial walls of fibers are perforated by small pits (1-2 µm). Fibers within the annual ring are round to poly-angular and thin- to thick-walled, while those at the ring boundary are rectangular and thick-walled (**Fig. 2**). Parenchyma is apotracheal in aggregates (**Fig. 3**). Rays are 2-4-seriate (**Fig. 4**), and homocellular with procumbent cells. Crystals are absent.

### Characteristics of the phloem and the cortex

The phloem is characterized by tangential bands of fiber-like sclereids (**Fig. 5**). Groups of sclereids occur in ray dilatations (**Fig. 6**). Non-functional sieve-tubes collapse and form tangential dark bands (**Fig. 7**). Many crystal druses occur in the phloem and in the cortex.

### Discussion in relation to previous studies

The genera *Juglans*, *Carya*, *Pterocarya* and others have been described many times (Gregory 1994). The present description confirms all results of previous studies of *Juglans regia*.




**Left Fig. 1.** Diffuse-porous wood with distinct annual rings. Vessel density is below 30/mm$^2$. Stem, tree, cultivated, Zürich, Switzerland. *Juglans regia*, transverse section.

**Right Fig. 2.** Ring boundary formed by thick-walled, rectangular fibers. Stem, tree, cultivated, Zürich, Switzerland. *Juglans regia*, transverse section.

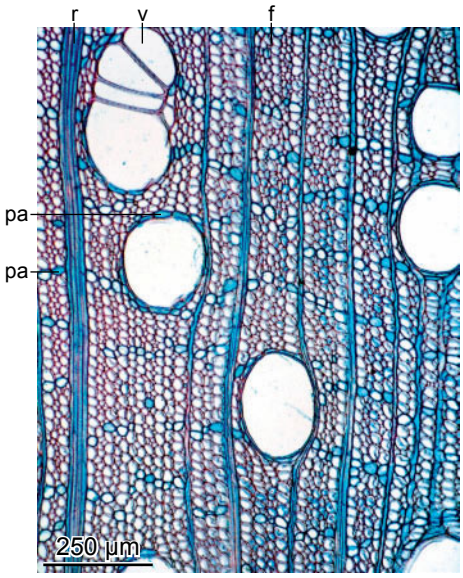



**Fig. 3.** Parenchyma is apotracheal in aggregates and paratracheal. Stem, tree, cultivated, Zürich, Switzerland. *Juglans regia*, tangential section.

**Fig. 4.** Homocellular, 2-4-seriate rays. Stem, tree, cultivated, Zürich, Switzerland. *Juglans regia*, tangential section.

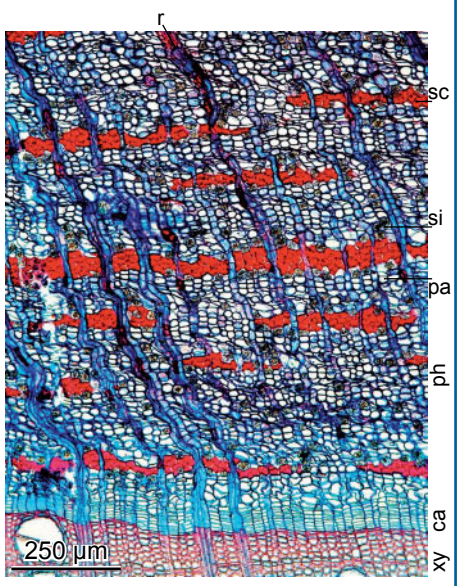
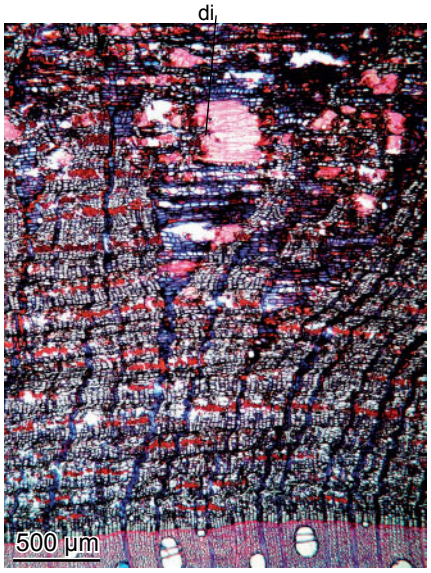
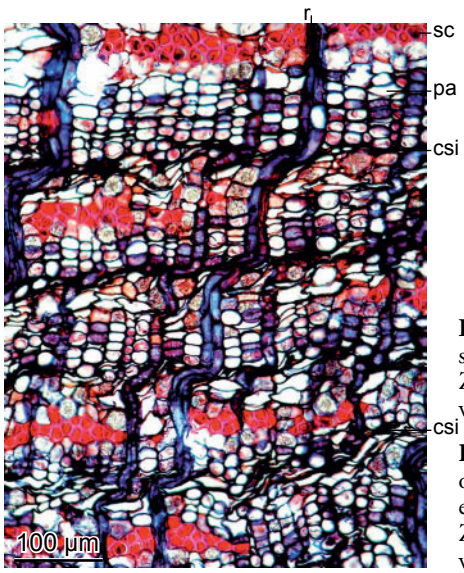



**Fig. 5.** Phloem with tangential bands of thick-walled fibers. Stem, tree, cultivated, Zürich, Switzerland. *Juglans regia*, transverse section.




**Left Fig. 6.** Ray dilatation with groups of sclerenchyma cells. Stem, tree, cultivated, Zürich, Switzerland. *Juglans regia*, transverse section.

**Right Fig. 7.** Tangetially arranged bands of collapsed sieve-tubes alternate large parenchymatic zones. Stem, tree, cultivated, Zürich, Switzerland. *Juglans regia*, transverse section.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **1** |
| 1 | growth rings distinct and recognizable | 1 |
| 5 | diffuse-porous | 1 |
| 9 | vessels predominantly solitary | 1 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 13 | vessels with simple perforation plates | 1 |
| 22 | intervessel pits alternate | 1 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 1 |
| 50 | <100 vessels per mm$^2$ in earlywood | 1 |
| 56 | tylosis with thin walls | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 1 |
| 70.2 | tension wood present | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 97 | ray width predominantly 1-3 cells | 1 |
| 98 | rays commonly 4-10-seriate | 1 |
| 104 | ray: all cells procumbent (radial section) | 1 |
| R1 | groups of sieve tubes present | 1 |
| R2 | groups of sieve tubes in tangential rows | 1 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R6.2 | sclereids in tangentially arranged groups, *Rhamnus* type | 1 |
| R8 | with crystal druses | 1 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 1 |

# Krameriaceae



### Number of species, worldwide and in Europe

The Krameriaceae family includes 1 genus with 15 species. Representatives of the family are absent Europe. The species occur in temperate to tropical regions of the New World particularly in warm and dry climate of Central America.

### Analyzed material

The xylem and phloem of 1 genera with 1 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 1 | 8 |
| **Plants analyzed from different vegetation zones:** | | |
| Arid | 1 | |

**Analyzed species:**
*Krameria grayi* Rose & Painter

*Krameria grayi*
(photos: Gary A. Monroe @ USDA-NRCS PLANTS Database)

### Characteristics of the xylem

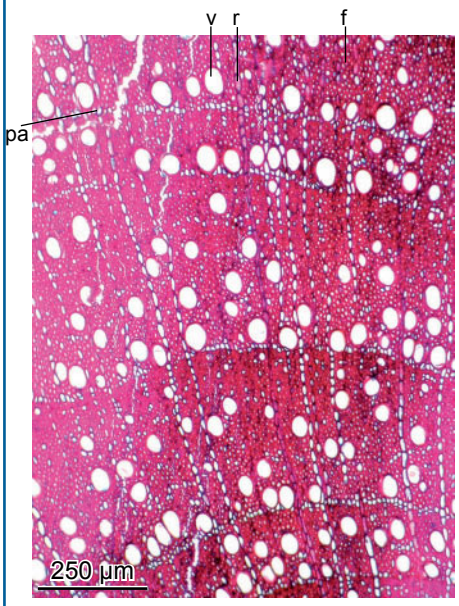
Annual rings are indistinct in the present material. Ring boundaries, if present, are represented by a marginal, uniseriate band of parenchyma cells (**Fig. 1**). Vessels are arranged solitary. The earlywood vessel diameter of the majority of species varies between 40-70 µm. Vessel density varies between 150-200/mm$^2$. Vessels contain exclusively simple perforations. Inter-vessel pits are predominantly small and round and arranged in alternating position. The radial walls of fibers in all species are perforated by fairly large round pits (2-3 µm; **Fig. 2**). Fibers are thick-walled. Parenchyma is apotracheal in aggregates and marginal. Rays are uniseriate (**Fig. 3**) and the cells are exclusively upright (**Fig. 4**). Crystals are absent.

### Characteristics of the phloem and the cortex

The phloem is characterized by isolated thick-walled sclereids, which are surrounded by a thin-walled tissue (**Fig. 5**). Parenchyma cells and sieve-tubes are difficult to distinguish. Many prismatic or irregularly formed crystals occur in the phloem.

### Discussion in relation to previous studies

Carlquist (2005) described 8 species of the genus *Krameria*. The present description is in agreement with that of Carlquist (2005).



**Left Fig. 1.** Diffuse-porous wood with indistinct annual rings, often containing uniseriate rows of marginal parenchyma. Stem, small shrub, shrub desert, California, USA. *Krameria grayi*, transverse section.

**Right Fig. 2.** Fibers with large, distinctly bordered pits. Stem, small shrub, shrub desert, California, USA. *Krameria grayi*, radial section.

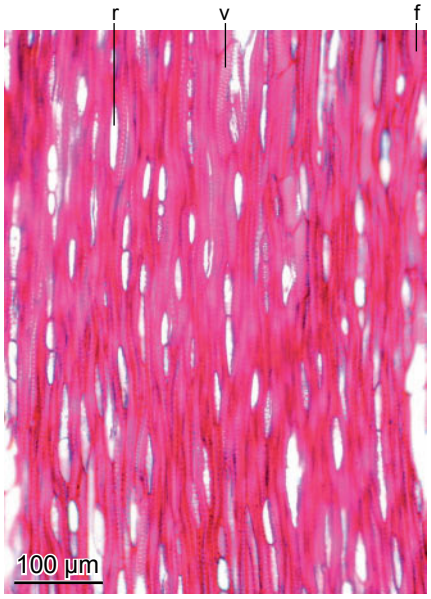



**Fig. 3.** Uniseriate rays. Stem, small shrub, shrub desert, California, USA. *Krameria grayi*, tangential section.

**Fig. 4.** Rays with thick-walled upright cells. Stem, small shrub, shrub desert, California, USA. *Krameria grayi*, radial section.

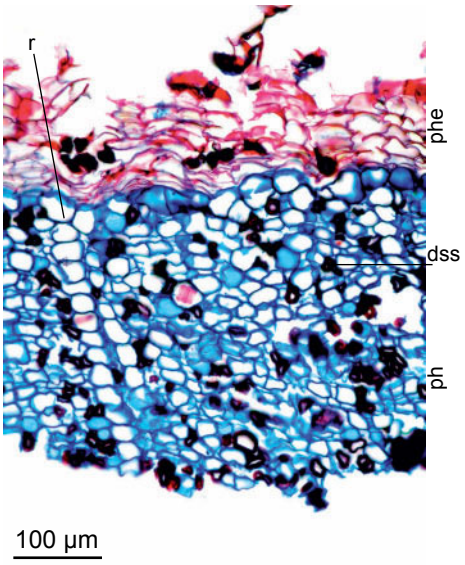



**Fig. 5.** Phloem with isolated thick-walled sclereids. Stem, small shrub, shrub desert, California, USA. *Krameria grayi*, transverse section.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **1** |
| 2 | growth rings absent | 1 |
| 5 | diffuse-porous | 1 |
| 9 | vessels predominantly solitary | 1 |
| 13 | vessels with simple perforation plates | 1 |
| 22 | intervessel pits alternate | 1 |
| 39.1 | vessel cell wall thick >2 µm | 1 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 1 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 1 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 1 |
| 69 | fibers thick-walled | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 89 | parenchyma marginal | 1 |
| 96 | rays uniseriate | 1 |
| 105 | ray: all cells upright or square | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R7 | with prismatic crystals | 1 |

# Lardizabalaceae



**Number of species, worldwide and in Europe**

The Lardizabalaceae family includes 8 genera with 45 species. Representatives occur mainly in SE-Asia, Taiwan, Japan and Chile (Mabberley 1997). Endemic members of the family are absent from Europe but a few species are often cultivated, e.g. *Akebia quinata*.

**Analyzed species:**

*Akebia quinata* Decn. (liana)
*Akebia trifoliata* Koidz. (liana)
*Decaisnea fargesii* French. (shrub)
*Holboellia coriaceae* Diels. (liana)
*Sinofranchetia chinensis* Hems. (liana)
*Stauntonia hexapetala* Decasn. (liana)

**Analyzed material**

The xylem and phloem of 5 genera with 6 species are analyzed here. They have been cultivated in the Botanical Gardens of Zürich and Halle.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 1 | 1 |
| Lianas | 5 | 7 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 6 | |

*Decaisnea fargesii*

*Decaisnea fargesii* (photo: Zinnert)

*Akebia quinata* (photo: Zinnert)

**Characteristics of the xylem**

The present material is divided into two groups: the shrub *Decaisnea fargesii* and the lianas.

*1. Decaisnea fargesii*

Annual rings are indicated by a slight semi-ring-porosity (**Fig. 1**). Vessel diameter varies from 40-60 µm. Perforations are scalariform with >10 bars and intervessel-pits are scalariform or rectangular and arranged in opposite position (**Fig. 2**). Vessel-ray pits have slightly horizontally elongated apertures. Fibers are thin- to thick-walled. Septate fibers with unlignified horizontal walls are frequent (**Fig. 2**). Rays are 3-5-seriate (**Fig. 3**) Axial parenchyma are rare and paratracheal. Rays are heterocellular and consist of a few rows of slightly procumbent cells and many marginal square cells. Crystals are absent.

*2. Lianas*

Annual rings are distinct (**Figs. 4** and **5**). The earlywood consists of both large and small vessels (vessel dimorphism). The aspect is ring-porous. The xylem has large, solitary vessels and small vessels in groups. Vessel diameter in the earlywood varies greatly: it is >100 µm for large vessels and 25-40 µm for small vessels. Vessel density is normally 100-200/mm$^2$.

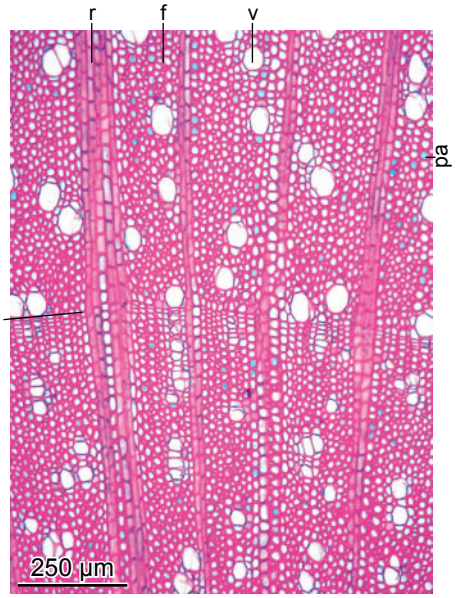



**Fig. 1.** Diffuse- to semi-ring-porous wood with solitary vessels in the earlywood and radial multiple vessels in the latewood. Stem of a 3 m-high shrub, cultivated, Botanical Garden Zürich, Switzerland. *Decaisnea fargesii*, transverse section.

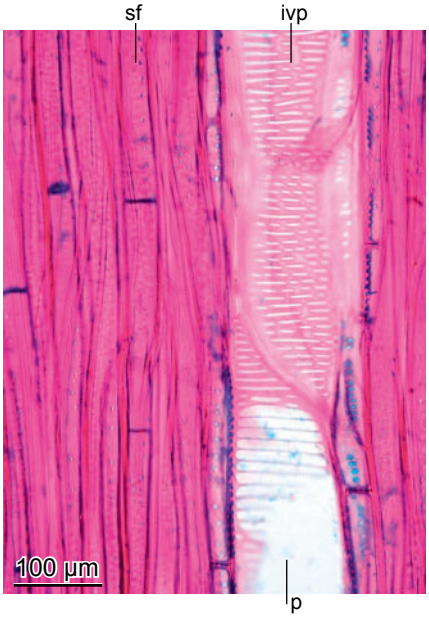
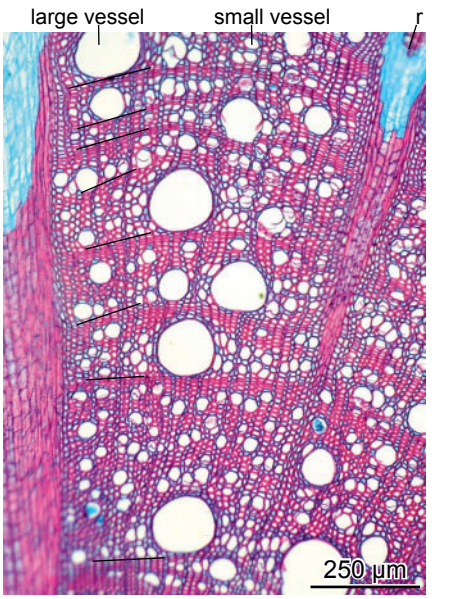
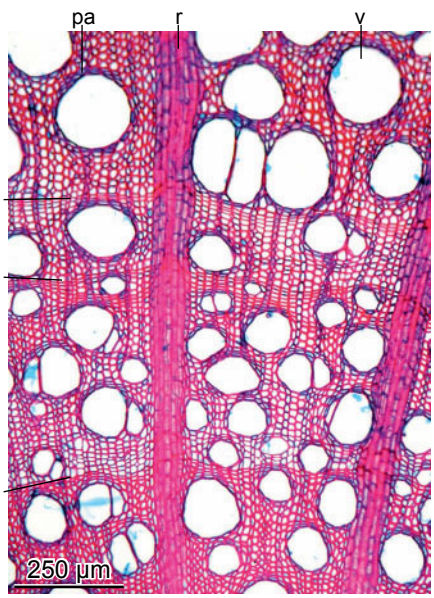



**Fig. 2.** Vessel with a perforation of 12 bars, scalariform intervessel pits, and pits arranged in opposite position. Stem of a 3 m-high shrub, cultivated, Botanical Garden Zürich, Switzerland. *Decaisnea fargesii*, radial section.

**Fig. 3.** Rays with 4-5 cells width. Stem of a 3 m-high shrub, cultivated, Botanical Garden Zürich, Switzerland. *Decaisnea fargesii*, tangential section.




**Left Fig. 4.** Ring-porous wood containing a few vessels 150 µm in diameter and many vessels with diameter between 40-50 µm. Large rays are unlignified at the periphery. Stem of a 4 m-long liana, cultivated, Botanical Garden Zürich, Switzerland. *Akebia trifoliata*, transverse section.




**Right Fig. 5.** Ring-porous wood with paratracheal parenchyma. Stem of a 4 m-long liana, cultivated, Botanical Garden Zürich, Switzerland. *Sinofranchetia chinensis*, transverse section.

Vessel perforations are simple (**Fig. 6**). Fine helical thickenings occur in fiber tracheids and partially in vessels (**Fig. 7**). Fiber pits have a diameter of approximately 3 µm (**Fig. 6**). Fibers are thin- to thick-walled and are in some cases storied. Septate fibers occur partially (**Fig. 8**). Axial parenchyma is vasicentric paratracheal and ocasionally apotracheal (**Fig. 5**). The primary form of vascular bundles is maintained by large rays (**Figs. 4**). Their cell walls are lignified in the center and unlignified at the periphery of the stem (**Fig. 4**). Large rays dominate the aspect of the tangential section (**Fig. 10**) and sometimes contain sheet cells (**Fig. 10**). Uniseriate rays with upright cells occur inside the xylem of the vascular bundles. They are often difficult to recognize in the tangential section because they are similar to axial parenchyma cells (**Fig. 9**). Prismatic crystals occur in the large rays.

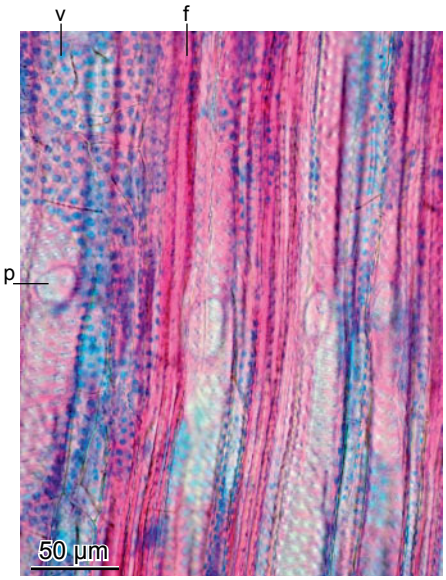
**Characteristics of the phloem and the cortex**

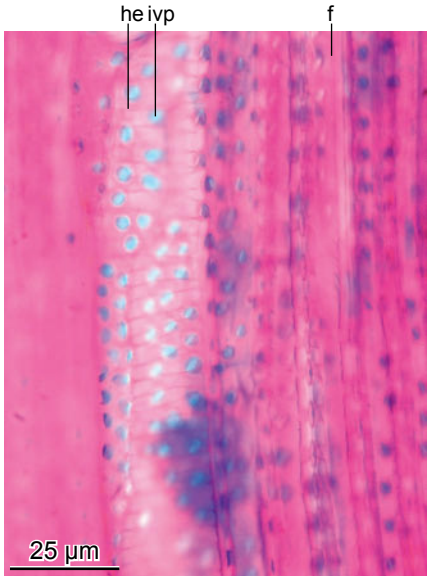
*1. Decaisnea fargesii*

Thin-walled parenchyma and sieve-tubes cannot be differentiated. Distinct ray dilatations occur. Older ray cells are seclerotised (**Fig. 11**). Crystals are absent.

*2. Lianas*

Thin-walled parenchyma and sieve-tubes are annually layered. Sieve-tubes collapse and parenchyma cells are round (**Fig. 12**). Vascular bundles are separated by ray dilatations. Groups of sclerotized cells occur in large rays (**Fig. 11**), inside of the cortex as groups (**Figs. 12** and **13**) or/and in a closed belt (**Fig. 12**). Many of the sclerotized cells contain prismatic crystals.




**Left Fig. 6.** Vessels with simple perforations and large intervessel pits. Stem of a 4 m-long liana, cultivated, Botanical Garden Halle, Germany. *Akebia quinata*, radial section.

**Right Fig. 7.** Vessel with very thin, helical thickenings. Stem of a 4 m-long liana, cultivated, Botanical Garden Zürich, Switzerland. *Stauntonia hexapetala*, radial section.

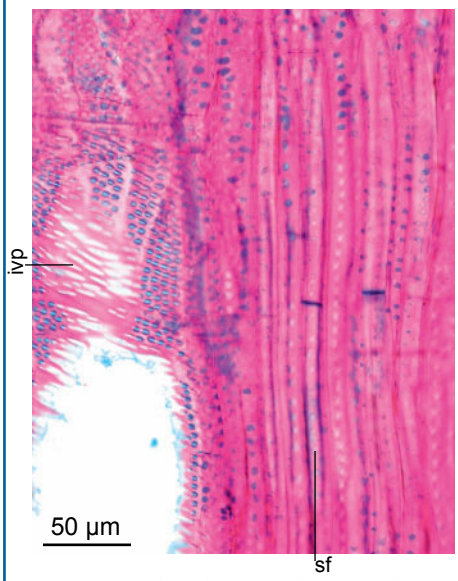



**Fig. 8.** Vessel with pits in horizontal position. Septate fibers with unlignified horizontal walls (blue). Stem of a 4 m-long liana, cultivated, Botanical Garden Zürich, Switzerland. *Sinofranchetia chinensis*, radial section.

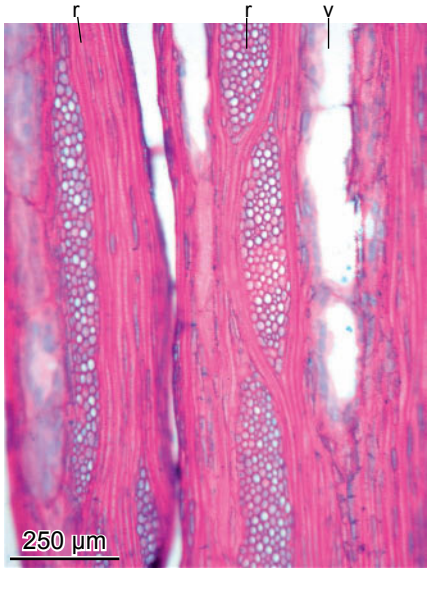



**Fig. 9.** Uniseriate and multiseriate rays. Stem of a 4 m-long liana, cultivated, Botanical Garden Zürich, Switzerland. *Sinofranchetia chinensis*, tangential section.

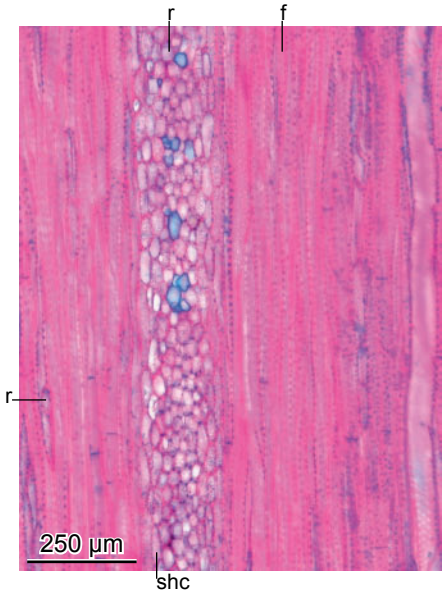



**Fig. 10.** Large ray with sheet cells. Stem of a 4 m-long liana, cultivated, Botanical Garden Zürich, Switzerland. *Stauntonia hexapetala*, tangential section.

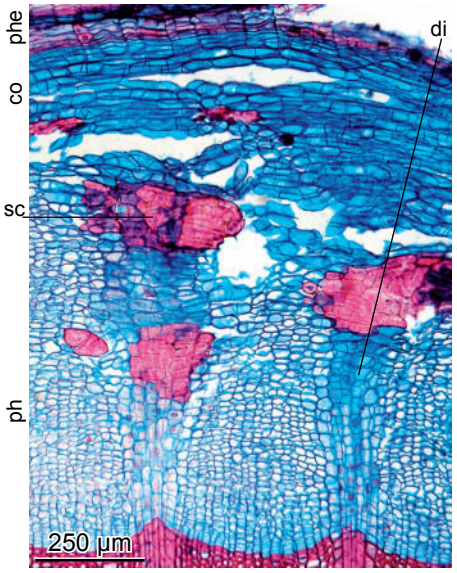



**Fig. 11.** Simply-structured phloem with ray dilatations. The external ray cells are thick-walled and lignified. Stem of a 3 m-high shrub, cultivated, Botanical Garden Zürich, Switzerland. *Decaisnea fargesii*, transverse section.

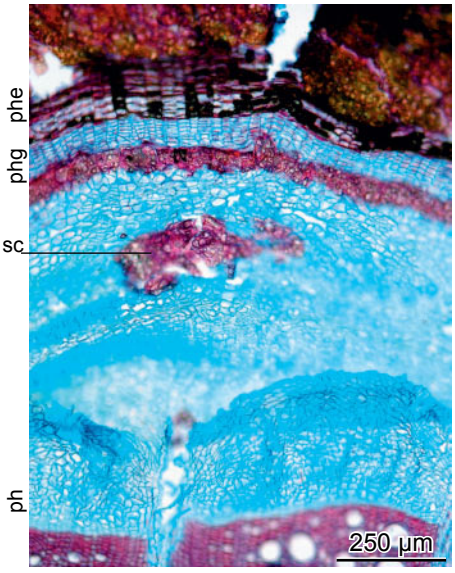



**Fig. 12.** Simply-structured phloem with a group of sclerenchyma cells. Below the phellogen is a belt of sclerenchyma. Stem of a 4 m-long liana, cultivated, Botanical Garden Zürich, Switzerland. *Akebia trifoliata*, transverse section.

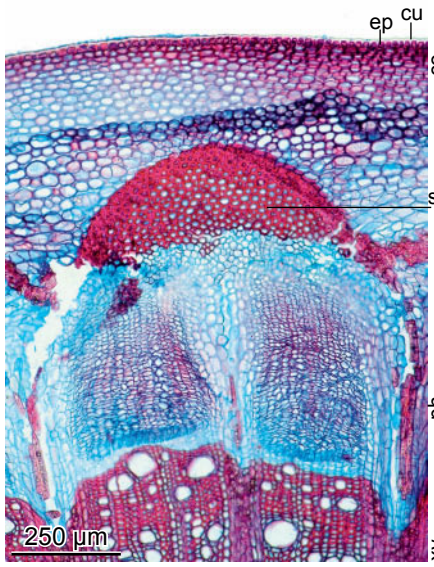



**Fig. 13.** Simply-structured phloem with ray dilatations and with a group of sclerenchyma in the cortex. Stem of a 4 m-long liana, cultivated, Botanical Garden Zürich, Switzerland. *Stauntonia hexapetala*, transverse section.



## Discussion in relation to previous studies

Carlquist (1984) characterized 7 species belonging to 7 genera of the Lardizabalaceae family in detail. The present observations agree with those of Carlquist (1984).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **6** |
| 1 | growth rings distinct and recognizable | 6 |
| 3 | ring-porous | 6 |
| 5 | diffuse-porous | 1 |
| 9 | vessels predominantly solitary | 6 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 5 |
| 14 | vessels with scalariform perforation plates | 1 |
| 20 | intervessel pits scalariform | 1 |
| 21 | intervessel pits opposite | 1 |
| 22 | intervessel pits alternate | 5 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 1 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 1 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 5 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 6 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 1 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 5 |
| 65 | septate fibers present | 1 |
| 68 | fibers thin-walled | 2 |
| 70 | fibers thin- to thick-walled | 4 |
| 75 | parenchyma absent or unrecognizable | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 5 |
| 79 | parenchyma paratracheal | 5 |
| 98 | rays commonly 4-10-seriate | 3 |
| 99 | rays commonly >10-seriate | 3 |
| 103 | rays of two distinct sizes (tangential section) | 5 |
| 102 | ray height >1 mm | 4 |
| 105 | ray: all cells upright or square | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 1 |
| 110 | rays with sheet cells tangential section | 1 |
| 136 | prismatic crystals present | 5 |
| R3 | distinct ray dilatations | 6 |
| R4 | sclereids in phloem and cortex | 6 |
| R6.1 | sclereids in tangential rows | 2 |
| R7 | with prismatic crystals | 5 |

# Lauraceae



**Number of species, worldwide and in Europe**

The Lauraceae family includes 50 genera with 2500 species. Species are widely distributed in tropical and subtropical climate regions. In Europe there is only one species (*Laurus nobilis*). 4 species are endemic to the Canary Islands (*Laurus azorica*, *Apollonias barbujana*, *Ocotea foetens*, *Persea indica*). Plantations of *Persea americana* exist in Southern Spain and on the Canary Islands.

**Analyzed species:**

*Apollonias barbujana* (Cav.) Bornm.
*Laurus azorica* (Seub.) Franco
*Laurus nobilis* L.
*Ocotea foetens* (Ait.) Benth. *et* Hook.
*Persea americana* Mill.
*Persea indica* (L.) Spreng

**Analyzed material**

The xylem and phloem of 6 Lauraceae species were analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 6 | ca. 600 |
| **Plants analyzed from different vegetation zones:** | | |
| Mediterranean | 1 | |
| Subtropical | 6 | |

**Right:** *Persea americana* (photo: Zinnert)

*Laurus nobilis*

*Ocotea foetens* (photo: Lauerer)

**Characteristics of the xylem**

Annual rings occur in the present material in *Apollonias barbujana*, *Laurus nobilis* and *L. azorica* (**Figs. 1-3**) but not in *Persea* (**Fig. 4**). Ring boundaries are defined by semi-ring porosity in *Apollonias barbujana* (**Figs. 1** and **10**) or radial flat latewood fibers in the other diffuse-porous species (**Figs. 2** and **3**). Vessels are solitary or arranged in mostly short (2-4 vessels) radial multiples (**Figs. 1-4**). Vessels are smaller than 100 µm in *Apollonias barbujana* but larger than 100 µm in all other species. Vessel perforations are scalariform in *Apollonias barbujana* (**Fig. 5**) and simple on all other species. Inter-vessel pits are opposite in A*pollonias barbujana* and alternate in all other species. Fine helical thickenings occur in *Apollonias* (**Fig. 5**). Ray-vessel pits are reticulate or gash-like (**Fig. 6**) except for *Apollonias* where they are round. Vessels of *Apollonias barbujana* contain dark-stained substances. Small, thin-walled, unlignified tylosis have been observed in *Laurus azorica*, *Ocotea foetens* and *Persea indica*. Tylosis of *Laurus azorica* contain distinct simple pits (**Fig. 7**). Radial walls of fibers are perforated by large pits in *Apollonias barbujana* (**Fig. 8**) and by small (<2 µm) pits with slit-like apertures in all other species. Septate fibers occur in *Apollonias barbujana*

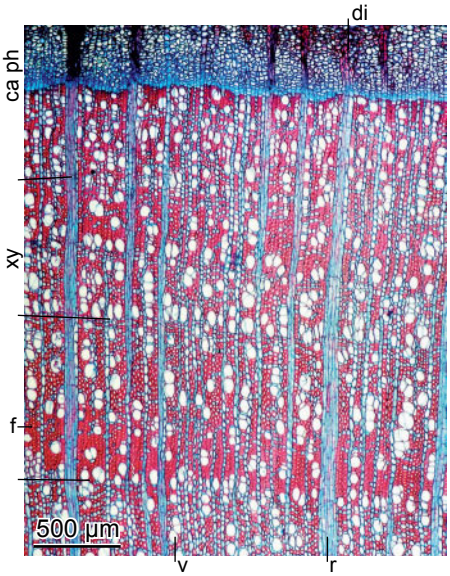



**Fig. 1.** Distinct rings in a diffuse-porous to slightly semi-ring-porous wood. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Apollonias barbujana*, transverse section.

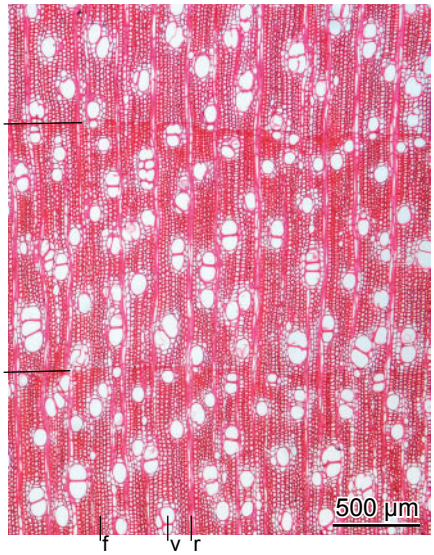



**Fig. 2.** Distinct rings in diffuse-porous to slightly semi-ring-porous wood. Vessels are primarily arrangend in short radial rows. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Laurus azorica*, transverse section.

**Fig. 3.** Distinct rings in a diffuse-porous wood. Ring boundaries are defined by thick-walled radial flat fiber cells. Xylem of a 3 m-high tree, *Quercus pubescens* forest, hill zone, Lago di Lugano, Switzerland. *Laurus nobilis*, transverse section.

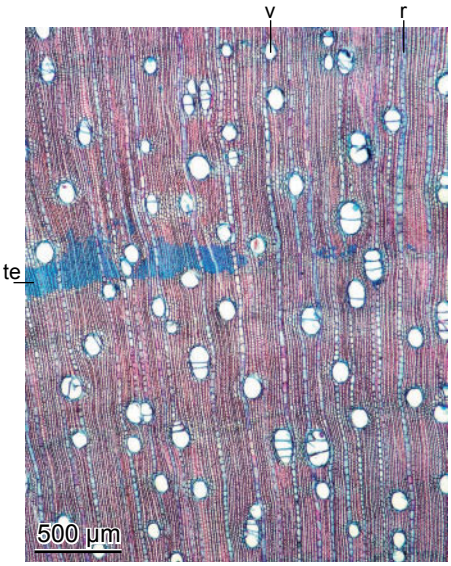



**Fig. 4.** Wood without annual rings and with tension wood. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Persea americana*, transverse section.

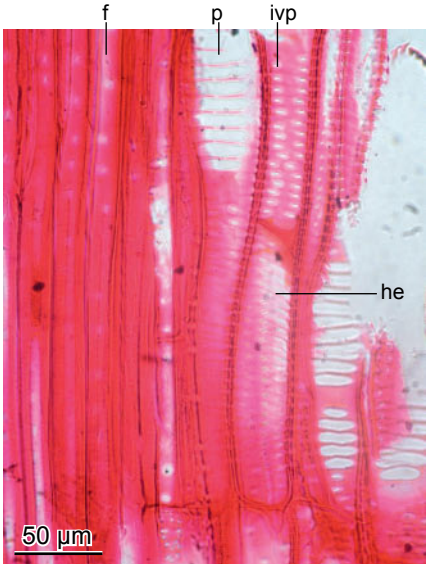



**Fig. 5.** Vessels with scalariform perforations and fine helical thickenings. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Apollonias barbujana*, radial section.

**Fig. 6.** Net-like and gash-like vessel-ray pits. Small prismatic crystals occur in ray cells. Xylem of a 5 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Laurus nobilis*, radial section.

and in both *Laurus* species (**Fig. 9**). Fibers are thin- or thin- to thick-walled. The axial parenchyma is diffuse in *Laurus* and *Ocotea*, diffuse in aggregates in *Apollonias barbujana* (**Fig. 10**) and vasicentric in *Persea* (**Fig. 11**). Rays are usually 2-3-seriate and slender (**Figs. 12** and **13**) except for *Persea americana* where the cells are round (**Fig. 14**). *Apollonias barbujana* has uniseriate and multiseriate (4-6 cells) rays (**Fig. 12**). Rays of all species consist of procumbent cells with 1-2 upright marginal cells except for *Apollonias barbujana* where 3-5 upright marginal cells are present. Oil cells associated with rays have been observed in *Laurus azorica* (**Fig. 15**) and in *Ocotea foetens*. Prismatic crystals occur in ray cells of *Laurus nobilis* (**Fig. 6**) and in axial parenchyma cells of both *Persea* species.

### Characteristic features of taxa

*Apollonias barbujana* differs from all other Lauraceae species in the occurrence of small vessels, large rays and the parenchyma that is diffuse in aggregates (**Fig. 10**). Diffuse parenchyma occur only in *Laurus* and *Ocotea* and vasicentric parenchyma is unique to *Persea* (**Fig. 11**).

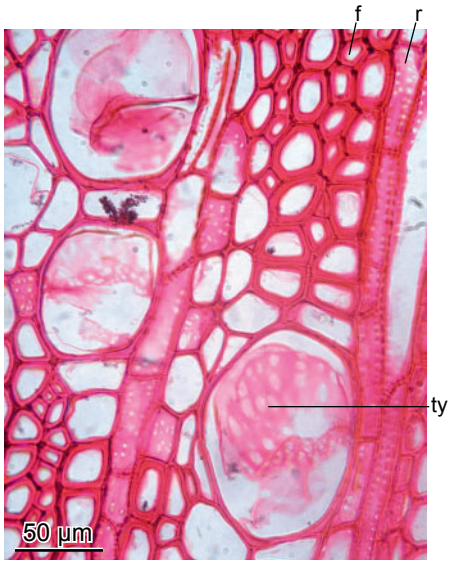



**Fig. 7.** Tylosis with simple pits. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Laurus azorica*, transverse section.

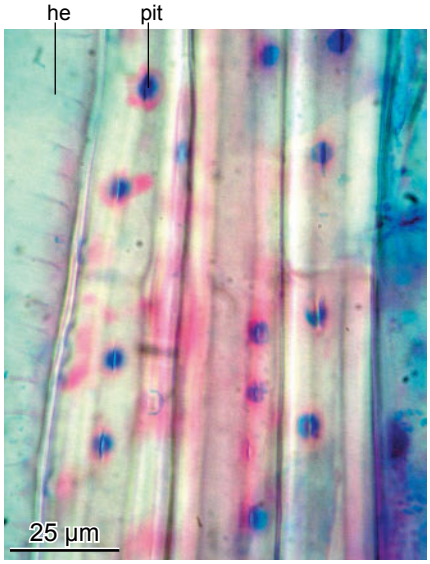



**Fig. 8.** Bordered pits in fibers with axially oriented slit-like apertures. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Apollonias barbujana*, radial section.

**Fig. 9.** Septate fibers. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Laurus azorica*, tangential section.

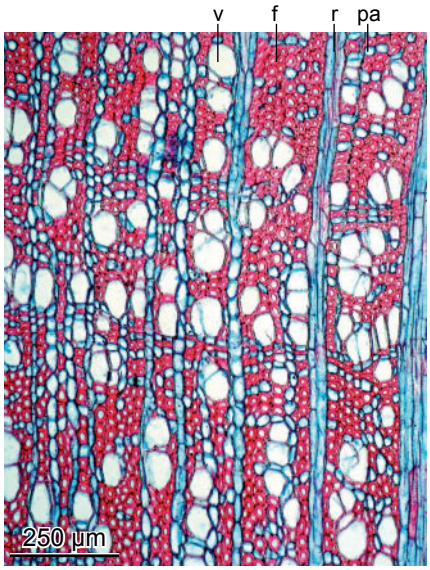



**Fig. 10.** Parenchyma diffuse in aggregates. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Apollonias barbujana*, transverse section.

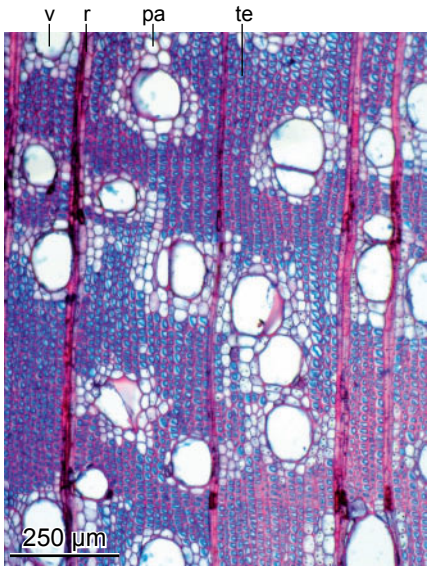



**Fig. 11.** Vasicentric parenchyma. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Persea indica*, transverse section.

**Fig. 12.** Uniseriate and multiseriate rays with axial elongated marginal cells. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Apollonias barbujana*, tangential section.

**Fig. 13.** Slender, 2-3-seriate rays. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Laurus azorica*, tangential section.

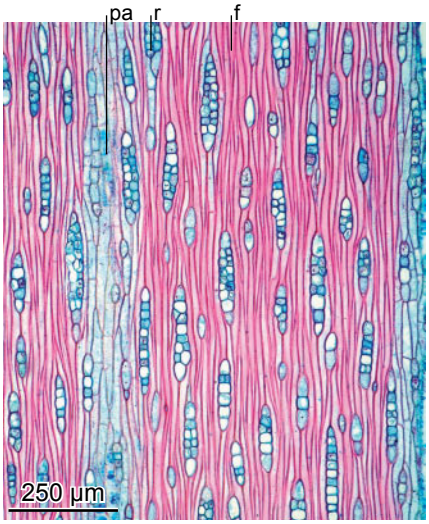



**Fig. 14.** Short, 1-2-seriate rays with round cells. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Apollonias barbujana*, tangential section.

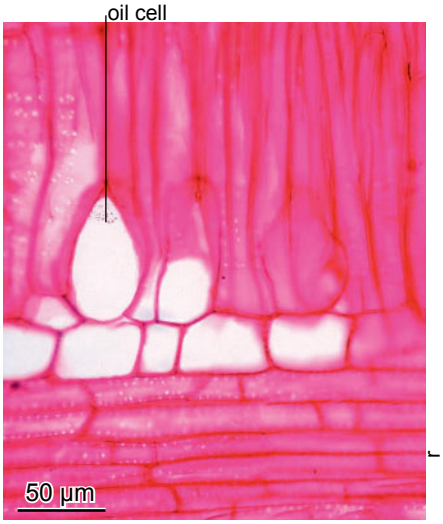



**Fig. 15.** Large oil cells associated with ray cells. Xylem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Laurus azorica*, radial section.



### Ecological trends and relations to life forms

No ecological trends were found because only a small number of species from subtropical climate and Mediterranean regions was analyzed.

### Characteristics of the phloem and the cortex

Two groups can be distinguished:

a) The phloem and the cortex of *Apollonias* (**Fig. 16**) and *Laurus* (**Fig. 17**) have simple structures. Sieve-tube elements and parenchyma cells are difficult to differentiate in transverse sections. Ray dilatations are characteristic. The presence of crystal sand in ray cells is unique to *Laurus azorica*.

b) Collapsed sieve-tube elements (**Figs. 18** and **20**) occur in both *Persea* species. Laticifers occur in *Persea indica* (**Fig. 19**). Intercellular ducts are surrounded by an epithelium in the phloem, the cortex (**Fig. 20**) and the pith (**Fig. 21**) of *Persea americana*. Irregular groups of sclereids are present in *Persea americana* (**Fig. 20**).

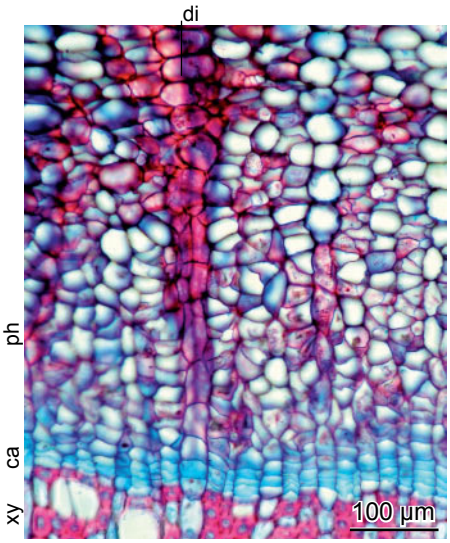



**Fig. 16.** Simple construction of the phloem. Sieve-tube elements and parenchyma cells cannot be differentiated. Phloem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Apollonias barbujana*, transverse section.

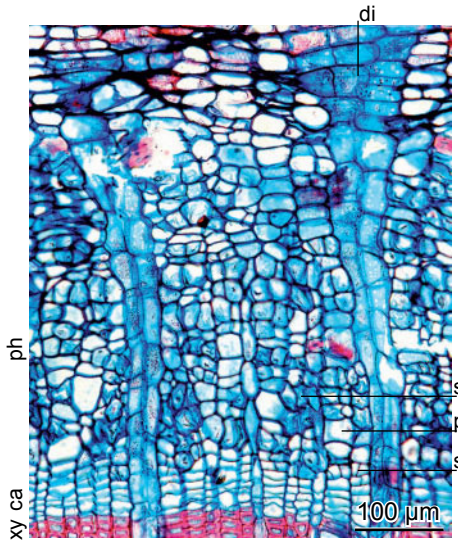



**Fig. 17.** Simple construction of the phloem. Sieve-tube elements and parenchyma cells are difficult to differentiate. Phloem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Laurus azorica*, transverse section.

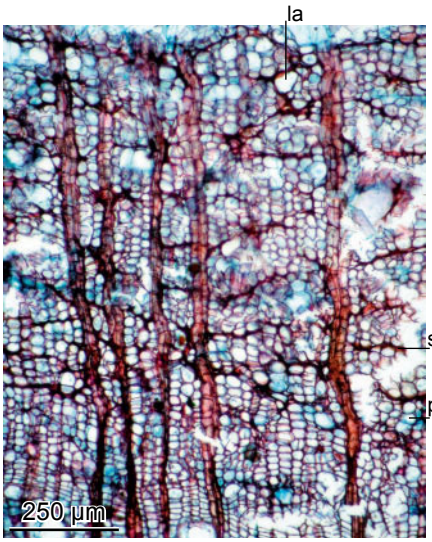



**Fig. 18.** Phloem with irregular lines of compressed sieve-tube elements. Phloem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Persea indica*, transverse section.

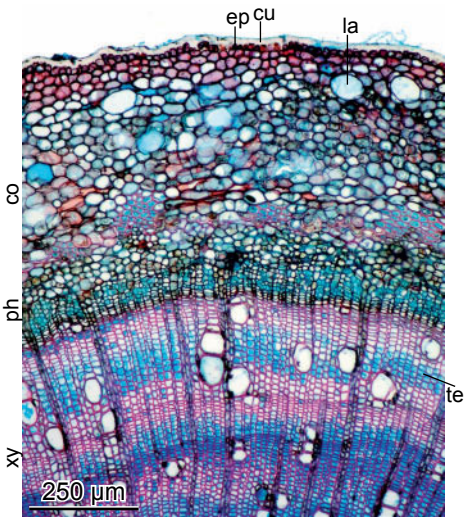



**Fig. 19.** Cortex with laticifers. Bark from a twig of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Persea indica*, transverse section.

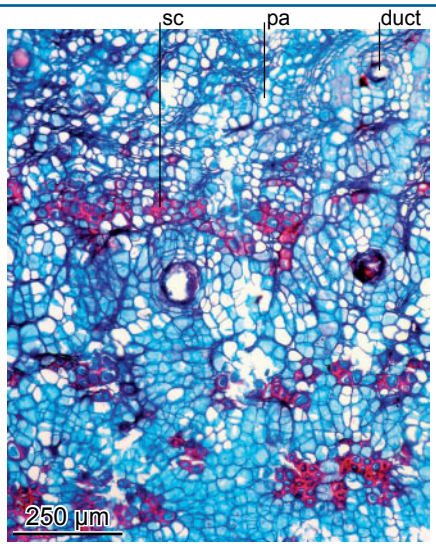



**Fig. 20.** Phloem with irregular groups of sclerenchyma cells and axial canals surrounded by epithelial cells. Phloem of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Persea americana*, transverse section.

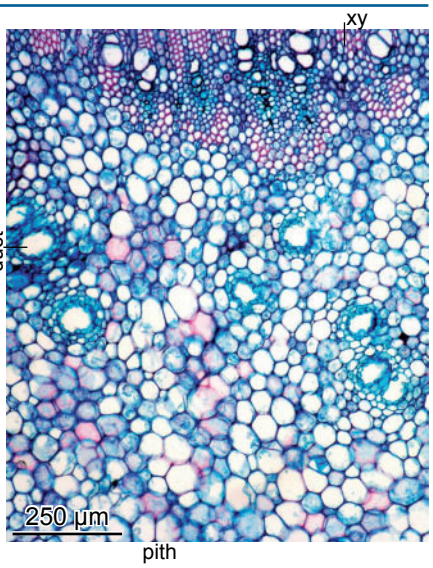



**Fig. 21.** Pith with axial canals surrounded by epithelial cells. Pith from a twig of a 4 m-high tree, *Laurus* forest, subtropical climate, Gomera, Canary Islands. *Persea americana*, transverse section.

### Discussion in relation to previous studies

A comprehensive wood anatomical study was performed by Richter (1981) in which he described the xylem and the phloem of 180 genera with 830 tree species. Schweingruber (1990) described the xylem of *Laurus nobilis*, *L. azorica*, *Persea indica* and *Ocotea foetens*. Gregory (1994) mentions further 190 references about the wood anatomy of mainly tropical Lauraceae.

The present study describes a few species occurring in Western Europe and on the Canary Islands, but it is far from representative for the whole family. Most representative for all Lauraceae species is the presence of paratracheal parenchyma and the occurence of alternating intervessel pits is a key feature of Lauraceae (Richter 1981).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| | **Total number of species** | **6** |
| 1 | growth rings distinct and recognizable | 4 |
| 2 | growth rings indistinct or absent | 2 |
| 4 | semi-ring-porous | 1 |
| 5 | diffuse-porous | 4 |
| 9 | vessels predominantly solitary | 3 |
| 9.1 | vessels in radial multiples of 2-4 common | 6 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 5 |
| 14 | vessels with scalariform perforation plates | 1 |
| 21 | intervessel pits opposite | 1 |
| 31 | vessel-ray pits with large apertures, *Salix/Laurus* type | 4 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 1 |
| 36 | helical thickenings present | 1 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 2 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 5 |
| 50 | <100 vessels per mm² in earlywood | 5 |
| 50.1 | 100-200 vessels per mm² in earlywood | 1 |
| 56 | tylosis with thin walls common | 3 |
| 58 | dark-stained substances in vessels and/or fibers present (gum, tannins) | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 5 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 1 |
| 65 | septate fibers present | 3 |
| 70 | fibers thin- to thick-walled | 6 |
| 70.2 | tension wood present | 3 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 3 |
| 79 | parenchyma paratracheal | 3 |
| 97 | rays width predominantly 1-3 cells | 5 |
| 98 | rays commonly 4-10-seriate | 2 |
| 100.2 | rays not visible in polarized light | 1 |
| 105 | ray: all cells upright or square | 3 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 3 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 3 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 1 |
| 110 | rays with sheet cells (tangential section) | 1 |
| 124 | oil and mucilage cells | 3 |
| 136 | prismatic crystals present | 3 |
| R3 | distinct ray dilatations | 3 |
| R4 | sclereids in phloem and cortex | 5 |
| R7 | with prismatic crystals | 4 |
| R9 | with crystal sand | 1 |
| R12 | with laticifers, oil ducts or mucilage ducts | 2 |
| P2 | with laticifers or intercellular canals | 1 |

# Linaceae



### Number of species, worldwide and in Europe

The cosmopolitan Linaceae family includes 6 genera with 220 species. Two genera with 37 species occur in Western Europe. The major genus *Linum* includes 16 species.

### Analyzed material

The xylem and phloem of 10 species of Linaceae has been analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Woody chamaephytes | 1 | 1 |
| Hemicryptophytes and geophytes | 7 | 1 |
| Therophytes | 2 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 3 | |
| Hill and mountain | 3 | |
| Mediterranean | 4 | |

**Analyzed species:**
*Adenolinum lewisii* A. Löve & D. Löve
*Linum alpinum* L.
*Linum austriacum* L.
*Linum bienne* Mill.
*Linum catharticum* L.
*Linum hypericifolium* E. Presl.
*Linum narbonense* L.
*Linum strictum* L.
*Linum suffruticosum* L.
*Linum tenuifolium* L.

*Linum catharticum* (photo: Zinnert)

*Linum austriacum* (photo: Zinnert)

*Linum alpinum* (photo: Landolt)

*Linum alpinum*

### Characteristics of the xylem

Annual species have only one ring (**Fig. 1**). Annual rings are distinct in all perennial species (**Figs. 2** and **3**). Ring distinctness is indicated by semi-ring-porosity (**Figs. 2** and **3**). Earlywood vessel diameter varies from 15-25 µm in annual and from 20-50 µm in perennial species. Vessel density varies from 300-500/mm$^2$. Simple perforations (**Fig. 4**) and fibers with distinctly bordered pits are characteristic of all species (**Fig. 5**). Fibers have large pits and are mostly fairly thick-walled (**Fig. 5**), especially in *Linum alpinum* and *L. suffruticosum*. Tension wood has been observed in the two annual species *Linum bienne* and *L. strictum* (**Fig. 6**). Parenchyma is apotracheal, diffuse (**Fig. 7**). Rays can be absent, uniseriate (**Fig. 8**) and 1-3-seriate (**Figs. 9** and **10**). All *Linum* species have square or upright ray cells (**Fig. 11**).

### Characteristic of the phloem and the cortex

Phloem structure is relatively uniform. Sieve tubes and parenchyma cells are mostly difficult to differentiate (**Figs. 12-14**). Sclereids are present in *Linum narbonense* and *L. suffruticosum*. Crystals are absent.

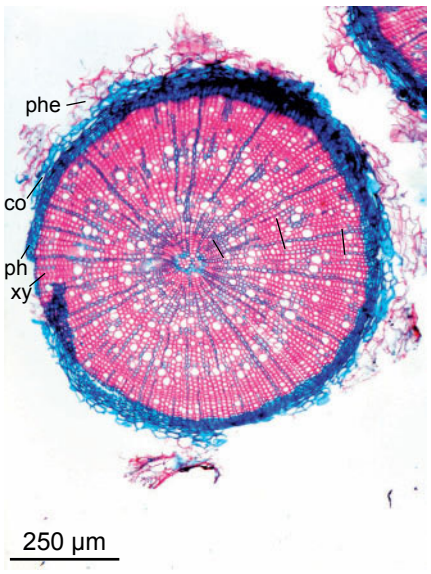



**Fig. 1.** Annual plant containing one ring with intra-annual structural fluctuations. Root collar of a 10 cm-high therophyte, meadow, Mediterranean zone, Provence, France. *Linum strictum*, transverse section.

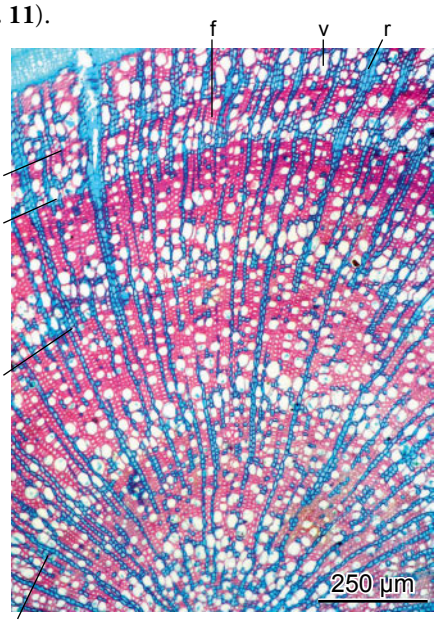



**Fig. 2.** Semi-ring-porous xylem. Root collar of a 40 cm-high hemicryptophyte, dry meadow, montane zone, Crested Butte, Colorado, USA. *Adenolinum lewisii*, transverse section.

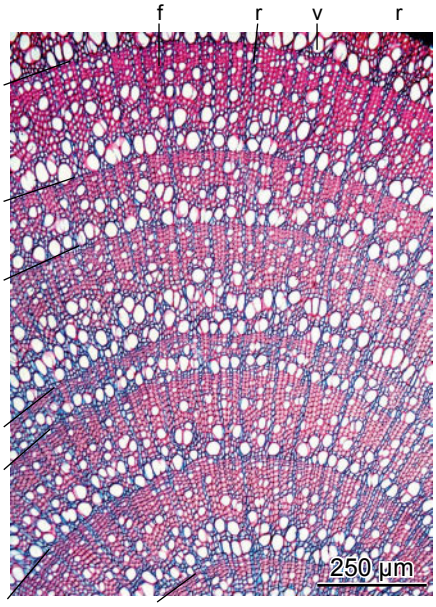
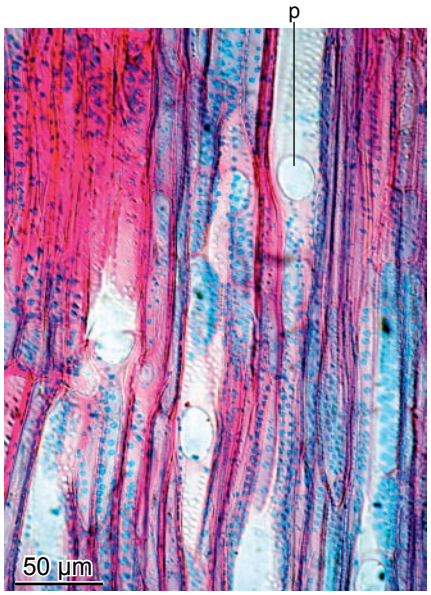
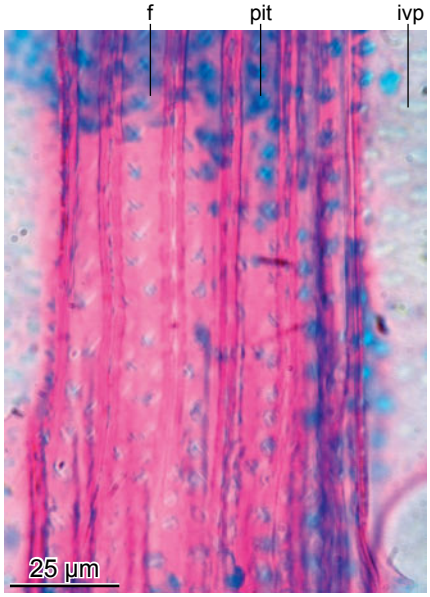



**Fig. 3.** Semi-ring-porous xylem. Root collar of a 40 cm-high dwarf chamaephyte, rock field, subalpine zone, French Alps. *Linum suffruticosum*, transverse section.




**Left Fig. 4.** Vessels with simple perforations and round pits in alternating position. Root collar of a 10 cm-high hemicryptophyte, meadow, subalpine zone, Caucasus, Georgia. *Linum hypericifolium*, radial section.




**Right Fig. 5.** Fibers with large pits (>3 µm) and gash-like apertures. Root collar of a 40 cm-high hemicryptophyte, dry meadow, montane zone, Crested Butte, Colorado, USA. *Adenolinum lewisii*, radial section.

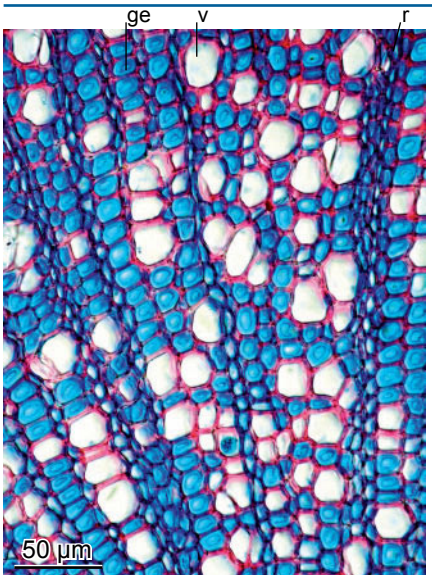



**Fig. 6.** Tension wood. Fibers contain large, unlignified secondary walls (gelatinous fibers). Root collar of a 10 cm-high therophyte, meadow, Mediterranean zone, Provence, France. *Linum strictum*, transverse section.

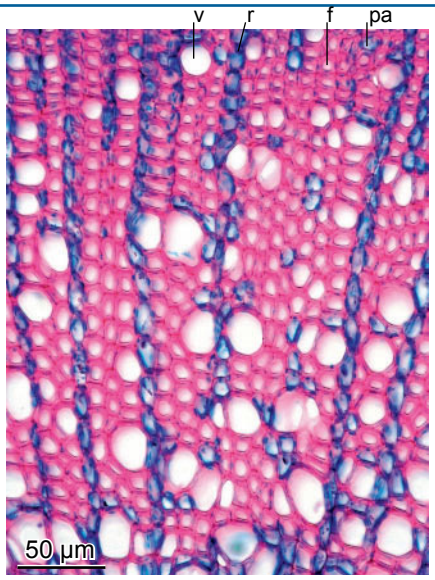



**Fig. 7.** Apotracheal, diffuse parenchyma. Root collar of a 20 cm-high hemicryptophyte, meadow, Mediterranean zone, Provence, France. *Linum tenuifolium*, transverse section.

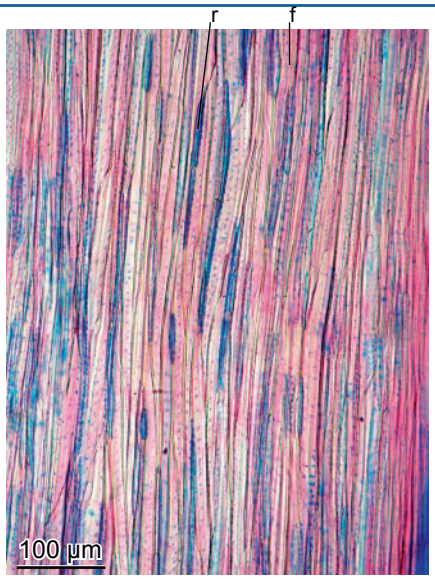
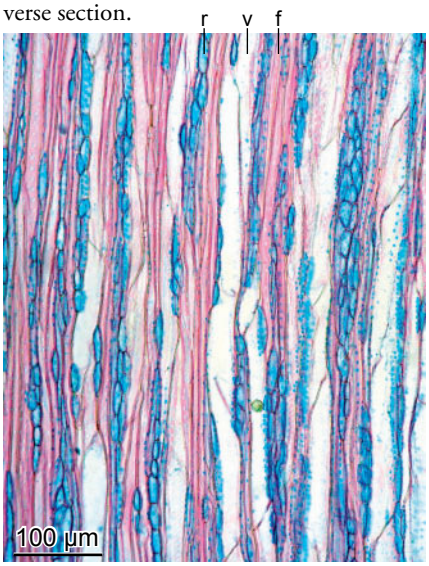
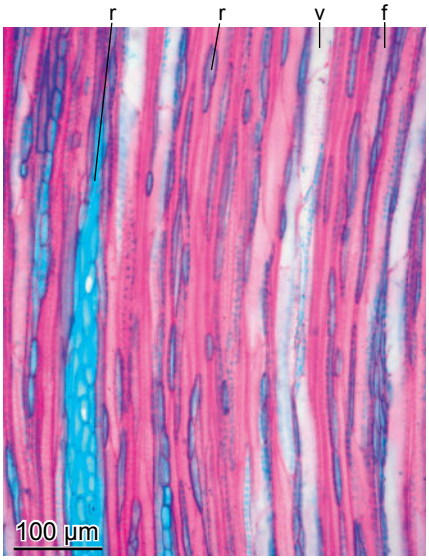


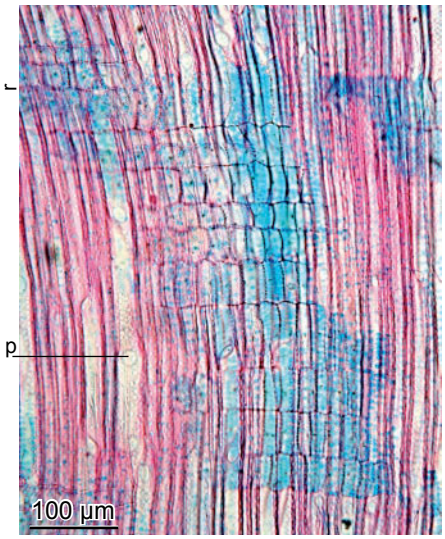

**Fig. 8.** Uniseriate rays with extremely elongated cells ressembling axial parenchyma cells. Root collar of a 12 cm-high herb, dry meadow, subtropical climate, Gomera, Canary Islands. *Linum bienne*, transverse section.

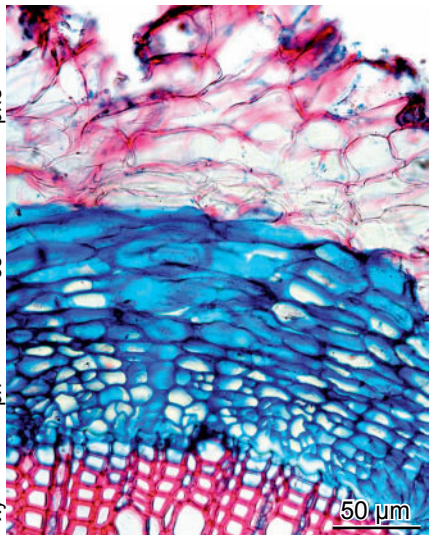



**Left Fig. 9.** Uni- and biseriate unlignified rays. Root collar of a 20 cm-high hemicryptophyte, vineyard hill zone, Burgenland, Austria. *Linum austriacum*, tangential section.

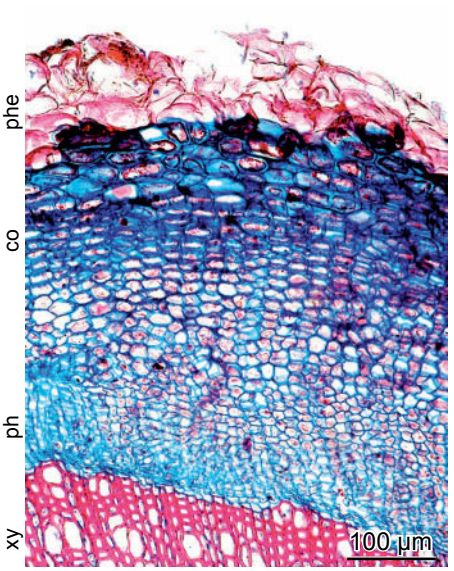
**Right Fig. 10.** 1-3-seriate unlignified rays. Root collar of a 40 cm-high hemicryptophyte, dry meadow, montane zone, Crested Butte, Colorado, USA. *Adenolinum lewisii*, tangential section.

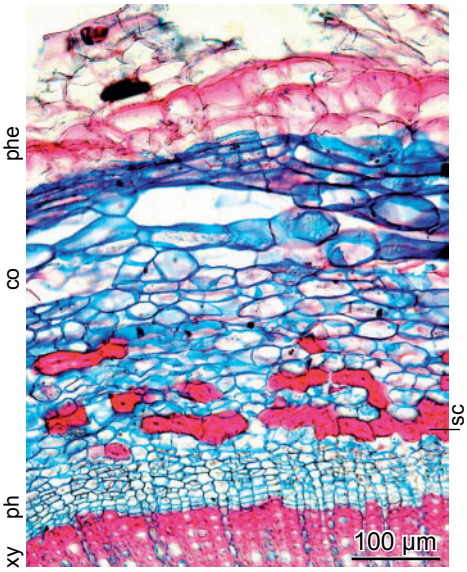



**Left Fig. 11.** Homocellular ray with both square and upright cells. Root collar of a 20 cm-high hemicryptophyte, vineyard hill zone, Burgenland, Austria. *Linum austriacum*, radial section.

**Right Fig. 12.** Bark with a small phloem consisting of small sieve-tubes and larger parenchyma cells, a small cortex consisting of large parenchyma cells and a large phellem. Root collar of a 10 cm-high therophyte, meadow, Mediterranean zone, Provence, France. *Linum strictum*, transverse section.




**Left Fig. 13.** A uniform phloem and cortex is covered by a phellem with irregular cell forms. Root collar of a 10 cm-high hemicryptophyte, meadow, subalpine zone, Caucasus, Georgia. *Linum hypericifolium*, transverse section.

**Right Fig. 14.** The small phloem consists of small sieve tubes and larger parenchyma cells. Tangentially elongated groups of sclerenchyma cells are embedded in the cortex. Phellem cells are produced by a small phellogen, and mature phellem cells are irregularly formed. Root collar of a 10 cm-high hemicryptophyte, meadow, subalpine zone, French Alps. *Linum narbonense*, transverse section.

### Ecological trends in the xylem and the bark

Vessels are smaller in small annual plants than in larger perennial plants.

### Discussion in relation to previous studies

Tropical genera have been described by many authors according to Gregory (1994), but *Linum* (*Linum suffruticosum* and *L. tenuifolium*) was only a detailed subject at Schweingruber (1990). The characterization of 7 *Linum* species and *Adenolinum lewisii* is new to this study.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **10** |
| 1 | growth rings distinct and recognizable | 9 |
| 2.1 | only one ring | 2 |
| 4 | semi-ring-porous | 10 |
| 9 | vessels predominantly solitary | 10 |
| 11 | vessels predominantly in clusters | 3 |
| 13 | vessels with simple perforation plates | 10 |
| 22 | intervessel pits alternate | 10 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 4 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 6 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 10 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 10 |
| 69 | fibers thick-walled | 2 |
| 70 | fibers thin- to thick-walled | 10 |
| 70.2 | tension wood present | 2 |
| 75 | parenchyma absent or unrecognizable | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 9 |
| 96 | rays uniseriate | 6 |
| 97 | rays width predominantly 1-3 cells | 3 |
| 100.2 | rays disappear in polarized light | 2 |
| 105 | ray: all cells upright or square | 9 |
| 117 | rayless | 1 |
| R1 | groups of sieve tubes present | 6 |
| R4 | sclereids in phloem and cortex | 2 |
| R10 | phloem not well structured | 1 |

# Loranthaceae and Viscaceae



### Number of species, worldwide and in Europe

The hemiparasitic species of Loranthaceae and Viscaceae (Santalales) are described together bacause the anatomical structures of species of both families are similar. The Loranthaceae family includes 60-70 genera with 800 species, the Viscaceae family includes 10 genera with 350 species. Distribution: Loranthaceae: pantropical, but no single genus spans the Old and New World. Viscaceae: pantropical, with some species extending into temperate regions. In Europe exist one species of Loranthaceae (*Loranthus europaeus*) and 2 genera with 3 species of Viscaceae (*Viscum album*, *V. cruciatum*, *Arecuthobium oxycedri*).

### Analyzed material

The xylem and phloem of 8 species has been analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Woody chamaephytes | 8 | ca. 20 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 4 | |
| Mediterranean | 1 | |
| Arid | 3 | |

The material was collected in Europe (3 species), in Arabia (1 species), in North America (3 species) and in Argentina (1 species).

**Analyzed species:**
*Loranthus acaciae* Zucc.
*Loranthus aphyllus* Miers *ex* DC.
*Loranthus europaeus* Jacq.
*Phoradendron californicum* Nutt.
*Phoradendron juniperinum* Engelm.
*Phoradendron tomentosum* (DC.) Gray
*Viscum album* L.
*Viscum cruciatum* Sieber ex Spreng

*Viscum album*

*Viscum album*

*Phoradendron juniperinum*

**Characteristics of the xylem**

In the presented material only *Loranthus europaeus* has distinct rings (**Fig. 1**). A few other species have somewhat distinct ring boundaries (**Fig. 2**), but some have no recognizable rings (**Fig. 3**). Ring distinctness is indicated by semi-ring porosity (**Fig. 1**) or slight differences in fiber size and cell-wall thickness between the latewood and the earlywood (**Fig. 2**). Earlywood vessel diameter varies from 20-40 µm and vessel density from 300-1000/mm$^2$.

Vessels are often arranged in radially uniseriate (**Fig. 4**) or multiseriate groups (**Figs. 2** and **5**). In some species vessels and fibers cannot be distinguished in transverse section as shown in *Phoradendron juniperinum* (**Fig. 6**). Characteristic are short, thick-walled vessels (**Figs. 7** and **8**) with simple perforations and small, bordered pits, often opposite each other. Pits with round and gash-like apertures have been observed (**Figs. 7** and **8**). Storied vessels and parenchyma occur in *Loranthus europaeus* (**Fig. 9**).

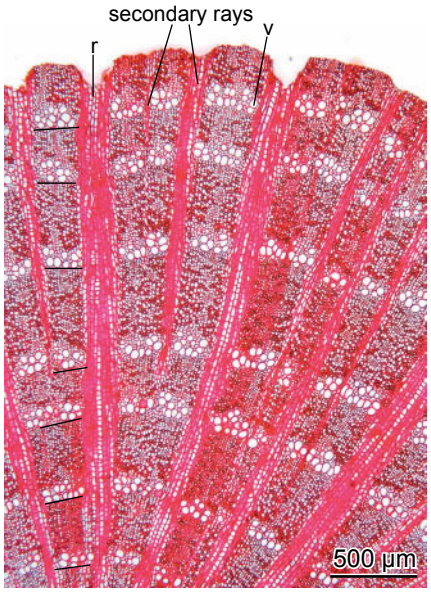



**Fig. 1.** Distinct rings in a semi-ring-porous wood. The peripheral ends of the large rays end in a wedge (Keilwuchs). Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Quercus petraea*, hill zone, Burgenland, Austria. *Loranthus europaeus*, transverse section.

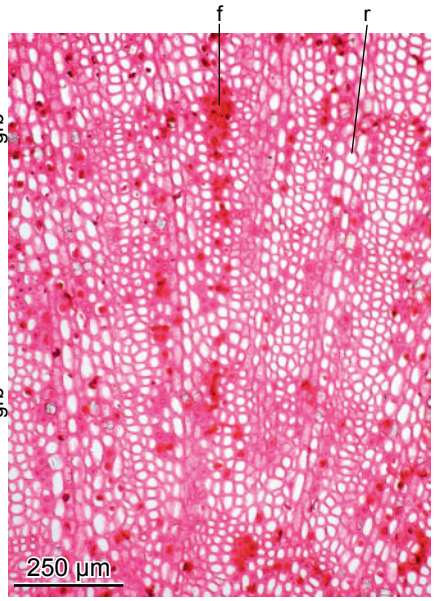
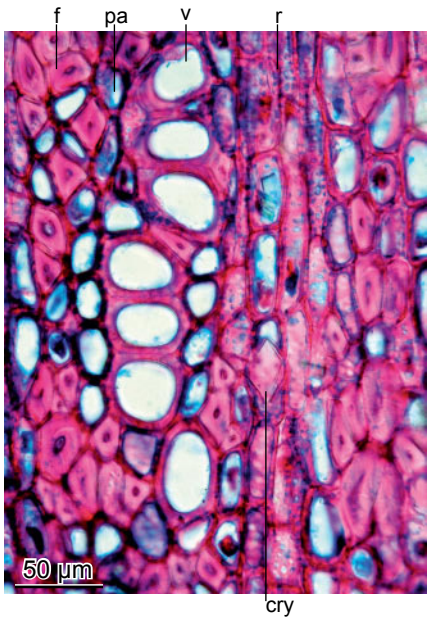
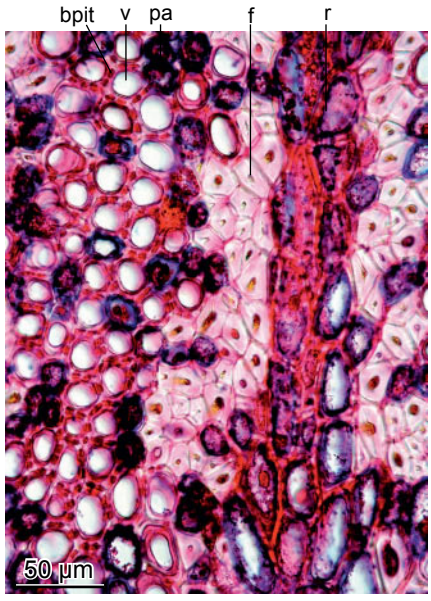



**Fig. 2.** Indistinct rings of a diffuse-porous wood. Since vessels, fibers and parenchyma cells have the same diameter, it is sometimes difficult to distinguish axial and horizontal elements. Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Malus sylvestris*, hill zone, Zürich, Switzerland. *Viscum album*, transverse section.

**Fig. 3.** Distinct rings of a diffuse-porous wood. Radial multiple vessel groups are concentrated between indistinct rays, thick-walled fibers, apotracheal and paratracheal parenchyma. Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Acacia* sp., subtropical climate, Dhofar, Oman. *Loranthus acaciae*, transverse section.




**Left Fig. 4.** A thick-walled radial vessel group is surrounded by paratracheal and apotracheal parenchyma, very thick-walled fibers and radially elongated ray cells. Ray cells contain partially prismatic crystals. Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Celtis laevigata*, mountain zone, arid climate, Arizona, USA. *Phoradendron tomentosum*, transverse section.

**Right Fig. 5.** Next to a group of thick-walled vessels with distinctly bordered pits and a few paratracheal parenchyma cells are two groups of very thick-walled fibers separated by a ray. Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Proustia cuneifolia*, mountain zone, arid climate, Uspallata, Argentina. *Loranthus aphyllus*, transverse section.

Fibers are primarely very thick-walled (**Figs. 4** and **5**) and radial cell walls have minutely bordered pits. Parenchyma is apotracheal or paratracheal (**Figs. 4-6**). The extremely large nuclei (diameter 10-15 µm) in the parenchyma cells are striking (**Fig. 8**).

All species have large rays (4-10 cells; **Figs. 9-11**) with square and upright cells, often with extremely thick cell walls. All species except *Loranthus europaeus* contain prismatic crystals and/or crystal druses (**Fig. 4**). Cone-like haustoria, consisting of predominately unlignified, thin-walled cells, are overgrown from the xylem and bark tissue of the host species (**Figs. 12** and **13**).

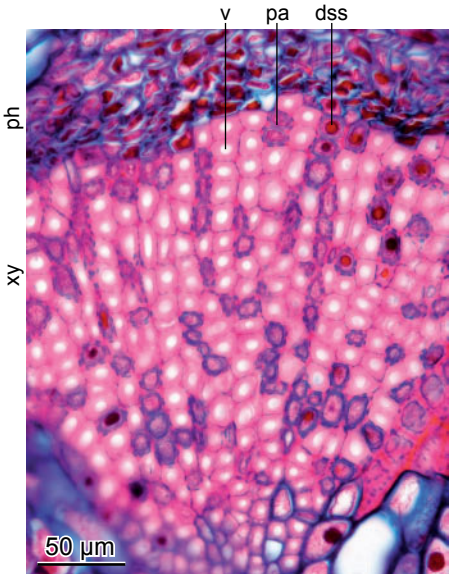



**Fig. 6.** The xylem consists of vessels and paratracheal parenchyma cells. Axial and horizontal elements cannot be distinguished. Fibers are absent. Stem of a 10 cm-high, hemi-parasitic dwarf shrub on *Juniperus* sp., mountain zone, arid climate, Arizona, USA. *Phoradendron juniperinum*, transverse section.

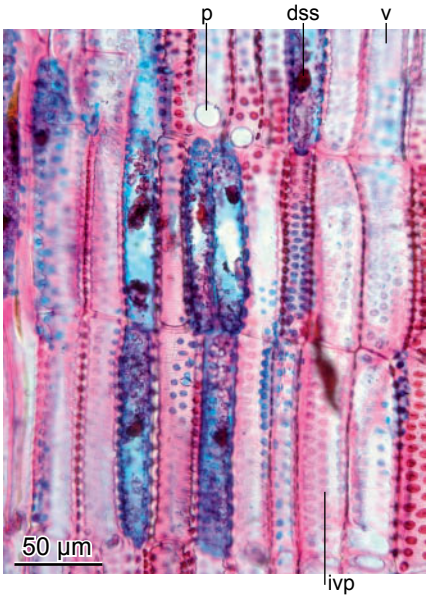



**Fig. 7.** Short vessels with simple perforations. Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Proustia cuneifolia*, mountain zone, arid climate, Uspallata, Argentina. *Loranthus aphyllus*, radial section.

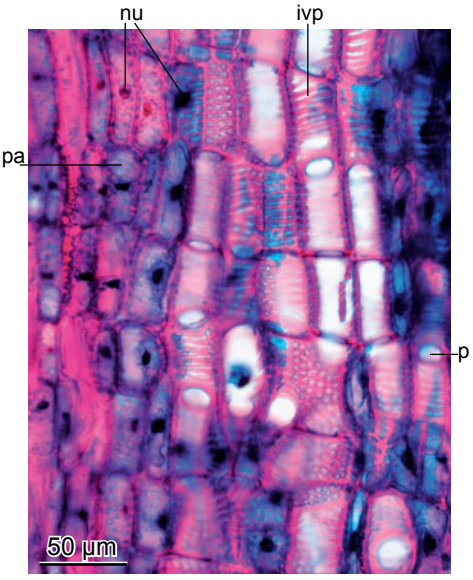



**Fig. 8.** Short vessels with simple perforations and round and scalariform inter-vessel pits. The small round pits are often arranged in horizontal rows (opposite). Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Prosopis glandulosa*, hill zone, arid climate, Arizona, USA. *Phoradendron californicum*, radial section.

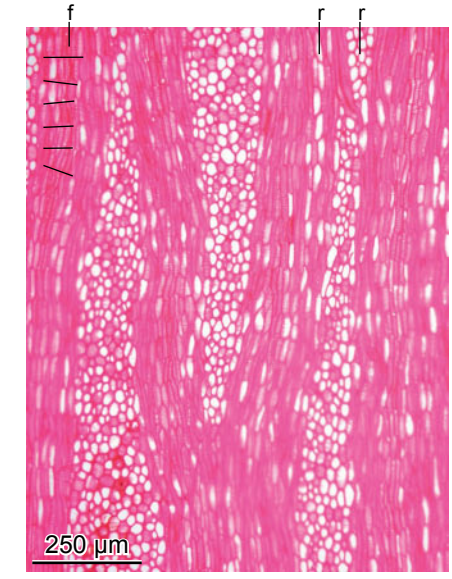



**Fig. 9.** Very large rays are embedded in a storied vessel/fiber tissue. Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Quercus petraea*, hill zone, Burgenland, Austria. *Loranthus europaeus*, tangential section.

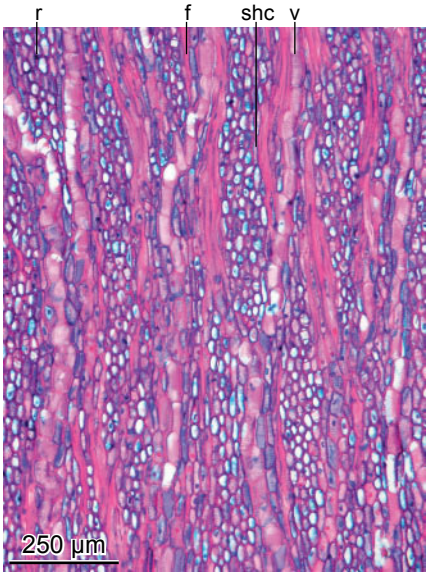



**Fig. 10.** Large rays partially with sheet cells are embedded in a non-storied vessel/fiber tissue. Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Celtis laevigata*, mountain zone, arid climate, Arizona, USA. *Phoradendron tomentosum*, tangential section.

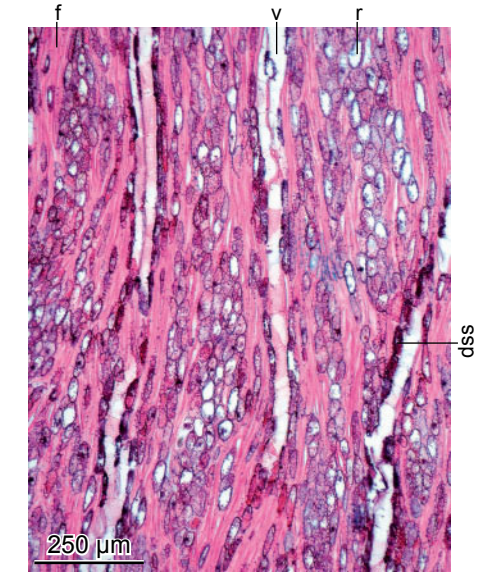
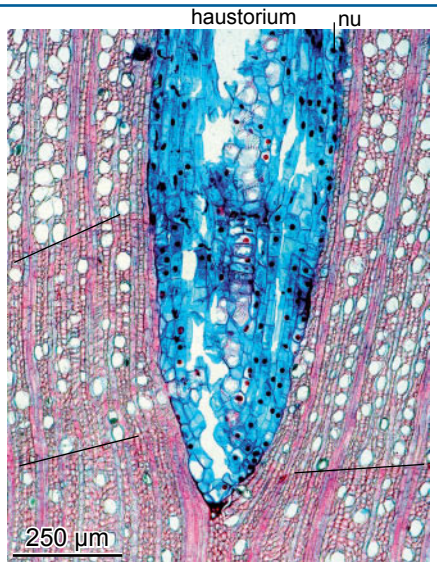
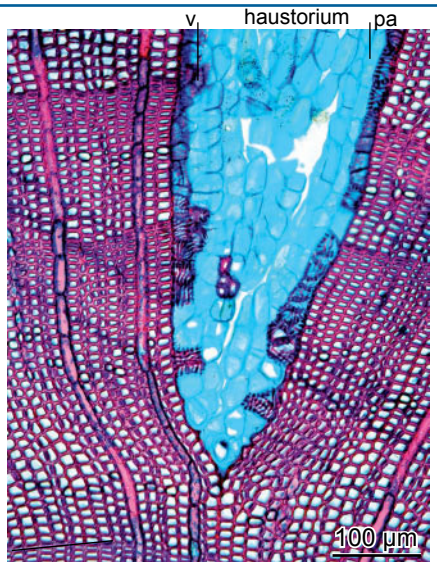



**Fig. 11.** Indistinct rays are embedded in a fiber/vessel tissue. Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Acacia* sp., subtropical climate, Dhofar, Oman. *Loranthus acaciae*, tangential section.




**Left Fig. 12.** Haustorium of a dwarf mistletoe in a branch of a deciduous tree. Characteristic are the thin-walled unlignified parenchymatic cells with large nuclei. Growth started in autumn just before the host tree formed its latewood. Stem of a 30 cm-high, hemi-parasitic dwarf mistletoe on *Malus sylvestris*, hill zone, Zürich, Switzerland. *Viscum album*, transverse section.

**Right Fig. 13.** Haustorium of a dwarf mistletoe in a conifer branch. The haustorium consists mainly of thin-walled unlignified parenchymatic cells and a few thick-walled, lignified vessels. Growth started in spring after the formation of the first seven tracheids. Stem of a 10 cm-high, hemi-parasitic dwarf shrub on *Juniperus* sp., mountain zone, arid climate, Arizona, USA. *Phoradendron juniperinum*, transverse section.

### Characteristics of the phloem and the cortex

Short dilatations divide small, more-or-less triangular phloem patches outside the vessel/fiber strips. Older sieve tubes are primarely not collapsed (**Figs. 14**, **15** and **17**). *Loranthus aphyllus* seems to be an exception (**Fig. 18**). Crystals (prismatic and druses) and groups of sclereids occur in all species. The epidermis, if preserved, is covered by an extremely thick cuticula (**Figs. 14**, **15** and **17**). Some vessels have been found in the cortex of *Phoradendron juniperinum* (**Fig. 16**). Xylem/phloem formation is not strictly bilateral in the family of Loranthaceae. Spot-like xylem enclosures in the cortex are shown in **Fig. 16**. In other species, e.g. *Nuytsia floribunda*, spot-like phloem enclosures occur in the xylem (**Fig. 19**). Predetermined breaking zones trigger twig dropping (cladaptosis; **Fig. 19**). It is characteristic of the Loranthaceae species.

### Ecological trends in the xylem and the bark

There is insufficient material to detect any ecological trends.

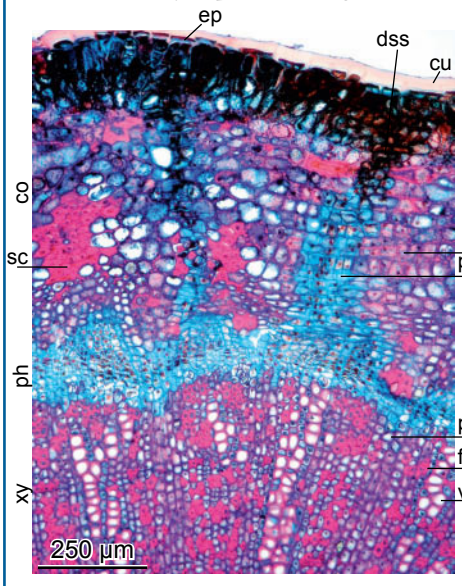



**Fig. 14.** The phloem consists of thin-walled cells with large nuclei. The phloem of the primary vascular bundles is in the prolongation of the radial vessel rows. Indistinct dilatations separate the bundles. Characteristic is the irregular structure in the cortex, consisting of groups of sclereids, round cortex cells and thin-walled callus cells. The cortex is covered by a thick cuticula. Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Prosopis glandulosa*, hill zone, arid climate, Arizona, USA. *Phoradendron californicum*, radial section.

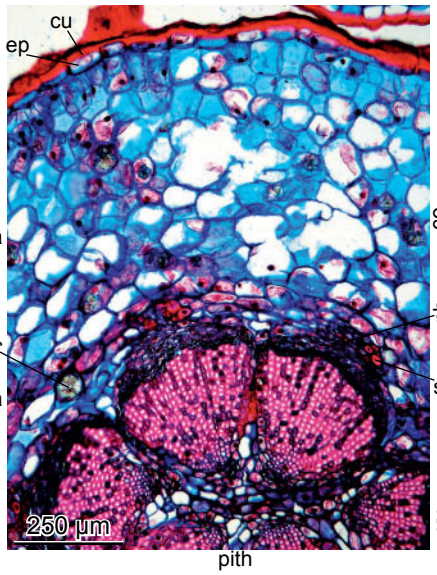



**Fig. 15.** The small phloem is surrounded by a large cortex. Some thin-walled parenchymatic cortex cells contain crystal druses. The cortex is covered by a thick cuticula. Stem of a 10 cm-high, hemi-parasitic dwarf shrub on *Juniperus* sp. mountain zone, arid climate, Arizona, USA. *Phoradendron juniperinum*, transverse section.

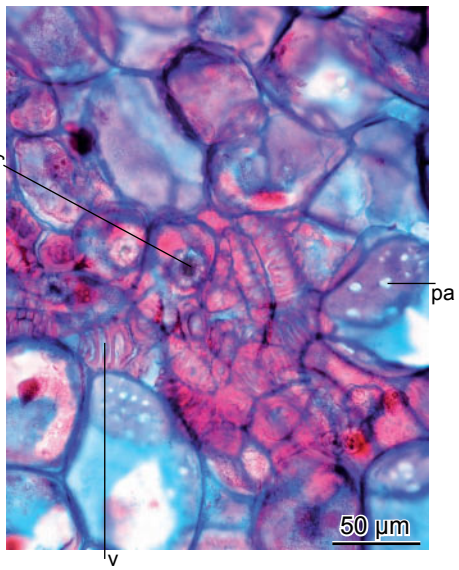
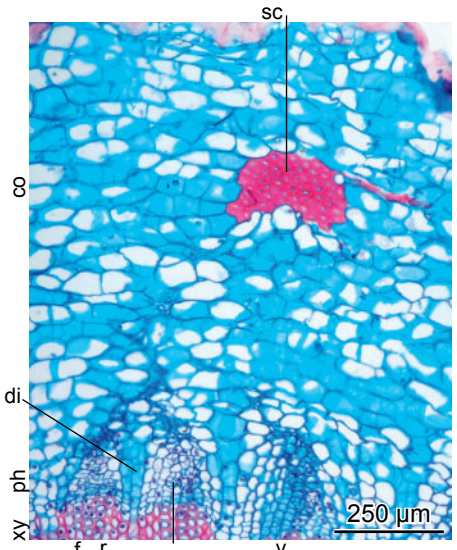
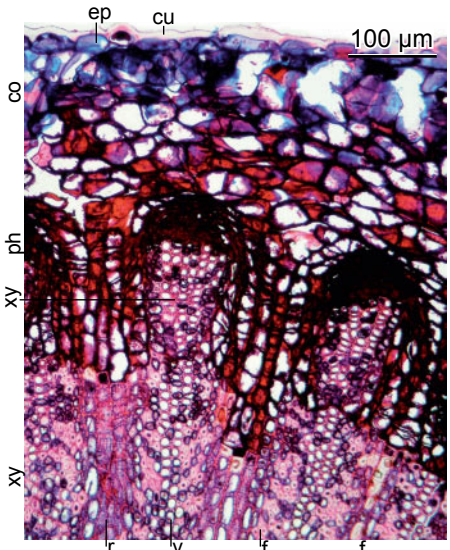


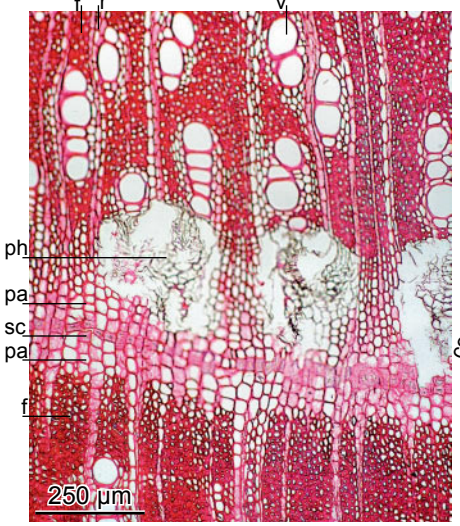

**Fig. 16.** Vessel enclosures in the cortex. The vessels are characterized by lignification and scalariform inter-vessel pits. Magnified part of **Fig. 15**.

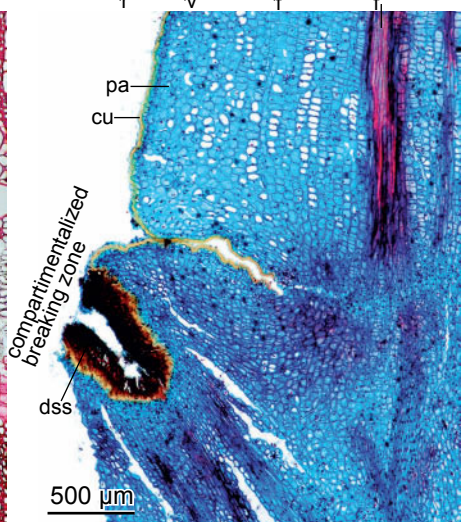



**Left Fig. 17.** Distinct triangular groups of phloem are in the continuation of the vessel groups in the xylem. A few conspicuous fiber groups are in the thin-walled parenchymatic cortex. Bark of a 30 cm-high, hemi-parasitic dwarf shrub on *Malus sylvestris*, hill zone, Zürich, Switzerland. *Viscum album*, transverse section.

**Right Fig. 18.** A phloem with collapsed sieve tubes is in the prolongation of the radial vessel/parenchyma strips of the xylem. The xylem ray formation remains behind that of the vessels and parenchyma (Keilwuchs). The cortex consists of large irregular cells and is covered by a thick cuticula. Stem of a 30 cm-high, hemi-parasitic dwarf shrub on *Proustia cuneifolia*, mountain zone, arid climate, Uspallata, Argentina. *Loranthus aphyllus*, radial section.




**Left Fig. 19.** Xylem with phloem enclosures (thin-walled cells). Characteristic of the xylem are the radial vessel groups and the sclerenchymatic tangential row in the tangential band of parenchymantic cells. Stem of a tree, savannah, Western Australia. *Nuytsia floribunda*, transverse section.

**Right Fig. 20.** Breaking zone of a twig. The axial xylem of the young and old shoot is separated by an unlignified meristematic zone and a groove around the shoot. The old shoots, as well as the young axial ends of the shoots, are covered with a thick cuticula. An already broken shoot is decayed and compartmentalized by a barrier zone. *Phoradendron juniperinum*, radial section.

## Discussion in relation to previous studies

*Loranthus europaeus* and *Viscum album* are described by Fahn et al. (1996), Greguss (1945), Huber and Roschal (1954) and Schweingruber (1990), *Phoradendron* sp. by Carlquist and Hoekman (1985) and *Phoradendron flavescens* by Inside wood (2004) and Ashworth and Dos Santos (1997). A few North American *Arceutobium* species have been described by by Wilson and Calvin (2000). Features of *Loranthus europaeus* and *Viscum album* agree with those of previous studies but there is not enough material available to elaborate common family characteristics and to explain large intra-familiy variations (Metcalfe and Chalk, 1957). Pfeiffer (1926) mentions phloem enclosures in the xylem.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **8** |
| 1 | growth rings distinct and recognizable | 6 |
| 2 | growth rings indistinct or absent | 2 |
| 4 | semi-ring-porous | 1 |
| 5 | diffuse-porous | 6 |
| 10 | vessels in radial multiples of 4 or more common | 6 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 8 |
| 20 | intervessel pits scalariform | 5 |
| 21 | intervessel pits opposite | 6 |
| 39.1 | vessel cell-wall thickness >2 µm | 7 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 6 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 8 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 6 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 8 |
| 69 | fibers thick-walled | 8 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 8 |
| 79 | parenchyma paratracheal | 4 |
| 98 | rays commonly 4-10-seriate | 7 |
| 99 | rays commonly >10-seriate | 1 |
| 99.1 | vascular-bundle form remaining | 1 |
| 104 | ray: all cells procumbent (radial section) | 7 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 1 |
| 117 | rayless | 1 |
| 135.1 | interxylary periderm (cork-band) | 6 |
| 136 | prismatic crystals present | 2 |
| 149 | rhaphides present | 5 |
| R2.1 | groups of sieve tubes in radial rows | 4 |
| R3 | distinct ray dilatations | 5 |
| R6 | sclereids in radial rows | 3 |
| R7.1 | with acicular crystals | 3 |

# Lythraceae



**Number of species, worldwide and in Europe**

The Lythraceae family includes 4 genera with 530 species and is mainly pantropical distributed. In Europe, there are 2 genera with 14 species.

**Analyzed material**

The xylem and phloem of 3 genera with 5 species were analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 2 | 10 genera (trees and shrubs) |
| Hemicryptophytes | 3 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 1 | |
| Mediterranean | 3 | |
| Subtropical | 1 | |

**Analyzed species:**

*Lythrum acutangulum* L.
*Lythrum hyssopifolia* L.
*Lythrum salicaria* L.
*Punica granatum* L.
*Woodfordia uniflora* Koehne

*Lythrum hyssopifolia* (photo: Zinnert)

*Punica granatum* (photo: Zinnert)

*Lythrum salicaria* (photo: Zinnert)

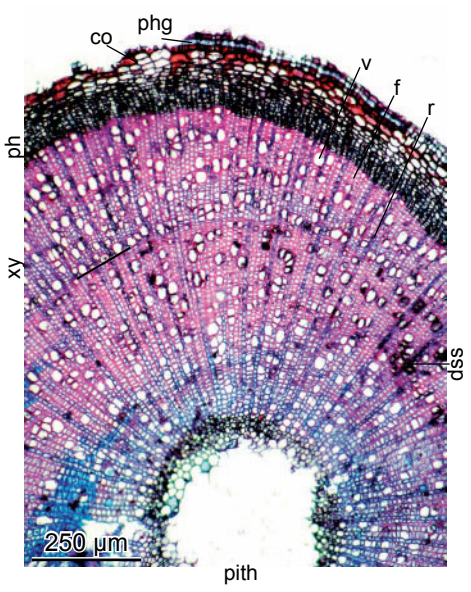
*Punica granatum* (photo: Zinnert)

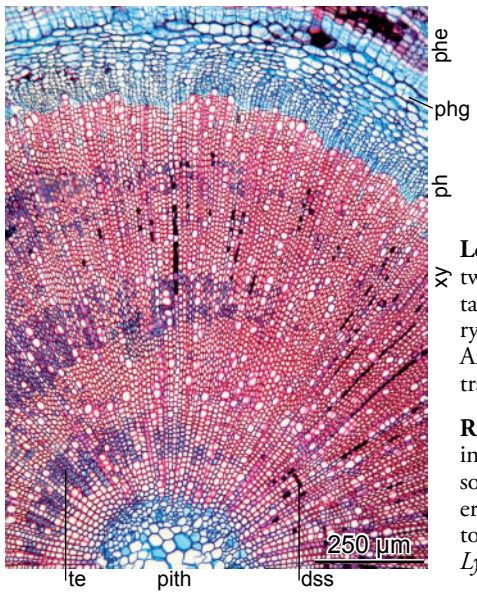
### Characteristics of the xylem

Rings of all species are diffuse-porous to semi-ring-porous and ring boundaries are distinct (**Figs. 1**, **4** and **5**) or at least recognizable (**Figs. 2** and **3**). Vessels are arranged solitary or in short radial multiples (**Figs. 4** and **5**). Vessel diameter varies from 20-40 µm in herbaceous plants (**Figs. 1-3**), and 50-100 µm in shrubs (**Figs. 4** and **5**). Vessels have exclusively simple perforations, and intervessel pits are round, arranged in opposite position (**Fig. 6**). Vessels of *Lythrum salicaria* and the shrubs contain phenolic substances in the heartwood (**Fig. 3**). Fibers are thin- to thick-walled (**Figs. 1-5** and **8**). Fiber pits are small with slit-like apertures. All species, including herbs, produce tension wood (**Figs. 2** and **7**). Axial parenchyma is mostly unrecognizable but it is sometimes paratracheal (**Fig. 8**). Rays are uniseriate, homocellular with square and upright cells (**Figs. 9** and **10**), or they are uni- and multiseriate (**Fig. 11**).

### Characteristics of the phloem and the cortex

The phloem of the herbs is simply structured. Sieve-tubes and parenchyma are difficult to distinguish on transverse sections (**Fig. 12**). The shrubs are characterized by tangential rows of parenchyma cells with crystal druses (**Fig. 13**).




**Left Fig. 1.** Diffuse-porous xylem with two rings. Vessels are arranged mostly solitary. Root collar of a 40 cm-high hemicryptophyte, wet meadow, Mediterranean, Andalusia, Spain. *Lythrum acutangulum*, transverse section.

**Right Fig. 2.** Diffuse-porous xylem with indistinct rings. Vessels are arranged mostly solitary. Tension wood appears in three layers. Root collar of a 20 cm-high hemicryptophyte, coast, hill zone, Galicia, Spain. *Lythrum hyssopifolia*, transverse section.

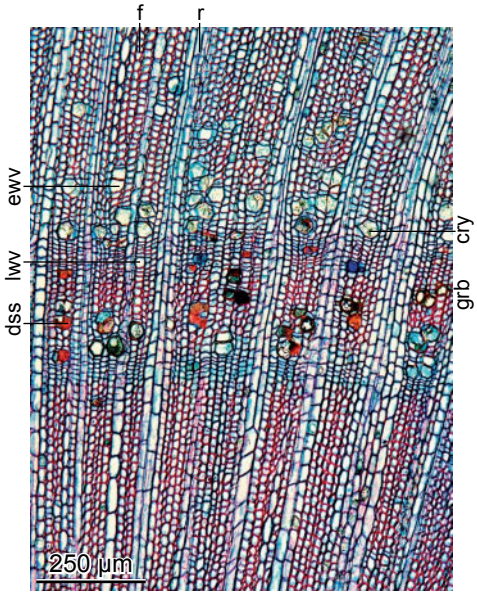



**Fig. 3.** Semi-ring-porous xylem with growth zone boundaries. Latewood vessels contain dark-staining substances. Root collar of a 50 cm-high hemicryptophyte, bog, hill zone, Schwyz, Switzerland. *Lythrum salicaria*, transverse section.

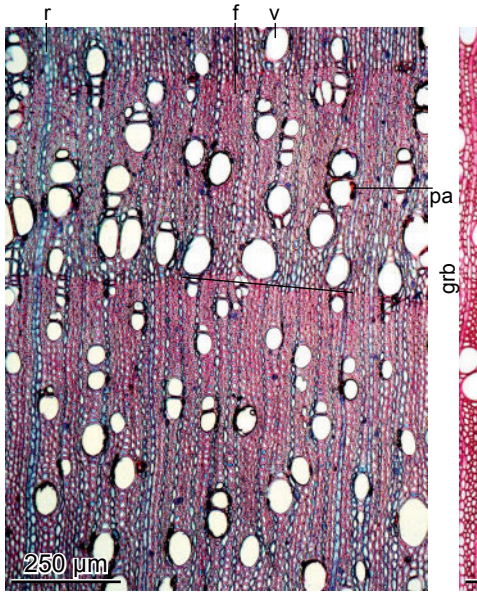
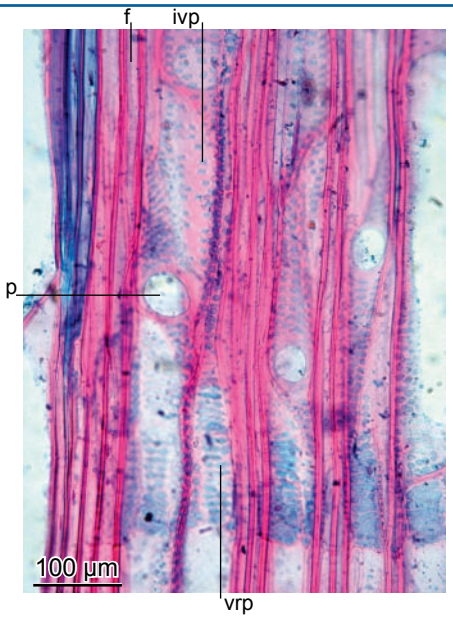
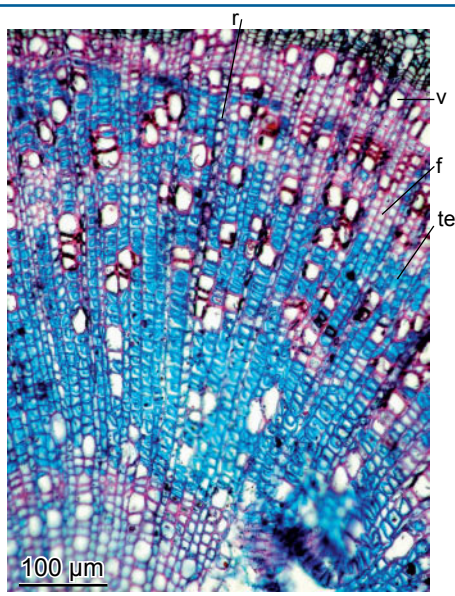



**Fig. 4.** Semi-ring-porous xylem with distinct rings. Stem of a 1.5 m-high shrub, coastal forest, subtropical climate, Salalah, Oman. *Woodfordia uniflora*, transverse section.

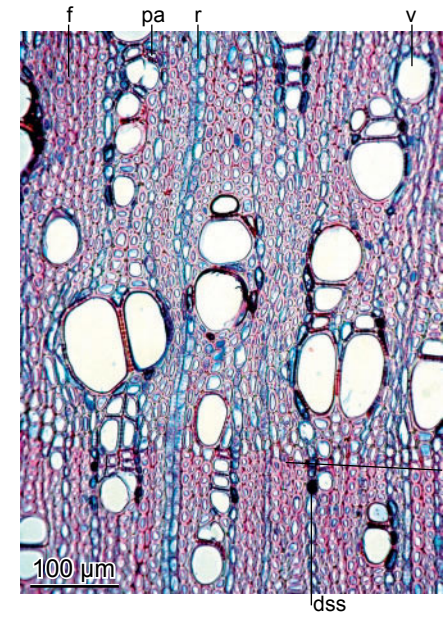
**Fig. 5.** Diffuse-porous xylem. Vessels are arranged in short radial multiples. Stem of a 2 m-high shrub, cultivated, mountain zone in subtropical climate, Nizwa, Oman. *Punica granatum*, transverse section.

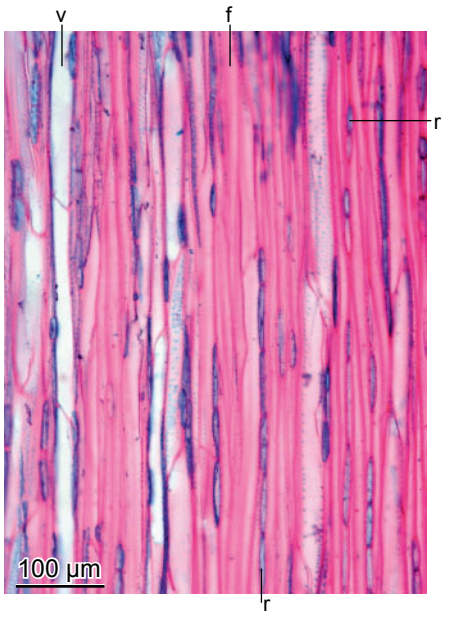



**Left Fig. 6.** Vessels with simple perforations and round intervessel pits in alternating position. Vessel-ray pits are slightly horizontally enlarged. Root collar of a 40 cm-high hemicryptophyte, wet meadow, Mediterranean, Andalusia, Spain. *Lythrum acutangulum*, radial section.

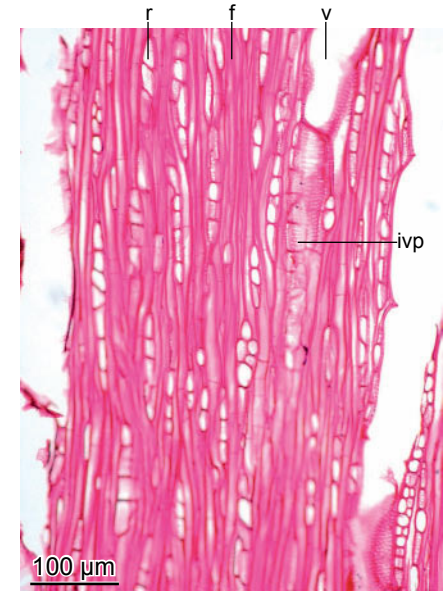
**Right Fig. 7.** Tension wood. Root collar of a 40 cm-high hemicryptophyte, wet meadow, Mediterranean, Andalusia, Spain. *Lythrum acutangulum*, transverse section.

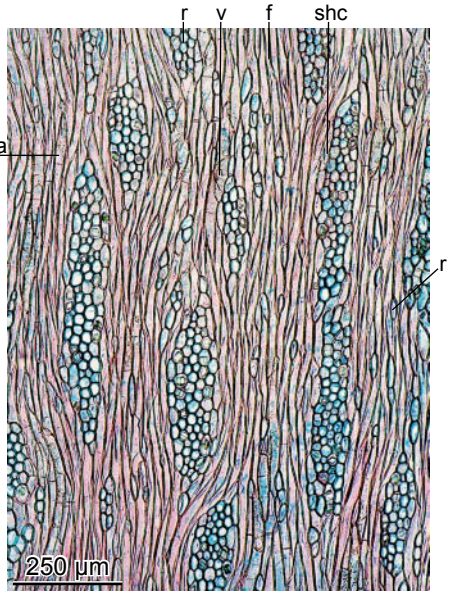



**Left Fig. 8.** Scanty paratracheal parenchyma. Stem of a 1.5 m-high shrub, coastal forest, subtropical climate, Salalah, Oman. *Woodfordia uniflora* transverse section.

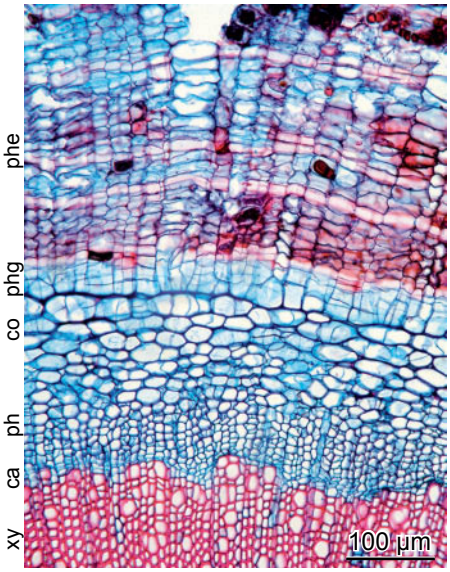
**Right Fig. 9.** Uniseriate rays with axially elongated unlignified cells. Root collar of a 40 cm-high hemicryptophyte, wet meadow, Mediterranean, Andalusia, Spain. *Lythrum acutangulum*, tangential section.

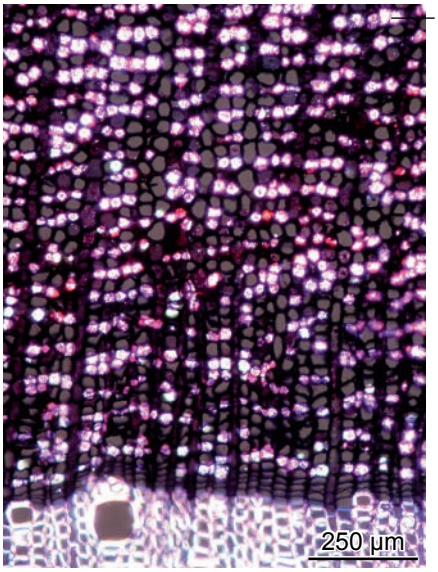



**Left Fig. 10.** Uni- and bi-seriate rays with large cells. Stem of a 2 m high shrub, cultivated, mountain zone in subtropical climate, Nizwa, Oman. *Punica granatum*, tangential section.

**Right Fig. 11.** Rays of two different sizes: short uniseriate and long 3-6-seriate, with sheet cells in some sections. Root collar of a 50 cm-high hemicryptophyte, bog, hill zone, Schwyz, Switzerland. *Lythrum salicaria*, tangential section.




**Left Fig. 12.** Uniform phloem, parenchyma and sieve-cells are not differentiated. The phellem consists of rectangular, radially arranged cork cells. Root collar of a 20 cm-high hemicryptophyte, coast, hill zone, Galicia, Spain. *Lythrum hyssopifolia*, transverse section.

**Right Fig. 13.** Phloem with tangential rows of crystal druses in parenchyma cells. Stem of a 2 m-high shrub, cultivated, mountain zone in subtropical climate, Nizwa, Oman. *Punica granatum*, transverse section, polarized light.



## Discussion in relation to previous studies

The xylem of *Punica granatum* (Punicaceae) has been described ten times (Gregory 1995), e.g. by Greguss (1945) and by Huber and Rouschal (1954). The description of all other species is new to this study.

Ecologically significant is the low vessel density in *Lythrum salicaria* which grows in wet environments.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **5** |
| 5 | diffuse-porous | 5 |
| 6 | vessels in intra-annual tangential rows | 1 |
| 9 | vessels predominantly solitary | 4 |
| 9.1 | vessels in radial multiples of 2-4 common | 5 |
| 11 | vessels predominantly in clusters | 2 |
| 13 | vessels with simple perforation plates | 5 |
| 22 | intervessel pits alternate | 5 |
| 39.1 | vessel cell-wall thickness >2 µm | 2 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 3 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 2 |
| 50 | <100 vessels per mm$^2$ in earlywood | 1 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 4 |
| 58 | dark-staining substances in vessels and/or fibers present (gum, tannins) | 1 |
| 60.1 | fibers absent | 5 |
| 65 | septate fibers present | 4 |
| 70 | fibers thin- to thick-walled | 5 |
| 70.2 | tension wood present | 3 |
| 75 | parenchyma absent or unrecognizable | 3 |
| 79 | parenchyma paratracheal | 2 |
| 96 | rays uniseriate | 2 |
| 97 | ray width predominantly 1-3 cells | 2 |
| 98 | rays commonly 4-10-seriate | 2 |
| 103 | rays of two distinct sizes (tangential section) | 1 |
| 105 | ray: all cells upright or square | 2 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 2 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 2 |
| 136 | prismatic crystals present | 2 |
| 144 | druses present | 2 |
| R1 | groups of sieve tubes present | 4 |
| R2 | groups of sieve tubes in tangential rows | 1 |
| R3 | distinct ray dilatations | 1 |
| R7 | with prismatic crystals | 2 |
| R8 | with crystal druses | 2 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 5 |

# Magnoliaceae



## Number of species, worldwide and in Europe

The Magnoliaceae family includes 2 genera with 220 species. The genus *Magnolia* includes 218 and *Liriodendron* 2 species (Judd et al. 2002). Species are distributed in temperate to tropical regions of eastern North America and eastern Asia, and tropical South America. No members of the family are endemic to Europe. *Liriodendron tulipifera* and several species of *Magnolia* are important ornamentals.

## Analyzed material

The xylem and phloem of 6 Magnoliaceae species were analyzed. These species are commonly planted in the hill zone of Central Europe.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 6 | >20 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 6 | |

**Analyzed species:**

*Liriodendron tulipifera* L.
*Magnolia acuminata* L.
*Magnolia denudata* Desr.
*Magnolia grandiflora* L.
*Magnolia x soulangiana* Soul. et Bod.
*Magnolia virginiana* L.

**Right:** *Liriodendron tulipifera* (photo: Zinnert)

*Magnolia grandiflora* (photo: Zinnert)

*Magnolia stellata*

**Characteristics of the xylem**

The anatomy of the Magnoliaceae-species analyzed here varies little. Annual rings occur in all species. Ring boundaries are defined by a slight semi-ring porosity (**Figs. 1** and **2**), rows of radial flat marginal tracheids and parenchyma cells (**Fig. 10**). Vessels are typically solitary or arranged in short radial multiples (2-4 vessels; **Figs. 1** and **2**). The earlywood vessel diameter varies between 30-70 µm. Vessel density varies between 100-200/mm$^2$. Vessel perforations are in the majority of cases simple (**Fig. 3**) but are scalariform in *Magnolia grandiflora* (**Fig. 4**) and in *Liriodendron tulipifera* (**Fig. 5**). Inter-vessel pits tend to be scalariform (**Fig. 6**) or round in opposite position (*Liriodendron tulipifera*; **Fig. 7**). Vessel-ray pits are round or have horizontal enlarged apertures (**Figs. 8** and **13**). In all species the radial walls of fibers are perforated by small slit-like or round pits (<3 µm; **Fig. 9**). Fibers are thin- to thick-walled (**Figs. 1**, **2** and **10**). Axial parenchyma is marginal (**Figs. 10** and **11**) but difficult to recognize within the annual ring. All species have rays with 1-3 cells in width (**Fig. 12**). Rays are homocellular or slightly heterocellular with 1-2 marginal upright cells (**Fig. 13**).

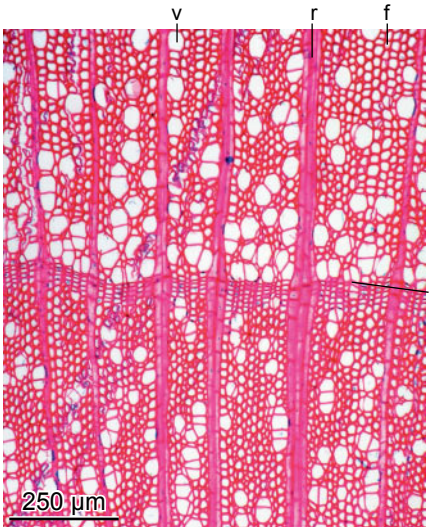



**Fig. 1.** Distinct annual rings. Ring boundaries are defined by semi-ring porosity and a marginal band of tracheids and parenchyma cells. Branch of a 4 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Magnolia soulangiana*, transverse section.

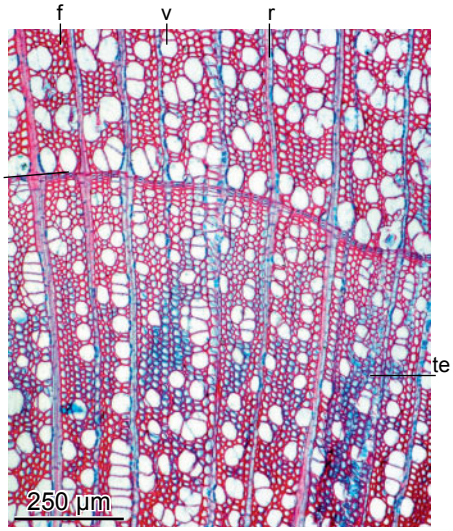



**Fig. 2.** Distinct annual rings. Ring boundaries are defined by semi-ring porosity. Branch of a 10 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Liriodendron tulipifera*, transverse section.

**Fig. 3.** Simple perforations present. Large, round vessel-ray pits in horizontal rows. Branch of a 4 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Magnolia acuminata*, radial section.

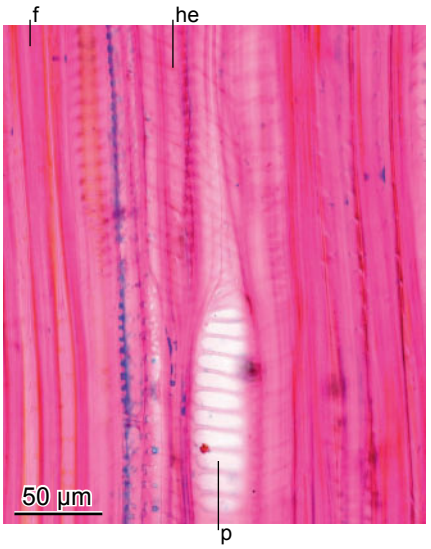



**Fig. 4.** Vessel with a scalariform perforation and thin helical thickenings. The ring boundary is defined by marginal tracheids and parenchyma cells with distinct simple pits (see **Fig. 11**). Branch of a 6 m-high tree, cultivated in a garden in Bakersfield, California, USA. *Magnolia grandiflora*, radial section.

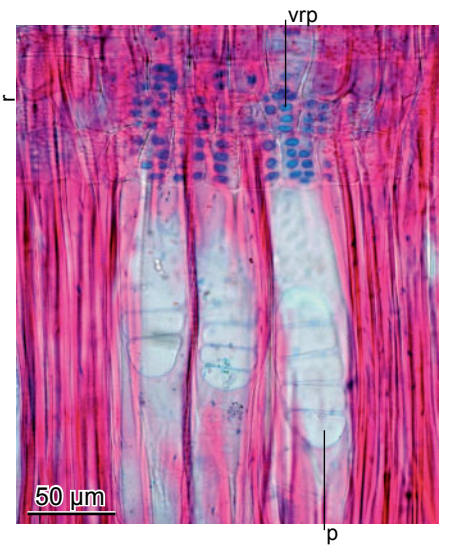



**Fig. 5.** Scalariform perforations with 3 and 4 bars. Large round vessel-ray pits in horizontal rows. Branch of a 10 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Liriodendron tulipifera*, radial section.

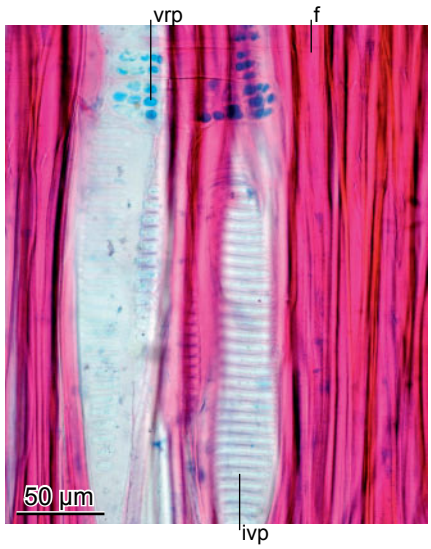



**Fig. 6.** Scalariform inter-vessel pits. Large round vessel-ray pits in horizontal rows. Branch of a 4 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Magnolia acuminata*, radial section.

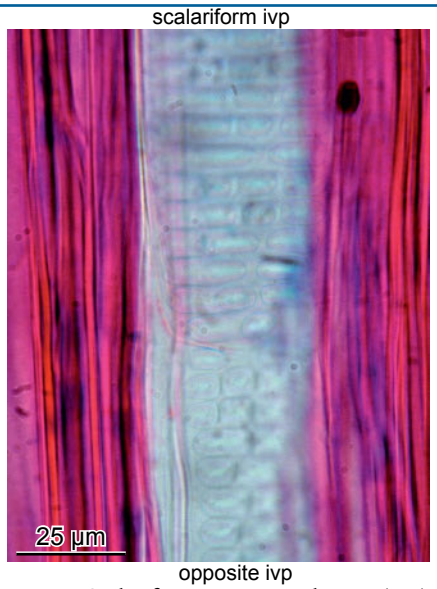
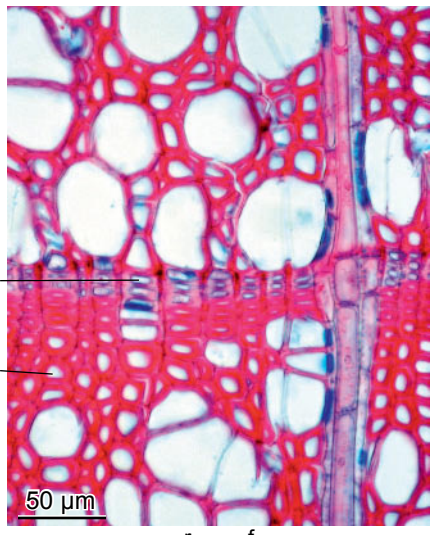
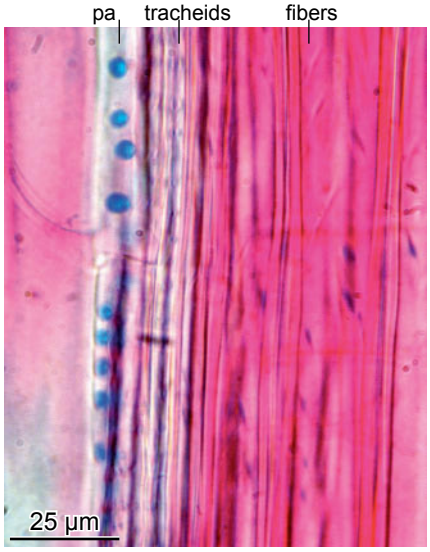



**Fig. 7.** Scalariform inter-vessel pits (top) and large round pits in opposite position. Branch of a 10 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Liriodendron tulipifera*, radial section.

**Fig. 8.** Vessel-ray pits with round apertures in central cells and with horizontally extended apertures in marginal cells (top). Branch of a 4 m-high tree, cultivated in the Botanical Garden Brissago Island, Switzerland. *Magnolia denudata*, radial section.

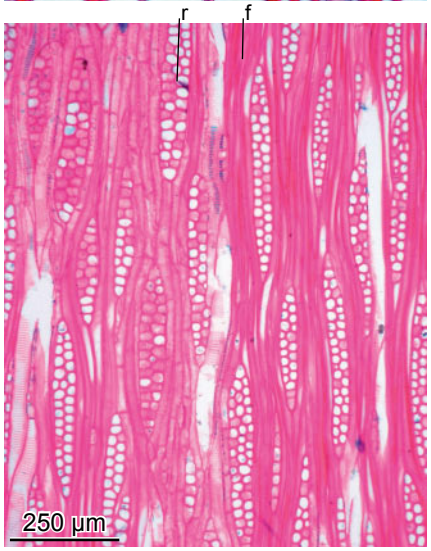
**Fig. 9.** Fibers with bordered pits with slit-like apertures. Branch of a 4 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Magnolia soulangiana*, radial section.

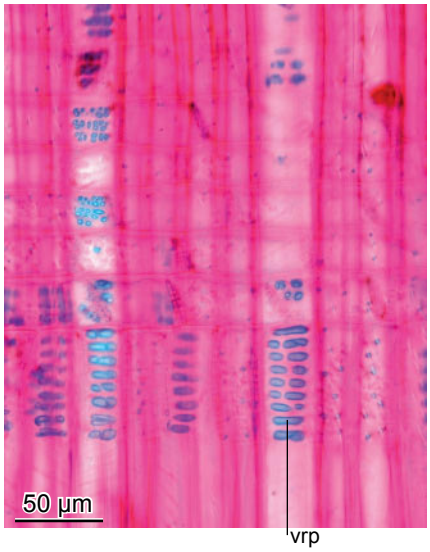



**Left Fig. 10.** Band of thick-walled marginal fibers. Branch of a 10 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Liriodendron tulipifera*, transverse section.

**Right Fig. 11.** Ring boundary. The latewood consists of intensively lignified fibers. The marginal zone is composed of a few rows of fibers with bordered pits (tracheids) and a single row of parenchyma with large simple pits. Branch of a 4 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Magnolia acuminata*, radial section.




**Left Fig. 12.** Ray with 2-3 cells wide. Branch of a 4 m-high tree. Cultivated in the Botanical Garden Zürich, Switzerland. *Magnolia soulangiana*, tangential section.

**Right Fig. 13.** Heterocellular ray with one row of marginal upright cells. Branch of a 6 m-high tree, cultivated in a garden in Bakersfield, California, USA. *Magnolia grandiflora*, radial section.

### Characteristics of the phloem and the cortex

The anatomy of the bark of the Magnoliaceae is very homogeneous (**Figs. 14** and **15**). Characteristic of all species is the presence of tangential arranged rectangular groups of thick-walled fibers and distinct ray dilatations and mucilage cells (Gregory and Baas 1989). In all species, mucilage cells occur in the cortex and at the periphery of the pith (**Fig. 16**).

### Characteristic features of taxa

Within the genus *Magnolia*, *Magnolia grandiflora* is differentiated from the other species analyzed here by the presence of scalariform perforations and helical thickenings. *Liriodendron tulipifera* is difficult to differentiate from *Magnolia* sp.; only the presence of intervascular pits in opposite position seems to be characteristic of *Liriodendron*.

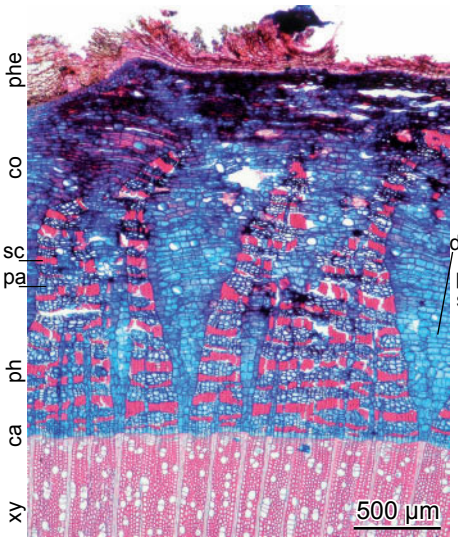



**Fig. 14.** Phloem with distinct tangential layers of intensively lignified fibers (red) and ray dilatations. Ray cell walls are unlignified (blue). Branch of a 4 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Magnolia acuminata*, transverse section.

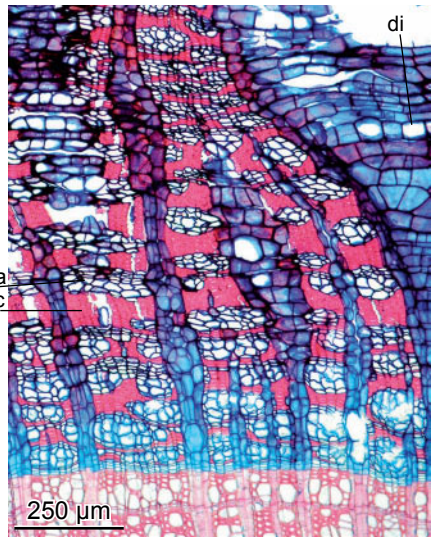



**Fig. 15.** Phloem with distinct tangential layers of fibers (red) and ray dilatations. A large mucilage cell occurs in the central ray. Branch of a 10 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Liriodendron tulipifera*, transverse section.

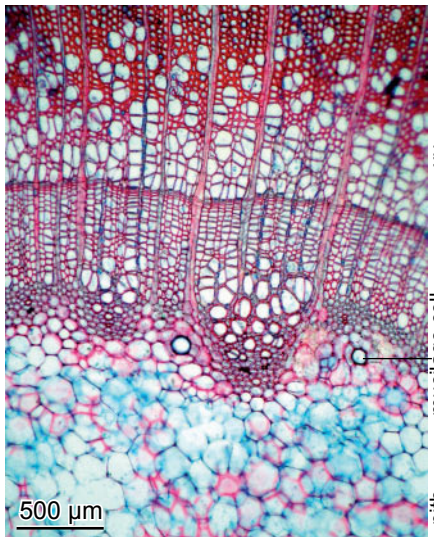



**Fig. 16.** Mucilage cells occur at the external border of the pit (dark walls). Twig of a 4 m-high tree, cultivated in the Botanical Garden Zürich, Switzerland. *Magnolia acuminata*, transverse section.

### Ecological trends and relations to life forms

No ecological trends were found.

### Discussion in relation to previous studies

A comprehensive wood anatomical study of the xylem of the family does not exists, but Gregory (1994) mentions 98 references in which single species or groups of species are discussed. *Liriodendron tulipifera* has been described numerous times e.g by Greguss (1945) and Grosser (1977). Jaquiot et al. (1973) and Zhang et al. (2000) describe *Magnolia acuminata* and *M. grandiflora*. Species descriptions presented here agree with those of previous studies, suggesting that this study should be fairly representative of the whole family.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| | **Total number of species** | **6** |
| 1 | growth rings distinct and recognizable | 6 |
| 4 | semi-ring-porous | 6 |
| 5 | diffuse-porous | 6 |
| 9 | vessels predominantly solitary | 2 |
| 9.1 | vessels in radial multiples of 2-4 common | 6 |
| 13 | vessels with simple perforation plates | 4 |
| 14 | vessels with scalariform perforation plates | 2 |
| 20 | intervessel pits scalariform | 2 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 6 |
| 36 | helical thickenings present | 6 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 6 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 3 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 6 |
| 61 | fiber-pits small and simple to minutely bordered (<3 µm = libriform fibers) | 6 |
| 70 | fibers thin- to thick-walled | 6 |
| 75 | parenchyma absent or unrecognizable | 5 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 89 | parenchyma marginal | 6 |
| 97 | ray width predominantly 1-3 cells | 6 |
| 104 | ray: all cells procumbent (radial section) | 6 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| R1 | groups of sieve tubes present | 5 |
| R3 | distinct ray dilatations | 5 |
| R4 | sclereids in phloem and cortex | 5 |
| R6.1 | sclereids in tangential rows | 5 |
| R12 | with laticifers, oil ducts or mucilage ducts | 5 |
| P2 | with laticifers or intercellular canals | 5 |

# Malvaceae



**Number of species, worldwide and in Europe**

The cosmopolitean Malvaceae family includes 75 genera with 1500 species. In Europe, there are 9 genera with 40 endemic species.

**Analyzed material**

The xylem and phloem of 11 genera with 25 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | | 15 genera |
| Nanophanerophytes 0.5-4 m | 9 | 3 genera |
| Woody chamaephytes | 2 | |
| Hemicryptophytes | 12 | |
| Therophytes | 2 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 8 | |
| Mediterranean | 8 | |
| Arid | 5 | |
| Suptropical | 4 | |

**Analyzed species:**

*Abelmoschus esculentus* (L.) Moench
*Abutilon palmeri* A. Grey
*Alcea rugosa* Alef.
*Althaea hirsuta* L.
*Althaea officinalis* L.
*Cristaria dissecta* Hook et Arn
*Gossypium herbaceum* L.
*Gossypium stoksii* Masters
*Hibiscus rosa-sinensis* L.
*Hibiscus syriacus* L.
*Lavatera acerifolia* Cav.
*Lavatera arborea* L.
*Lavatera assurgentiflora* Kellog.
*Lavatera maritima* Gouhan
*Lavatera oblongifolia* Boiss.
*Lavatera olbia* L.
*Malva moschata* L.
*Malva neglecta* Wallr.
*Malva parviflora* L.
*Malva sylvestris* L.
*Senra incana* Cav.
*Sphaeralcea ambigua* A. Grey
*Sphaeralcea coccinea* Rydb.
*Sphaeralcea coulteri* Brandeg.
*Sphaeralcea miniata* (Cav.) Spach

*Gossypium* sp. (photo: Lauerer)

*Hibiscus syriacus*

*Alcea rosea* (photo: Zinnert)

**Characteristics of the xylem**

Rings are exceptionally distinct in *Hibiscus syriacus* (**Fig. 1**), and distinct in *Lavatera oblongifolia* and all *Sphaeralacea* species (**Figs. 2** and **3**). Ring boundaries of most species are rather indistinct or absent (**Figs. 4-10**). Only *Hibiscus syriacus* is ring-porous. Semi-ring-porosity to diffuse-porosity are the dominant vessel distribution patterns within the family (**Figs. 2** and **3**). Tangentially arranged vessel bands occur in different species of the genera *Malva* and *Lavatera* (**Fig. 10**). Vessel groups of *Lavatera oblongifolia* are in radial to diagonal patterns (**Fig. 11**). Earlywood vessels usually vary from 50-100 µm in diameter and vessel density varies from 100-200/mm$^2$. Vessels with a diameter larger 100 µm are characteristic of *Abelmoschus*, *Gossypium* and *Senra*. Low vessel density occurs in various species throughout the family. Vessels of all species have simple perforations. Intervessel pits are round and mostly arranged in alternating position. Thin helical thickenings occur in *Hibiscus syriaca*, *Lavatera olbia* and *Spharalcea coulteri* (**Figs. 12** and **13**). Transitional forms between scalariform intervessel pits and helical thickening occur in *Lavatera oblongifolia* (**Fig. 13**).

Fibers have small pits with slit-like apertures. Fibers vary from a combination of thin- and thin- to thick-walled (**Figs. 8** and **9**) to only thick-walled (**Figs. 7**, **11**, **14** and **15**). Both features can occur within one individual.

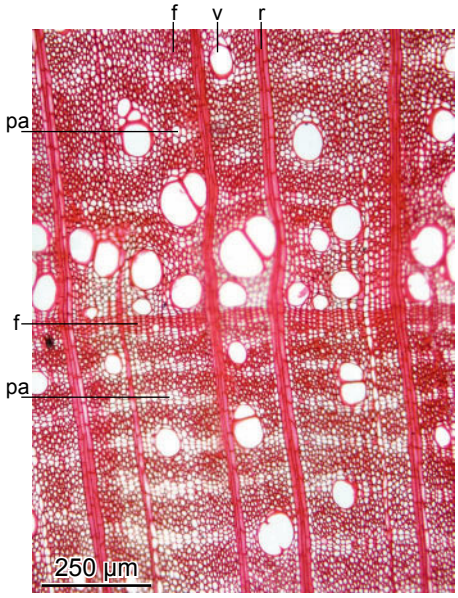



**Fig. 1.** Distinct ring boundary of a ring-porous-wood. Interrupted tangential parenchyma bands occur mainly in the latewood. Stem of a 2 m-high shrub, cultivated, hill zone, Zürich, Switzerland. *Hibiscus syriacus*, transverse section.

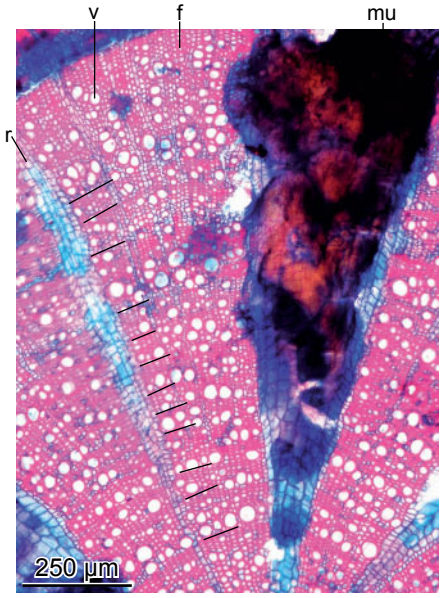



**Fig. 2.** Semi-ring-porous xylem with fairly distinct rings. The large dilated ray contains mucilage. Root collar of a 40 cm-high hemicryptophyte, steppe, mountain zone, Monte Vista, Colorado, USA. *Sphaeralcea coccinea*, transverse section.

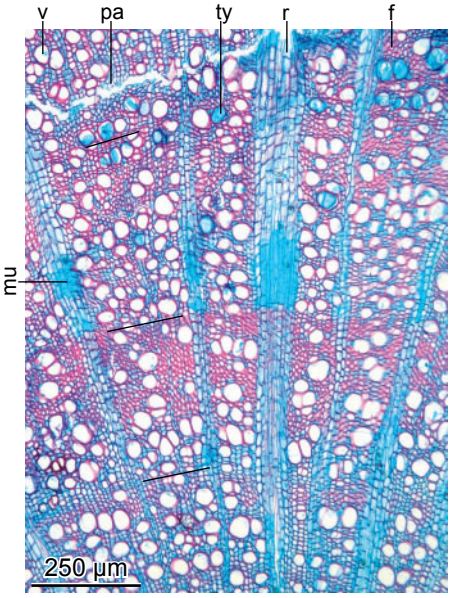
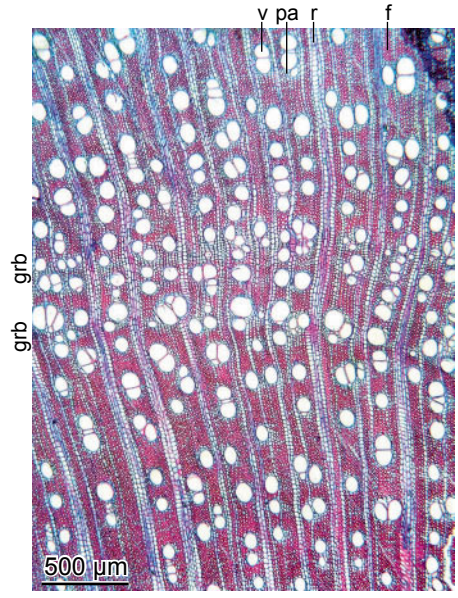
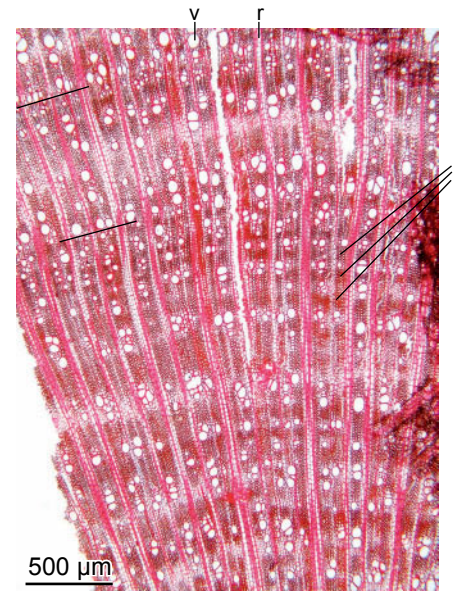



**Fig. 3.** Semi-ring-porous xylem with distinct rings. Some vessels contain tylosis. Root collar of a 40 cm-high hemicryptophyte, steppe, mountain zone, Canyon de Chelly, Colorado, USA. *Sphaeralcea coulteri*, transverse section.




**Left Fig. 4.** Semi-ring-porous wood with growth zones. Vessels are solitary and in short radial multiples. Parenchyma is mainly vasicentric paratracheal. Stem of a 2 m-high shrub, ruderal site, subtropical climate, Tenerife, Canary Islands. *Gossypium herbaceum*, transverse section.

**Right Fig. 5.** Growth zones are characterized by tangentially arranged vessel groups and fibers of variable thickness. Stem of a 1.5 m-high shrub, ruderal site, Mediterranean, Thermon, Greece. *Lavatera arborea*, transverse section.

The distribution of axial parenchyma is mostly scanty paratracheal (**Fig. 14**) or apotracheal in uni- or multiseriate tangential bands (**Fig. 15**). Transitions occur within one individual. Parenchyma strands are storied in *Hibiscus* and *Lavatera* (**Fig. 15**). Most species are characterized by large ray cells. Ray width varies from uni- to multiseriate (<10 cells). Uni- and bi-seriate rays occur mainly in *Cristaria* (**Fig. 17**), while rays are 2-4- (**Figs. 18** and **19**) or 3-6-seriate in most other species (**Figs. 20** and **21**). Rays are unlignified in a few species (*Alcea rugosa*, *Lavatera hirsuta*, *Malva parviflora*; **Fig. 21**). Most species are characterized by homocellular rays with upright and square cells (**Fig. 22**) or by heterocellular rays with one to a few cells of square and upright cells (**Figs. 23** and **24**). Transitions between the different types of rays are frequent. Many species contain mucilage. It is mainly produced in ray cells (**Figs. 2** and **10**) but also in axial parenchyma cells (**Fig. 25**) . Crystals (prismatic crystals or crystal druses) occur in all species except in *Cristaria dissecta*.

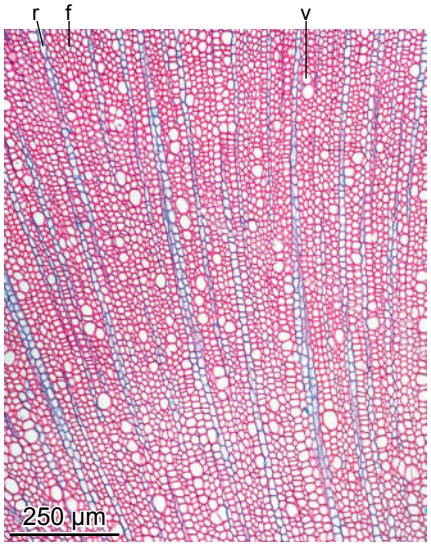



**Fig. 6.** Ring boundaries are absent. Small vessels are solitary and in small radial groups. The fiber tissue is thin-walled. Root collar of a 40 cm-high chamaephyte, shrub desert, arid zone, Vallenar, Patagonia, Chile. *Cristaria dissecta*, transverse section.

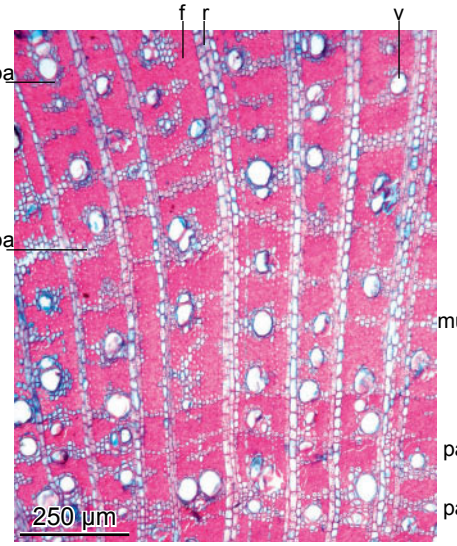



**Fig. 7.** Solitary vessels are surrounded by thick-walled fibers and tangentially arranged parenchyma bands. Stem of a 1.5 m-high shrub, rock field, thermophile zone, subtropical climate, Buena Vista, Tenerife, Canary Islands. *Lavatera acerifolia*, transverse section.

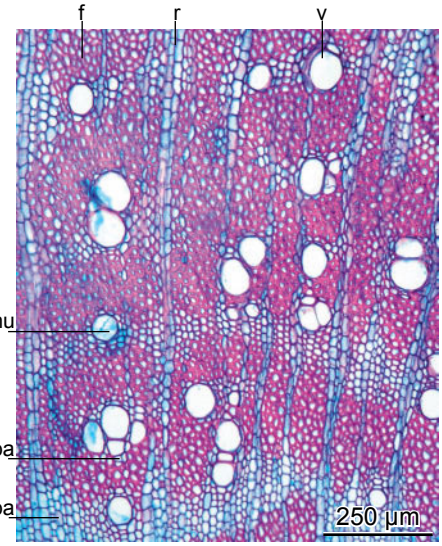



**Fig. 8.** Large vessels are surrounded by fibers and irregular tangentially arranged parenchyma bands. Stem of a 1.5 m-high therophyte, cultivated, hill zone, Birmensdorf, Switzerland. *Althaea officinalis*, transverse section.

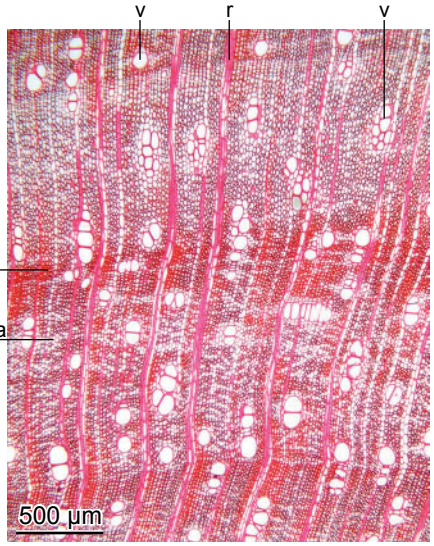



**Fig. 9.** Short and long radial multiples are surrounded by an irregular fiber/parenchyma tissue. Stem of a 2 m-high shrub, hedge, cultivated, Mediterranean zone, Paphos, Cyprus, Greece. *Hibiscus rosa-sinensis*, transverse section.

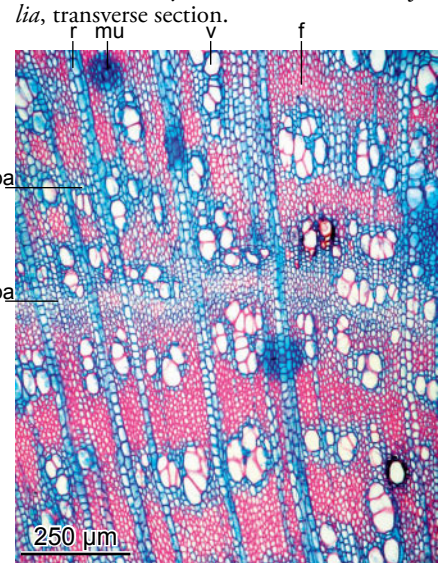



Fig. 10. Irregular vessel groups are arranged in tangential bands. Parenchyma is paratracheal vasicentric and arranged in tangential bands. Blue diffuse dots represent mucilage. Root collar of a 30 cm-high hemicryptophyte, abandoned field, submediterranean, Le Puy en Velais, France. *Malva moschata*, transverse section.

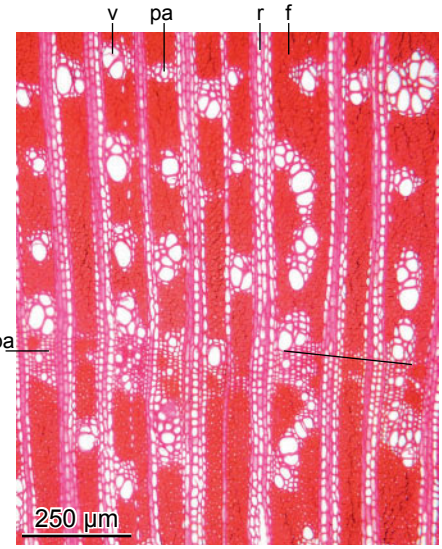



**Fig. 11.** Radial vessel groups are surrounded by paratracheal parenchyma and thick-walled fibers. Parenchyma cells are concentrated in the latewood. Stem of a 1 m-high shrub, maccia, Mediterranean, Agra, Andalusia, Spain. *Lavatera oblongifolia*, transverse section.

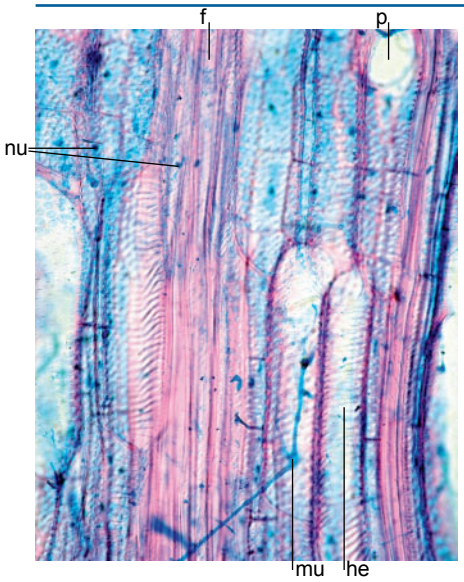



**Fig. 12.** Vessel with helical-like thickenings and a simple perforation. Root collar of a 40 cm-high hemicryptophyte, steppe, mountain zone, Canyon de Chelly, Colorado, USA. *Sphaeralcea coulteri*, radial section.

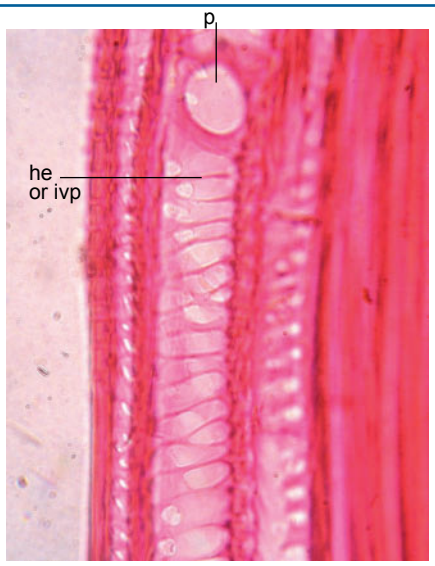



**Fig. 13.** Vessel with simple perforation and transitions between helical thickenings and intervessel pits. Stem of a 1 m-high shrub, maccia, Mediterranean, Agra, Andalusia, Spain. *Lavatera oblongifolia*, radial section.

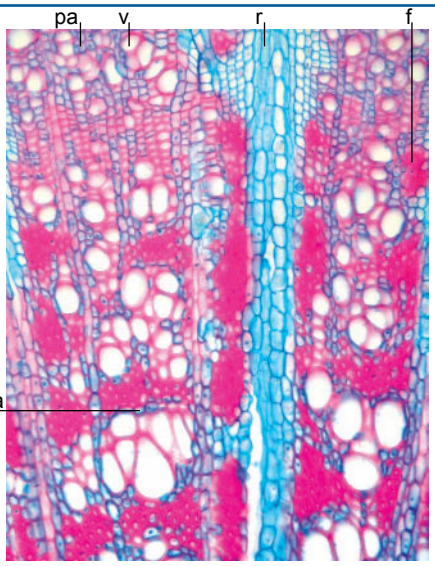
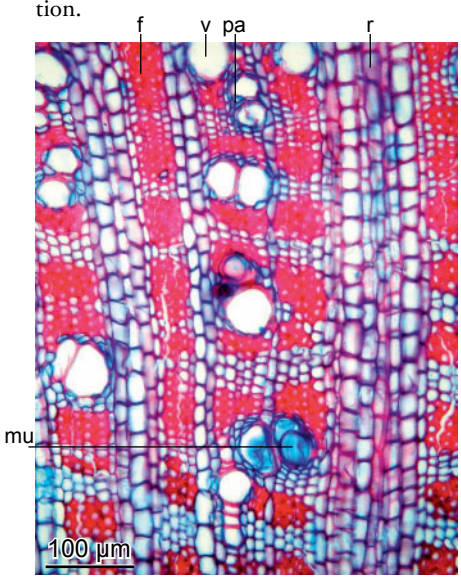
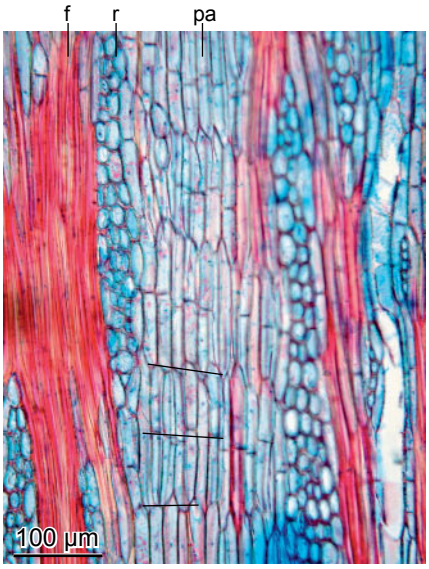


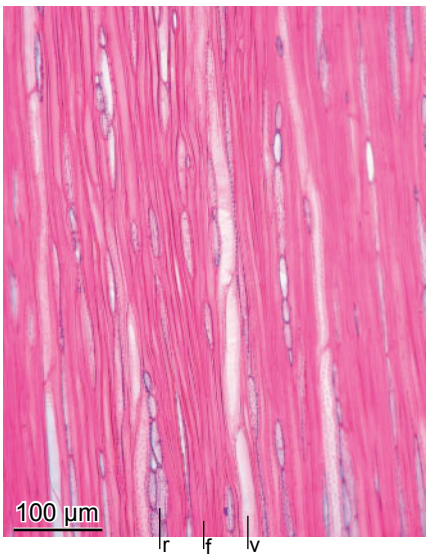

**Fig. 14.** Vessel groups are surrounded by vasicentric parenchyma, and thick-walled fibers. The large ray is unlignified. Root collar of a 40 cm-high hemicryptophyte, steppe, arid zone, Twentynine Palms, California, USA. *Sphaeralcea ambigua*, transverse section.

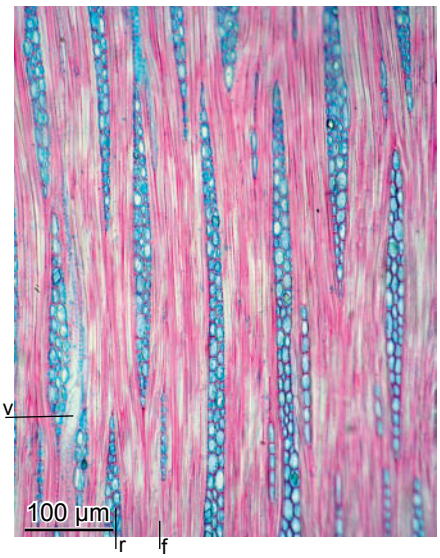



**Left Fig. 15.** Vessels are surrounded by vasicentric parenchyma. Bands of thin-walled parenchyma occur between bands of thick-walled fibers. Two vessels contain mucilage. Root collar of an 80 cm-high hemicryptophyte, Mediterranean zone, Botanical Garden Santa Barbara, California, USA. *Lavatera assurgentiflora*, transverse section.

**Right Fig. 16.** Strands of storied parenchyma between fibers and 1-5-seriate rays. Stem of a 1.5 m-high shrub, rock field, thermophile zone, subtropical, Buena Vista, Tenerife, Canary Islands. *Lavatera acerifolia*, tangential section.




**Left Fig. 17.** Uni-and biseriate rays. Many ray-cells are axially elongated. Root collar of a 40 cm-high chamaephyte, shrub desert, arid zone, Vallenar, Chile. *Cristaria dissecta*, tangential section.

**Right Fig. 18.** 2-3-seriate rays with round cells. Root collar of an 80 cm-high hemicryptophyte, Mediterranean zone, Botanical Garden Santa Barbara, California, USA. *Abutilon palmeri*, tangential section.

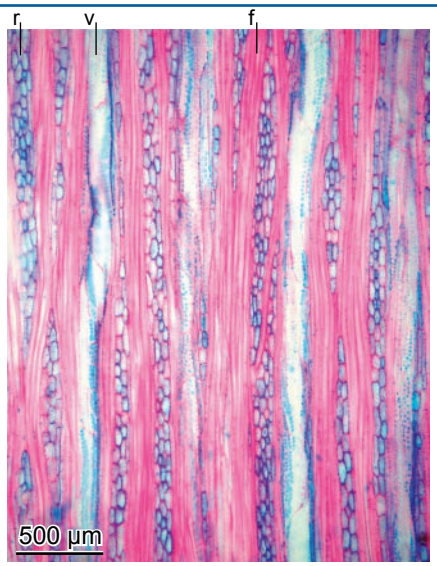



**Fig. 19.** 2-4-seriate rays. Root collar of a 50 cm-high hemicryptophyte, steppe, Valle Fertil, Patagonia, Argentina. *Sphaeralcea miniata*, tangential section.

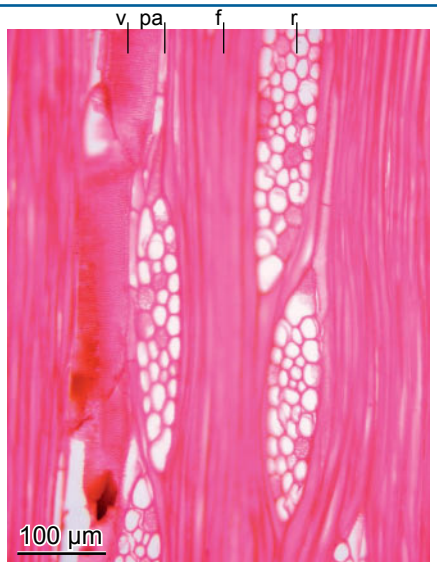



**Fig. 20.** 4-5-seriate rays with large cells. Stem of a 2 m-high shrub, hedge, cultivated, Mediterranean zone, Paphos, Cyprus, Greece. *Hibiscus rosa-sinensis*, tangential section.

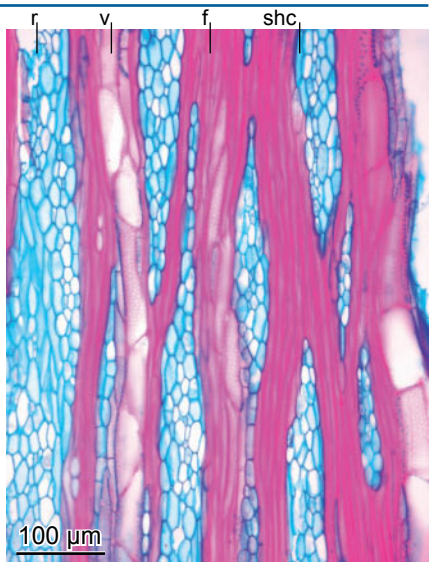
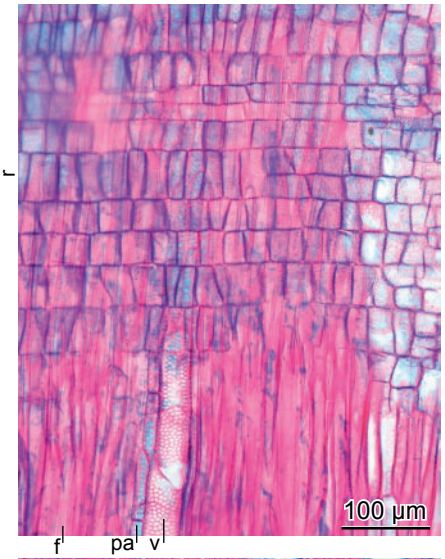
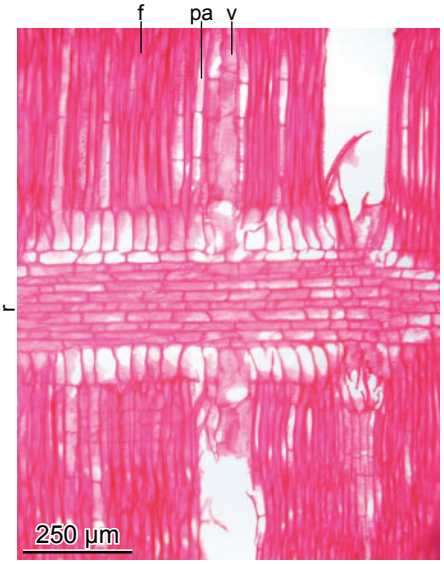


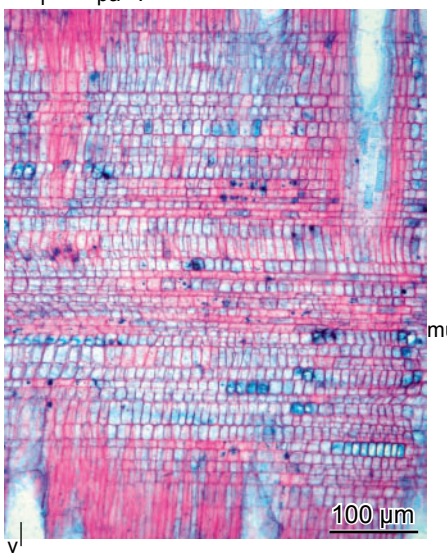

**Fig. 21.** Large rays with sheet cells consisting of unlignified cells. Root collar of an 80 cm-high hemicryptophyte, dry abandoned field, hill zone, Tibilisi, Georgia. *Alcea rugosa*, tangential section.

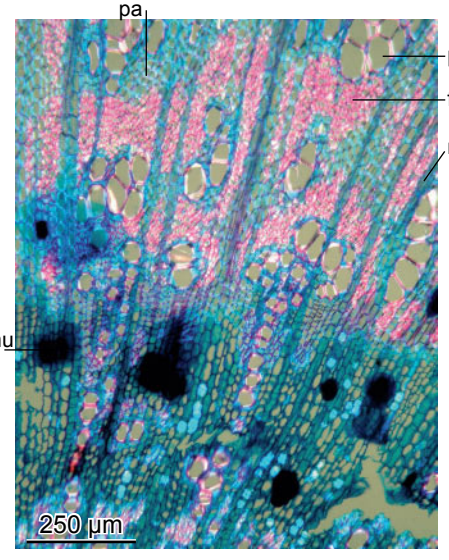



**Left Fig. 22.** Homocellular ray consisting of upright and square cells. Stem of a 1.5 m-high therophyte, cultivated, hill zone, Birmensdorf, Switzerland. *Althaea officinalis*, radial section.

**Right Fig. 23.** Heterocellular ray consisting of procumbent central cells, and upright and square marginal cells. Stem of a 2 m-high shrub, hedge, cultivated, Mediterranean zone, Paphos, Cyprus, Greece. *Hibiscus rosa-sinensis*, radial section.




**Left Fig. 24.** Heterocellular ray consisting of a few procumbent and many upright and square marginal cells. Stem of a 2 m-high shrub, ruderal site, subtropical climate, Tenerife, Canary Islands. *Gossypium herbaceum*, radial section.

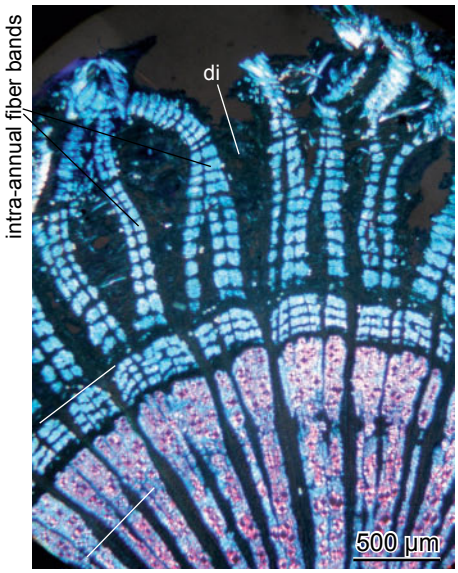
**Right Fig. 25.** Mucilage patches in the inner parenchymatic part of the stem. Root collar of a 60 cm-high hemicryptophyte, ruderal site, hill zone, Le Puy en Velais, France. *Malva sylvestris*, transverse section, polarized light.

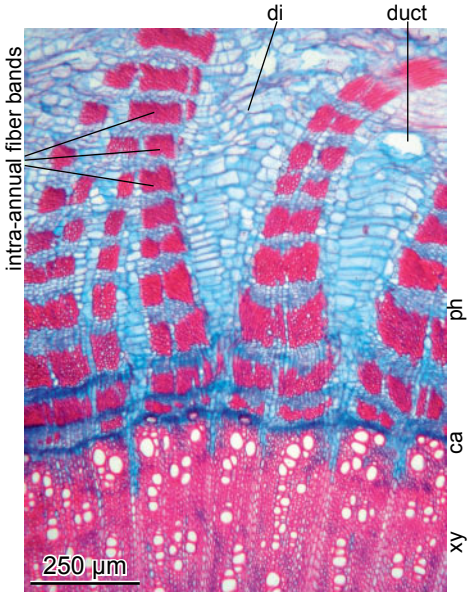
### Characteristics of the phloem and the cortex

Tangentially arranged rectangular groups of sclerenchyma (**Figs. 26** and **27**) and the presence of mucilage and crystal druses and/or prismatic crystals and mucilage are characteristic of well-grown individuals. Mucilage is produced in parenchymatic ray cells (**Fig. 28**) or in ducts within rays (**Fig. 29**). All of these features are absent in *Cristaria dissecta*.

### Characteristic features of taxa

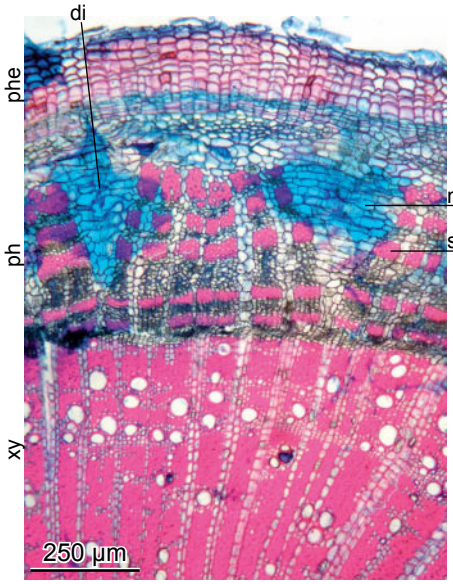
Characteristic of the family are many species with large vessels and tangential parenchymatic bands in the xylem. Species with indistinct large rings are common. Bark structures of different species within the family are very similar. Characteristic are the tangential bands of sclerenchyma and the mucilage producing parenchyma cells.

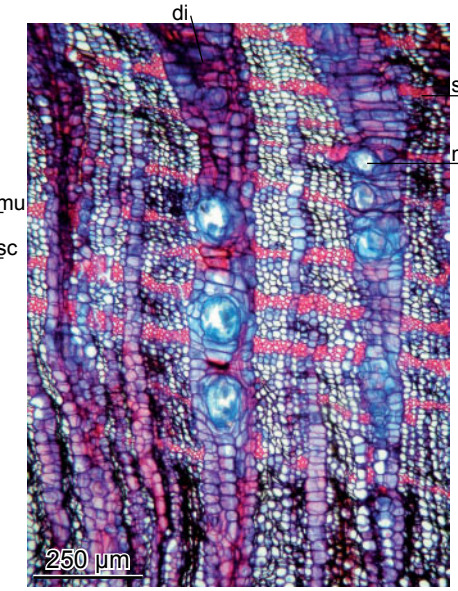



**Left Fig. 26.** Phloem with distinct ray dilatations and many tangential layers of sclerenchyma located in a bi-annual plant. Root collar of a 40 cm-high hemicryptophyte, abandoned field, submediterranean, Le Puy en Velais, France. *Malva moschata*, transverse section, polarized light.

**Right Fig. 27.** Phloem with distinct ray dilatations and many tangential layers of sclerenchyma located in a bi-annual plant. Root collar of a 40 cm-high hemicryptophyte, ruderal site, submediterranean, Postoina, Slovenia. *Malva neglecta*, transverse section.




**Left Fig. 28.** Phloem with distinct ray dilatations and many tangential layers of sclerenchyma. Dilated rings are filled with mucilage (blue). The phellem consists of rectangular, regularly radial oriented cells. Stem of a 1.5 m-high shrub, rock field, thermophile zone, subtropical zone, Buena Vista, Tenerife, Canary Islands. *Lavatera acerifolia*, transverse section.

**Right Fig. 29.** Mucilage ducts in large rays. Stem of a 2 m-high shrub, ruderal site, subtropical climate, Tenerife, Canary Islands. *Gossypium herbaceum*, transverse section.

### Ecological trends and relations to life forms

Dominant anatomical differences are mainly caused by taxonomy. *Cristaria dissecta* is very different from all other species. Anatomical differences between life forms (shrubs and dwarf shrubs), from different vegetation belts and life forms cannot be recognized.

### Discussion in relation to previous studies

Most previous studies have described tropical species (Gregory 1994). Many authors described different species of *Hibiscus* and *Gossypium* and a few described the genera *Abutilion*, *Lavatera* and *Sphaeralcea*. Detailed descriptions of the genera *Abelmoschus*, *Althaea*, *Cristaria*, *Malva* and *Senra* are new here along with all bark descriptions.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **25** |
| 1 | growth rings distinct and recognizable | 12 |
| 2 | growth rings absent | 15 |
| 2.1 | only one ring | 2 |
| 3 | ring-porous | 2 |
| 4 | semi-ring-porous | 2 |
| 5 | diffuse-porous | 5 |
| 6 | vessels in intra-annual tangential rows | 7 |
| 9 | vessels predominantly solitary | 11 |
| 9.1 | vessels in radial multiples of 2-4 common | 10 |
| 10 | vessels in radial multiples of 4 or more common | 8 |
| 11 | vessels predominantly in clusters | 10 |
| 13 | vessels with simple perforation plates | 25 |
| 21 | intervessel pits opposite | 3 |
| 22 | intervessel pits alternate | 24 |
| 31 | vessel-ray pits with large apertures, *Salix/Laurus* type | 1 |
| 36 | helical thickenings present | 4 |
| 39.1 | vessel cell-wall thickness >2 µm | 4 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 3 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 18 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 5 |
| 50 | <100 vessels per mm$^2$ in earlywood | 12 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 15 |
| 56 | tylosis with thin walls | 3 |
| 58 | dark staining substances in vessels and/or fibers (gum, tannins) | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 25 |
| 68 | fibers thin-walled | 2 |
| 69 | fibers thick-walled | 5 |
| 70 | fibers thin- to thick-walled | 19 |
| 70.1 | intra-annual thick-walled tangential fiber-bands | 2 |
| 75 | parenchyma absent or unrecognizable | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 10 |
| 79 | parenchyma paratracheal | 22 |
| 85 | axial parenchyma bands more than three cells wide, *Ficus/Urtica* type | 9 |
| 89 | parenchyma marginal | 2 |
| 97 | rays width predominantly 1-3 cells | 11 |
| 98 | rays commonly 4-10-seriate | 15 |
| 99 | rays commonly >10-seriate | 3 |
| 100.2 | rays disappear in polarized light | 3 |
| 102 | ray height >1 mm | 1 |
| 104 | ray: all cells procumbent (radial section) | 3 |
| 105 | ray: all cells upright or square | 17 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 2 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 2 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 7 |
| 110 | rays with sheet cells (tangential section) | 10 |
| 120 | storied axial tissue (parenchyma, fibers, vessels in tangential section) | 3 |
| 124 | oil and mucilage cells | 3 |
| 136 | prismatic crystals present | 10 |
| 144 | druses present | 14 |
| 153 | crystal sand present | 1 |
| R1 | groups of sieve tubes present | 4 |
| R3 | distinct ray dilatations | 17 |
| R4 | sclereids in phloem and cortex | 18 |
| R6 | sclereids in radial rows | 1 |
| R6.2 | sclereids in tangentially arranged groups, *Rhamnus* type | 17 |
| R8 | with crystal druses | 17 |
| R9 | with crystal sand | 1 |
| R12 | with laticifers, oil ducts or mucilage ducts | 16 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 3 |

# Menispermaceae

**Number of species, worldwide and in Europe**

The pantropical Menispermaceae family has 71 genera with 450 species. Representatives of the family are absent from Europe.

**Analyzed material**

The xylem and phloem of the stem of one liana-like species (*Cocculus pendulus*) growing in a wadi of the central Sahara (arid climate) is described.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Liana | 1 | 77 |
| **Plants analyzed from different vegetation zones:** | | |
| Arid | 1 | |

**Analyzed species:**
*Cocculus pendulus* (J.R. Forst. & G. Forst.) Diels

*Cocculus pendulus* (photos: Cohen)

**Characteristics of the xylem**

Annual rings are absent in the analyzed species (**Figs. 1** and **2**). Vessels are solitary with a diameter of 50-160 µm (**Fig. 3**). Vessel density varies between 30-50/mm$^2$. Vessels contain exclusively simple perforations often in a horizontal position. Inter-vessel pits are round and distinctly bordered. Radial walls of fibers are perforated by round pits with slit-like apertures (tracheids; **Fig. 4**). Fibers are thin- to thick-walled (**Fig. 3**). Septate fibers are present (**Fig. 5**). Axial parenchyma is apotracheal (diffuse) and paratracheal (diffuse). Ray width varies between 4-8 cells (**Fig. 6**). Many new rays are initiated by the second row of vascular bundles (**Fig. 2**). Rays are heterocellular with 1-2 square and upright marginal cells (**Fig. 7**) and sheet cells (**Fig. 6**). Successive cambia are common. Vascular bundles are concentric and separated from each other. Each vascular bundle consists of a phloem with collapsed cells at the external side and a group of thick-walled fibers with small, slit-like pits (libriform fibers; **Figs. 3** and **8**). The conjunctive tissue outside the first zone of vascular bundles consists of a band of thick-walled sclereids and a band of thin-walled, unlignified cells (**Figs. 2** and **3**). Prismatic crystals occur in ray cells.

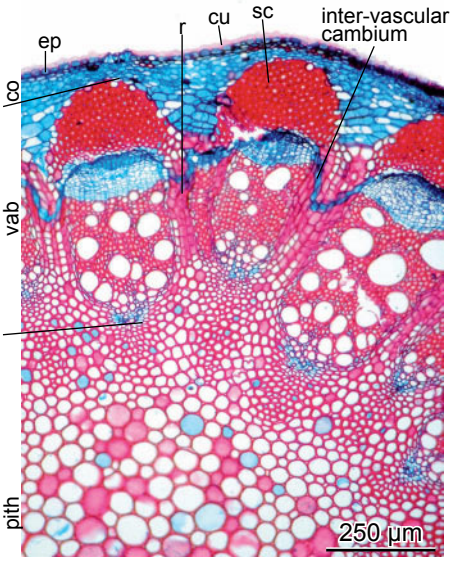



**Fig. 1.** Annual shoot with one row of concentrically arranged vascular bundles. The bundles are separated from each other by rays. Each bundle consists of a xylem, a phloem (blue) and a group of thick-walled fibers. Stem of a 3 m-long liana in a dry canyon (wadi), hyperarid zone of the Sahara, Fezzan, Libya. *Cocculus pendulus*, transverse section.

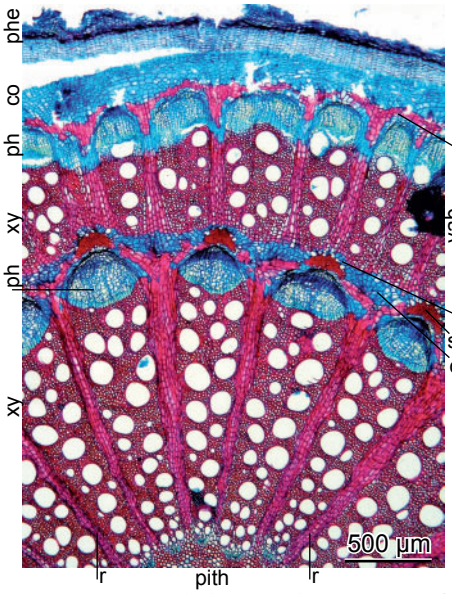



**Fig. 2.** Perennial shoot with two rows of concentrically vascular bundles. The second row contains more bundles than the first. See **Fig. 1** for origin, transverse section.

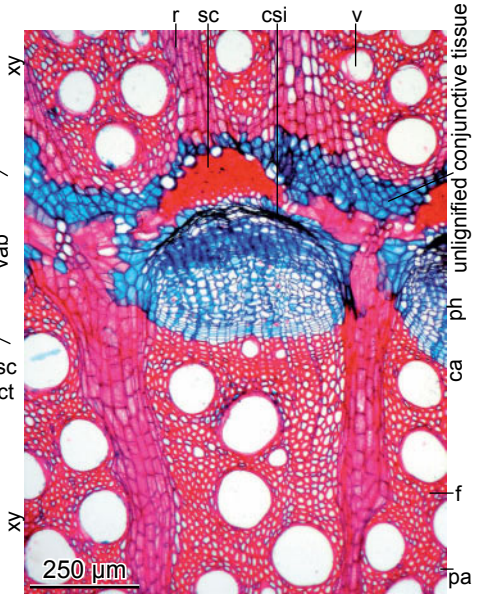
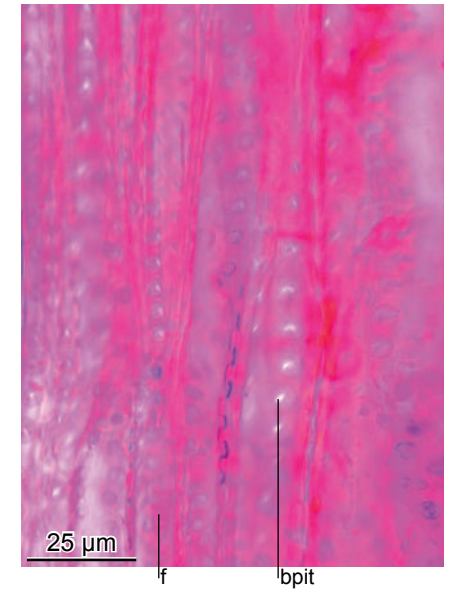
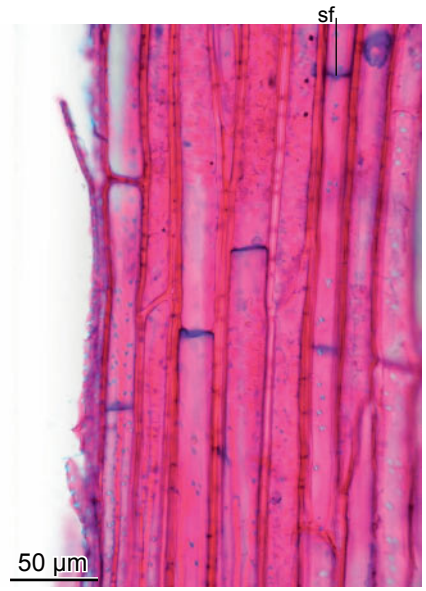



**Fig. 3.** Zone between the first and second row of vascular bundles. The bundles are tangentially separated by conjunctive tissue consisting of thick-walled sclereids and unlignified thin-walled parenchyma cells. Inactive phloem cells are collapsed. Parenchyma in the xylem is apotracheal and paratracheal. See **Fig. 1** for origin, transverse section.




**Left Fig. 4.** Tracheids with large, bordered pits. See **Fig. 1** for origin, radial section.

**Right Fig. 5.** Septate fibers. See **Fig. 1** for origin, radial section.

## Characteristic features of taxa

Jacques and Franceschi (2007) demonstrated, that the anatomical structure of species described here is similar to the majority of the family. The presence of concentric single vascular bundles (successive cambia) is characteristic.

## Characteristics of the phloem and the cortex

The bark is identical to the internal vascular bundles of the stem. The cortex zone is covered with a phellem consisting of many tangential rows of prismatic, thin-walled cork cells (**Fig. 8**).

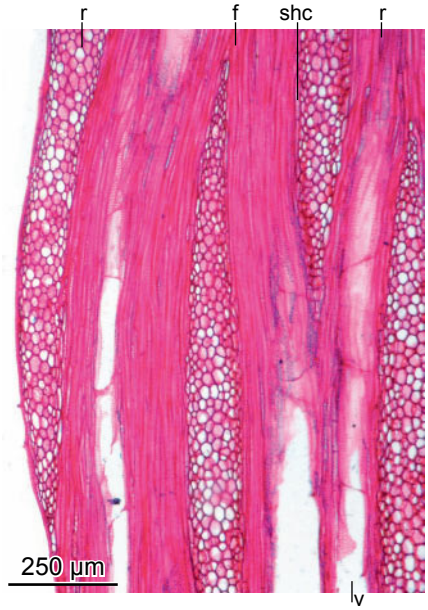



**Fig. 6.** Multiseriate rays partially bordered by sheet cells. See **Fig. 1** for origin, tangential section.

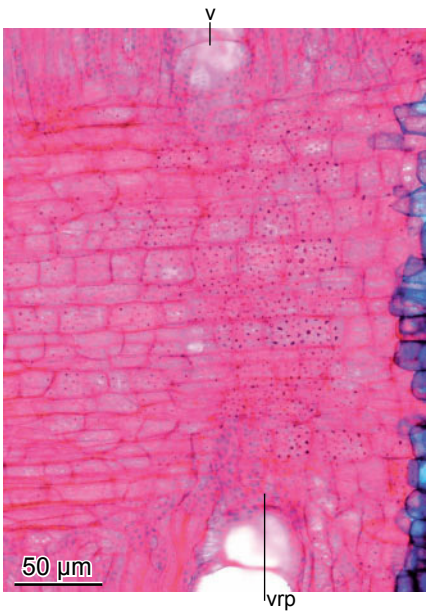



**Fig. 7.** Slightly heterocellular ray with one row of square to upright marginal cells. See **Fig. 1** for origin, radial section.

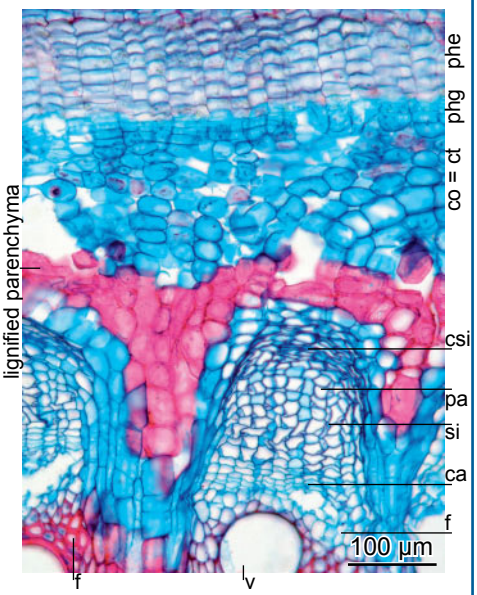



**Fig. 8.** Periphery of the perennial stem. The bark consists of phloem, conjunctive tissue, cortex and phellem. The cortex is characterized by round, thin-walled parenchyma cells and the phellem by a thick layer of thin-walled prismatic cork cells. See **Fig. 1** for origin, transverse section.

## Discussion in relation to previous studies

Carlquist (1996) describes 15 species from 15 genera and Jacques and Franceschi (2007) 77 species from 44 genera. The only species described here fits perfectly in the anatomical spectrum of the majority of species (Jacques and Franceschi 2007).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **1** |
| 2 | growth rings absent | 1 |
| 9 | vessels predominantly solitary | 1 |
| 13 | vessels with simple perforation plates | 1 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 1 |
| 50 | <100 vessels per mm² in earlywood | 1 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 1 |
| 65 | septate fibers present | 1 |
| 70 | fibers thin- to thick-walled | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 79 | parenchyma paratracheal | 1 |
| 98 | rays commonly 4-10-seriate | 1 |
| 99.1 | vascular-bundle form remaining | 1 |
| 110 | rays with sheet cells tangential section | 1 |
| 133.1 | successive cambia, concentrically arranged single vascular bundles | 1 |
| 134.1 | conjunctive tissue thin-walled | 1 |
| 136 | prismatic crystals present | 1 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R6.1 | sclereids in tangential rows | 1 |
| R7.1 | with acicular crystals | 1 |

# Menyanthaceae



**Number of species, worldwide and in Europe**

The cosmopolitean Menyanthaceae family includes 5 genera, 40 species. In Europe there are two genera with one species each (*Menyanthes trifoliata* and *Nymphoides peltata*).

**Analyzed species:**
*Menyanthes trifoliata* L. (rhizome)
*Nymphoides peltata* G.M. Kuntze (annual shoot)

**Analyzed material**
The xylem and phloem of 2 genera with 2 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Hydrophytes and Helophytes | 2 | 2 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 2 | |

*Nymphoides peltata*

*Menyanthes trifoliata* (photo: Zinnert)

*Menyanthes trifoliata* (photo: Zinnert)

### Characteristics of the xylem

Rayless vascular bundles without annual rings form a siphonostele without an inter-fascicular cambium in *Menyanthes* and the annual shoot of *Nymphoides peltata*. (**Figs. 1** and **2**). They are laterally isolated in *Menyanthes* (**Fig. 3**), but form a more-or-less compact circle in the rhizome of *Nymphoides* (**Fig. 5**). A one-cell thick endodermis surrounds the siphonostele (**Fig. 5**). The xylem contains vessels with diameters <50 µm, which stay solitary or form radial multiples (**Fig. 4**). Radial vessel walls with scalariform perforations are characteristic of *Menyanthes* (**Fig. 6**). Solitary vessels with simple perforations are typical for *Nymphoides* (**Fig. 7**). Both species have scalariform inter-vessel pits (**Figs. 6** and 7). Vessels are surrounded by a pervasive parenchyma (**Figs. 4** and **5**). Small strands of fibers occur along the pit side of the vascular bundles of *Menyanthes* (**Fig. 4**).

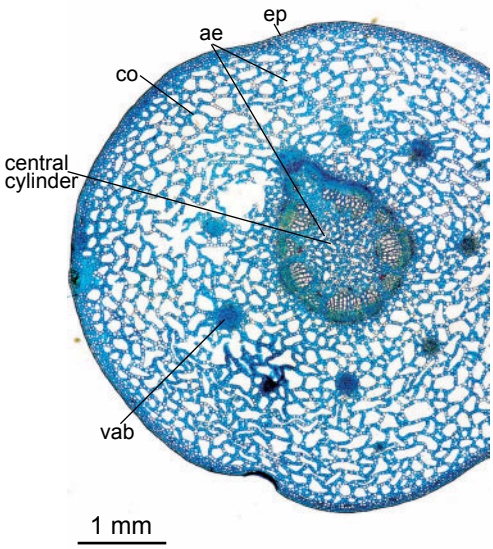



**Fig. 1.** Central cylinder with isolated vascular bundles. Large cortex with vascular bundles. Inter-cellular spaces exist in the cortex and the pith. Rhizome of plant in a pond in the mountain zone of the Alps, Switzerland. *Menyanthes trifoliata*, transverse section.

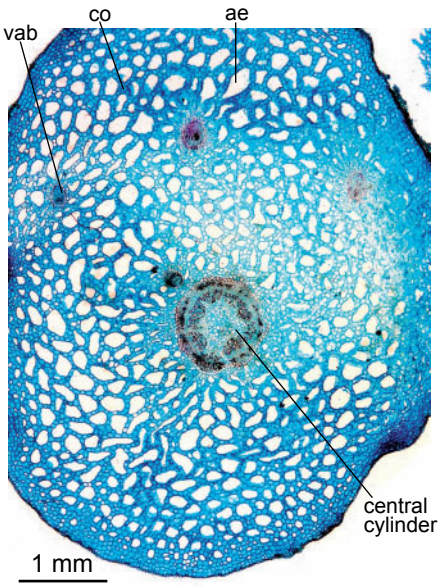



**Fig. 2.** Central cylinder with vascular bundles inside a cortex with small vascular bundles and many large inter-cellular spaces. Rhizome of plant in a pond, hill zone, Botanical Garden Zürich, Switzerland. *Nymphoides peltata*, transverse section.

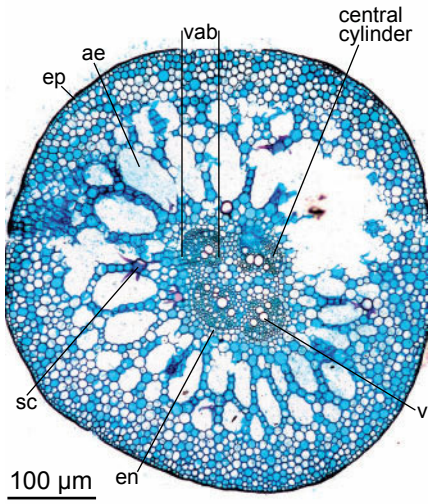
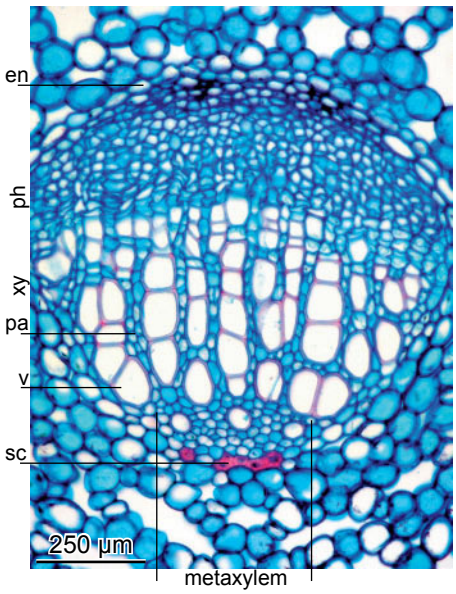
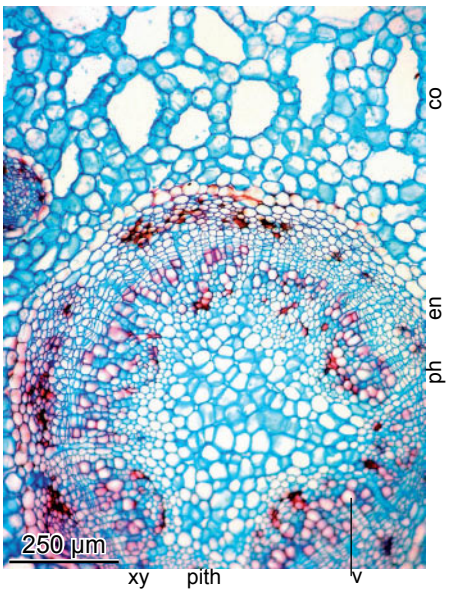


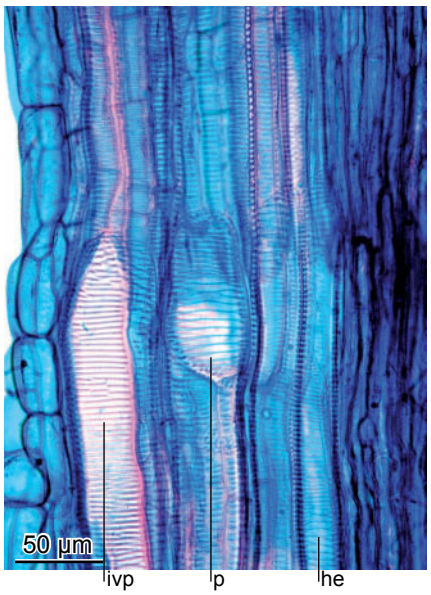

**Fig. 3.** Central cylinder with isolated vascular bundles. Large inter-cellular spaces in the cortex. Annual shoot of plant in a pond, hill zone, Botanical Garden Zürich, Switzerland. *Nymphoides peltata*, transverse section.

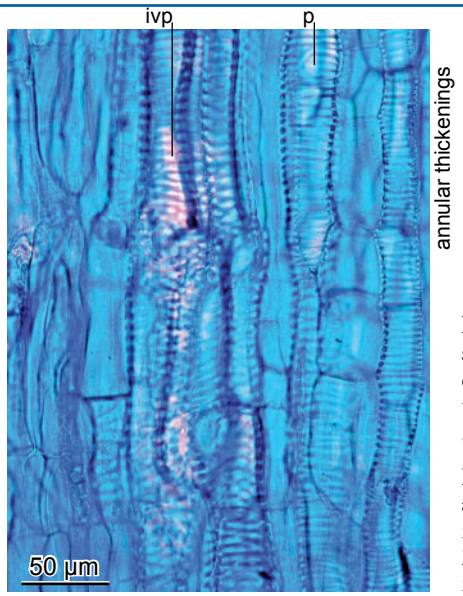



**Left Fig. 4.** Single rayless vascular bundle with vessels in radial multiples. On the outside is a thin-walled endodermis and on the inside few thick-walled lignified cells (red). Rhizome of plant in a pond, mountain zone, Alps, Switzerland. *Menyanthes trifoliata*, transverse section.




**Right Fig. 5.** Central cylinder with vascular bundles inside a cortex with large inter-cellular spaces. The pith has no intercellular cavities. The central cylinder is surrounded by a one cell-thick, thin-walled endodermis. Rhizome of plant in a pond, hill zone, Botanical Garden Zürich, Switzerland. *Nymphoides peltata*, transverse section.




**Left Fig. 6.** Scalariform inter-vessel pits, scalariform perforations and helical thickenings. Rhizome of plant in a pond, mountain zone, Alps, Switzerland. *Menyanthes trifoliat*a, radial section.

**Right Fig. 7.** Scalariform inter-vessel pits and simple perforations. Rhizome of plant in a pond, hill zone, Botanical Garden Zürich, Switzerland. *Nymphoides peltata*, radial section.

### Characteristics of the phloem and the cortex

Parenchyma and sieve tubes cannot be differentiated in the phloem (**Figs. 4** and **5**). Cortical vascular bundles are embedded in a net-like parenchyma with irregular intercellular spaces (**Figs. 1** and **2**). The cell walls of *Menyanthes* are perforated with sieve-area and sieve-plate-like openings (**Fig. 8**). Phellem exists only around the nodes (**Fig. 9**).

Characteristic of the cortex of annual shoots of *Nymphoides peltata* are isolated, thick-walled, lignified idioblasts with star-like, pointed protuberances (**Figs. 10** and **11**). The epidermis is thin-walled (**Fig. 12**).

### Characteristic of the pith

The pith of *Menyanthes* has a similar structure as the cortex but does not contains vascular bundles (**Fig. 1**). Large inter-cellular spaces are missing in *Nymphoides* (**Fig. 2**).

### Ecological trends in the phloem and the pith

The net-like construction of the cortex and the pith, the thin-walled epidermis and the missing phellem seems to be an adoption to the submerse environment.

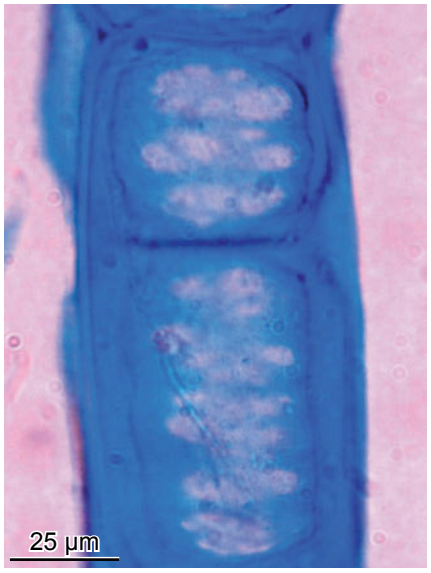



**Fig. 8.** Sieve area-like perforations in parenchyma cells of the cortex. Rhizome of plant in a pond, mountain zone, Alps, Switzerland. *Menyanthes trifoliata*, radial section.

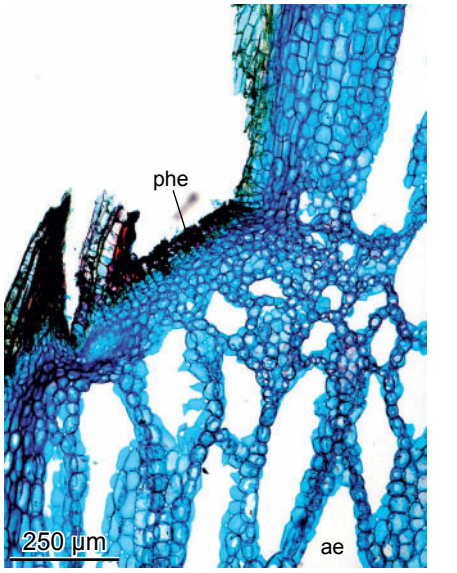



**Fig. 9.** Phellem and leaf basis at a node of rhizome with cortical inter-cellular spaces. Rhizome of plant in a pond, mountain zone, Alps, Switzerland. *Menyanthes trifoliata*, radial section.

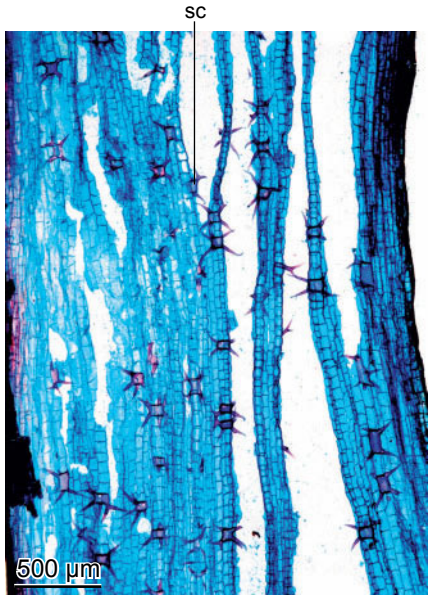
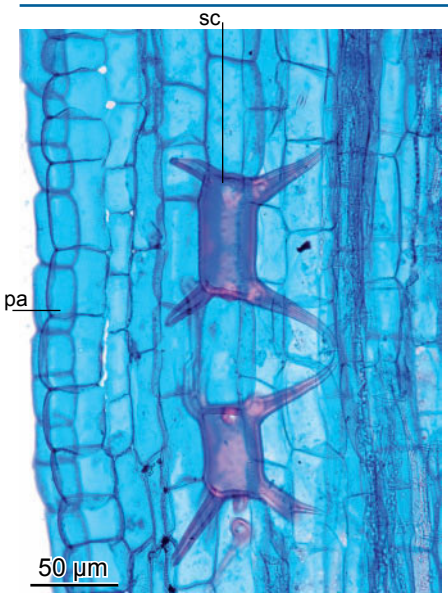
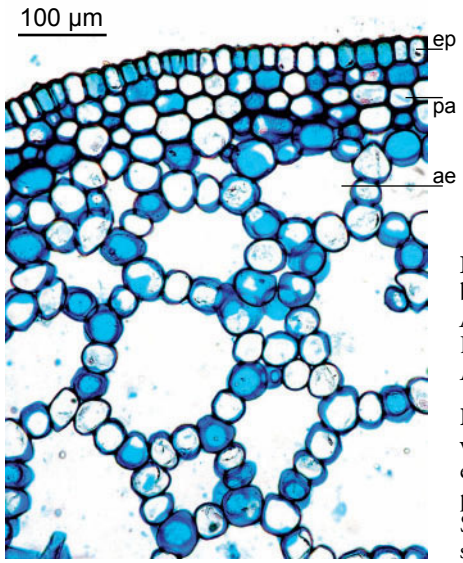



**Fig. 10.** Thick-walled lignified idioblasts with star-like, pointed protuberances. Annual shoot of plant in a pond, hill zone, Botanical Garden Zürich, Switzerland. *Nymphoides peltata*, tangential section.




**Left Fig. 11.** Thick-walled, lignified idioblasts with star-like, pointed protuberances. Annual shoot of plant in a pond, hill zone, Botanical Garden Zürich, Switzerland. *Nymphoides peltata*, tangential section.

**Right Fig. 12.** Thin-walled epidermis without cuticula around a cortical parenchymatic tissue. Rhizome of plant in a pond, hill zone, Botanical Garden Zürich, Switzerland. *Nymphoides peltata*, transverse section.



## Discussion in relation to previous studies

The rhizome anatomy of *Menyanthes trifoliata* is described by Linsday (1938). Metcalfe and Chalk (1957) described a rhizome of *Menyanthes trifoliata* and an annual shoot of *Nymphoides peltata*. The results of the present study agree with those of previous authors.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **2** |
| 2 | growth rings absent | 1 |
| 2.1 | only one ring | 1 |
| 9 | vessels predominantly solitary | 1 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 1 |
| 14 | vessels with scalariform perforation plates | 1 |
| 20 | intervessel pits scalariform | 2 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 2 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 2 |
| 60.1 | fibers absent | 2 |
| 79.1 | parenchyma pervasive | 2 |
| 99.1 | vascular bundle form remaining | 2 |
| 117 | rayless | 2 |
| R4 | sclereids in phloem and cortex | 1 |
| R10 | phloem not well structured | 2 |

# Moraceae



**Number of species, worldwide and in Europe**

The cosmopolitan Moraceae family includes 53 genera with 1500 species. *Ficus* is the most abundant genus (800 species). In Europe, there are 2 native (*Morus* and *Ficus*) and 2 introduced genera (*Broussonetia* and *Maclura*).

**Analyzed material**

The xylem and phloem of 3 genera with 8 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes 4 - >20 m | 8 | numerous |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 3 | |
| Mediterranean | 1 | |
| Suptropical | 4 | |

**Analyzed species:**

*Broussonetia papyrifera* (L.) Vent
*Ficus carica* L.
*Ficus elastica* Roxb.
*Ficus salicifolia* Vahl
*Ficus sycomorus* L.
*Ficus vasta* Forsk.
*Morus alba* L.
*Morus nigra* L.

*Morus alba*

*Morus nigra* (photo: Zinnert)

*Ficus carica* (photo: Zinnert)

*Ficus carica*

## Characteristics of the xylem

The family is divided into two groups: Group a) *Morus* and *Broussonetia* have distinct ring boundaries and are ring-porous (**Figs. 1** and **2**). Both species have helical thickenings in latewood vessels (**Fig. 3**). Latewood vessels are arranged in groups in *Morus* and are solitary in *Broussonetia* (**Figs. 1** and **2**). Parenchyma is paratracheal and marginal. Group b) All *Ficus* species have indistinct rings and are diffuse porous (**Figs. 4** and **5**). Large tangential parenchyma bands are characteristic of well-grown *Ficus* specimens (**Fig. 4**). Vessels of all species have simple perforations, contain tylosis, are large (150-250 µm in diameter) and vessel density is low (40-100/mm$^2$; **Figs. 4** and **5**). Fibers are thick- and thin- to thick-walled (**Figs. 1**, **2**, **4** and **5**) and have small pits with slit-like apertures. Tension wood occurs in all analyzed species (**Fig. 1**). Ray width varies from 2-3-seriate in *Ficus carica* (**Fig. 6**) to 4-6-seriate in *Broussonetia* (**Fig. 7**) to 5-11-seriate in *Ficus sycomorus* (**Fig. 8**). Rays of all species are slightly heterocellular with 1-2 marginal square or upright cells (**Fig. 9**). Prismatic crystals occur in all species though frequency varies.

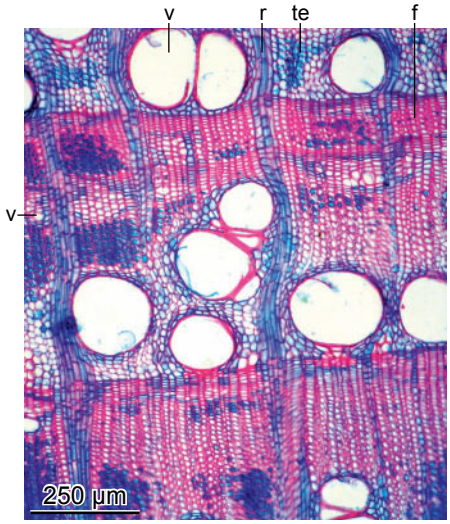



**Fig. 1.** Ring-porous xylem with a distinct annual ring boundary. Small latewood vessel are arranged in groups. Blue cells contain gelatinous fibers (tension wood). Stem of a 5 m-high tree, road side, Mediterranean, Provence, France. *Broussonetia papyrifera*, transverse section.

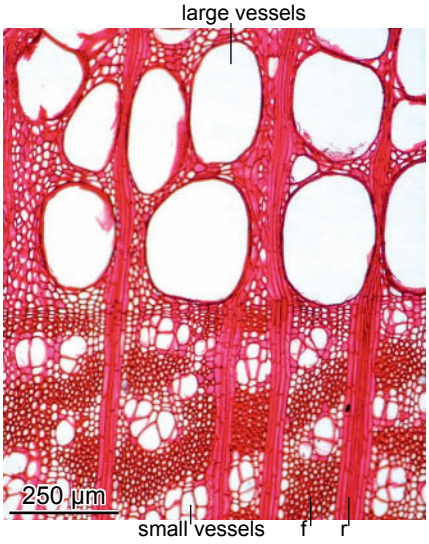



**Fig. 2.** Ring-porous xylem with a distinct annual ring boundary. Latewood vessels and thin- to thick-walled fibers are arranged in diagonal groups. Stem of a 10 m-high tree, cultivated, Samos, Greece. *Morus alba*, transverse section.

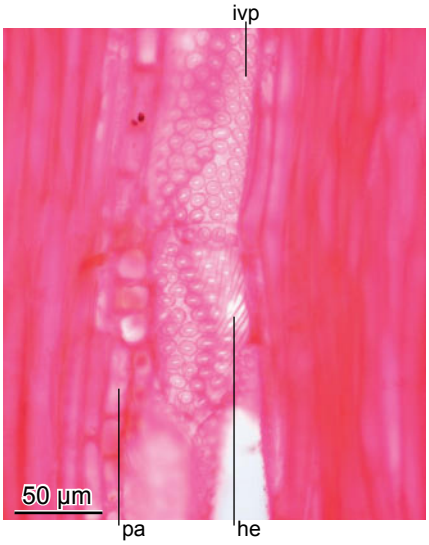



**Fig. 3.** Helical thickenings in small latewood vessels. Stem of a 10 m-high tree, cultivated, Samos, Greece. *Morus alba*, radial section.

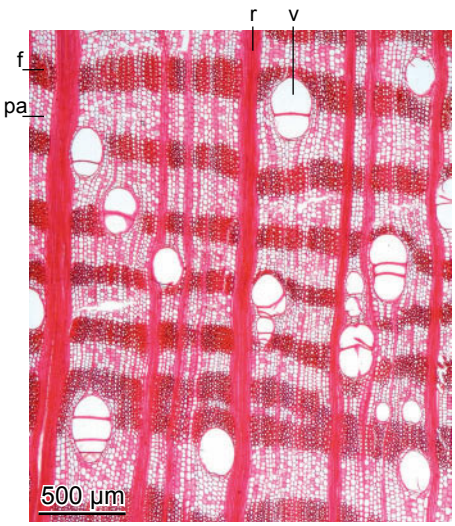



**Fig. 4.** Xylem with a few large vessels and alternating bands of thick-walled fibers and thin-walled parenchyma. Stem of a 6 m-high tree, wadi, near Tel Aviv, Mediterranean, Israel. *Ficus sycomorus*, transverse section.

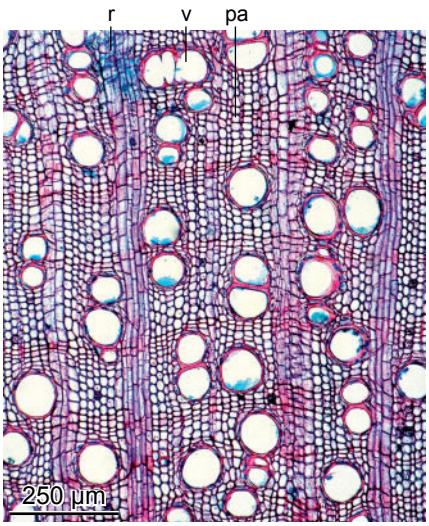



**Fig. 5.** Xylem with solitary vessels embedded in thin-walled parenchyma cells. Due to poor growing conditions fibers occur only in the latewood. Stem of a 5 m-high tree, cultivated, arid zone, Sabah, Libya. *Ficus carica*, transverse section.

**Fig. 6.** Ray with 2-3 cells width. Stem of a 5 m-high tree, cultivated, arid zone, Sabah, Lybia. *Ficus carica*, tangential section.

**Fig. 7.** Ray with 2-3 cells in width. Stem of a 5 m-high tree, road side, Mediterranean, Provence, France. *Broussonetia papyrifera*, tangential section.

**Fig. 8.** Ray with 3, 9 and 11 cells in width. Stem of a 6 m-high tree, wadi, near Tel Aviv, Mediterranean, Israel. *Ficus sycomorus*, tangential section.

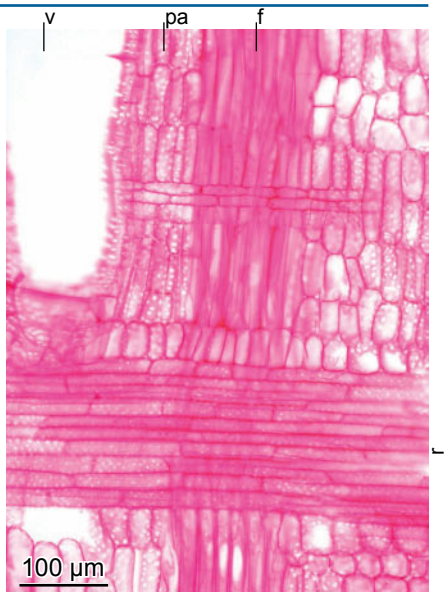


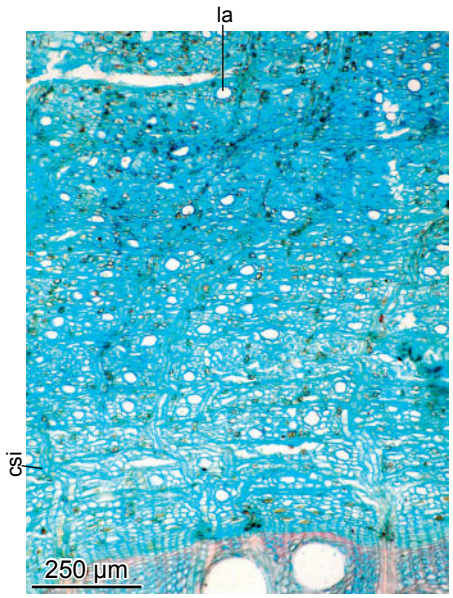

**Fig. 9.** Heterocellular ray with many central procumbent cells and one row of upright cells. Stem of a 6 m-high tree, wadi, near Tel Aviv, Mediterranean, Israel. *Ficus sycomorus*, radial section.

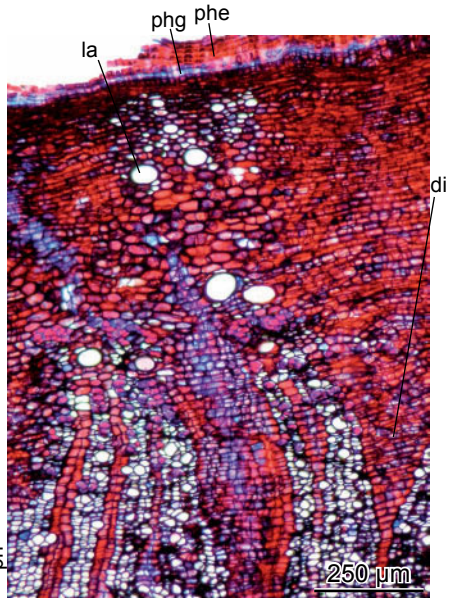
### Characteristics of the phloem and the cortex

Characteristic of all species is the presence of laticifers (**Figs. 10** and **11**) and prismatic crystals. Sieve-tubes and parenchyma are arranged in tangential layers in *Broussonetia* (**Fig. 10**) and are irregularly distributed in *Ficus* and *Morus* (**Fig. 12**). Sclereids are absent in *Broussonetia* and *Ficus* (**Figs. 10** to **12**). The occurrence of many isolated sclereids is characteristic for *Morus* (**Fig. 13**). Prismatic crystals occur in the axial parenchyma of all species.

### Discussion in relation to previous studies

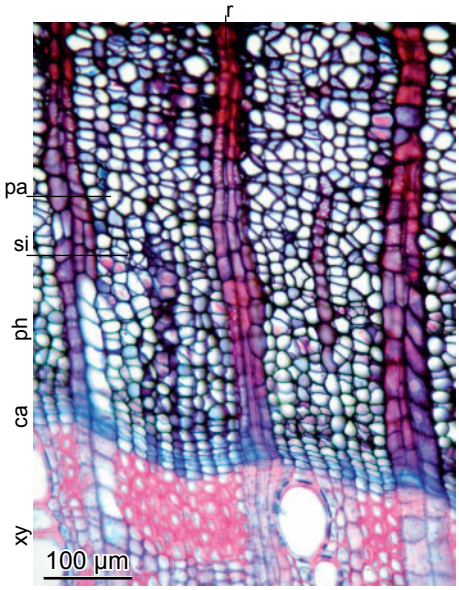
The xylem of all genera analyzed here have been characterized before. Gregory (1994) mentioned 177 references concerning numerous tropical genera. Holdheide (1951) described the bark of *Morus rubra*. Described here for the first time is the bark of 3 species. The few specimens analyzed here do not allow differentiation of species within genera. Since all species grow in the submediterranean or in the hill zone of the temperate climate, anatomical differences seem to be absent.

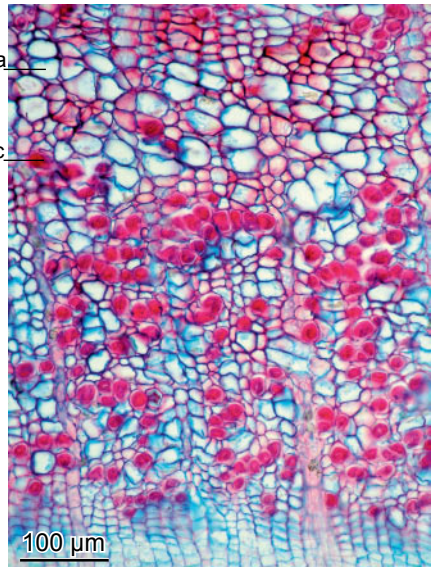



**Left Fig. 10.** Phloem with tangential layers of sieve-tubes and parenchyma cells and many lacitifers. Stem of a 5 m-high tree, road side, Mediterranean, Provence, France. *Broussonetia papyrifera*, transverse section.

**Right Fig. 11.** Large lacitifers lateral to a dilatation in the phloem and the cortex. Stem of a 5 m-high tree, cultivated, arid zone, Sabah, Libya. *Ficus carica*, transverse section.




**Left Fig. 12.** Irregular distribution of parenchyma cells and sieve-tubes. Stem of a 5 m-high tree, cultivated, arid zone, Sabah, Libya. *Ficus carica* , transverse section.

**Right Fig. 13.** Isolated thick-walled sclerenchyma cells and thin-walled parenchyma cells. Stem of a 12 m-high tree, cultivated, hill zone, Zürich, Switzerland. *Morus alba*, transverse section.



**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **8** |
| 1 | growth rings distinct and recognizable | 3 |
| 2 | growth rings absent | 5 |
| 3 | ring-porous | 3 |
| 9 | vessels predominantly solitary | 1 |
| 9.1 | vessels in radial multiples of 2-4 common | 8 |
| 11 | vessels predominantly in clusters | 2 |
| 13 | vessels with simple perforation plates | 8 |
| 22 | intervessel pits alternate | 8 |
| 36 | helical thickenings present | 3 |
| 39.1 | vessel cell-wall thickness >2 µm | 4 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 8 |
| 50 | <100 vessels per mm$^2$ in earlywood | 8 |
| 56 | tylosis with thin walls | 7 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 1 |
| 61 | fiber-pits small and simple to minutely bordered (<3 µm = libriform fibers) | 8 |
| 70 | fibers thin- to thick-walled | 8 |
| 70.2 | tension wood present | 7 |
| 79 | parenchyma paratracheal | 8 |
| 85 | axial parenchyma bands more than three cells wide, *Ficus*/*Urtica* type | 5 |
| 89 | parenchyma marginal | 3 |
| 97 | ray width predominantly 1-3 cells | 3 |
| 98 | rays commonly 4-10-seriate | 7 |
| 99 | rays commonly >10-seriate | 3 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 8 |
| 136 | prismatic crystals present | 6 |
| 142 | prismatic crystals in axial chambered cells | 1 |
| R2 | groups of sieve tubes in tangential rows | 2 |
| R3 | distinct ray dilatations | 3 |
| R4 | sclereids in phloem and cortex | 1 |
| R6.1 | sclereids in tangential rows | 1 |
| R7 | with prismatic crystals | 4 |
| R12 | with laticifers, oil ducts or mucilage ducts | 4 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 4 |

# Myricaceae



**Number of species, worldwide and in Europe**

The cosmopolitan Myricaceae family includes 3 genera with 45 species. *Myrica gale* is endemic to Europe and *Myrica faya* is endemic on the Canary Islands and Madeira (Macaronesia).

**Analyzed species:**

*Myrica californica* Cham.
*Myrica faya* L.
*Myrica gale* L.

**Analyzed material**

The xylem and phloem of 1 genus with 3 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 3 | numerous |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 1 | |
| Mediterranean | 1 | |
| Suptropical | 1 | |

*Myrica faya* (photo: Lauerer)

**Characteristics of the xylem**

Annual rings are distinct. Ring boundaries are marked by marginal, uni- and biseriate rows of rectangular, thick-walled fibers (**Figs. 1-3**). *Myrica californica* and *M. faya* are diffuse-porous with solitary vessels (**Figs. 1** and **2**). *M. gale* is semi-ring-porous and vessels are arranged in irregular groups (**Fig. 3**). The earlywood vessel diameter varies from 100-200 µm and vessel density from 100-200/mm$^2$. Particular for *Myrica gale* is the vessel-free latewood zone (**Fig. 3**). Vessels contain mostly scalariform perforations (**Fig. 4**). Inter-vessel pits are predominantly large and round and are arranged in alternating position. Radial walls of fibers are perforated by large pits (ca. 3 µm; **Fig. 4**). Fibers of *Myrica californica* and *M. faya* are thin- to thick-walled (**Figs. 1** and **2**). Those of *M. gale* are thin-walled and arranged in straight radial lines (conifer-like; **Fig. 3**). Parenchyma is apotracheal diffuse and sporadically marginal (**Fig. 1**). Rays are 2-4-seriate. Particular is the occurrence of uniseriate and multiseriate rays in *Myrica gale* (**Fig. 5**). Rays are heterocellular in *Myrica californica* and *M. faya* and are homocellular with upright cells in *M. gale*. Prismatic crystals occur in *M. faya* in axial parenchymatic cells (**Fig. 6**).

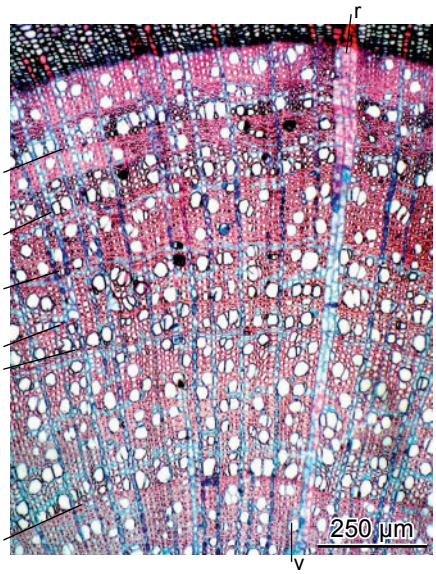



**Fig. 1.** Diffuse-porous wood with distinct annual rings. Stem, shrub, Mediterranean climate, Botanical Garden Santa Barbara, USA. *Myrica californica*, transverse section.

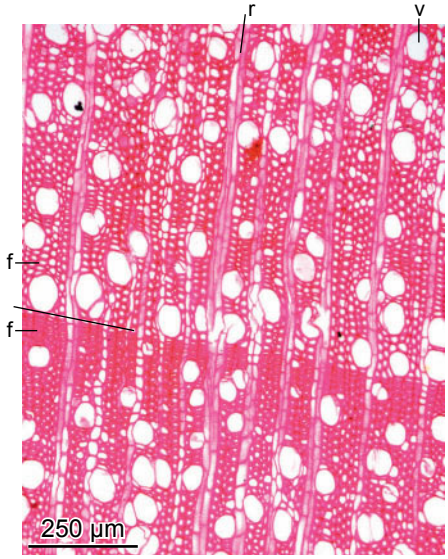



**Fig. 2.** Diffuse-porous wood with distinct annual rings. The ring boundary is formed of thick-walled, rectangular fibers. Stem, shrub, subtropical climate, *Laurus* forest, Madeira, Portugal. *Myrica faya*, transverse section.

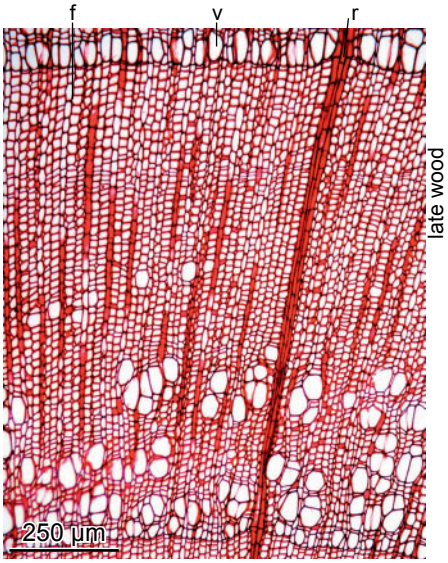



**Fig. 3.** Semi-ring-porous wood with distinct annual rings. Characteristic is the vessel-free latewood zone and the straight radially orientated fibers. Stem, shrub, coastal swamp, temperate climate, Wilhelmshaven, Germany. *Myrica gale*, transverse section.

**Fig. 4.** Vessels with scalariform perforations and fibers with large pits. Stem, shrub, Mediterranean climate, Botanical Garden Santa Barbara, USA. *Myrica californica*, transverse section.

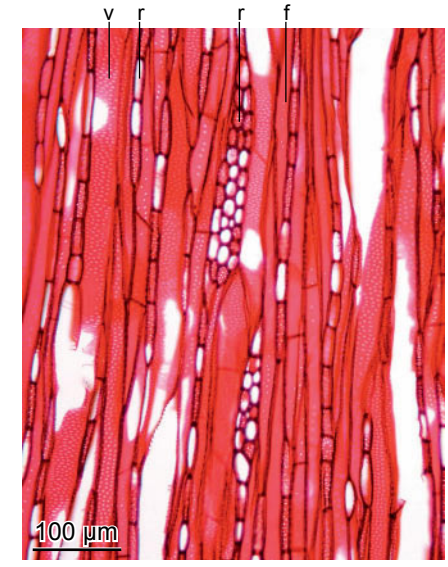



**Fig. 5.** Rays dimorphism: uniseriate with axially elongated cells and 2-3-seriate heterocellular. Stem, shrub, coastal swamp, temperate climate, Wilhelmshaven, Germany. *Myrica gale*, tangential section.

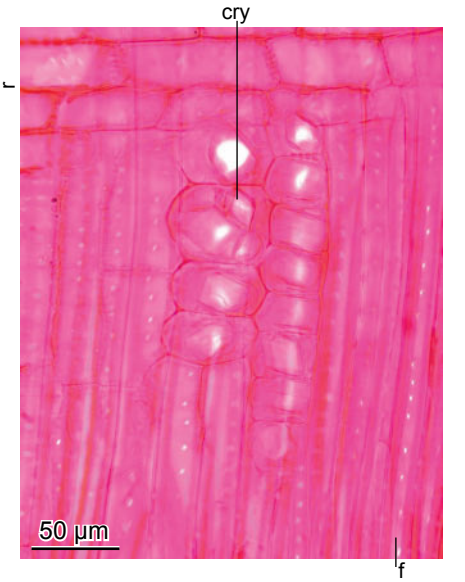



**Fig. 6.** Prismatic crystals in axially oriented chambers. Stem, shrub, subtropical climate, *Laurus* forest, Madeira, Portugal. *Myrica faya*, radial section.

### Characteristics of the phloem and the cortex

The phloem of *Myrica californica* is fairly uniform (**Fig. 7**). Ray dilatations are present. A band of sclereids separates the phloem from the cortex (**Fig. 7**). Many crystal druses occur in the phloem and the cortex.

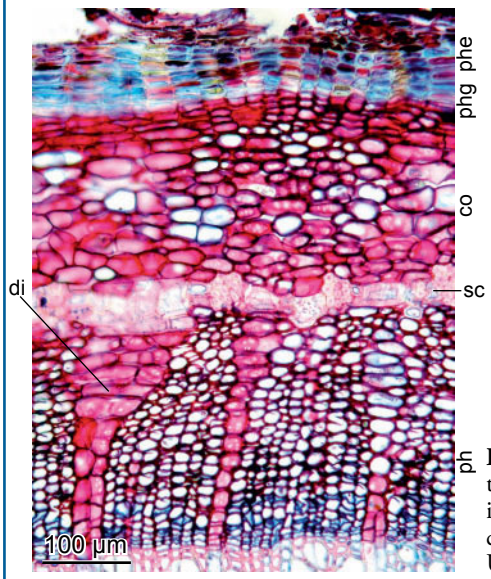



**Fig. 7.** Uniform phloem with ray dilatations. A tangential band of sclereids occurs in the cortex. Stem, shrub, Mediterranean climate, Botanical Garden Santa Barbara, USA. *Myrica californica*, transverse section.

### Discussion in relation to previous studies

The genus *Myrica* has been described by 29 authors (Gregory 1994). The present description confirms all results of previous studies.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| | **Total number of species** | **3** |
| 1 | growth rings distinct and recognizable | 2 |
| 4 | semi-ring-porous | 1 |
| 5 | diffuse-porous | 1 |
| 9 | vessels predominantly solitary | 2 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 13 | vessels with simple perforation plates | 1 |
| 14 | vessels with scalariform perforation plates | 3 |
| 22 | intervessel pits alternate | 3 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 2 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 3 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 3 |
| 61 | fiber-pits small and simple to minutely bordered (<3 µm = libriform fibers) | 1 |
| 62 | fiber-pits large and distinctly bordered (>3 µm = fiber tracheids) | 2 |
| 68 | fibers thin-walled | 1 |
| 70 | fibers thin- to thick-walled | 2 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 3 |
| 89 | parenchyma marginal | 1 |
| 96 | rays exclusively uniseriate | 1 |
| 97 | ray width predominantly 1-3 cells | 2 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 2 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 1 |

# Myrtaceae

**Number of species, worldwide and in Europe**

The Myrtaceae family includes 148 genera with 3500 species and is mainly pantropical distributed. Here we describe *Myrtus communis*, widely distributed in the Mediterranean climate of Europe.

**Analyzed species:**
*Myrtus communis* L.

**Analyzed material**
The xylem and phloem of 1 genus with 1 species are analyzed here.

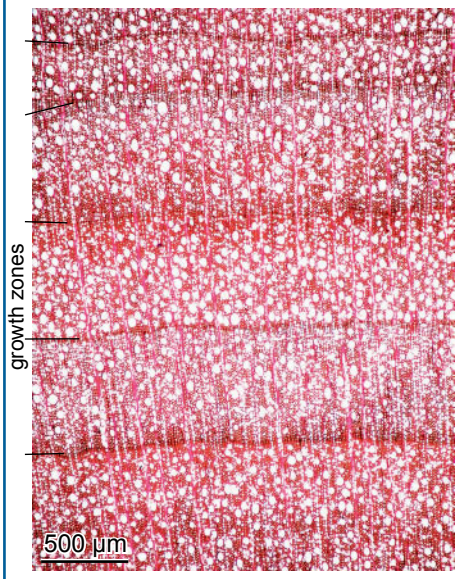
| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | | many, especially *Eucalyptus* |
| Nanophanerophytes 0.5-4 m | 1 | |
| **Plants analyzed from different vegetation zones:** | | |
| Mediterranean | 1 | |

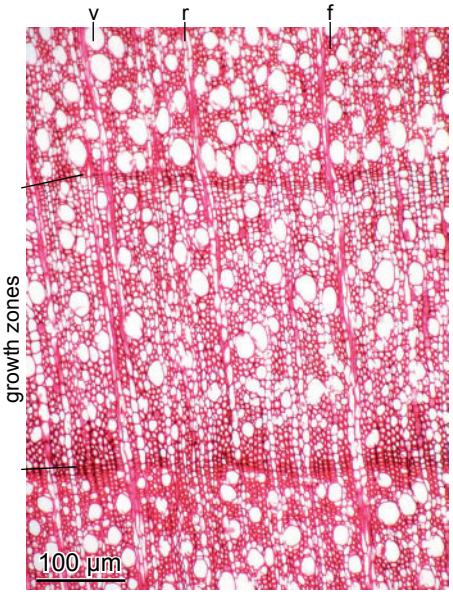
**Right:** *Myrtus communis* (photo: Zinnert)

*Myrtus communis* (photo: Lauerer)

**Characteristics of the xylem**

Annual rings can be distinct or indistinct. Ring boundaries are marked by marginal, multiseriate rows of rectangular thick-walled fibers (**Figs. 1** and **2**). The xylem is diffuse-porous with solitary vessels (**Figs. 1** and **2**). The earlywood vessel diameter varies between 30-50 µm and vessel density is between 300-500/mm$^2$. Vessels contain simple perforations and thin helical thickenings. Inter-vessel pits are predominantly large and round and arranged in alternating position. Radial walls of fibers are perforated by large pits (ca. 3 µm; **Fig. 3**). Fibers are thin- to thick-walled (**Fig. 2**). Parenchyma is mainly apotracheal diffuse in aggregates. Rays are 2-3-seriate (**Fig. 4**), and are heterocellular with 4-6 rows of upright cells (**Fig. 5**).




**Left Fig. 1.** Diffuse-porous wood with distinct and indistinct or growth zones. Stem, shrub, maccia, Mediterranean climate, Mallorca, Spain. *Myrtus communis*, transverse section.

**Right Fig. 2.** Diffuse-porous wood. The growth zone boundary is formed by thick-walled, rectangular fibers. Large vessels occur at the beginning or in the middle part of the ring. Stem, shrub, maccia, Mediterranean climate, Mallorca, Spain. *Myrtus communis*, transverse section.

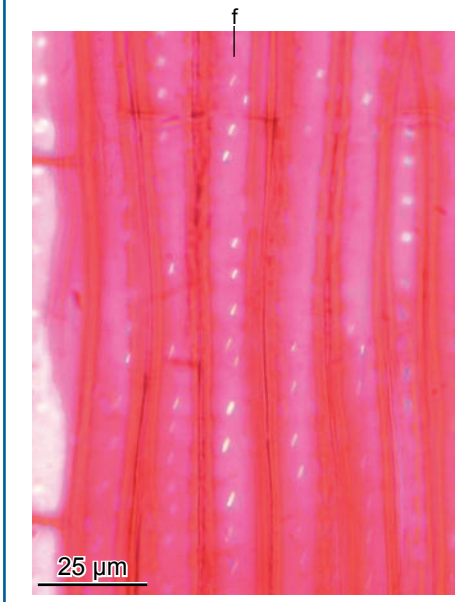



**Fig. 3.** Fibers containing large pits with slit-like apertures. Stem, shrub, maccia, Mediterranean climate, Mallorca, Spain. *Myrtus communis*, radial section.

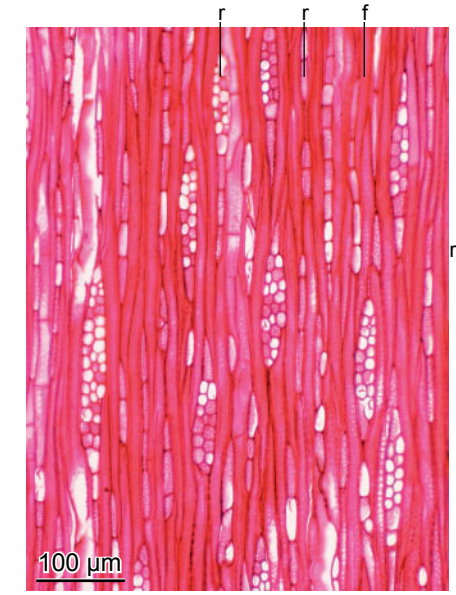



**Fig. 4.** Uniseriate rays with axially elongated cells and 2-3 heterocellular rays with round central cells and elongated marginal cells. Stem, shrub, maccia, Mallorca, Spain. *Myrtus communis*, tangential section.

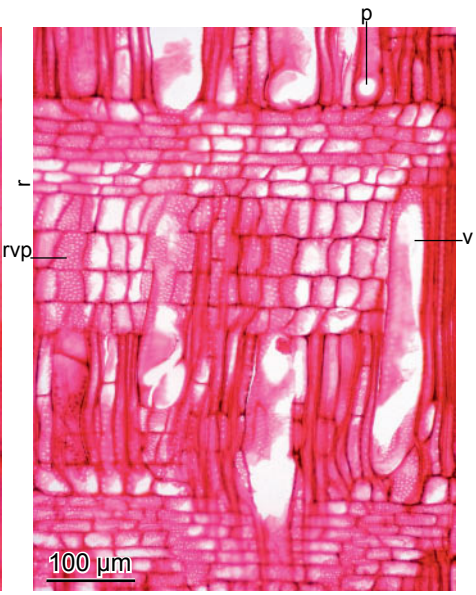



**Fig. 5.** Heterocellular rays with some central procumbent cells and some marginal upright cells. Stem, shrub, Mediterranean climate, Mallorca, Spain. *Myrtus communis*, radial section.

### Characteristics of the phloem and the cortex

Characteristic of the phloem are uni- and biseriate layers of sieve-tubes and parenchyma cells (**Fig. 6**). Ray dilatations are present. A few small groups of sclereids occur in the cortex (**Fig. 6**). Many crystal druses fill the parenchyma cells in the phloem.

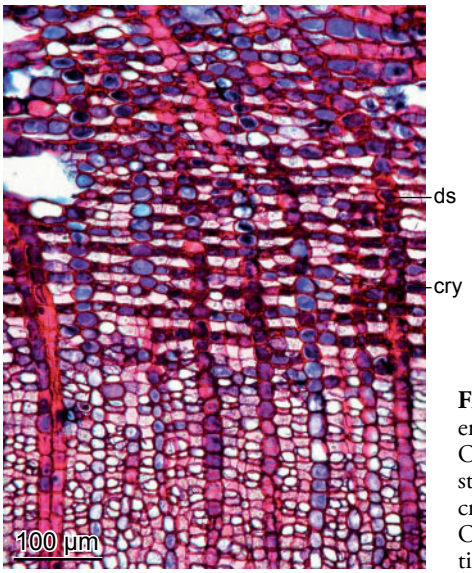



**Fig. 6.** Phloem containing tangential layers with sieve-tubes and parenchyma cells. Older sieve-tubes are filled with blue-stained substances and parenchyma with crystal druses. Stem, shrub, maccia, Nizwa, Oman. *Myrtus communis*, transverse section.

### Discussion in relation to previous studies

*Myrtus communis* has been described by Huber and Rouschal (1954), Fahn et al. (1986) and Schweingruber (1990). The present description confirms all results of previous studies.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **1** |
| 1 | growth rings distinct and recognizable | 1 |
| 5 | diffuse-porous | 1 |
| 9 | vessels predominantly solitary | 1 |
| 14 | vessels with scalariform perforation plates | 1 |
| 22 | intervessel pits alternate | 1 |
| 36 | helical thickenings present | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 1 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 1 |
| 62 | fiber-pits large and distinctly bordered (>3 µm = fiber tracheids) | 1 |
| 70 | fibers thin- to thick-walled | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 97 | ray width predominantly 1-3 cells | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| R2 | groups of sieve tubes in tangential rows | 1 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R8 | with crystal druses | 1 |

# Nepenthaceae



**Number of species, worldwide and in Europe**

The Nepenthaceae family includes 1 genus with75 species. All species grow in the tropics of the old world. No representatives of the family exist in Europe and on the Canary Islands.

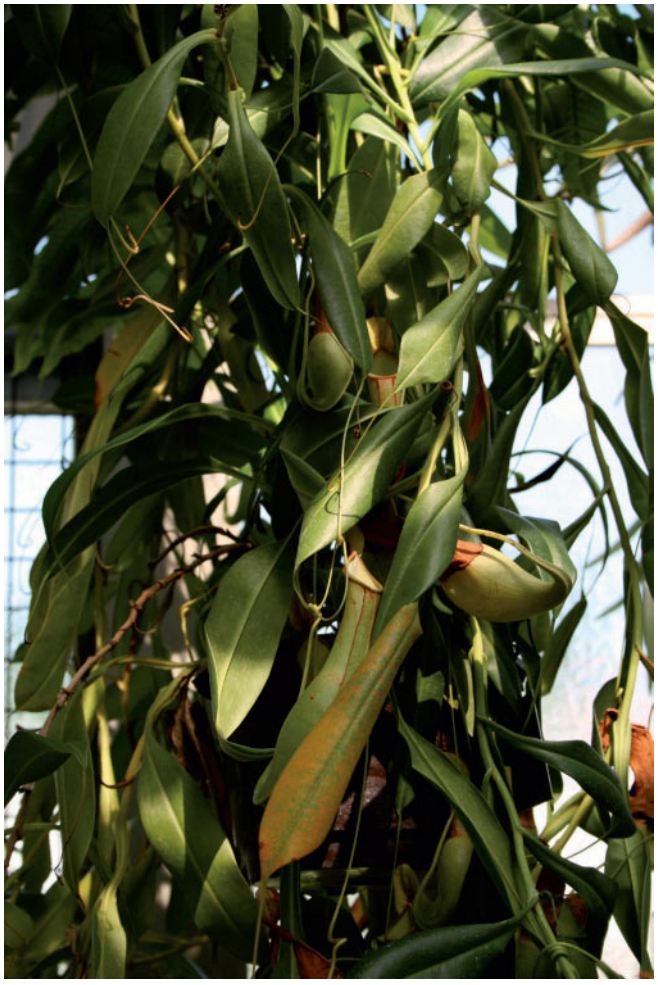
**Analyzed material**

The stem base of two terrestrial tropical dwarf shrubs growing in greenhouse of the Botanical Garden of Zürich are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 2 | 5 |
| **Plants analyzed from different vegetation zones:** | | |
| Tropical | 2 | |

**Analyzed species:**

*Nepenthes alata* Blanco
*Nepenthes ampullaria* Juck

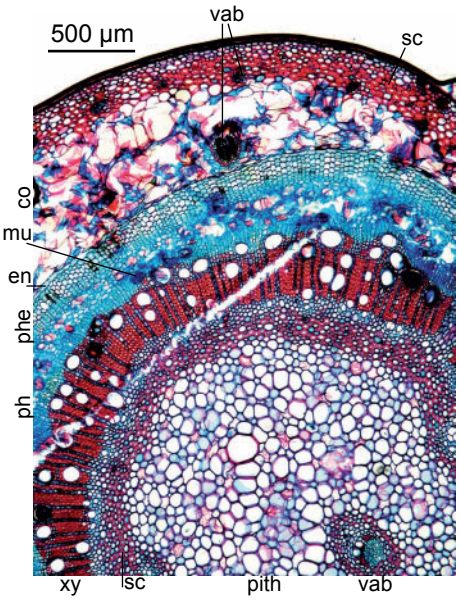


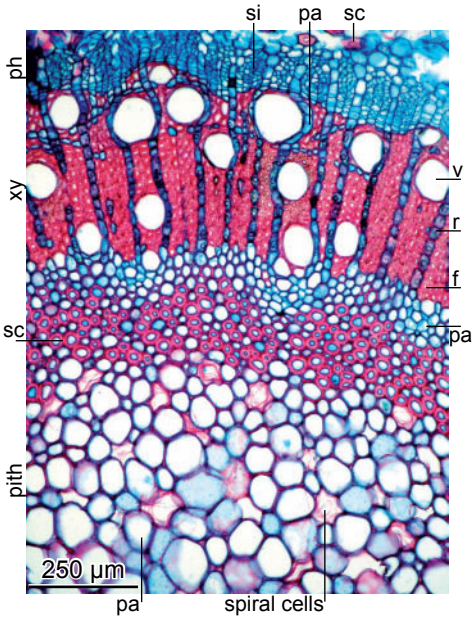
*Nepenthes alata*

*Nepenthes* sp. (photo: Lauerer)

### Characteristics of the xylem

Annual rings are absent. Vessels are solitary (**Figs. 1** and **2**). Vessel diameter varies from 50-120 µm and vessel density from 100-150/mm$^2$. Large simple perforations are oblique at the distal ends of the vessels. Inter-vessel pits are round. Some vessels contain dark-staining substances. Fiber cell walls contain small, round pits (**Fig. 3**). Parenchyma cells are arranged mainly in uniseriate tangential bands (**Fig. 2**). Rays 1-3 cells in width are very high (>25 cells; **Fig. 4**). Rays are exclusively homocellular with square and upright cells. Ray cells of *Nepenthes ampullaria* contain irregular bowl-like inclusions (oil?; **Fig. 5**).




**Left Fig. 1.** A large pith is surrounded by a small xylem (red), phloem, a phellem (blue) and a bark (red). The cortex and the pith contain vascular bundles. 60 cm-high dwarf shrub, understory, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Nepenthes ampullaria*, transverse section.

**Right Fig. 2.** Solitary parenchyma cells in tangential bands, large vessels and uniseriate rays are characteristic. Cells of the central part of the pith are thin-walled. The pith is surrounded by a belt of thick-walled lignified cells and a belt of thin-walled unlignified cells. The phloem contains many small sieve-tube groups. 60 cm-high dwarf shrub, understory, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Nepenthes ampullaria*, transverse section.

**Fig. 3.** Small round bordered pits at the radial walls of fibers. 60 cm-high dwarf shrub, understory, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Nepenthes alata*, radial section.

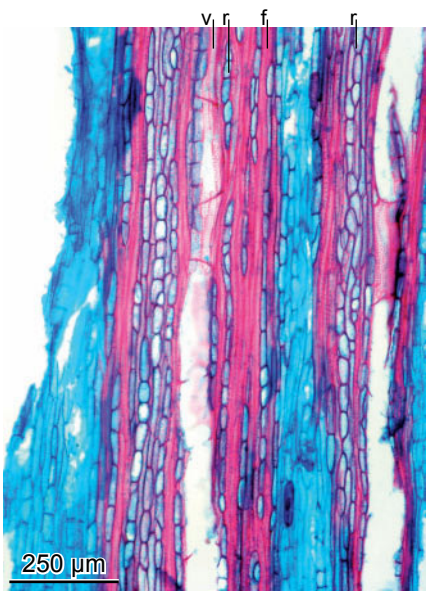



**Fig. 4.** Mainly high, uniseriate rays with upright cells characterize the two species analyzed. 60 cm-high dwarf shrub, understory, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Nepenthes alata*, tangential section.

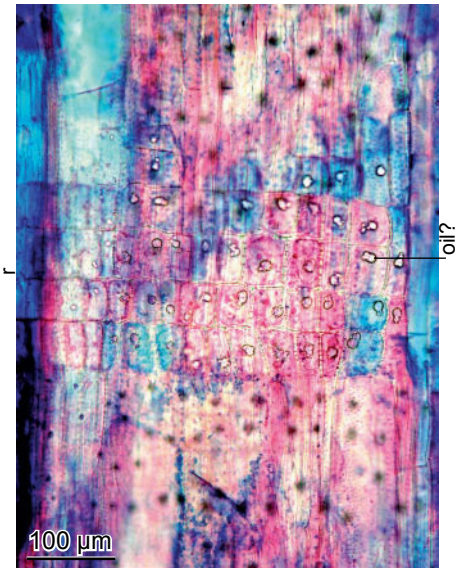
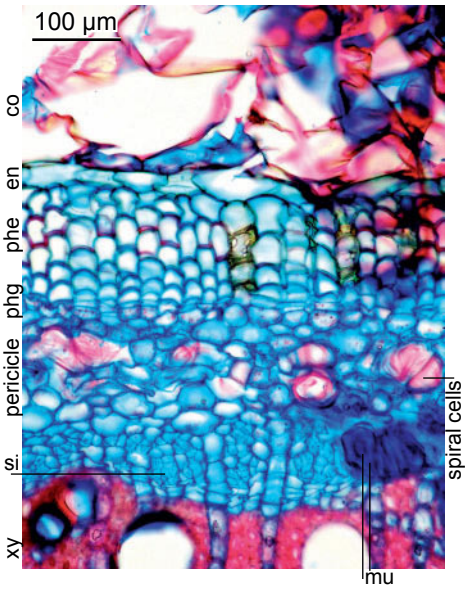


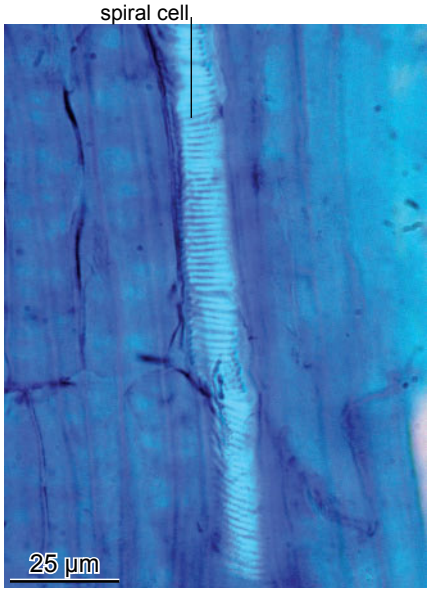

**Fig. 5.** Bowl-like inclusions (oil?) in upright ray cells. 60 cm-high dwarf shrub, understory, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Nepenthes ampullaria*, radial section.

**Characteristics of the phloem, the cortex and the pith**

Following Metcalfe and Chalk (1957), the cortex is divided in three zones (**Fig. 1**): Under the epidermis are thin-walled parenchymatic cells (assimilating tissue). Below is a belt with central vascular bundles (phloem in the center), embedded in slightly sclerotized cells. An endodermis seperates the cortex from the cork zone consisting square, pitless prismatic cells (shoe box-like; **Fig. 6**). This zone arises from the pericycle zone, which consists mainly of spirally thickened, very long, unlignified cells. The phloem consists of radially grouped sieve tubes and parenchyma and spiral cells (**Fig. 6**).

Thin-walled parenchymatic cells with scattered "spiral cells" (Metcalfe and Chalk 1957) characterize the inner part of the pith (**Figs. 7** and **8**). Cell walls of some pith cells have thin spiral thickenings (**Fig. 9**). A belt of thick-walled cells is typical for the border zone towards the xylem. In both parts collateral vascular bundles occur (**Figs. 1** and **10**).




**Left Fig. 6.** The bark is composed of a phloem with small sieve-tube groups, a pericycle zone with some "spiral cells", a phellogen, a phellem, an endodermis and a cortex. 60 cm-high dwarf shrub, understory, tropical greenhouse climate, Botanical Garden Zürich, Switzerland. *Nepenthes alata*, transverse section.

**Right Fig. 7.** Spiral cell of the pericycle zone. The spirals of the extremely long cells are loosely connected with the primary walls. 60 cm-high dwarf shrub, understory, tropical greenhouse climate, Botanical Garden Zürich, Switzerland. *Nepenthes alata*, radial section.

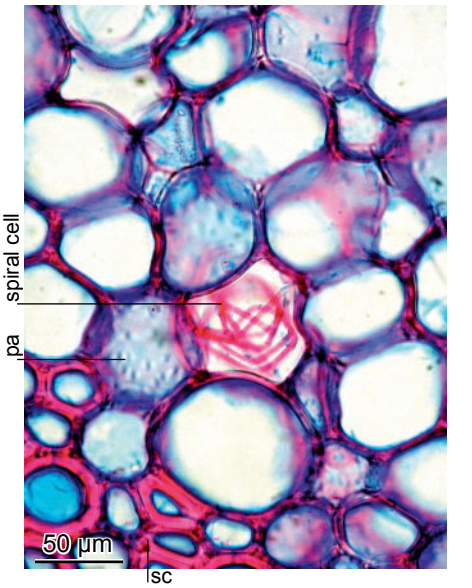



**Fig. 8.** Spiral cell embedded in parenchyma cells of the pith. The spirals have been displaced by the mechanical force of the cutting knife. 60 cm-high dwarf shrub, understory, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Nepenthes ampullaria*, transverse section.

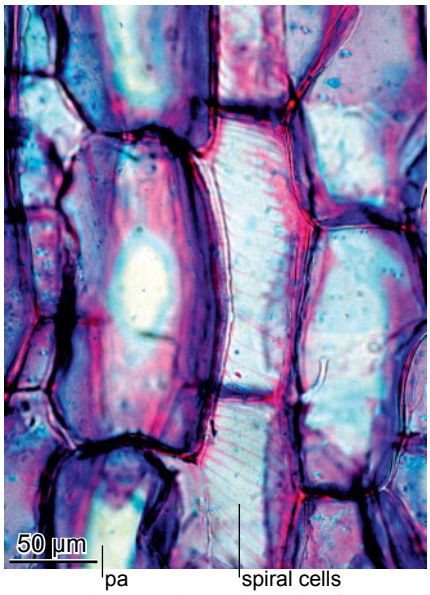



**Fig. 9.** Thin spirals on the walls of a parenchyma cells in the pith. 60 cm-high dwarf shrub, growing in the understory, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Nepenthes ampullaria*, radial section.

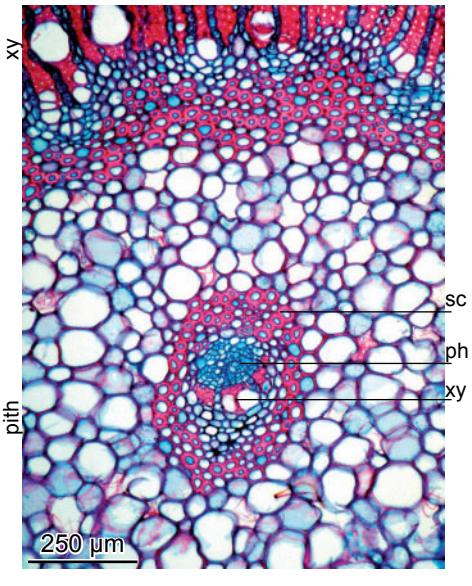



**Fig. 10.** Collateral vascular bundle in the pith. The bundle is surrounded by thick-walled cells. 60 cm-high dwarf shrub, understory, tropical greenhouse, Botanical Garden Zürich, Switzerland. *Nepenthes ampullaria*, transverse section.

**Discussion in relation to previous studies**

Metcalfe and Chalk (1957) described the xylem and phloem of 3 species. These authors identified all the features we summarize below. Carlquist (1981) studied the xylem of three species, including *Nepenthes ampullaria*.

The results of the present study agree in general with those of previous studies. Different in the present material is the presence of oil-like inclusions in ray cells. Absent are scalariform perforations and bordered ray pits. Very special are the cells in the bark and the pith with spirally constructed cell walls.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **2** |
| 2 | growth rings absent | 2 |
| 9 | vessels predominantly solitary | 2 |
| 13 | vessels with simple perforation plates | 2 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 2 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 2 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 2 |
| 69 | fibers thick-walled | 2 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 2 |
| 86 | axial parenchyma in narrow bands or lines, *Quercus* type | 2 |
| 96 | rays uniseriate | 2 |
| 97 | ray width predominently 1-3 cells | 1 |
| 105 | ray: all cells upright or square | 2 |
| R1 | groups of sieve tubes present | 2 |
| R4 | sclereids in phloem and cortex | 1 |

# Nyctaginaceae



**Number of species, worldwide and in Europe**

The Nyctaginaceae family includes 31 genera with 350 species. Species are widely distributed, in tropical and subtropical regions. In Europe there is only one endemic species (*Commicarpus plumbagineus*). Two species, not present in the described material, are endemic to the Canary Islands.

**Analyzed species:**

*Abronia fragrans* Nutall
*Abronia latifolia* Eschsch.
*Bougainvillea spectabilis* Willd.
*Bougainvillea spinosa* Willd.
*Commicarpus boissieri* Cufod

**Analyzed material**

The xylem and phloem of 5 Nyctaginaceae were analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | | ca. 10 |
| Liana | 3 | |
| Hemicryptophytes and geophytes | 2 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 2 | |
| Mediterranean | 2 | |
| Suptropical | 1 | |

*Bougainvillea spectabilis* (photo: Lauerer)

*Bougainvillea spectabilis* (photo: Zinnert)

**Characteristics of the xylem**

In the present material annual rings are absent or indistinct (**Fig. 1**). Vessels are solitary or in the majority of cases arranged in short radial multiples or groups (2-4 vessels; **Figs. 2-4**). Earlywood vessel diameter varies between 40-140 µm. Especially lianas have large vessels (*Bougainvillea*, *Commicarpus*; **Figs. 1** and **3**). Vessels contain exclusively simple perforations. Intervessel pits are in the majority of cases small and round, but are sometimes partially slit-like or can be scalariform (*Abronia latifolia*; **Fig. 5**). Vestured pits are clearly visible with the light microscope on material stained only with safranin. Dark-staining substances occur in the center of the stem of *Bougainvillea* and *Commicarpus*. The radial walls of fibers of all species are perforated by very small slit-like or round pits (<2 µm). Fibers can be thin- or thin- to thick-walled or are absent in the prostrate *Abronia latifolia* (**Fig. 3**). Paratracheal parenchyma occurs in 3 species and pervasive parenchyma is characteristic of *Abronia latifolia* (**Fig. 3**). Rays are absent in *Commicarpus boissieri* and 4 species have rays with 1-4 cells. All species contain lateral cambia which produce open vascular bundles arranged in more-or-less distinct concentric bands (**Figs. 1-4**). Rays are absent within vascular-bundles. The conjunctive tissue is storied, except in *Abronia fragrans*, and thin-walled (**Figs. 1-4**). Medullary vascular bundles (**Figs. 6** and **7**) and rhaphides in idioblasts (**Figs. 8** and **9**) were found in all species analyzed.

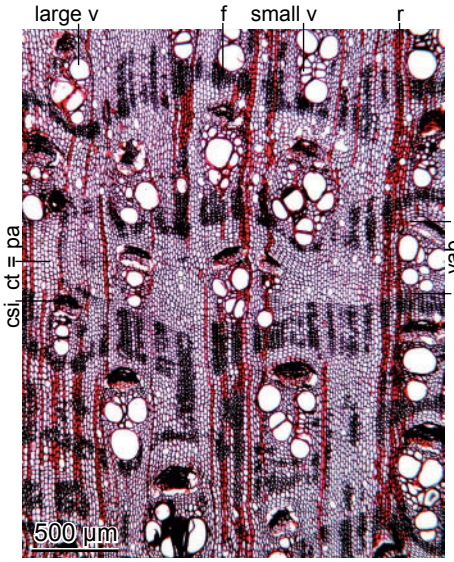



**Fig. 1.** Concentrically arranged vascular bundles are surrounded by thin-walled conjunctive tissue (parenchyma) and thin- to thick-walled fibers. Characteristic of the liana is the presence of large and small vessels. The two growth ring boundaries are barely discernible. Liana on a wall, cultivated, subtropical climate, Mt. Isa, Australia. *Bougainvillea spectabilis*, transverse section.

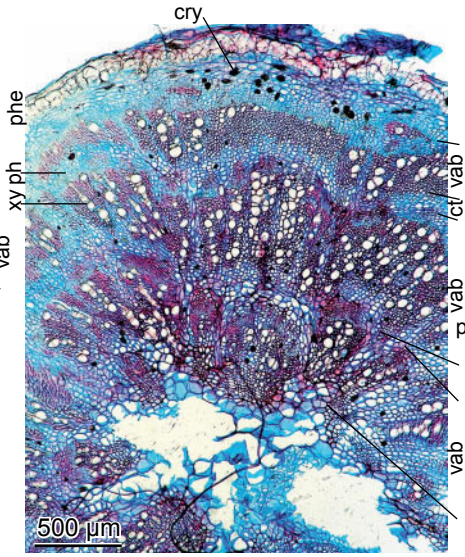



**Fig. 2.** More-or-less concentrically arranged vascular bundles. Some vascular bundles stay solitary, but some are linked with a continuous fiber band and conjunctive tissue. Vessels stand in radial multiples. Long prostrate hemicryptophyte, embedded in sand, cold steppe, Great Sand Dunes, Colorado, USA. *Abronia fragrans*, transverse section.

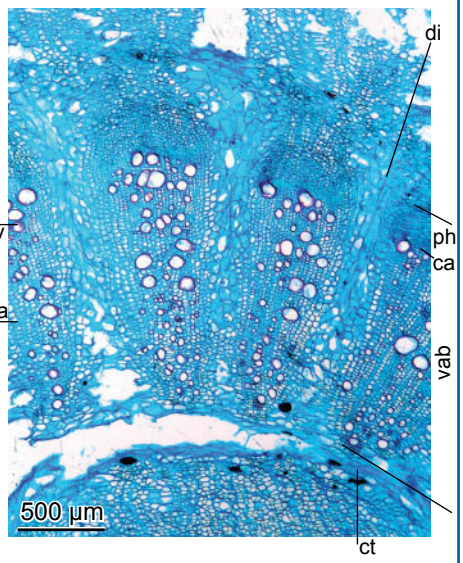
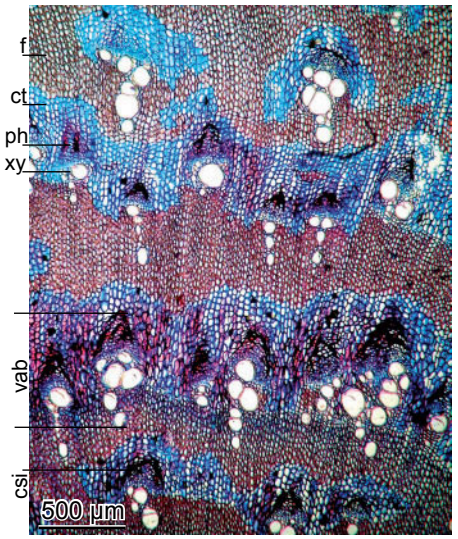
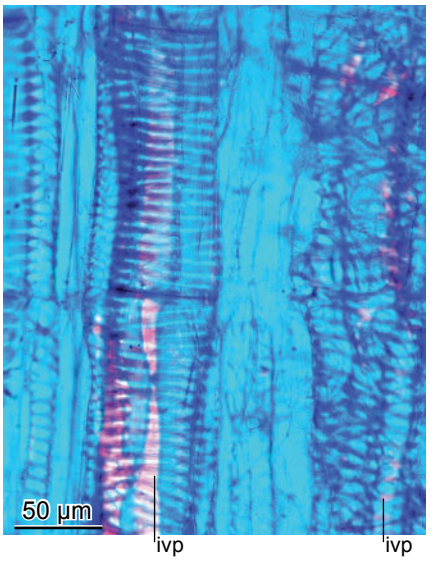


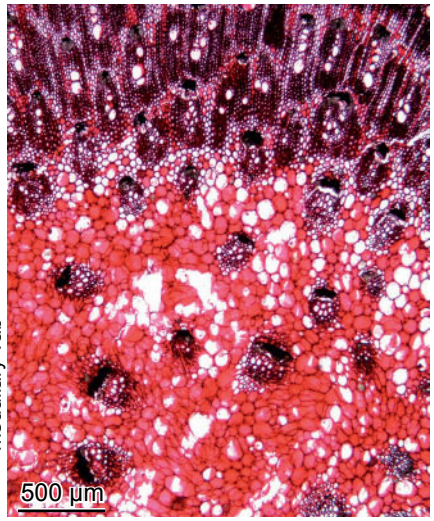

**Fig. 3.** Single vascular bundles are surrounded by thin-walled, unlignified conjunctive parenchyma. The parenchyma between the vessels is ray-like. Vessels are surrounded by pervasive parenchyma. Fibers are missing. Only the vessel walls are lignified. Long prostrate hemicryptophyte, embedded in sand, coast-line, Astoria, Oregon, USA. *Abronia latifolia*, transverse section.

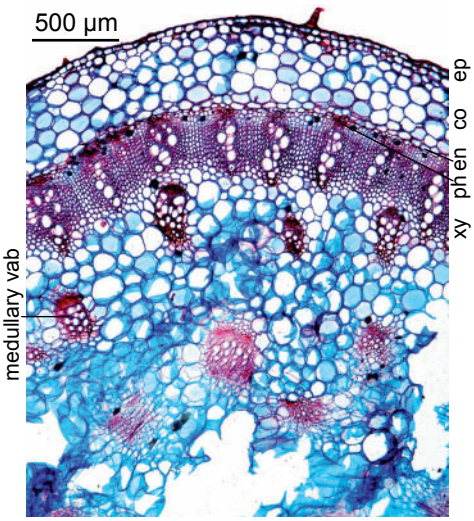



**Left Fig. 4.** More-or-less concentrically arranged vascular bundles. The vascular bundles are linked by a continuous fiber band and a thin-walled unlignified conjunctive tissue (parenchyma). 4 m-long prostrate liana, sea shore, subtropical climate, Dhofar, Oman. *Commicarpus boissieri*, transverse section.

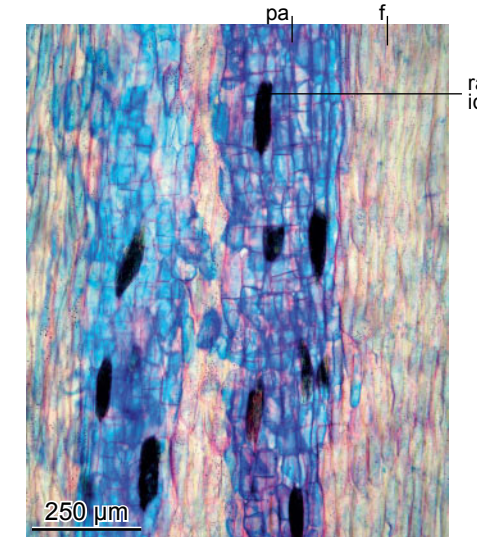
**Right Fig. 5.** Scalariform inter-vessel pitting. Only the vessel walls are lignified. Long prostrate hemicryptophyte, embedded in sand, coast-line, Astoria, Oregon, USA. *Abronia latifolia*, transverse section.




**Left Fig. 6.** Vascular bundles in the pith (medullary vascular bundles). Liana on a wall, cultivated, subtropical climate, Mt. Isa, Australia. *Bougainvillea spectabilis*, transverse section.

**Right Fig. 7.** Vascular bundles in the pith of an annual shoot (medullary vascular bundles). Long prostrate hemicryptophyte, embedded in sand, cold steppe, Great Sand Dunes, Colorado, USA. *Abronia fragrans*, transverse section.




**Left Fig. 8.** Rhaphides in parenchyma cells of the xylem. Liana on a wall, cultivated, subtropical climate, Mt. Isa, Australia. *Bougainvillea spectabilis*, radial section, polarized light.

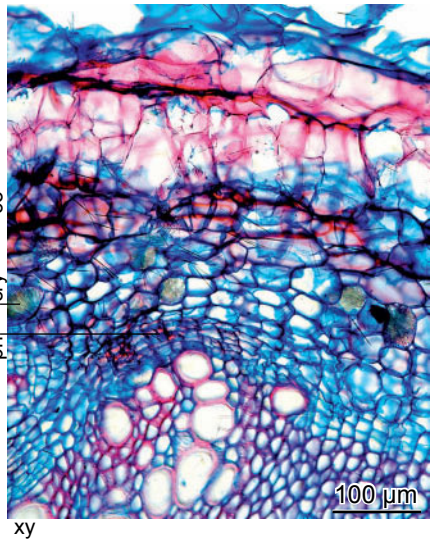
**Right Fig. 9.** Rhaphides in idioblasts (black dots) in the thin-walled conjunctive parenchyma. 4 m-long prostrate liana, seashore, subtropical climate, Dhofar, Oman. *Commicarpus boissieri*, radial section.

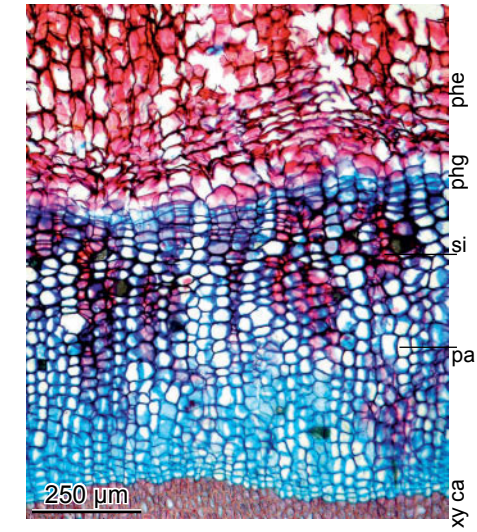
## Characteristics of the phloem and the cortex

The anatomy of the bark of all species is characterized by the absence of sieve tubes, the presence of parenchyma cells in different sizes and the presence of rhaphides (**Figs. 10** and **11**).

## Ecological trends in the phloem and the pith

There is not sufficient material to identify any ecological trends or characteristic features of species.




**Left Fig. 10.** Simple construction of the phloem and the cortex. Dilatation expands the cortex cells from the cambium to the periphery. Long prostrate hemicryptophyte, embedded in sand, cold steppe, Great Sand Dunes, Colorado, USA. *Abronia fragrans*, transverse section.

**Right Fig. 11.** Simple construction of the phloem and the cortex. The parenchyma stays in regular radial rows. 4 m-long prostrate liana, seashore, subtropical climate, Dhofar, Oman. *Commicarpus boissieri*, transverse section.

**Discussion in relation to previous studies**

Many authors have described the xylem of woody species from the genera *Pisonia*, *Neea*, *Torrubia* and *Heimerliodendron* (Gregory1994). Metcalfe and Chalk (1957) summarized the results of studies done before that date. Carlquist (2004) studied the lateral meristems and their products of seven woody species (*Abronia latifolia*, *Bougainvillea spectabilis*, *Guapira*, *Heimerliodendron*, *Mirabilis*, *Pisonia*, *Torrubia*).

The results of the present study agree with those of previous studies, however, it demonstrates the presence of medullary vascular bundles. The anatomical spectrum of the family is not fully covered with the present study.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **5** |
| 2 | growth rings absent | 5 |
| 3 | ring porous | 1 |
| 9 | vessels predominantly solitary | 4 |
| 11 | vessels predominantly in clusters | 3 |
| 13 | vessels with simple perforation plates | 5 |
| 20 | intervessel pits scalariform | 2 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 4 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 3 |
| 50 | <100 vessels per $mm^2$ in earlywood | 3 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 2 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 5 |
| 68 | fibers thin-walled | 2 |
| 70 | fibers thin- to thick-walled | 3 |
| 79 | parenchyma paratracheal | 4 |
| 79.1 | parenchyma pervasive | 1 |
| 97 | rays width predominantly 1-3 cells | 1 |
| 98 | rays commonly 4-10-seriate | 4 |
| 100.1 | rays confluent with ground tissue | 1 |
| 105 | ray: all cells upright or square | 3 |
| 117 | rayless | 1 |
| 120 | storied axial tissue (parenchyma, fibers, vessels, tangential section) | 4 |
| 133.1 | successive cambia: concentrically arranged single vascular bundles | 1 |
| 133.2 | successive cambia: concentric continuous | 4 |
| 134.1 | conjunctive tissue thin-walled | 4 |
| 149 | rhaphides present | 5 |
| R10 | phloem not well structured | 5 |
| R11 | with rhaphides | 5 |
| P1 | with medullary phloem or vascular bundles | 5 |

# Nymphaeaceae



**Number of species, worldwide and in Europe**

The cosmopolitan Nymphaeaceae family (incl. Cabombaceae) includes 6 genera with 68 species. In Europe there are 2 genera with 5 species.

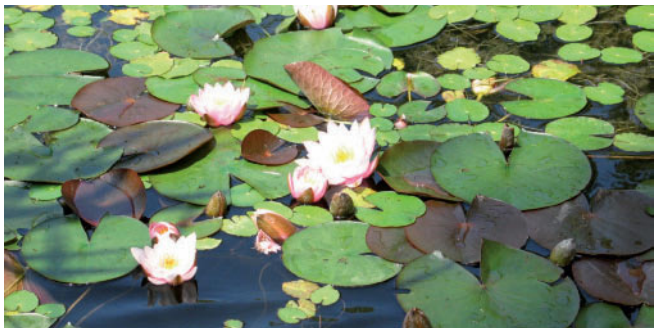
**Analyzed species:**

*Nuphar lutea* (L.) Sm.
*Nymphaea alba* L.
*Nymphaea candida* C. Presl

**Analyzed material**

The xylem and phloem of 3 Nymphaeaceae were analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Hydrophytes and helophytes | 3 | ca. 5 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 3 | |



*Nymphaea alba*

*Nuphar lutea*

*Nuphar lutea*

**Characteristics of the stem**

***1. Annual flower stems***

Secondary growth does not take place. Monocotyledon-like distributed, closed collateral vascular bundles stand in the parenchymatic tissue with large aerenchymatic lacunes (**Figs. 1-3**). The closed collateral vascular bundles contain a barely differentiated xylem and phloem (**Figs. 4-6**) as well as air ducts, which are surrounded by small parenchyma cells (**Figs. 4-6**). Single, large ducts stay outside the vascular bundle near the protoxylem on *Nuphar lutea* and *Nymphaea alba* (**Figs. 4** and **5**). Several small ducts stay within the vascular bundle of *Nympaea candida* (**Fig. 6**). Simple perforations and annular to helical thickenings (**Fig. 7**) are characteristic of the always unlignified vessels of all three species. The construction of aerenchyma is species-specific: net-like with larger cells in nodal points of *Nuphar lutea* (**Fig. 1**), and *Nymphaea candida* (**Fig. 3**) and tube-like in *Nymphaea alba* (**Fig. 2**). Specific for *Nuphar lutea* (**Fig. 8**) and *Nymphaea alba* (**Fig. 9**) are the star-shaped hairs with secondary walls which are covered with prismatic crystals. The hairs are located in both species in border cells of air ducts (**Figs. 8** and **9**). Isolated long, needle-shaped, thick-walled fibers with crystal mantels are below the epidermis in the collenchyma tissue and in intercellulares of *Nymphaea alba* (**Figs. 10-12**). A few crystals, sand and agglomerated grains (**Fig. 13**) occur in the aerenchymatic tissues of *Nymphaea candida*.

***2. Rhizomes***

The anatomical differences between rhizomes and stems are the following: The amount of aerenchyma is reduced and there are no metaxylem-borne lacunes (**Figs. 14** and **15**). Crystallized fibers and crystals are absent.

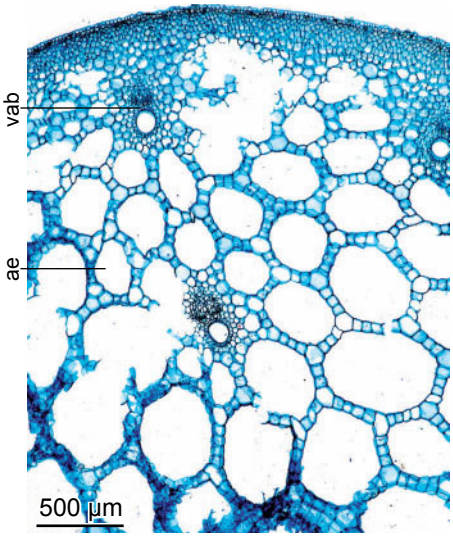



**Fig. 1.** Stem with scattered vascular bundles surrounded by a loose aerenchymatic tissue. Flower stem of a hydrophyte, 1 m below water level, hill zone, Federsee, Bavaria, Germany. *Nuphar lutea*, transverse section.

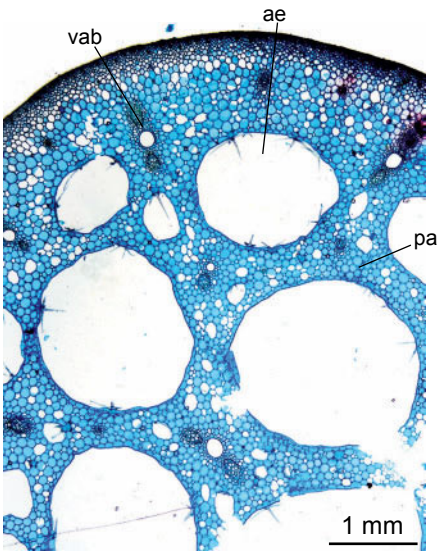



**Fig. 2.** Stem with scattered vascular bundles in a parenchymatic tissue and large and small air ducts. Flower stem of a hydrophyte, 1 m below water level, pond, hill zone, Switzerland. *Nymphaea alba*, transverse section.

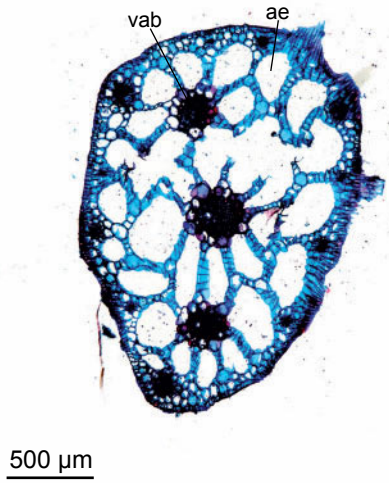
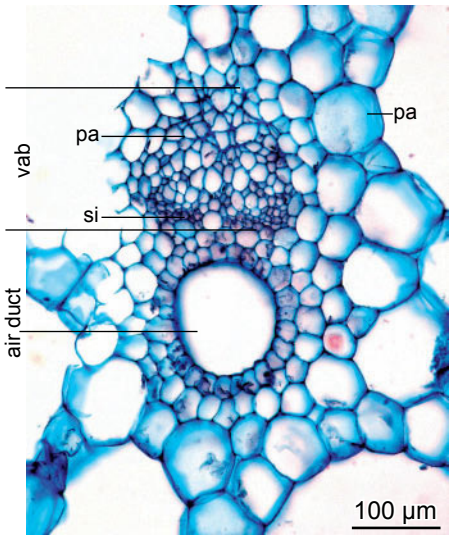
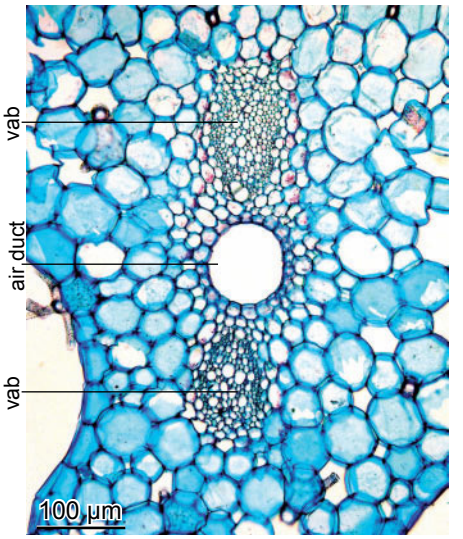


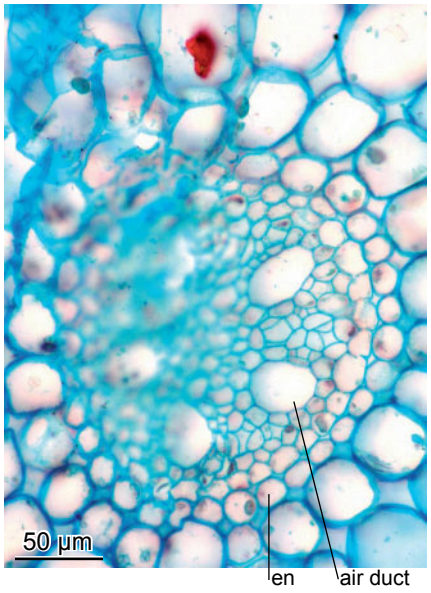

**Fig. 3.** Stem with scattered vascular bundles surrounded by a loose aerenchymatic tissue. Flower stem of a hydrophyte, 50 cm below water level, backwater of the Danube, hill zone, Slovakia. *Nymphaea candida*, transverse section.

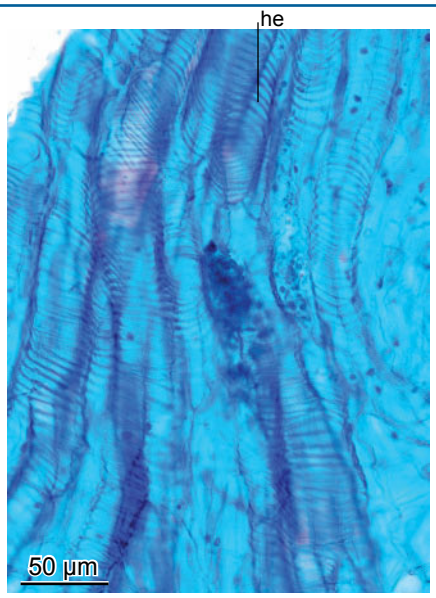



**Left Fig. 4.** Closed collateral vascular bundle. An air duct stays outside the vascular bundle. The xylem does not contain vessels and consists of small and large parenchyma cells. The phloem consists of parenchyma cells and collapsed sieve tubes. Flower stem of a hydrophyte, 1 m below water level, hill zone, Federsee, Bavaria, Germany. *Nuphar lutea*, transverse section.

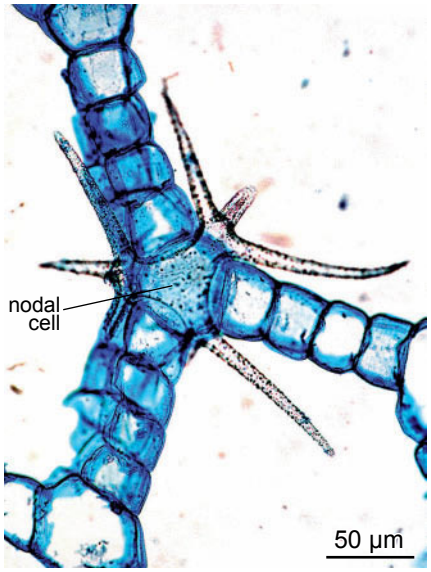
**Right Fig. 5.** Two closed collateral vascular bundles in opposite orientation with an air duct between them. The construction is similar to that of *Nuphar lutea*, but the external bundle (top) has at least one vessel (near the air duct). Flower stem of a hydrophyte, 1 m below water level, pond, hill zone, Switzerland. *Nymphaea alba*, transverse section.

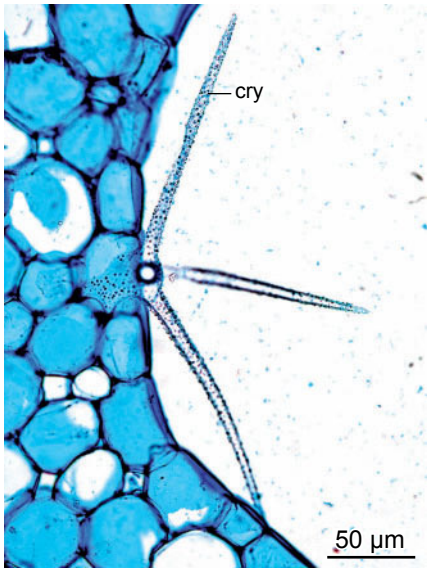



**Left Fig. 6.** Central radial vascular bundle with large air ducts. Phloem and xylem cannot be differentiated. Flower stem of a hydrophyte, 50 cm below water level, backwater of the Danube, hill zone, Slovakia. *Nymphaea candida*, transverse section.

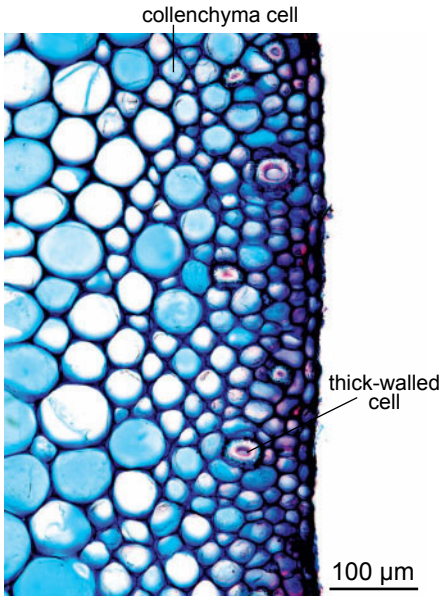
**Right Fig. 7.** Unlignified vessels with helical thickenings. Flower stem of a hydrophyte, 1 m below water level, hill zone, Federsee, Bavaria, Germany. *Nuphar lutea*, radial section.

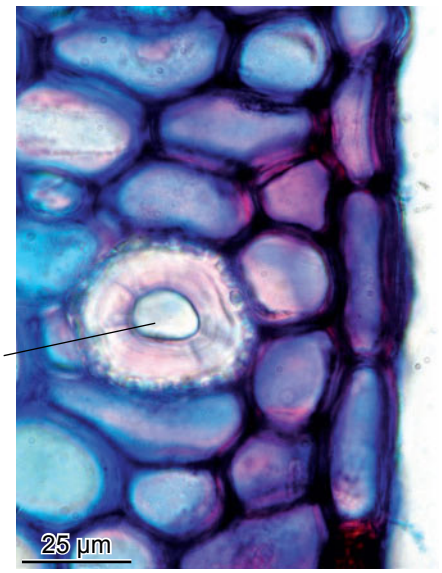



**Left Fig. 8.** A star-shaped hair is based in a nodal cell of aerenchymatic tissue. Small crystals occupy the hair. Flower stem of a hydrophyte, 1 m below water level, hill zone, Federsee, Bavaria, Germany. *Nuphar lutea*, transverse section.

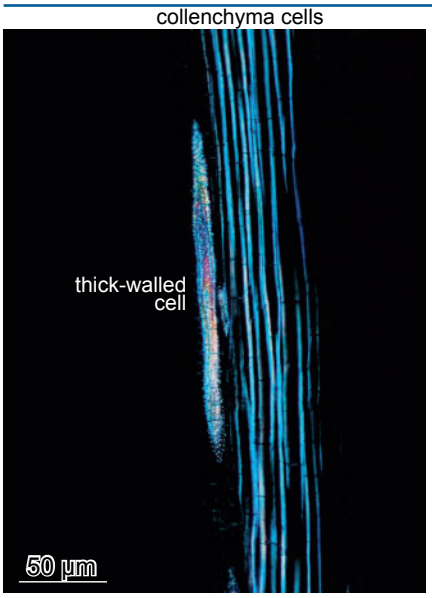
**Right Fig. 9.** A star-shaped hair is located in a border cell of an air duct. Small crystals occupy the hair. Flower stem of a hydrophyte, 1 m below water level, pond, hill zone, Switzerland. *Nymphaea alba*, transverse section.

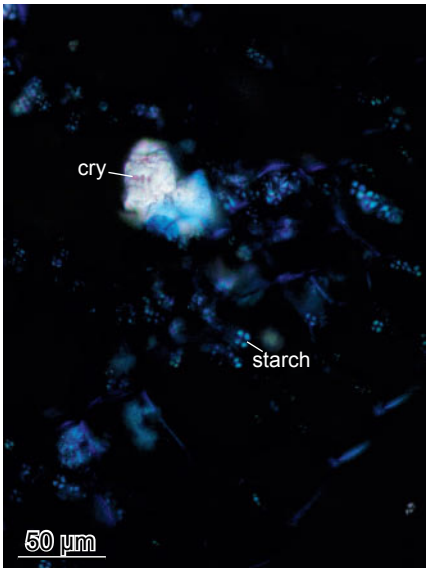



**Left Fig. 10.** Epidermis and a subepidermal collenchyma zone. A few cells have very thick cell walls. See also **Figs. 11** and **12**. Flower stem of a hydrophyte, 1 m below water level, pond, hill zone, Switzerland. *Nymphaea alba*, transverse section.

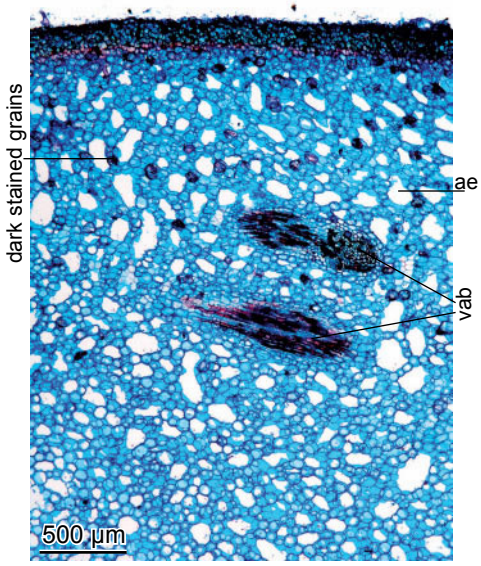
**Right Fig. 11.** The thick-walled cell is surrounded by small prismatic crystals. See also Fig. **12**. Flower stem of a hydrophyte, 1 m below water level, pond, hill zone, Switzerland. *Nymphaea alba*, transverse section.




**Left Fig. 12.** Longitudinal view of a single thick-walled cell, which is occupied by small prismatic crystals. The adjacent cells represent collenchyma. Flower stem of a hydrophyte, 1 m below water level, pond, hill zone, Switzerland. *Nymphaea alba*, radial section.

**Right Fig. 13.** Irregular group of small crystals in an air duct. Flower stem of a hydrophyte, 50 cm below water level, backwater of the Danube, hill zone, Slovakia. *Nymphaea candida*, transverse section, polarized light.



**Left Fig. 14.** Rhizome with two vascular bundles surrounded by aerenchymatic tissue. Some cells contain dark-staining grains (not starch). Rhizome of a hydrophyte, 1 m below water level, hill zone, Federsee, Bavaria, Germany. *Nuphar lutea*, transverse section.

**Right Fig. 15.** Rhizome with a central zone of densly packed vascular bundles. This zone is surrounded by small aerenchymatic tissue and an epidermis. Flower stem of a hydrophyte, 50 cm below water level, backwater of the Danube, hill zone, Slovakia. *Nymphaea candida*, transverse section.

## Discussion in relation to previous studies

Metcalfe and Chalk (1957) described some Nymphaeaceae species including *Nuphar* and *Nymphaea*. Schneider and Carlquist (1995a and b) concentrated on roots of the hydrophyte *Barclaya rotundifolia*, *Euryale* and *Victoria*. Special attention found the diaphragms, which traverse the intercellular spaces (Bruyne 1922). Kuo-Hang and Chen (1999) describe the crystals, which are deposited between a thin-walled primary wall and a thick-walled lignified secondary wall of the sclerenchymatic structures in the aerenchymatic zone. The distribution and construction of vascular bundles put these species in the neighborhood of monocotyledons. The results of the present study agree with observations by Metcalfe and Chalk (1957).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **3** |
| 2.1 | only one ring | 3 |
| 2.2 | without secondary growth | 3 |
| 9 | vessels predominantly solitary | 1 |
| 20 | intervessel pits scalariform | 3 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 3 |
| 50 | <100 vessels per mm$^2$ in earlywood | 3 |
| 60.1 | fibers absent | 3 |
| 79.1 | parenchyma pervasive | 3 |
| 99.1 | vascular-bundle form remaining | 3 |
| 117 | rayless | 3 |
| 127 | intercellular canals | 3 |
| 134 | successive cambia, diffuse = foraminate | 3 |
| 136 | prismatic crystals present | 3 |
| R14 | cortex with aerenchyma | 3 |
| P1 | with medullary phloem or vascular bundles | 3 |

# Onagraceae



**Number of species, worldwide and in Europe**

The Onagraceae family includes 17 genera with 675 species. Species occur in temperate and subtropical climates. In Europe, there are 5 genera with 46 endemic species.

**Analyzed material**

The xylem and phloem of 4 genera with 14 species were analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | | >10 |
| Hemicryptophytes | 10 | |
| Therophytes | 4 | 2 |
| **Plants analyzed from different vegetation zones:** | | |
| Boreal | 2 | |
| Mountain to subalpine | 4 | |
| Hill and mountain | 8 | |

**Analyzed species:**

*Circaea lutetiana* L.
*Clarkia purpurea* A. Nelson & J.F. Macbr.
*Epilobium alpestre* Kroker
*Epilobium angustifolium* L.
*Epilobium collinum* C. C. Gmelin
*Epilobium dodonaei* Vill.
*Epilobium fleischeri* Hochst.
*Epilobium hirsutum* L.
*Epilobium latifolium* L.
*Epilobium obscurum* Schreber
*Epilobium roseum* Schreber
*Oenothera biennis* L.
*Oenothera flava* Munz
*Oenothera glazioviana* Micheli

*Epilobium angustifolium*

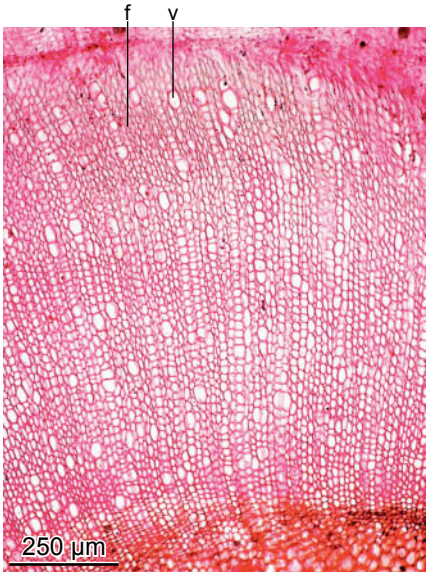
*Epilobium fleischeri*

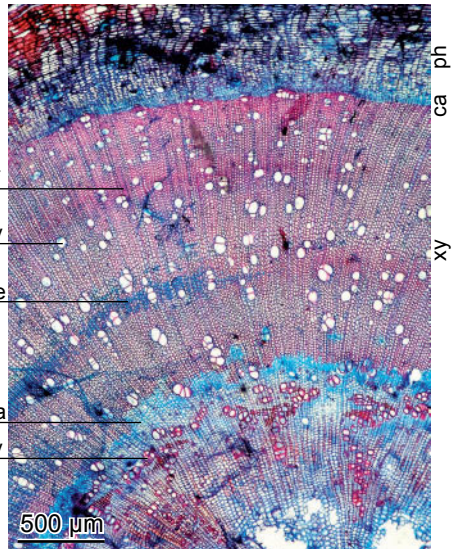
*Circaea lutetiana*

*Oenothera glazioviana*

**Characteristics of the xylem**

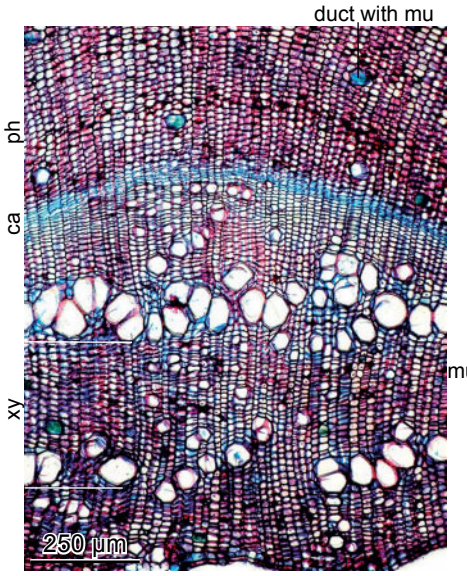
Annual and biannual species, as well as a few hemicryptophytes, have only one ring (**Figs. 1** and **2**). Growth-ring boundaries are marked by ring-porosity on *Epilobium angustifolium* (**Fig. 3**), and by semi-ring-porosity in *Epilobium fleischeri* (**Fig. 4**). Vessels are arranged mostly solitary or in short radial multiples (**Figs. 1-4** and **10**). Earlywood vessel diameter varies between 50-100 µm, e.g. in *Epilobium angustifolium* (**Fig. 3**) and *Oenothera biennis*, and between 20-40 µm, e.g. in *Circaea lutetiana* and *Epilobium obscurum* (**Figs. 1**, **2** and **9**). Vessels of all species have simple perforations (**Figs. 5** and **6**). Intervessel pits are scalariform (**Figs. 5** and 7) or round and are arranged in alternating position (**Fig. 6**). Vestured pits could be observed in *Epilobium dodonaei* (**Fig. 7**). Vessels of a few species are thick-walled, e.g. *Oenothera glazioviana* (**Fig. 8**). Fibers with small pits and slit-like apertures are in the radial walls of all species. Tension wood is present in most species (**Figs. 9** and **10**). The occurence of axial parenchyma greatly varies: It is unrecognizable (**Fig. 1**), scanty paratracheal (**Fig. 10**) or pervasive in the center and paratracheal on the periphery (**Figs. 8**, **11** and **12**). Rays are rarely absent, e.g. in *Epilobium angustifolium*, and uni- or biseriate (**Figs. 13-15**) with square and upright cells. The xylem of a few *Epilobium* and *Oenothera* species includes enlarged cells containing mucilage and raphides (**Figs. 16**, **17** and **18**). Raphides are present in the pith of all species. Included sieve tubes have been observed in *Epilobium angustifolium*, *Oenothera biennis* and *O. glazioviana* (**Figs. 8**, **12**, **19** and **20**). Interxylary periderm is present in *Epilobium angustifolium*, *E. dodonaei* and *E. latifolium* (**Figs. 21** and **22**).




**Left Fig. 1.** One ring with solitary vessels. Root collar of an 80 cm-high therophyte, riparian, hill zone, Birmensdorf, Switzerland. *Epilobium hirsutum*, transverse section.

**Right Fig. 2.** One ring with growth zones. The center consists mainly of unlignified parenchyma cells, while the periphery is formed by lignified fibers. Root collar of a 1 m-high therophyte, ruderal site, hill zone, Birmensdorf, Switzerland. *Oenothera glazioviana*, transverse section.



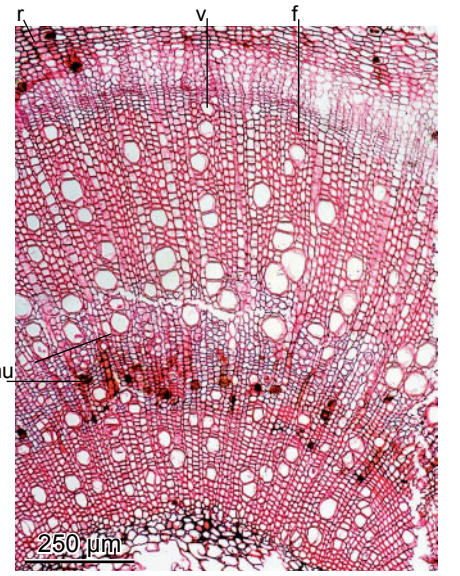



**Fig. 3.** Distinct rings due to ring-porosity. Rhizome of a 40 cm-high hemicryptophyte, riparian, subalpine zone, Engadin, Switzerland. *Epilobium latifolium*, transverse section.

**Fig. 4.** Semi-ring-porous xylem. Dark cells in the middle of the xylem show enlarged cells with mucilage and raphides. Rhizome of a 40 cm-high hemicryptophyte, riparian, subalpine zone, Engadin, Switzerland. *Epilobium fleischeri*, transverse section.

**Fig. 5.** Vessels with simple perforations and scalariform intervessel pits. Rhizome of a 40 cm-high hemicryptophyte, riparian, subalpine zone, Engadin, Switzerland. *Epilobium fleischeri*, radial section.

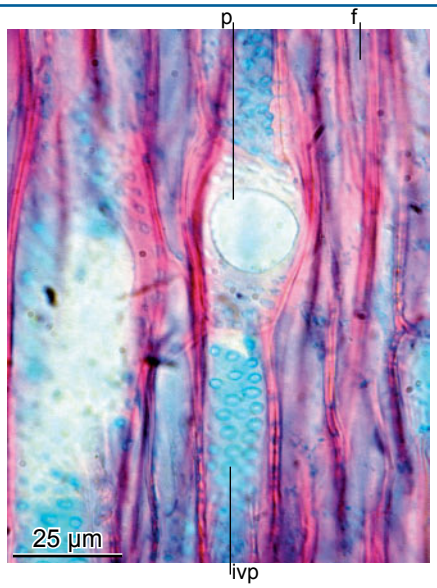



**Fig. 6.** Vessels with simple perforations and large, round intervessel pits. Root collar of a 20 cm-high hemicryptophyte, on a wall, hill zone, Ticino, Switzerland. *Epilobium collinum*, radial section.

**Fig. 7.** Scalariform, vestured pits. Rhizome of a 50 cm-high hemicryptophyte, rock field, montane zone, Klosters, Switzerland. *Epilobium dodonaei*, radial section.

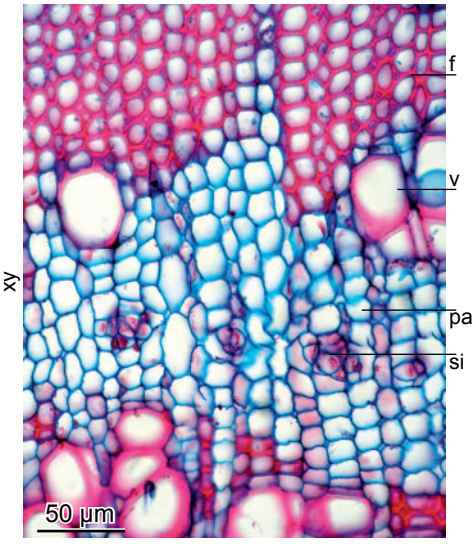
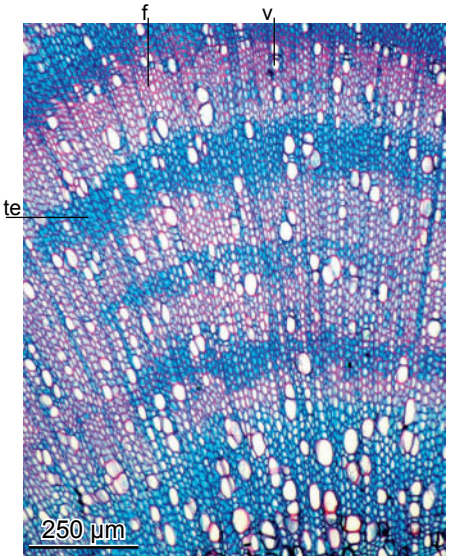
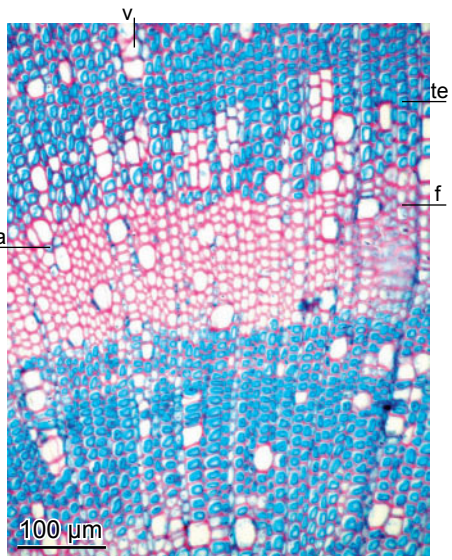


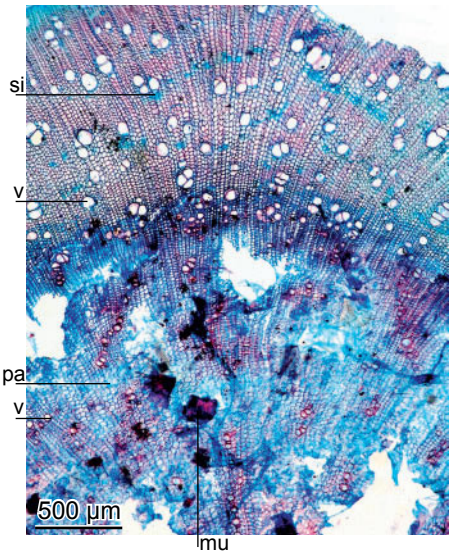

**Fig. 8.** Thick-walled vessels surrounded by pervasive parenchyma and two groups of small sieve-tubes (lower part). Root collar of a 1 m-high therophyte, ruderal site, hill zone, Birmensdorf, Switzerland. *Oenothera glazioviana*, transverse section.

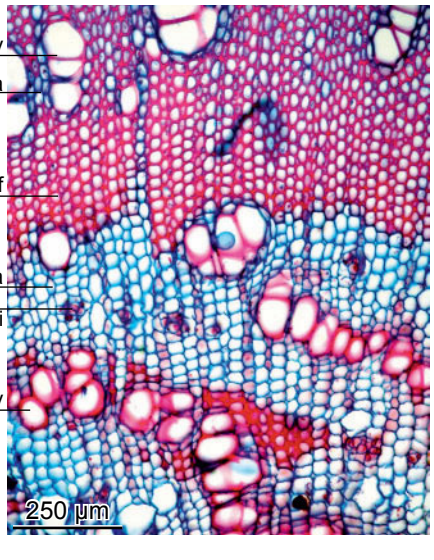



**Left Fig. 9.** Rhythmic occurrence of intra-annual tension wood. Root collar of a 0.5 m-high hemicryptophyte, ruderal site, hill zone, Jura, Lons le Saunier, France. *Epilobium obscurum*, transverse section.

**Right Fig. 10.** A zone of fibers and vessels with scanty paratracheal parenchyma lies between two zones of gelatinous fibers. Rays are absent. Root collar of a 20 cm-high hemicryptophyte, on a wall, hill zone, Ticino, Switzerland. *Epilobium collinum*, transverse section.




**Left Fig. 11.** Variable occurrence of parenchyma: pervasive in the center and paratracheal on the periphery. Root collar of a 1 m-high therophyte, ruderal site, hill zone, Birmensdorf, Switzerland. *Oenothera biennis*, transverse section.

**Right Fig. 12.** Variable occurrence of parenchyma and fibers. Center: Pervasive parenchyma dominates; included are a few vessels, groups of fibers and groups of sieve-tubes. Periphery: fibers dominate; included are a few vessels with paratracheal parenchyma. Root collar of a 1 m-high therophyte, ruderal site, hill zone, Birmensdorf, Switzerland. *Oenothera glazioviana*, transverse section.

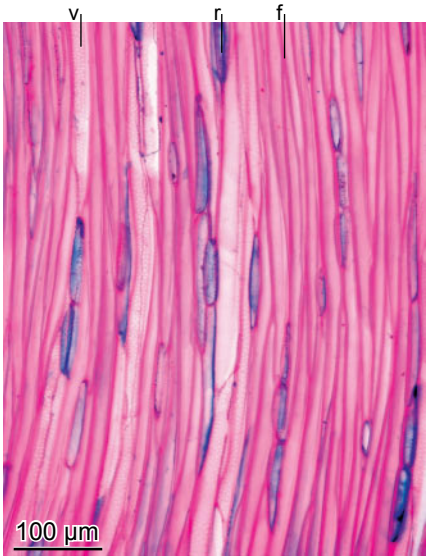



**Fig. 13.** Uniseriate rays consisting of axially elongated long cells. Root collar of a 1 m-high therophyte, dry meadow, arid zone, Bakersfield, California, USA. *Clarkia purpurea*, tangential section.

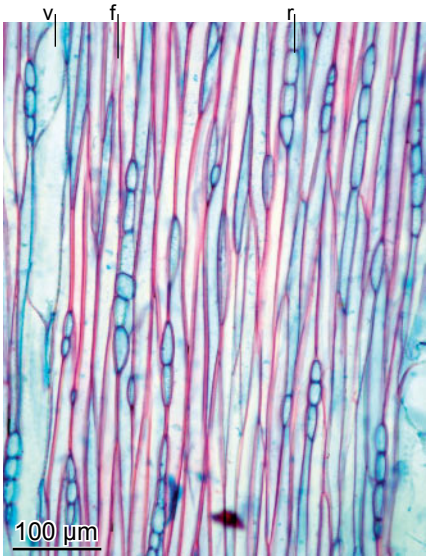



**Fig. 14.** Uniseriate rays. Root collar of a 1 m-high therophyte, ruderal site, hill zone, Birmensdorf, Switzerland. *Oenothera biennis*, tangential section.

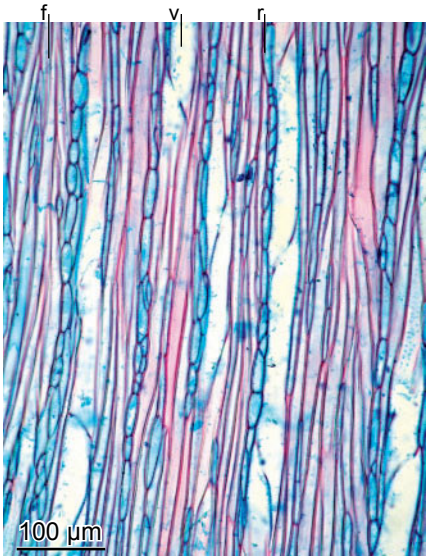
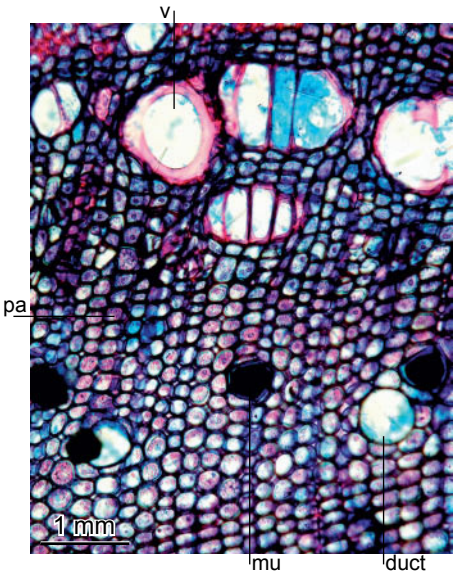
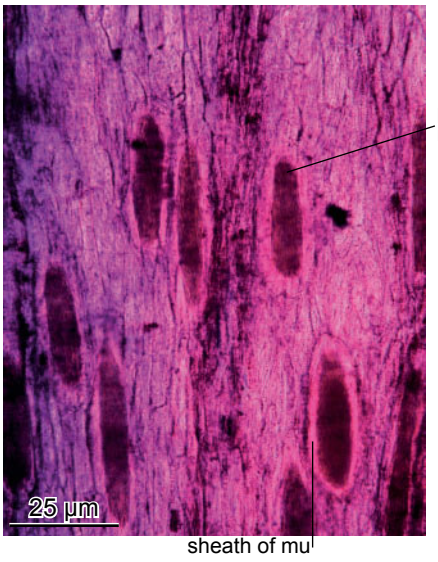


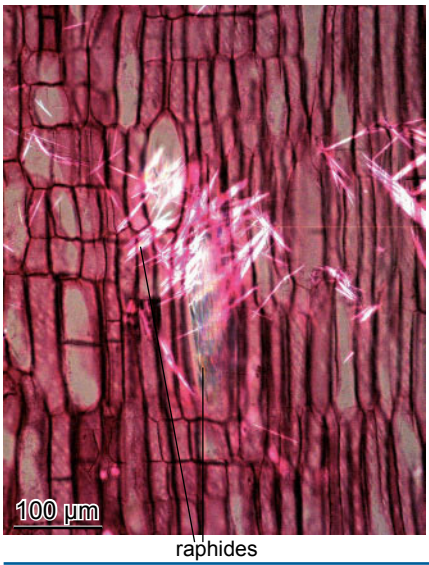

**Fig. 15.** Uni- and biseriate rays. Root collar of a 1 m-high therophyte, riparian, hill zone, Birmensdorf, Switzerland. *Circaea lutetiana*, tangential section.

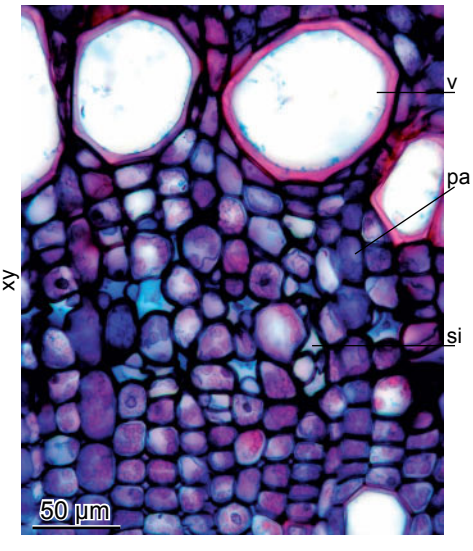



**Left Fig. 16.** Vessels, mucilage cells and sieve-tubes are embedded in a parenchymatic tissue. Rhizome of an 80 cm-high hemicryptophyte, rock field, subalpine, Engadin, Switzerland. *Epilobium angustifolium*, transverse section.

**Right Fig. 17.** The axially elongated cells contain mucilage (light red border) and bundles of raphides (dark part). Root collar of a 20 m-high therophyte, dry meadow, montane zone, Monte Vista, Colorado, USA. *Oenothera flava*, tangential section.




**Left Fig. 18.** Isolated raphides and a bundle of raphides in an axially elongated cell. Rhizome of a 50 cm-high hemicryptophyte, rock field, montane zone, Klosters, Switzerland. *Epilobium dodonaei*, radial section.

**Right Fig. 19.** Groups of sieve-tubes embedded in a parenchymatic tissue. Rhizome of an 80 cm-high hemicryptophyte, rock field, subalpine zone, Engadin, Switzerland. *Epilobium angustifolium*, transverse section.

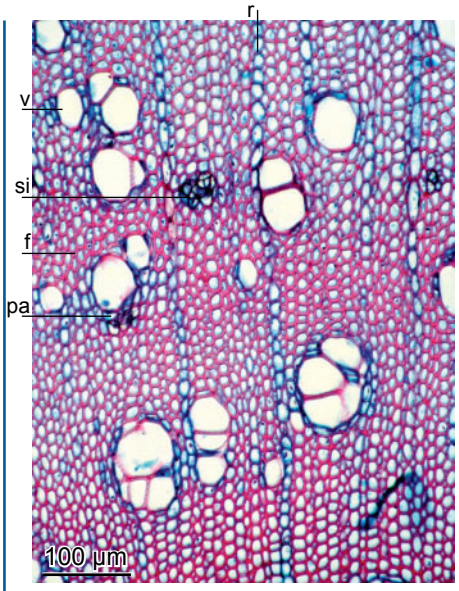



**Fig. 20.** Groups of sieve-tubes surrounded by a fiber tissue and vessels with paratracheal parenchyma. Root collar of a 1 m-high therophyte, ruderal site, hill zone, Birmensdorf, Switzerland. *Oenothera glazioviana*, transverse section.

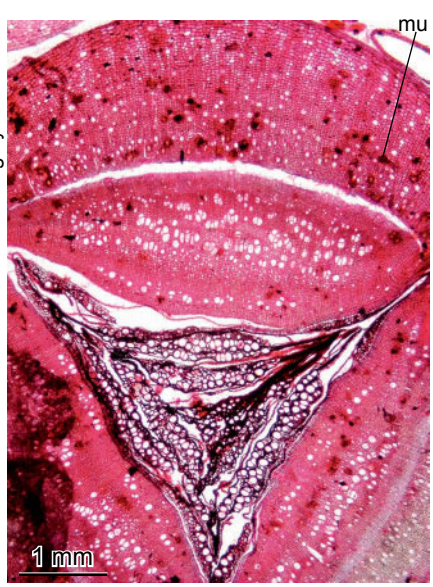



**Fig. 21.** Dead inter-xylary rhytidiome is surrounded by a living xylem. The inner part consists of dead inter-xylary periderm and dead xylem. Rhizome of an 80 cm-high hemicryptophyte, rock field, subalpine zone, Engadin, Switzerland. *Epilobium angustifolium*, transverse section.

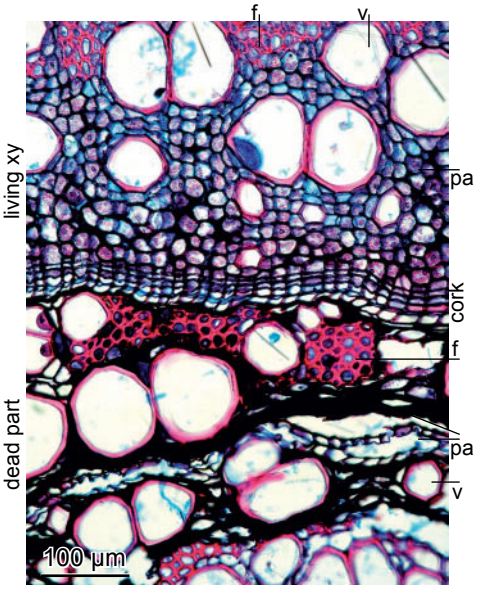
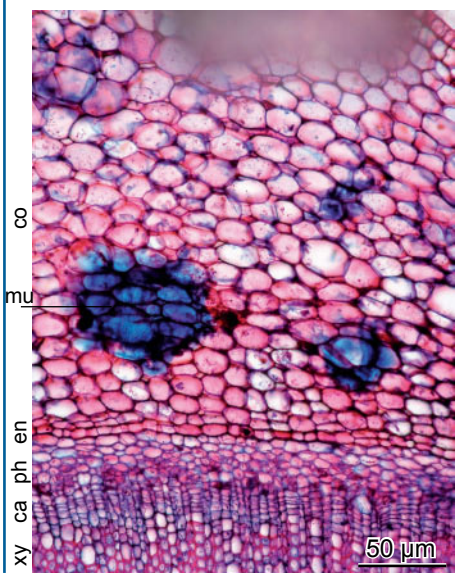
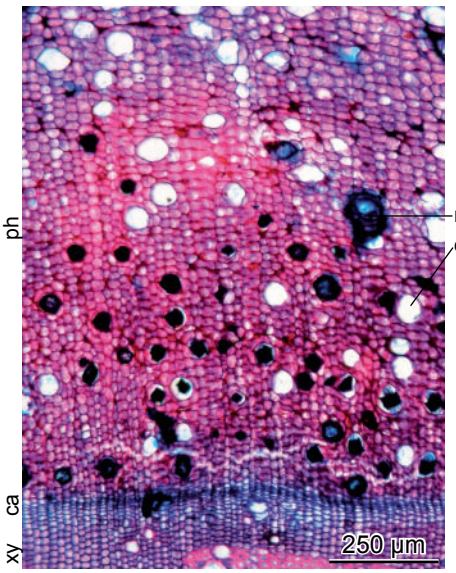



**Fig. 22.** Living xylem, phellogen, phellem and phelloderm (upper part); dead rhytidiome (lower part). Rhizome of an 80 cm-high hemicryptophyte, rock field, subalpine zone, Engadin, Switzerland. *Epilobium angustifolium*, transverse section.

### Characteristics of the phloem and the cortex

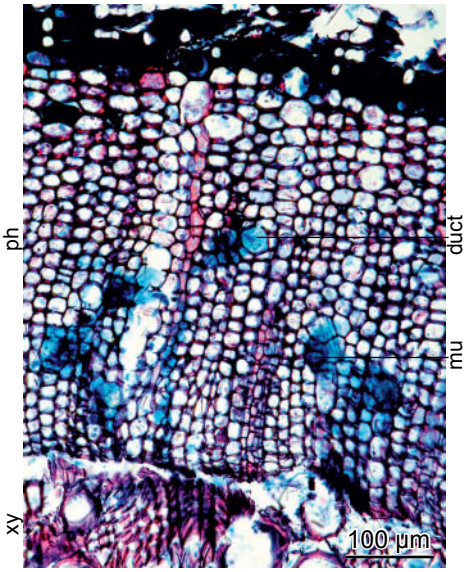
Common to all species analyzed are enlarged cells containing mucilage and raphides in the phloem and the cortex (**Figs. 23-26**). Prismatic crystals occur only in ray cells of *Clarkia purpurea*. In most species the phloem and parenchyma cells cannot be differentiated (**Figs. 24** and **25**) or the parenchymatic tissue of the phloem includes small groups of small sieve-tubes (**Fig. 23**).

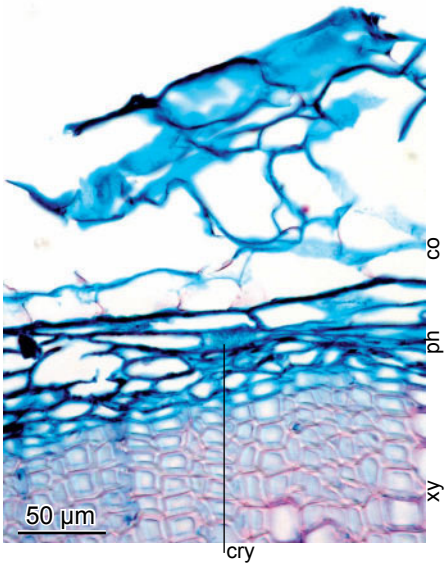



**Left Fig. 23.** Cortex containing a few zones with mucilages. Root collar of a 1 m-high therophyte, moist meadow, subalpine zone, Furka Pass, Valais, Switzerland. *Epilobium alpestre*, transverse section.

**Right Fig. 24.** Simply structured phloem and cortex containing many mucilage cells. Rhizome of an 80 cm-high hemicryptophyte, rock field, subalpine zone, Engadin, Switzerland. *Epilobium angustifolium*, transverse section.




**Left Fig. 25.** Simply structured phloem and cortex, containing mucilage cells with raphides. Rhizome of a 50 cm-high hemicryptophyte, rock field, montane zone, Klosters, Switzerland. *Epilobium dodonaei*, transverse section.

**Right Fig. 26.** The phloem consists of small cells and larger cells (idioblasts) with short raphides and a cortex with large cells. Root collar of a 1 m-high therophyte, dry meadow, arid zone, Bakersfield, California, USA. *Clarkia purpurea*, transverse section.



### Discussion in relation to previous studies

All species described here occur in cool temperate regions. Carlquist (1975, 1977 and 1982) described 10 shrubs and 2 therophytes (*Circaea lutetiana* and *Oenothera deltoids*). *Fuchsia* species were subject of many studies (Gregory 1994). Moss (1936) studied *Epilobium angustifolium* in detail. Newly described here are 8 hemicryptophytes and 3 therophytes. The present results are principally in accordance with previous findings. We can confirm the general presence of raphides and mucilage canals. In contrast, included sieve-tubes and included periderm are species-specific. This study shows that remarkable anatomical variability exists within the genus *Epilobium*. Anatomical structures related to environmental conditions could not be recognized.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **14** |
| 1 | growth rings distinct and recognizable | 4 |
| 2.1 | only one ring | 10 |
| 3 | ring-porous | 1 |
| 5 | diffuse-porous | 2 |
| 9 | vessels predominantly solitary | 10 |
| 9.1 | vessels in radial multiples of 2-4 common | 8 |
| 10 | vessels in radial multiples of 4 or more common | 2 |
| 11 | vessels predominantly in clusters | 2 |
| 13 | vessels with simple perforation plates | 14 |
| 20 | intervessel pits scalariform | 8 |
| 21 | intervessel pits opposite | 2 |
| 22 | intervessel pits alternate | 10 |
| 39.1 | vessel cell-wall thickness >2 µm | 4 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 7 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 7 |
| 50 | <100 vessels per mm² in earlywood | 12 |
| 50.1 | 100-200 vessels per mm² in earlywood | 2 |
| 56 | tylosis with thin walls | 1 |
| 60.1 | fibers absent | 3 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 14 |
| 68 | fibers thin-walled | 10 |
| 70 | fibers thin- to thick-walled | 2 |
| 70.2 | tension wood present | 7 |
| 75 | parenchyma absent or unrecognizable | 7 |
| 79 | parenchyma paratracheal | 3 |
| 79.1 | parenchyma pervasive | 4 |
| 96 | rays uniseriate | 8 |
| 97 | rays width predominantly 1-3 cells | 4 |
| 98 | rays commonly 4-10-seriate | 1 |
| 105 | ray: all cells upright or square | 10 |
| 117 | rayless | 4 |
| 124 | oil and mucilage cells | 4 |
| 135 | interxylary phloem present | 3 |
| 135.1 | interxylary periderm (cork band) | 3 |
| 136 | prismatic crystals present | 1 |
| 149 | rhaphides present | 13 |
| R1 | groups of sieve tubes present | 5 |
| R7.1 | with acicular crystals | 1 |
| R7.2 | with raphides | 14 |
| R8 | with crystal druses | 0 |
| R9 | with crystal sand | 0 |
| R10 | phloem not well structured | 7 |
| R11 | with rhaphides | 0 |
| R12 | with laticifers, oil ducts or mucilage ducts | 14 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 9 |

# Oxalidaceae



**Number of species, worldwide and in Europe**

The cosmopolitan Oxalidaceae family includes 6 genera with 880 species. In Europe there is one genus with 12 species (*Oxalis*). All *Oxalis* species in Makaronesia are adventitious.

**Analyzed species:**

*Oxalis corniculata* L.
*Oxalis pres-caprae* L.
*Oxalis stricta* L.
*Oxalis subacaulis* Gilles

**Analyzed material**

The xylem and phloem of 1 genus with 4 species were analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | | 2 |
| Hemicryptophytes/therophytes | 4 | |
| **Plants analyzed from different vegetation zones:** | | Studies from other authors: |
| Tropical | | 2 |
| Suptropical | 1 | |
| Hill and mountain | 3 | |

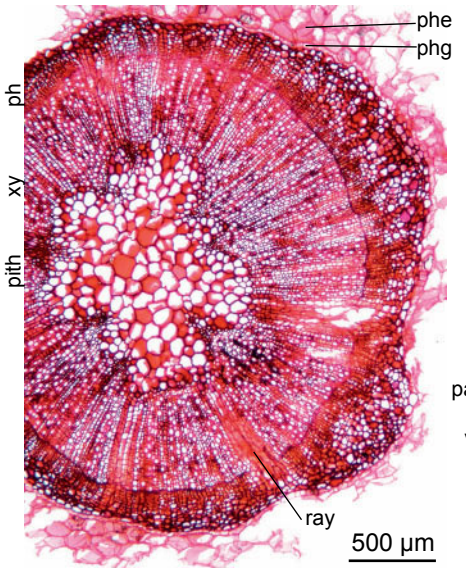
**Right:** *Oxalis pres-caprae*

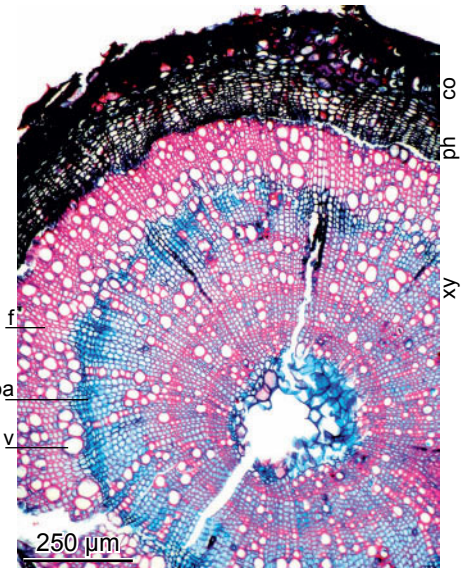
*Oxalis stricta*

*Oxalis acetosella*

**Characteristics of the xylem**

Rings are absent or indistinct in the present material (**Figs. 1-4**). Ring boundaries, if present, are marked by slight semi-ring- porosity (**Figs. 2-4**). Vessels are arranged mostly solitary (**Figs. 1-4**). The earlywood vessel diameter of the majority of species varies between 20-50 µm. Vessel density is usually between 200-300/mm$^2$. Vessel walls are thick-walled in most species. Vessels contain exclusively simple perforations (**Fig. 5**). Inter-vessel pits are predominantly small and round in alternating position but are scalariform in *Oxalis subacaulis* (**Fig. 6**). The radial walls of fibers in all species are perforated by small to medium-sized round pits (2-3 µm). Fibers are absent (**Fig. 7**) or thin- to thick-walled (**Figs. 2** and **3**). *Oxalis stricta* has few septate fibers (**Fig. 8**). *Oxalis corniculata* and *O. stricta* have paratracheal parenchyma (**Fig. 12**). Parenchyma is pervasive in *Oxalis pres-caprae* and *O. subacaulis* (**Fig. 7**). Rays are absent in *Oxalis corniculata* (**Fig. 2**), rare and 1-3 cells wide in *Oxalis stricta* (**Fig. 9**) and large, but not well differentiated from the axial tissue in *Oxalis pres-caprae* (**Fig. 1**) and *Oxalis subacaulis* (**Fig. 10**). The primary form of vascular bundles remains in *Oxalis subacaulis* (**Fig. 4**). Ray cells, if present, are exclusively upright. Prismatic crystals have been observed in *Oxalis pres-caprae*.




**Left Fig. 1.** Stem with one ring, small vessels and large rays. Root collar of a 30 cm-high therophyte, ruderal site, subtropical arid zone, La Palma, Canary Islands. *Oxalis pres-caprae*, transverse section.

**Right Fig. 2.** Stem with growth zones. The last ring is delimitated from the previous by a parenchymatic zone consisting of cells with unlignified walls. Root collar of a 15 cm-high hemicryptophyte, ruderal site, hill zone, Switzerland. *Oxalis corniculata*, transverse section.

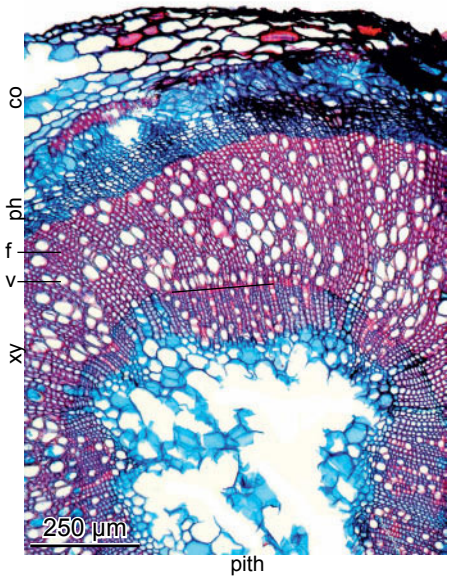



**Fig. 3.** Semi-ring-porous xylem with two rings. Root collar of a 20 cm-high hemicryptophyte, ruderal site, hill zone, Switzerland. *Oxalis stricta*, transverse section.

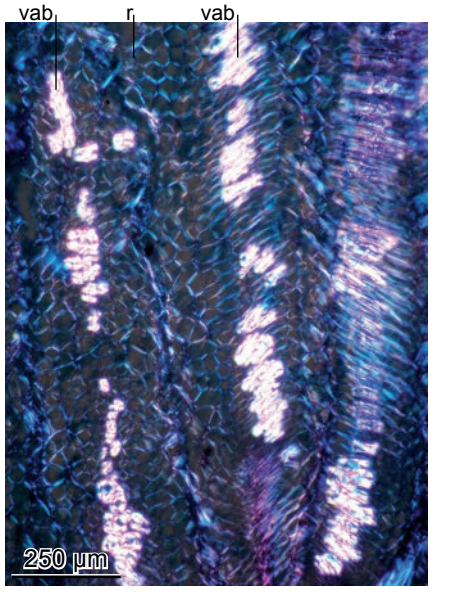



**Fig. 4.** Semi-ring-porous xylem with large rays and radial strips consiting of vessels. Root collar of a 30 cm-high hemicryptophyte, ruderal site, hill zone, Andes, Argentina. *Oxalis subacaulis*, transverse section, polarized light.

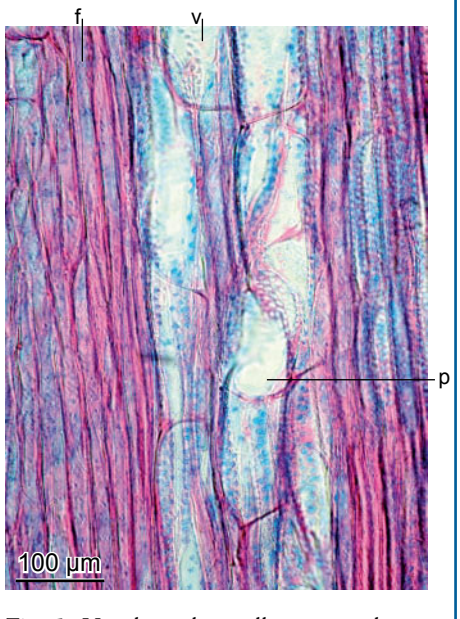



**Fig. 5.** Vessels with small intervessel pits and simple perorations. Root collar of a 20 cm-high hemicryptophyte, ruderal site, hill zone, Switzerland. *Oxalis stricta*, radial section.

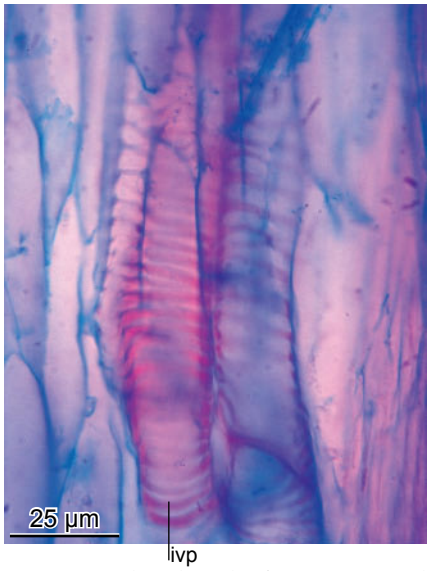



**Fig. 6.** Vessel with scalariform inter-vessel pits. Root collar of a 30 cm-high hemicryptophyte, ruderal site, hill zone, Andes, Argentina. *Oxalis subacaulis*, radial section.

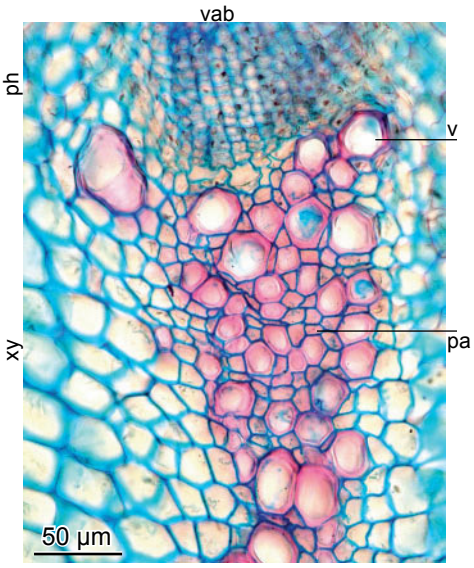



**Fig. 7.** Thick-walled vessels surrounded by pervasive parenchyma. Root collar of a 30 cm-high hemicryptophyte, ruderal site, hill zone, Andes, Argentina. *Oxalis subacaulis*, transverse section.

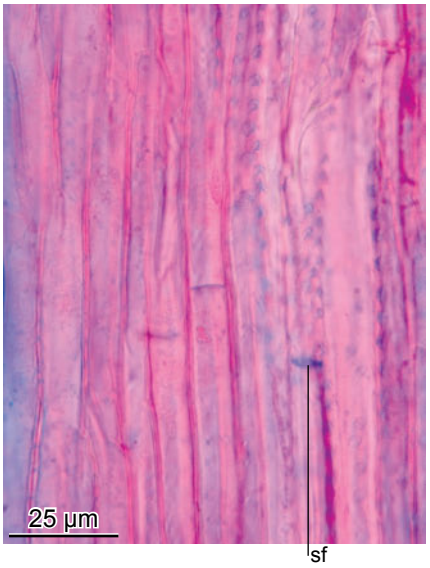
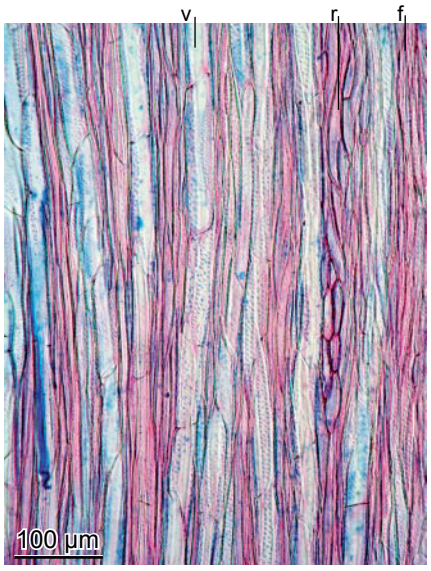
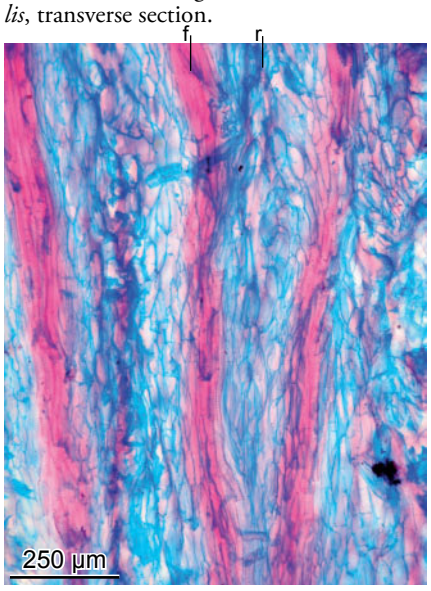



**Fig. 8.** Septate fibers with large fiber pits. Root collar of a 20 cm-high hemicryptophyte, ruderal site, hill zone, Switzerland. *Oxalis stricta*, radial section.




**Left Fig. 9.** One ray with 2-3 cells width. Rays are rare. Root collar of a 20 cm-high hemicryptophyte, ruderal site, hill zone, Switzerland. *Oxalis stricta*, tangential section.

**Right Fig. 10.** Very large, confluent rays with unlignified cell walls. Root collar of a 30 cm-high hemicryptophyte, ruderal site, hill zone Andes, Argentina. *Oxalis subacaulis*, tangential section.

### Characteristics of the phloem, the cortex and the pith

All species have a simply structured phloem (**Fig. 11**). Sieve tubes and parenchyma cells are difficult to differentiae. Sclereids are present in *Oxalis stricta* (**Fig. 12**). Large, irregularly formed crystal bodies occur in the bark of *Oxalis pres-caprae* (**Fig.13**). Such crystals also occur in the pith of *Oxalis subacaulis*. The cortex of *Oxalis stricta* and *O. pres-caprae* is divided into two parts. The inner part consists of thick-walled small cells and the outer part of thin-walled, large parenchymatic cells. The two parts are delimitated by an endodermis (**Figs. 2**, **12** and **14**). A phellem is present in *Oxalis corniculata* (**Fig. 11**) and in *O. subacaulis* (**Fig. 15**).

### Characteristic features of taxa

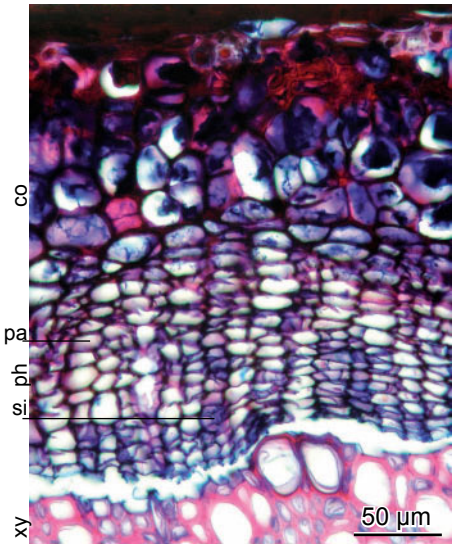
Ray and intervessel pit features and the presence or absence of crystals can be used for species differentiation.

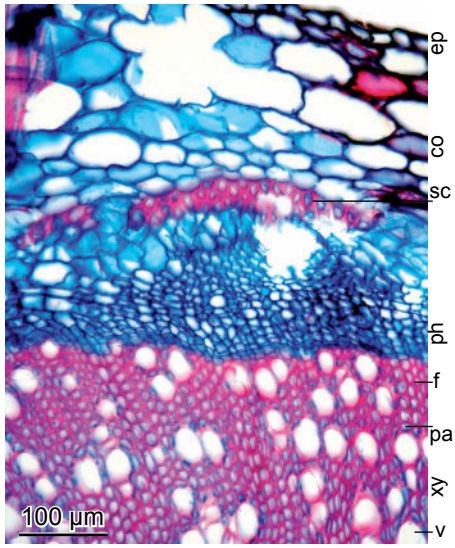
### Ecological trends and relations to life forms

The analyzed material is too limited to detect ecological trends.

### Discussion in relation to previous studies

The xylem of the tree-like genera *Averrhoa* and *Sarcotheca* have been described by several authors (see Gregory 1994). Heimsch (1942) mentioned ray characteristics in *Oxalis* species. The species presented here have never been described before.




**Left Fig. 11.** Bark with a simply structured phloem. Outside of the small cortex is a phellem consisting of collapsed cells. Root collar of a 15 cm-high hemicryptophyte, ruderal site, hill zone, Switzerland. *Oxalis corniculata*, transverse section.

**Right Fig. 12.** Bark with an outer thin-walled part, which is divided by a small band of sclerenchyma from the inner part containing thicker-walled smaller cells. The phloem is simply structured. Root collar of a 20 cm-high hemicryptophyte, ruderal site, hill zone, Switzerland. *Oxalis stricta*, radial section.

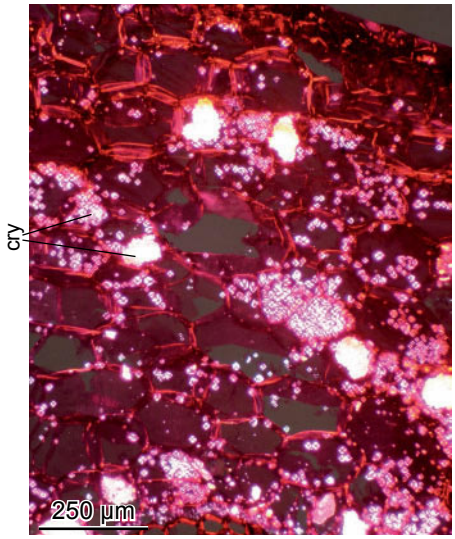



**Fig. 13.** Irregularly formed crystal bodies in the outer part of the cortex. Root collar of a 30 cm-high therophyte, ruderal site, subtropical arid zone, La Palma, Canary Islands. *Oxalis pres-caprae*, transverse section, polarized light.

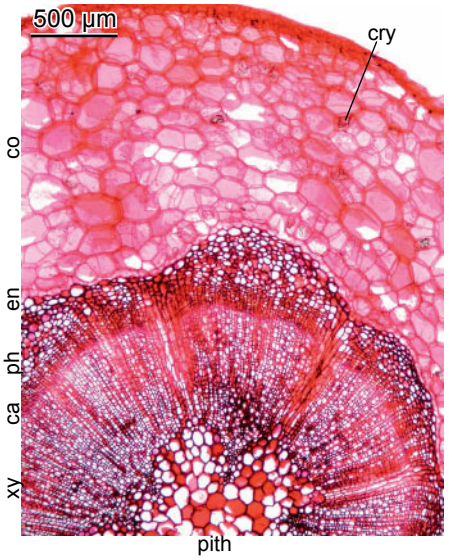



**Fig. 14.** Bark with an outer thin-walled part, which is divided by a uniseriate endodermis from the inner part containing thicker-walled smaller cells. The phloem is simply structured. Root collar of a 30 cm-high therophyte, ruderal site, subtropical arid zone, La Palma, Canary Islands. *Oxalis pres-caprae*, transverse section.

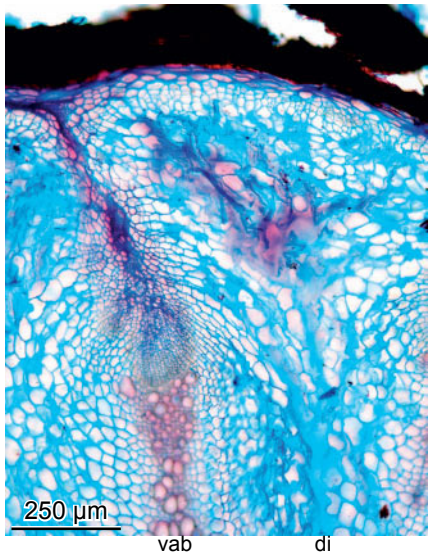



**Fig. 15.** A simply structured phloem located between large ray dilatations in the radial continuation of a vessel strip. Outside of the small cortex is a phellem consisting of collapsed cells (dark layer). Root collar of a 30 cm-high hemicryptophyte, ruderal site, hill zone, Andes, Argentina. *Oxalis subacaulis*, transverse section.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **4** |
| 2 | growth rings absent | 3 |
| 2.1 | only one ring | 1 |
| 5 | diffuse-porous | 4 |
| 9 | vessels predominantly solitary | 4 |
| 13 | vessels with simple perforation plates | 4 |
| 20 | intervessel pits scalariform | 1 |
| 20.1 | intervessel pits pseudoscariform to reticulate | 1 |
| 22 | intervessel pits alternate | 3 |
| 39.1 | vessel cell-wall thickness >2 µm | 3 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 4 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 4 |
| 60.1 | fibers absent | 2 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 2 |
| 70 | fibers thin- to thick-walled | 2 |
| 79 | parenchyma paratracheal | 1 |
| 79.1 | parenchyma pervasive | 3 |
| 89 | parenchyma marginal | 1 |
| 97 | ray width predominant 1-3 cells | 1 |
| 99 | rays commonly >10-seriate | 1 |
| 99.1 | vascular-bundle form remaining | 1 |
| 100.1 | rays confluent with ground tissue | 1 |
| 105 | ray: all cells upright or square | 3 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 1 |
| 117 | rayless | 2 |
| 142 | prismatic crystals in axial chambered cells | 1 |
| R3 | distinct ray dilatations | 1 |
| R6.1 | sclereids in tangential rows | 2 |
| R7 | with prismatic crystals | 1 |
| R8 | with crystal druses | 1 |
| R10 | phloem not well structured | 4 |

# Paeoniaceae



**Number of species, worldwide and in Europe**

The Paeoniaceae family includes 1 genus with 30 species. Most species grow in the temperate zone of the Northern hemisphere, Eurasia and North West America. The family is represented by 10 species in Western Europe.

**Analyzed material**

The xylem and phloem of 3 taxa from Central Europe were analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 1 | 4 |
| Hemicryptophytes/geophytes | 2 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 3 | |

**Analyzed species:**

*Paeonia officinalis* ssp. *officinalis* L., wild form
*Paeonia officinalis*, cultivar
*Paeonia suffruticosa* Andrews

*Paeonia officinalis*

*Paeonia tenuifolia*

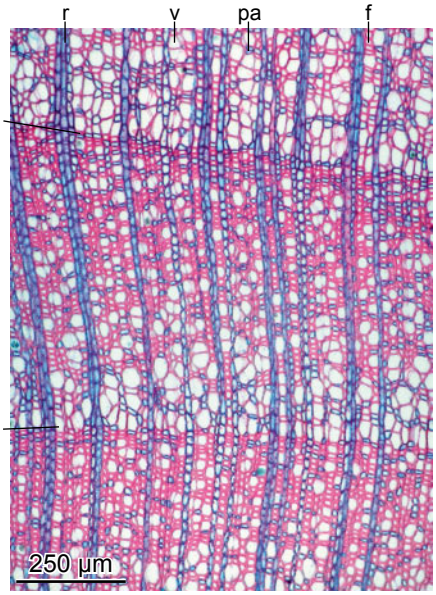
*Paeonia lutea*

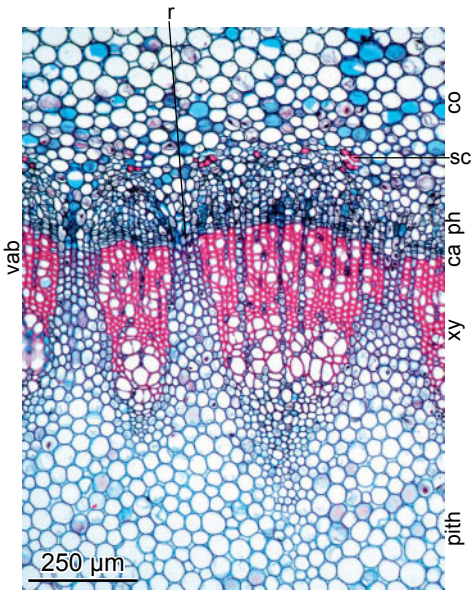
### Characteristics of the xylem

Annual rings are very distinct inthe stem of *Paeonia suffruticosa* (**Fig. 1**). There is only one ring in the annual shoot of *Paeonia officinalis* (**Fig. 2**). Ring distinctness is indicated by semi-ring porosity (**Fig. 1**). Earlywood vessel diameter varies from 30-60 µm and vessel density from 300-500/mm$^2$. Scalariform perforations with 2-4 bars and fibers with distinctly bordered pits are characteristic of the perennial xylem of *P. suffruticosa* and the annual xylem of *P. officinalis* (**Figs. 3** and **4**). Parenchyma is apotracheal (**Fig. 1**). 1-3-seriate homocellular rays with square and upright cells as well as heterocellular rays with several rows of upright cells could be observed (**Figs. 5** and **6**). The structure of the bulb of *Paeonia officinalis* is different. Rings are indistinct and a few vascular rayless vascular bundles are embedded in a large parenchymatic tissue (**Fig. 7**).

### Characteristics of the phloem and the cortex

The phloem is fairly uniform (**Figs. 8** and **10**). In all analyzed species small groups of fibers can be found (**Figs. 10** and **11**) as well as variable numbers of crystal druses in the phloem (**Fig. 8**), cortex and pith. *P. suffruticosa* has a well-developed phellem (**Fig. 9**).




**Left Fig. 1.** Distinct rings of the semi-ring-porous xylem with apotracheal parenchyma. Stem of a 1 m-high, cultivated shrub, hill zone, Switzerland. *Paeonia suffruticosa*, transverse section.

**Right Fig. 2.** Circular arranged vascular bundle (siphonostele). Rays are uniseriate in the vascular bundle and large between them. Annual shoot of a cultivated wild, hemicryptic form, hill zone, Switzerland. *Paeonia officinalis*, transverse section.

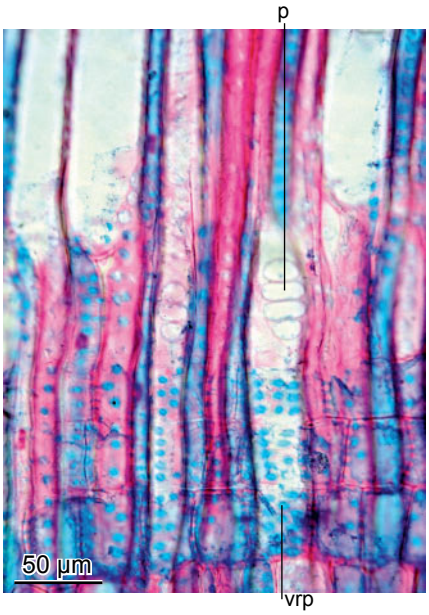



**Fig. 3.** Perforations with 3 bars. Ray cells with small pits. Stem of a 1 m-high, cultivated shrub, hill zone, Switzerland. *Paeonia suffruticosa*, radial section.

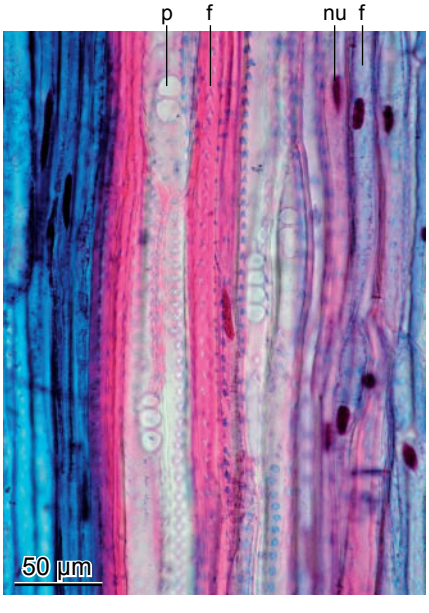



**Fig. 4.** Perforations with 3 bars and living fibers (nuclei in red). Annual shoot of a cultivated wild, hemicryptic form, hill zone, Switzerland. *Paeonia officinalis*, radial section.

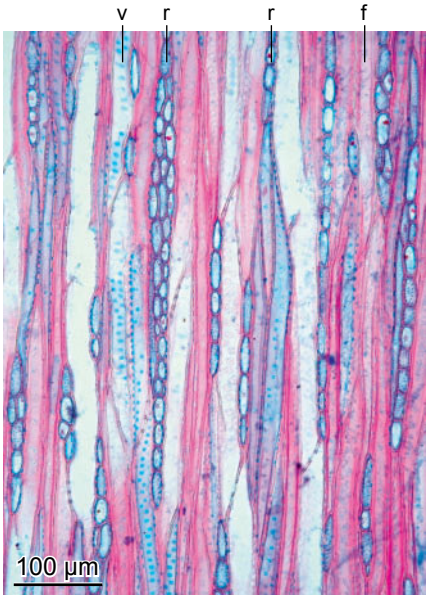
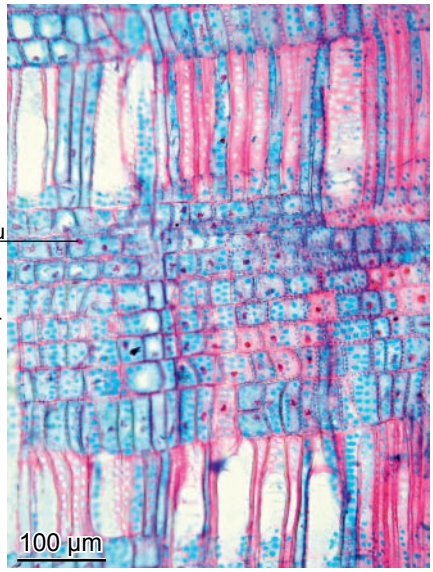



**Fig. 5.** 1-3-seriate rays with axially elongated cells. Stem of a 1 m-high, cultivated shrub, hill zone, Switzerland. *Paeonia suffruticosa*, tangential section.



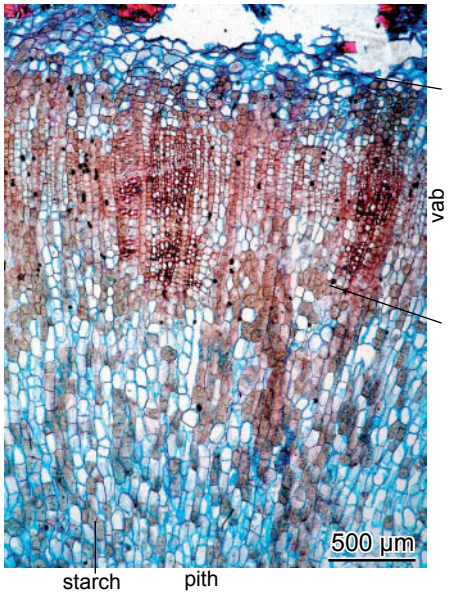
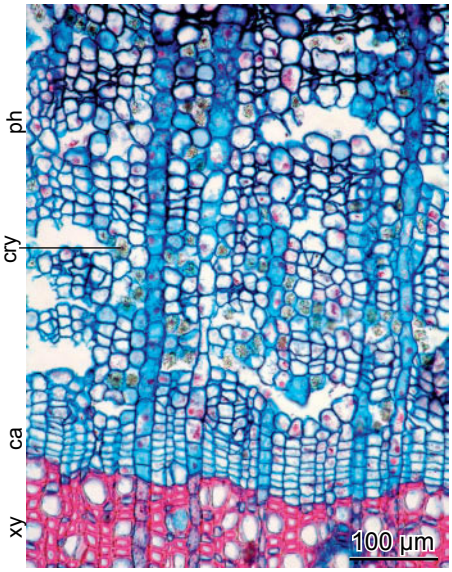
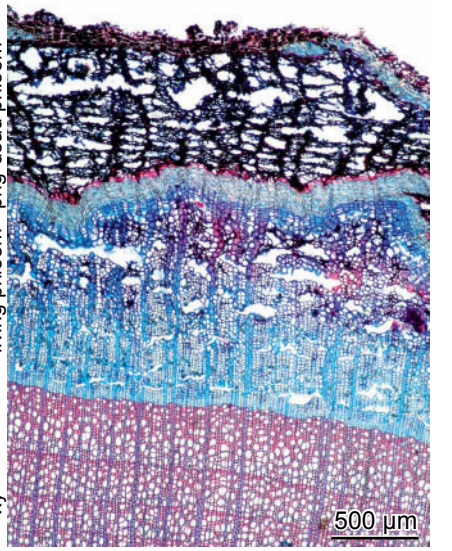




**Fig. 6.** Heterocellular ray with several square and upright marginal cells. Intervessel pits are in an alternating position. Stem of a 1 m-high, cultivated shrub, hill zone, Switzerland. *Paeonia suffruticosa*, radial section.

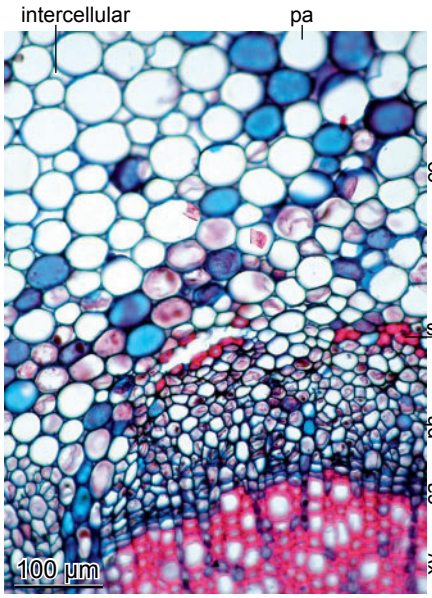
**Fig. 7.** Vascular bundles are embedded in a parenchymatic tissue. The annual rings in the xylem are indistinct. Bulb of a cultivated wild, hemicryptic form, hill zone, Switzerland. *Paeonia officinalis*, cultivated form, transverse section.

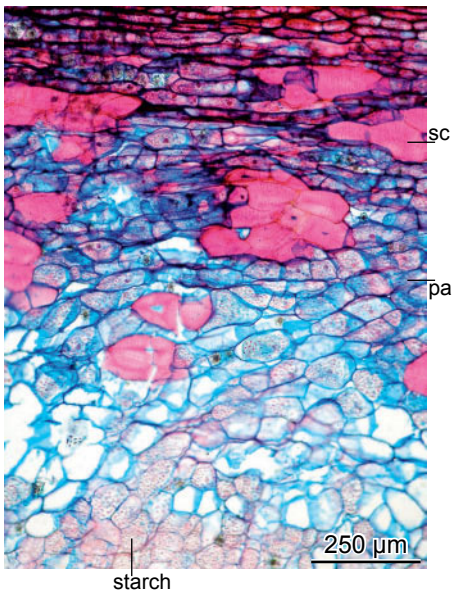



**Left Fig. 8.** Uniform phloem with indistinct groups of small sieve tubes and uniseriate rays. Crystal druses are in the parenchyma cells. Stem of a 1 m-high, cultivated shrub, hill zone, Switzerland. *Paeonia suffruticosa*, transverse section.

**Right Fig. 9.** Distinct phellem zones separate living phloem from dead phloem. Stem of a 1 m-high, cultivated shrub, hill zone, Switzerland. *Paeonia suffruticosa*, transverse section.




**Left Fig. 10.** Uniform phloem with irregular parenchyma and sieve tubes. Small groups of thick-walled fibers are at the external side of the phloem. There are intercellulares between the large parenchyma cells of the cortex. Annual shoot of a cultivated wild, hemicryptic form, hill zone, Switzerland. *Paeonia officinalis*, transverse section.

**Right Fig. 11.** Cortex with irregular groups of sclereids. Bulb of a cultivated wild, hemicryotic form, hill zone, Switzerland. *Paeonia officinalis*, transverse section.

## Ecological trends in the xylem and the bark

There is not enough material to detect any trends

## Discussion in relation to previous studies

The xylem and phloem of *Paeonia suffruticosa* have been described by Kumazawa (1935) and Takahashi (1985). The most extensive wood anatomical study is that of Keefe and Moseley (1978), which includes 4 shrubby species. Lemesle (1956) described the xylem of *Paeonia officinalis*.

The results of the present study of shrubby *Paeonia* species confirm previous observations. The anatomical structure of bulbs and annual shoots differs in many respects. However, scalariform perforations occur in herbaceous and shrubby species.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **3** |
| 1 | growth rings distinct and recognizable | 1 |
| 2.1 | only one ring | 2 |
| 5 | diffuse-porous | 3 |
| 9 | vessels predominantly solitary | 3 |
| 11 | vessels predominantly in clusters | 2 |
| 14 | vessels with scalariform perforation plates | 3 |
| 22 | intervessel pits alternate | 3 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 3 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 3 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 3 |
| 70 | fibers thin- to thick-walled | 3 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 3 |
| 97 | ray width predominantly 1-3 cells | 1 |
| 98 | rays commonly 4-10-seriate | 2 |
| 104 | ray: all cells procumbent (radial section) | 2 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 1 |
| 144 | druses present | 1 |
| R1 | groups of sieve tubes present | 3 |
| R4 | sclereids in phloem and cortex | 2 |
| R8 | with crystal druses | 3 |

# Papaveraceae



**Number of species, worldwide and in Europe**

The Papaveraceae family includes 40 genera with 770 species. Species are mainly distributed in temperate regions in the Northern Hemisphere. In Europe there are 14 genera with 93 species. The majority belongs to *Fumaria* (33 species), *Papaver* (33 species) and *Corydalis* (14 species).

**Analyzed material**

The xylem and phloem of 22 Papaveraceae species were analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 1 | 9 |
| Hemicryptophytes and geophytes | 13 | 3 |
| Therophytes | 8 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 4 | |
| Hill and mountain | 12 | |
| Arid | 3 | |
| Subtropical | 3 | |

**Analyzed species:**

Papaveroidea
- *Argemone chisosensis* G. B. Ownbay
- *Argemone ochroleuca* Sweet
- *Argemone pleiacantha* Greene
- *Chelidonium majus* L.
- *Dendromecon rigidum* Benth
- *Eschscholzia californica* Cham.
- *Eschscholzia minutiflora* Greene
- *Glaucium flavum* Crantz
- *Meconopsis cambrica* (L.) Vig.
- *Papaver alpinum* (group, Putorana Mts.).
- *Papaver alpinum* ssp. *rhaeticum* Lerersche
- *Papaver auranthiacum* Loisel.
- *Papaver dubium* L.
- *Papaver rhoeas* L.
- *Papaver somniferum* L.
- *Papaver variegatum* Tolm

Fumaroideae
- *Corydalis aurea* Willd.
- *Corydalis cava* (L.) Schweigg.
- *Corydalis solida* Swartz
- *Dicentra formosa* Walp.
- *Fumaria officinalis* L.
- *Fumaria vaillantii* Loisel.

*Papaver rhoeas* (photo: Zinnert)

*Dicentra spectabilis*

*Fumaria officinalis* (photo: Landolt)

*Corydalis cava* (photo: Landolt)

*Chelidonium majus*

*Meconopsis robusta* (photo: Landolt)

*Papaver alpinum* (photo: Landolt)

*Papaver somniferum*

*Eschscholzia californica* (photo: Zinnert)

**Characteristics of the xylem**

Anatomical stem structures are very diverse within the family of Papaveraceae. In the present material annual rings occur in most perennial species in all vegetation zones. Rings are absent in annual species (**Fig. 1**), and in the bulbs of *Corydalis* species (**Fig. 2**). Ring boundaries of most species are defined by semi-ring porosity (6 out of 8 species) or diffuse porosity (**Fig. 3**). Vessels are solitary (**Fig. 4**) or are arranged in short (2-4 vessels) or long radial multiples (>4 vessels; **Fig. 1**) or groups (**Fig. 5**). Vessels of fast-growing individuals can be arranged in tangential rows (**Fig. 5**). Vessels are smaller than 20 µm in the bulb of *Corydalis solida* (**Fig. 2**). Earlywood vessel diameter of the majority of species varies between 30-60 µm. Diameter exceeds 100 µm in the second ring of *Glaucium flavum* grown in the subtropical climate (**Fig. 14**). Vessel density varies in the majority of cases between 200-300/mm$^2$ (**Figs. 3-5**). It is only lower in the second ring of *Glaucium flavum* (subtropical climate; **Fig. 14**). Vessels contain exclusively simple perforations (**Figs. 6** and **7**). The shape of inter-vessel pits is very variable. They can be round (**Fig. 6**), laterally extended (**Fig. 7**), distinctly scalariform (**Fig. 8**), and almost annular (*Papaver variegatum*; **Fig. 9**).

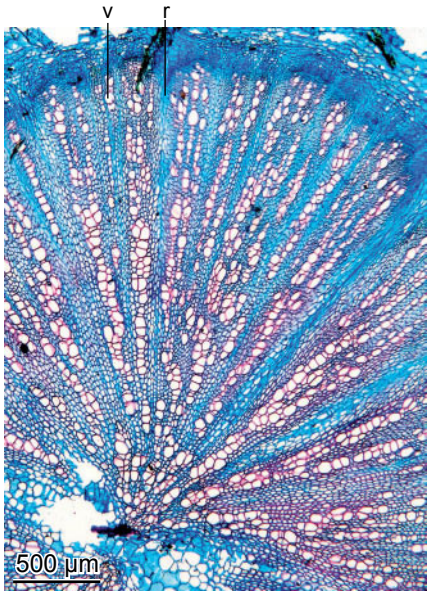



**Fig. 1.** One ring in an annual plant. Vessels stand in long radial and multiple groups between rays with unlignified cell walls. Root collar of a 30 cm-high annual herb, mountain zone, ruderal site, Briançon, France. *Fumaria officinalis*, transverse section.

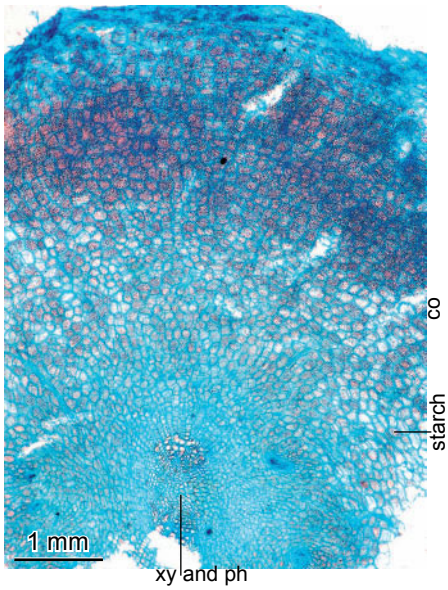



**Fig. 2.** One ring in a bulb. All cells in the very small xylem of the center are unlignified. The phloem is small and the cortex extremely large. Top of a bulb of a 10 cm-high perennial herb (geophyte), hill zone, dry meadow, Martigny, Valais, Switzerland. *Corydalis solida*, transverse section.

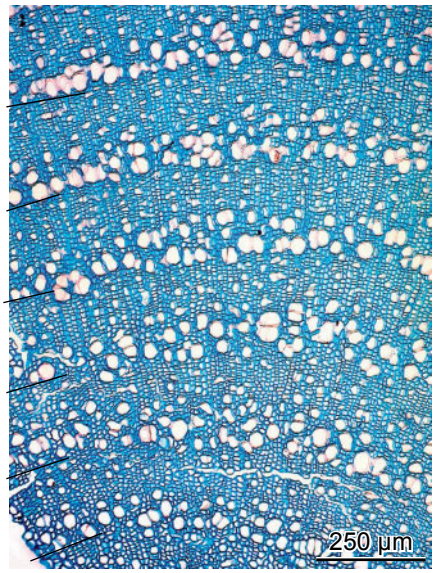
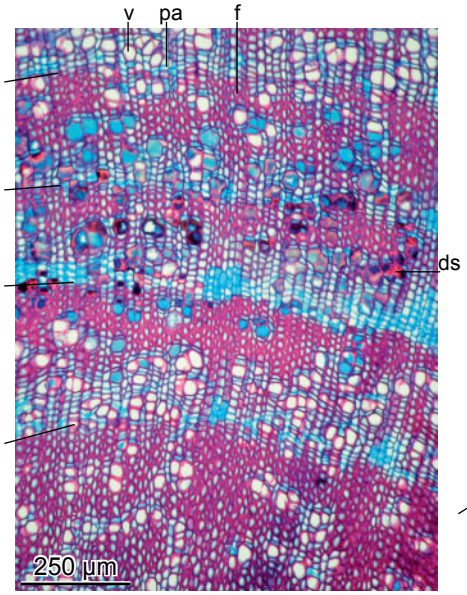
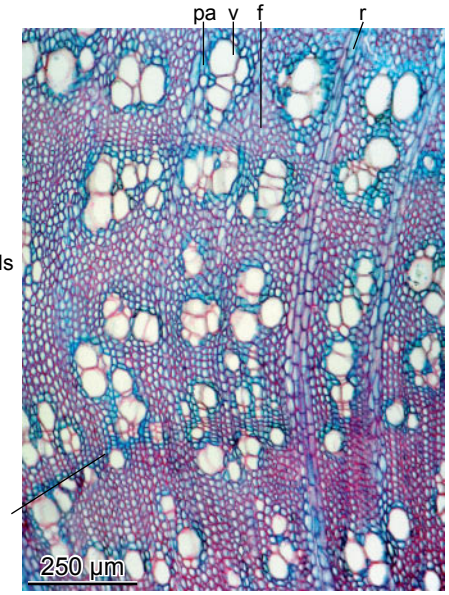



**Fig. 3.** Distinct rings of a semi-ring-porous xylem. All cell walls are unlignified. Rays are absent. Root collar of 20 cm-high perennial hemicryptophyte, subalpine zone, limestone gravel, Mt. Ventoux, France. *Papaver auranthiacum*, transverse section.




**Left Fig. 4.** Distinct rings of a diffuse-porous wood. Ring boundaries are mainly defined by marginal parenchyma (blue). Many vessels are filled with blue and dark-stained substances. Root collar of a 20 cm-high perennial hemicryptophyte, boreal zone, limestone gravel, Putorana Mountains, Siberia. *Papaver alpinum*, transverse section.

**Right Fig. 5.** Indistinct rings of a diffuse-porous wood with paratracheal parenchyma. The ring boundary is mainly defined by radial flat fibers. Root collar of a 40 cm-high biannual plant, subtropical climate, ruderal site, Tenerife, Canary Islands. *Argemone ochroleuca*, transverse section.

Dark-staining substances have been observed in vessels of *Papaver alpinum* (**Fig. 4**) and in necrotic tissue of the long-living *Papaver auranthiacum*. The radial walls of fibers are perforated by very small slit-like or round pits (<2 µm) in all species (**Fig. 11**). Fibers are in the majority of cases thin- or thin- to thick-walled (**Figs. 4**, **5** and **14**). They are thick-walled in the desert species *Argemone chisosensis* (**Fig. 10**). Fibers are missing in the alpine species (*Papaver alpinum*, *P. auranthiacum*, *P. variegatum*; **Fig. 12**), the bulbs of *Corydalis* (**Fig. 2**) and in the vascular bundles of *Chelidonium majus* and *Dicentra formosa*.

Axial parenchyma can be scanty paratracheal (**Fig. 5**), marginal (**Fig. 4**) or pervasive (**Figs. 3**, **12**, and **13**). It is exclusively paratracheal in 8 species, pervasive in the center of the stem and paratracheal outside (3 species) or exclusively pervasive (8 species). Rays are diverse, varying from absent to very large. They are completely absent in 6 species (**Figs. 3** and **4**). Normally, ray width varies between 4-8 cells (**Figs. 14** and **15**) and reaches a maximum of 12 cells (**Fig. 12**). The primary vascular bundle form is found in 5 species (**Fig. 17**). In such cases, ray width between vascular bundles exceeds 10 cells. Crystals are absent in the xylem.

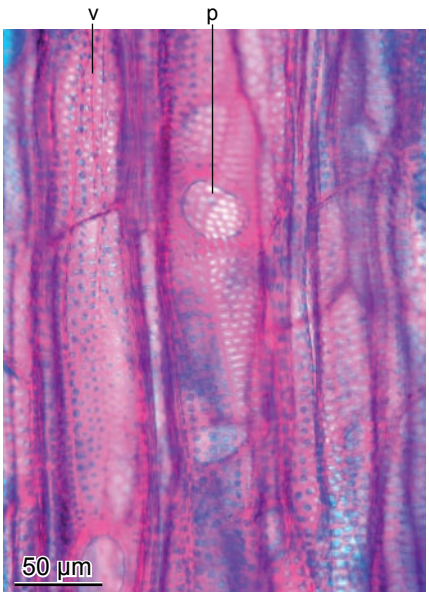



**Fig. 6.** Vessels with simple perforations and small, round pits. Rhizome of a 50 cm-high perennial hemicryptophyte, subalpine zone, moist meadow, Mt. St. Helens, Washington, USA. *Dicentra formosa*, radial section.

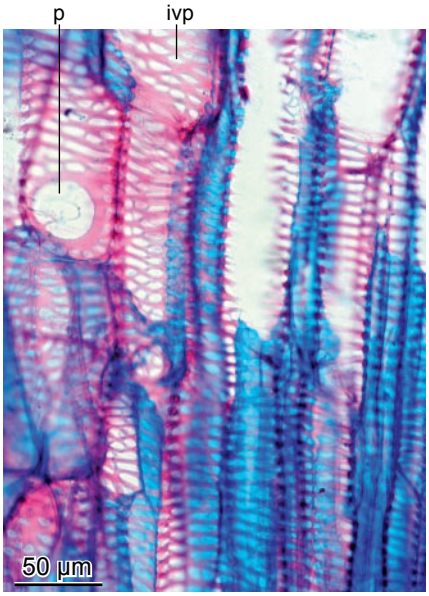



**Fig. 7.** Vessels with simple perforations and pits with horizontally enlarged apertures. Root collar of an annual plant, mountain zone, meadow, Monte Vista, Colorado, USA. *Corydalis aurea*, radial section.

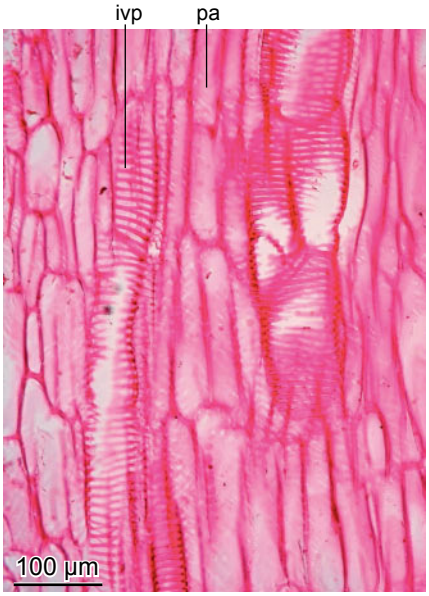



**Fig. 8.** Vessels with scalariform pits. Root collar of a 30 cm-high annual plant, hill zone, ruderal site, Trento, Italy. *Papaver rhoeas*, radial section.

**Left Fig. 9.** Vessels with scalariform pits to annular cell-wall thickenings. Root collar of a 15 cm-high perennial hemicryptophyte, boreal zone, riverbed, Ayan Lake, Putorana Mountains, Siberia. *Papaver variegatum*, radial section.

**Right Fig. 10.** Rays with unlignified cell walls between a tissue of very thick-walled fibers. Root collar of a 50 cm-high perennial herb, arid zone, ruderal site, Stafford, Arizona, USA. *Argemone chisosensis*, transverse section.

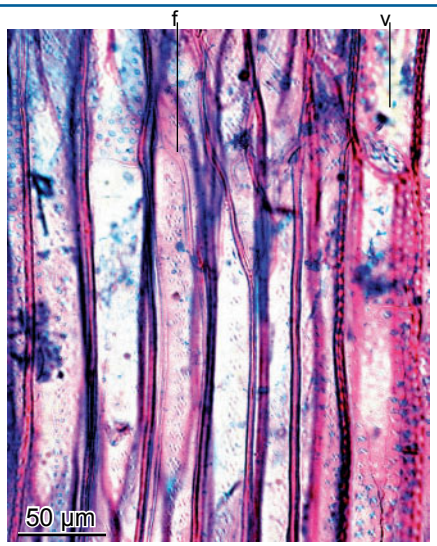



**Fig. 11.** Short fibers with small, slit-like pits. Root collar of a 30 cm-high annual herb, mountain zone, ruderal site, Briançon, France. *Fumaria officinalis*, radial section.

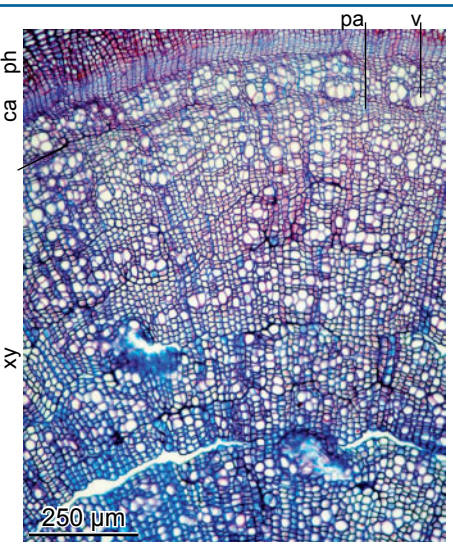



**Fig. 12.** Xylem without fibers. Vessels are embedded in pervasive parenchyma. Root collar of a 15 cm-high perennial hemicryptophyte, boreal zone, riverbed, Ayan Lake, Putorana Mountains, Siberia. *Papaver variegatum*, transverse section.

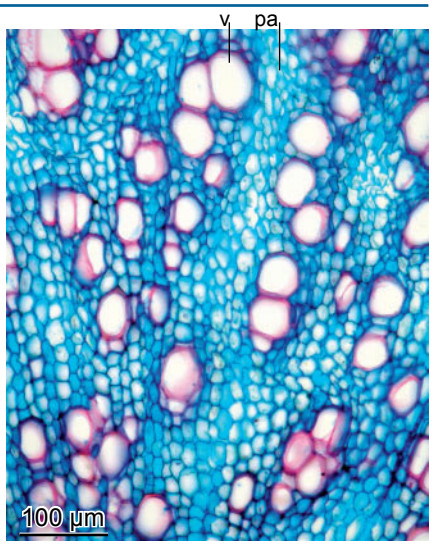
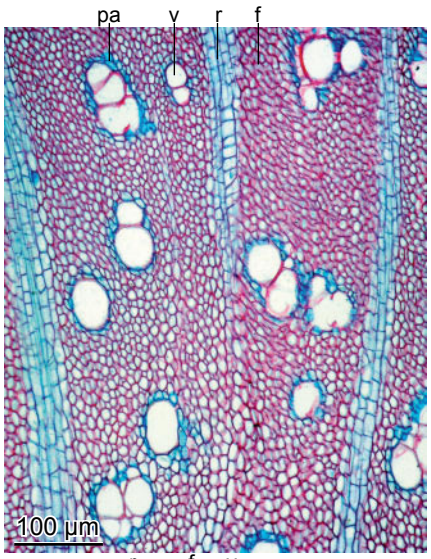
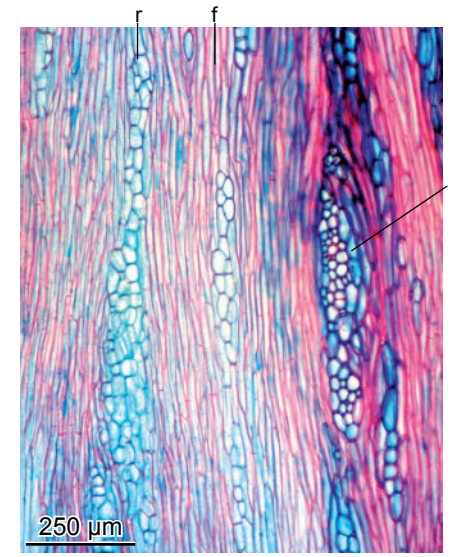


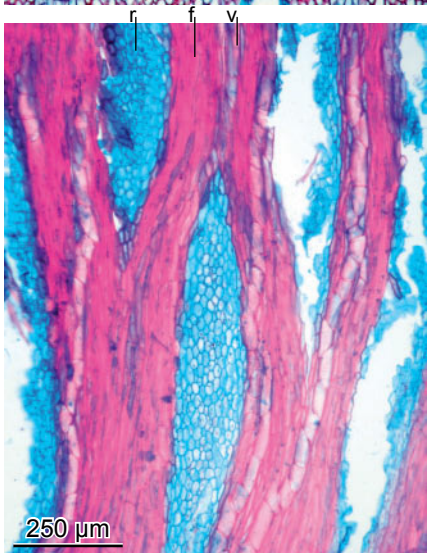

**Fig. 13.** Pervasive parenchyma with unlignified cell walls around vessels with lignified walls. Central part of a root collar of a 50 cm-high biannual plant, subtropical climate, ruderal site, Gran Canaria, Canary Islands. *Glaucium flavum*, transverse section.

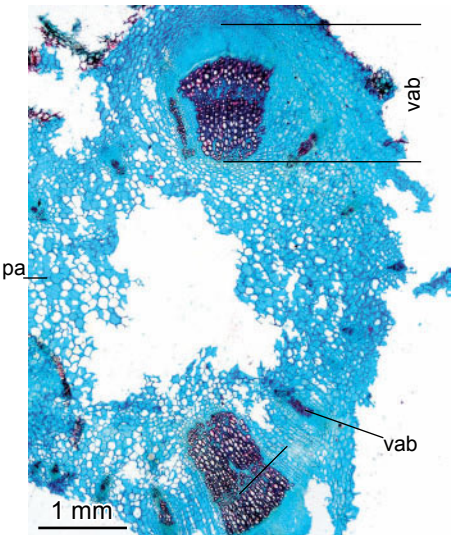



**Left Fig. 14.** Scanty parenchyma around vessels. Fibers are thin-walled. External part of a root collar of a 50 cm-high biannual plant, subtropical climate, ruderal site, Gran Canaria, Canary Islands. *Glaucium flavum*, transverse section.

**Right Fig. 15.** Rays 1-5 cells wide. One ray contains sheet cells. Root collar of a 50 cm-high annual plant, subtropical climate, ruderal site, Tenerife, Canary Islands. *Argemone ochroleuca*, tangential section.




**Left Fig. 16.** Very large rays (8->10 cells wide) with unlignified cells. Root collar of a 50 cm-high perennial herb, arid zone, ruderal site, Stafford, Arizona, USA. *Argemone chisosensis*, tangential section.

**Right Fig. 17.** Vascular bundles in a parenchymatic tissue. The xylem of the large vascular bundles have two annual rings. The intervascular parenchyma can be interpreted as very large rays. Rhizome of a 50 cm-high perennial hemicryptophyte, subalpine zone, moist meadow, Mt. St. Helens, Washington, USA. *Dicentra formosa*, transverse section.

### Taxa-characteristic features

Some features characterize single species or groups of species: There is a high probability that most species or genera have specific xylem characteristics but we do not have enough material from different sites to identify any species-specific features. The presence of vascular bundles e.g. in *Chelidonium majus*, *Dicentra formosa* (**Fig. 1**), the shape of inter-vessel pits (**Figs. 6-9**) and the radial arrangement of vessels (**Figs. 1-5**) seem to be species-specific.

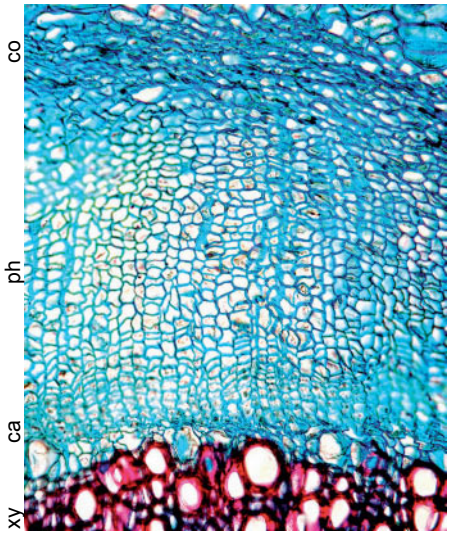
### Ecological trends and relations to life forms

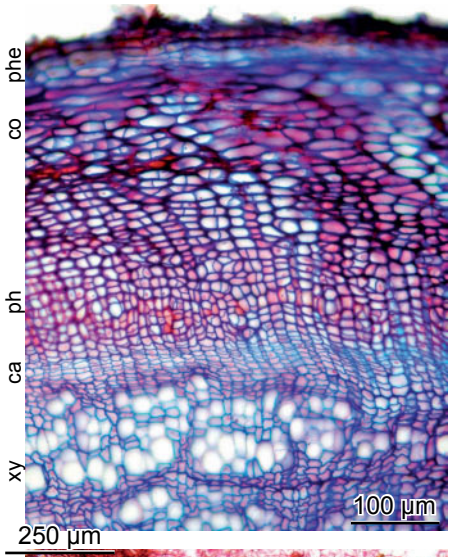
Ecological trends were found only in plant age. Relatively old plant (6-17 years) are typical for some *Papaver* species in cold climates. The age of all species in other genera varies between 1-3 years.

### Characteristics of the phloem and the cortex

The phloem and the cortex are in the majority of cases simply structured by the radial arrangement of parenchyma and sieve tubes (**Figs. 18** and **19**). Groups of sieve tubes in tangential rows occur in most genera (**Figs. 20** and **21**). Groups of sclereids occur only in *Argemone chisosensis* and *Papaver alpinum* (**Fig. 23**). Ray dilatations occur in 9 of 19 species but are in the majority of cases not very distinct (**Figs. 22** and **23**).

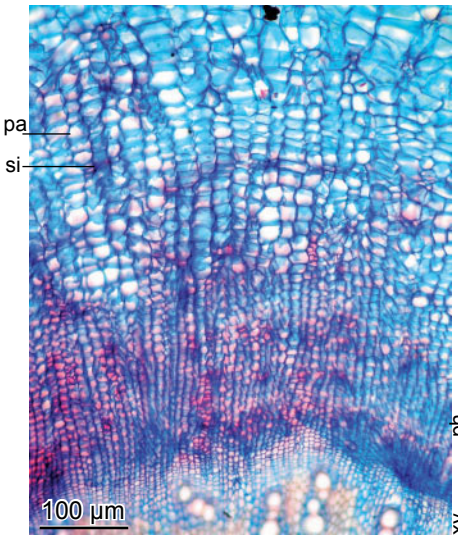
Characteristic of all species is the absence of prismatic crystals and crystal druses. A few round particles of crystal sand (<2 µm, silica bodies?) were found in the cortex of *Chelidonium majus* and in the phloem of *Papaver auranthiacum* and in *Argemone ochroleuca*.

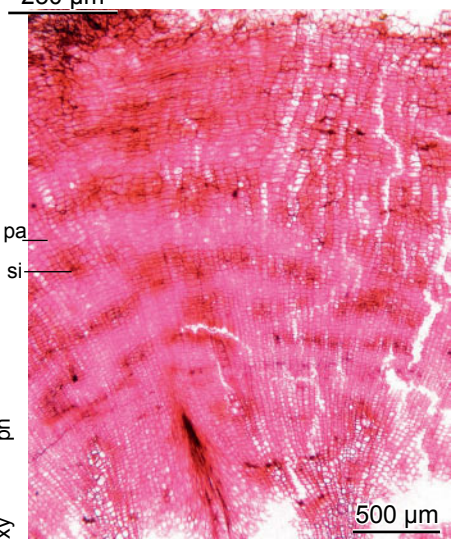



**Left Fig. 18.** Simple construction of the phloem and xylem. Parenchyma and sieve tubes stand in radial rows and cannot be distinguished. Rhizome of a 50 cm-high perennial hemicryptophyte, subalpine zone, moist meadow, Mt. St. Helens, Washington, USA. *Dicentra formosa*, transverse section.

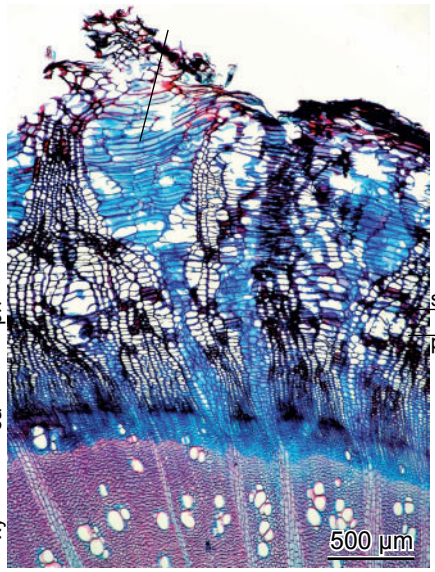
**Right Fig. 19.** Simple construction of the phloem and xylem. Phloem cells form a small belt of small rectangular cells. Cortex cells are round and often separated by a straight cell wall. Bark of the root collar of a 15 cm-high perennial hemicryptophyte, riverbed, Ayan Lake, Putorana Mountains, Siberia. *Papaver variegatum*, transverse section.

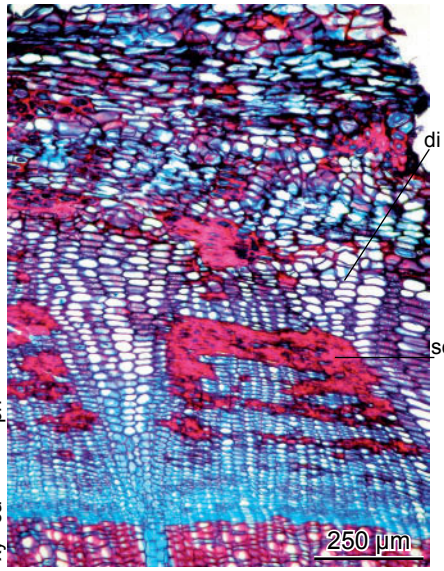



**Left Fig. 20.** Simple construction of the phloem and xylem. Red-stained flecks might represent sieve-cell areas. Bark of the root collar of an annual plant, ruderal site, subtropical climate, Gran Canaria, Canary Islands. *Eschscholzia californica*, transverse section.

**Right Fig. 21.** Simple construction of the phloem and xylem. Red-stained spots are arranged in tangential rows and might represent sieve-cell areas. Bark of the rhizome of a 40 cm-high perennial therophyte, ruderal site, hill zone, Birmensdorf, Switzerland. *Chelidonium majus*, transverse section.




**Left Fig. 22.** Radial rows of parenchyma and sieve tubes are separated by ray dilatations. Bark of the root collar of a 50 cm-high biannual plant, ruderal site, subtropical climate, Gran Canaria, Canary Islands. *Glaucium flavum*, transverse section.

**Right Fig. 23.** Tangential zones of thick-walled groups of sclereids are visible on both sides of a ray dialatation. They interrupt the radial arrangement of parenchyma and sieve tubes. Bark of the root collar of a 20 cm-high perennial hemicryptophyte, boreal zone, limestone gravel, Putorana Mountains, Siberia. *Papaver alpinum*, transverse section.

**Discussion in relation to previous studies**

Metcalfe and Chalk (1957) described briefly the upper parts of annual shoots of *Chelidonium majus*, *Fumaria muralis* and *Dicentra spectabilis*. The most extended wood anatomical study is that of Carlquist and Zona (1988) on the basis of 9 woody species (*Bocconia*, *Dendromecon*, *Dicentra chrysantha*, *Hunnemannia*, *Romneya*). Carlquist et al. (1994) characterized the xylem and the bark of woody *Argemone fruticosa* and the herbaceous *Argemone turnerae*. For further information see Gregory (1994).

Earlier studies concentrate on the xylem of shrubs and dwarf shrubs from dry regions. This study includes many annual and perennial herbaceous species including those of humid regions of different vegetation zones. The anatomical variability is larger than shown in previous studies. Common family-specific characteristics could not be found.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **22** |
| 1 | growth rings distinct and recognizable | 9 |
| 2 | growth rings absent | 2 |
| 2.1 | only one ring | 11 |
| 4 | semi-ring-porous | 6 |
| 5 | diffuse-porous | 3 |
| 6 | vessels in intra-annual tangential rows | 3 |
| 7 | vessels in diagonal and/or radial patterns | 1 |
| 9 | vessels predominantly solitary | 10 |
| 9.1 | vessels in radial multiples of 2-4 common | 7 |
| 10 | vessels in radial multiples of 4 or more common | 4 |
| 11 | vessels predominantly in clusters | 15 |
| 13 | vessels with simple perforation plates | 22 |
| 20 | intervessel pits scalariform | 9 |
| 20.1 | intervessel pits pseudoscariform to reticulate | 3 |
| 21 | intervessel pits opposite | 1 |
| 36 | helical thickenings present | 1 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 16 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 9 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 1 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 8 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 14 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 2 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 2 |
| 60.1 | fibers absent | 8 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 14 |
| 68 | fibers thin-walled | 9 |
| 69 | fibers thick-walled | 1 |
| 79 | parenchyma paratracheal | 14 |
| 79.1 | parenchyma pervasive | 11 |
| 89 | parenchyma marginal | 2 |
| 89.1 | parenchyma marginal thin walled, dark in polarized light | 9 |
| 89.2 | ring shake, *Saxifraga* type | 1 |
| 97 | ray width predominantly 1-3 cells | 1 |
| 98 | rays commonly 4-10-seriate | 10 |
| 99 | rays commonly >10-seriate | 2 |
| 99.1 | vascular bundle form remaining | 5 |
| 100.1 | rays confluent with ground tissue | 1 |
| 100.2 | rays not visible in polarized light | 8 |
| 105 | ray: all cells upright or square | 15 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 1 |
| 110 | rays with sheet cells (tangential section) | 5 |
| 117 | rayless | 8 |
| R1 | groups of sieve tubes present | 12 |
| R2 | groups of sieve tubes in tangential rows | 9 |
| R3 | distinct ray dilatations | 10 |
| R4 | sclereids in phloem and cortex | 2 |
| R7 | with prismatic crystals | 1 |
| R9 | with crystal sand | 5 |
| R10 | phloem not well structured | 6 |
| R11 | with rhaphides | 6 |

# Phytolaccaceae

**Number of species, worldwide and in Europe**

The Phytolaccaceae family includes 4 genera with 30 species. The majority is represented by *Phytolacca* (24). Most species are distributed mainly in tropical and warm temperate regions of America. Three *Phytolacca* species are naturalized in Europe.

**Analyzed material**

Analyzed here is the rhizome of *Phytolacca americana*.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Hemicryptophytes and geophytes | 1 | 1 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 1 | |

**Analyzed species:**
*Phytolacca americana* L.

*Phytolacca americana* (photo: Zinnert)

*Phytolacca americana* (photo: Zinnert)

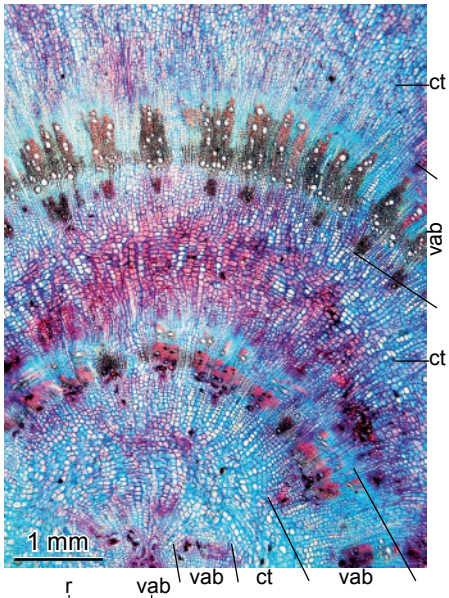
*Phytolacca americana* (photo: Zinnert)

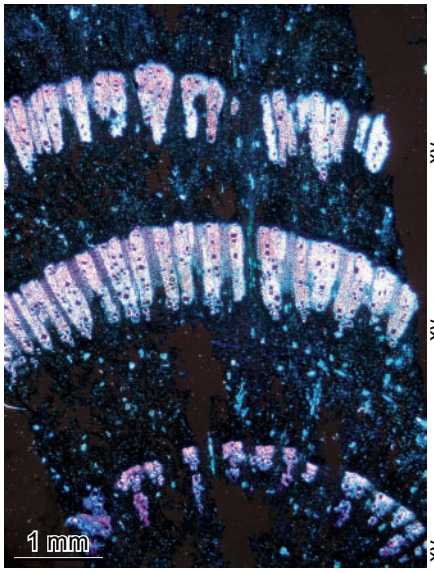
### Characteristics of the xylem

Annual rings are probably absent or unrecognizable. Characteristic are circular vascular bundles between parenchymatic zones (successive cambia; **Figs. 1** and **2**). Perforations are simple and inter-vessel pits are small and round. Fibers, probably libriform fibers, are thin-walled Carlquist (2000). The axial parenchyma is scanty paratracheal (**Fig. 3**). Rays are very large, often irregularly formed and confluent to axial fibers (**Fig. 4**). Ray cell walls are thin and unlignified. Short rhaphides (20 µm) are bundled in few idioblasts in the inter-vascular bundle zone (**Fig. 5**).

### Characteristics of the phloem

Outside the peripheral circle of vascular bundles is a parenchymatic zone which is bordered by the phellem.




**Left Fig. 1.** Circular arrangement of vascular bundles. The bundels are tangentially interrupted by a large zone of thin-walled, unlignified parenchyma cells. 1-2 m-high hemicryptophyte, hill zone, Switzerland. *Phytolacca americana*, transverse section.

**Right Fig. 2.** Circular arrangement of vascular bundles. The bundels are tangentially interrupted by a large zone of thin-walled, unlignified parenchyma cells. 1-2 m-high hemicryptophyte, hill zone, Switzerland. *Phytolacca americana*, transverse section, polarized light.

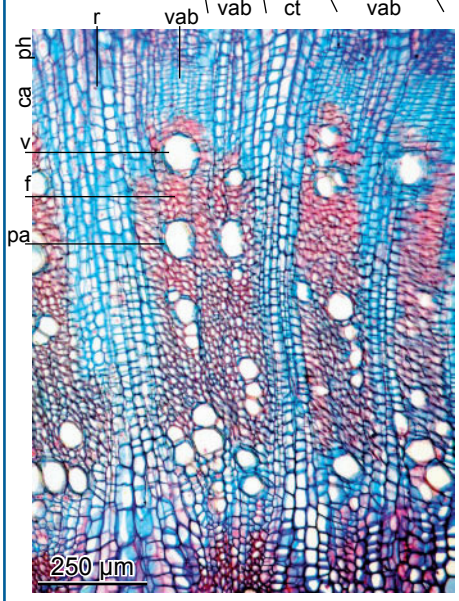



**Fig. 3.** Vascular bundles. The initial point of the bundles contain lignified fibers, which are interrupted by a zone of unlignified cells. Vessels with paratracheal parenchyma are surrounded by thin- to thick-walled fibers. 1-2 m-high hemicryptophyte, hill zone, Switzerland. *Phytolacca americana*, transverse section.

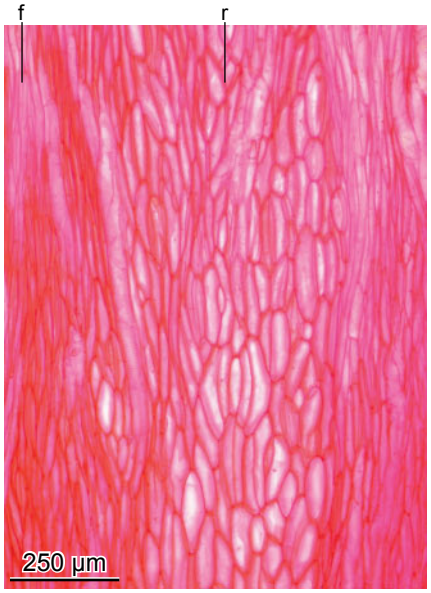



**Fig. 4.** Very large confluent rays with irregular cells. 1-2 m-high hemicryptophyte, hill zone, Switzerland. *Phytolacca americana*, tangential section.

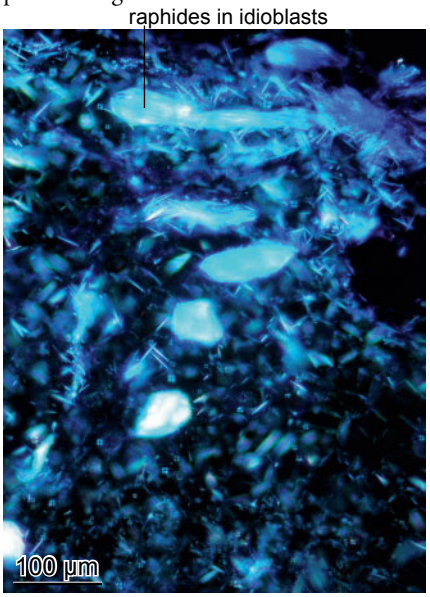



**Fig. 5.** Rhaphides in idioblasts are concentrated in the tangential parenchyma bands. 1-2 m-high hemicryptophyte, hill zone, Switzerland. *Phytolacca americana*, transverse section, polarized light.

## Discussion in relation to previous studies

Mikesell (1979) summarizes the results of the previous studies of Metcalfe and Chalk (1950), Chalk and Chattaway (1937) and Pfeiffer (1926). Mikesell (1979) and Carlquist (2000) studied in detail the ontogenic development of the primary thickening meristem of *Phytolacca americana*.

The results of the present study agree with the studies from Mikesell (1979) and Carlquist (2000).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **1** |
| 2 | growth rings absent | 1 |
| 9 | vessels predominantly solitary | 1 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 1 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 1 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 1 |
| 70 | fibers thin- to thick-walled | 1 |
| 79 | parenchyma paratracheal | 1 |
| 99 | rays commonly >10-seriate | 1 |
| 105 | ray: all cells upright or square | 1 |
| 133 | successive cambia, Caryophyllaceae type | 1 |
| 149 | rhaphides present | 1 |
| R10 | phloem not well structured | 1 |

# Piperaceae



**Number of species, worldwide and in Europe**

The Piperaceae family includes 6 genera with 2020 species. Major genera are *Peperomia* (1000 species) and *Piper* (1000 species). Most species are distributed in tropical and subtropical regions.

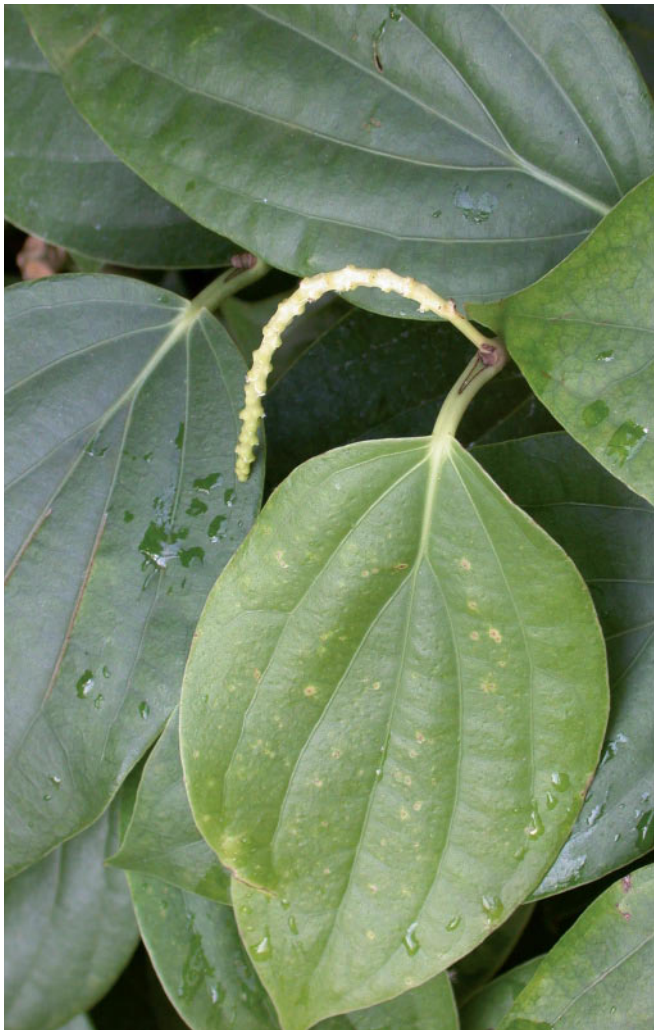
**Analyzed species:**

*Peperomia caperata* Yuncker
*Piper nigrum* L.
*Piper methysticum* G. Forst

**Analyzed material**

The xylem and phloem of 3 Piperaceae species are analyzed. The material was collected in the tropical greenhouse of the Botanical Garden Basel, Switzerland.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 3 | |
| **Plants analyzed from different vegetation zones:** | | |
| Tropical | 3 | |



*Piper nigrum*

*Peperomia caperata*

### Characteristics of the xylem

In the present material annual rings are absent. *Peperomia caperata* does not have secondary growth (**Fig. 1**). Therefore we characterize only the xylem of *Piper methysticum* and *P. nigrum* (**Figs. 2** and **3**). Vessels remain solitary (**Fig. 2**). Vessel diameter of *Piper nigrum* varies from 50-80 µm whereas it exceeds 100 µm in *Piper methysticum*. The vessel density is low (<100/mm$^2$; **Fig. 4**). Vessels contain exclusively simple perforations. Perforations stand more-or-less perpendicular to the stem axis. Inter-vessel pits are predominantly annular in the vascular bundles and scalariform in the secondary xylem (**Fig. 5**). *Piper methysticum* produces locally small, thin-walled, unlignified tyloses (**Fig. 4**). The radial walls of fibers are perforated by very small slit-like or round pits (<2 µm; **Fig. 6**). Fibers are in the majority of cases thin- or thin- to thick-walled. Fibers of *Piper methysticum* are storied. Septate fibers have been found in *Piper nigrum* (**Fig. 7**). Axial parenchyma is paratracheal (**Fig. 4**). It surrounds mostly the whole circumference of the vessels. Large rays with more than 10 cells separate the remaining vascular bundles (**Figs. 2**, **3**, **8** and **9**). Ray cells with small round pits are upright (**Fig. 10**). Medullary vascular bundles are found in all species and secretory canals exist in the pith of *Piper methysticum* and *P. nigrum* (**Figs. 11** and **12**).

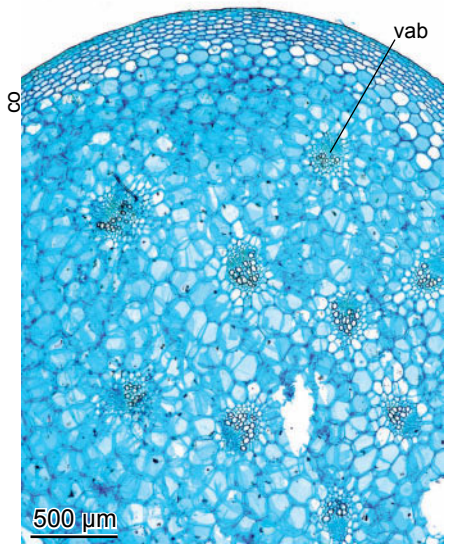



**Fig. 1.** Species without secondary growth. Characteristic are the isolated vascular bundles inside the cortex. Stem of a 100 cm-long, hanging, 2-4-year-old shoot, tropical greenhouse, Botanical Garden Basel, Switzerland. *Peperomia caperata*, transverse section.

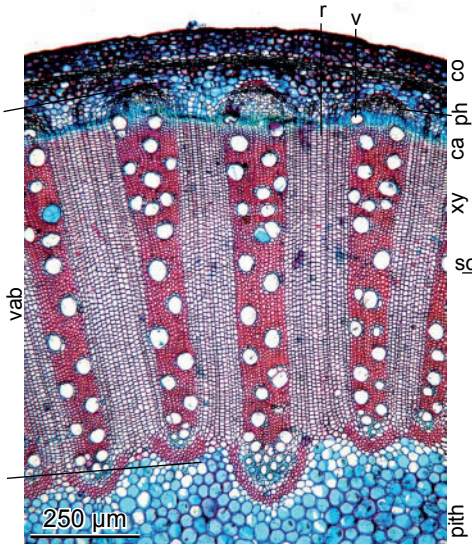



**Fig. 2.** Xylem with radial vessel/fiber strips. The pith is delimitated from the xylem by a wavy band of thick-walled fibers. Stem of a 1 m-high, 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper methysticum*, transverse section.

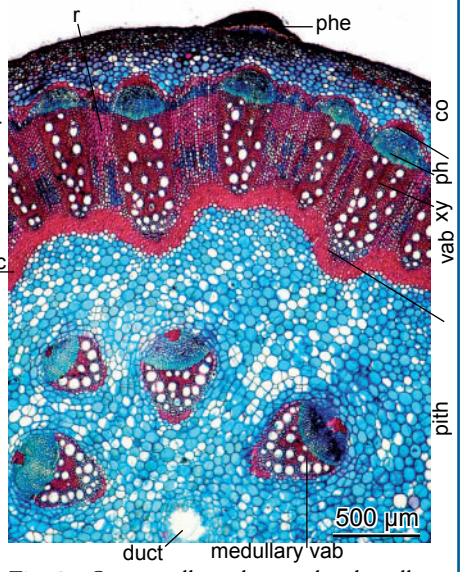
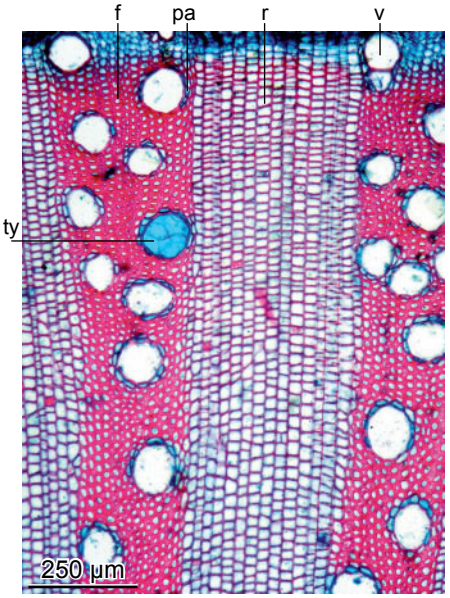
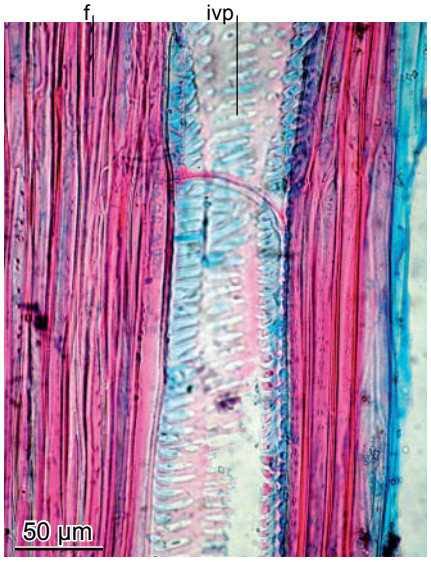


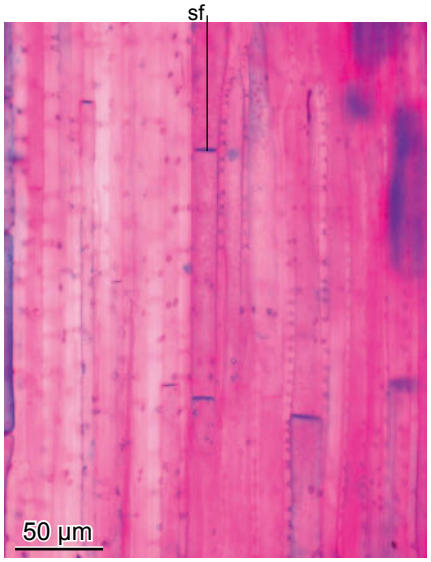

**Fig. 3.** Open collateral vascular bundles are outside the pith; they are connected by an intervascular cambium. The pith is delimitated from the xylem by a wavy band of thick-walled fibers. Stem of an 80 cm-high 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper nigrum*, transverse section.




**Left Fig. 4.** Large, solitary vessels are surrounded by paratracheal parenchyma. One vessel contains unlignified tyloses. There are very large rays between radial vessel/fiber strips. Stem of a 1 m-high 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper methysticum*, transverse section.

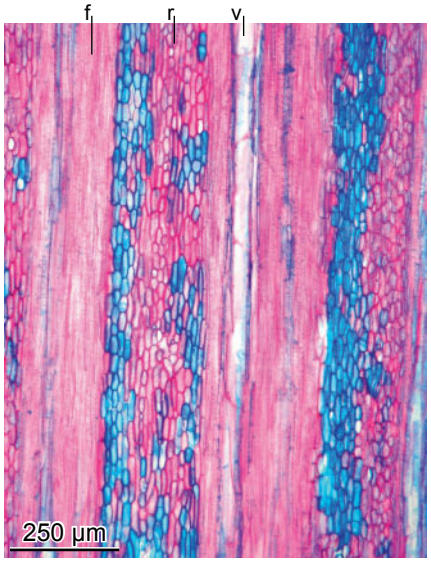
**Right Fig. 5.** Vessels with annular thickenings in a vascular bundle in the center of the stem. Stem of a 100 cm-long, hanging, 2-4-year-old shoot, tropical greenhouse, Botanical Garden Basel, Switzerland. *Peperomia caperata*, radial section.




**Left Fig. 6.** Vessels with scalariform pits and fibers with small pits with slit-like apertures. Stem of a 1 m-high 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper methysticum*, radial section.

**Right Fig. 7.** Septate fibers with unlignified (blue) horizontal cell walls. Stem of an 80 cm-high 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper nigrum*, radial section.




**Left Fig. 8.** High (>5 mm) large rays with >10 cells in width and with sheet cells. Cells are thin-walled. Stem of a 1 m-high 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper methysticum*, tangential section.

**Right Fig. 9.** High (>5 mm) and large rays (>10 cells in width). Cells are thin-walled and partially unlignified (blue). Stem of an 80 cm-high 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper nigrum*, tangential section.

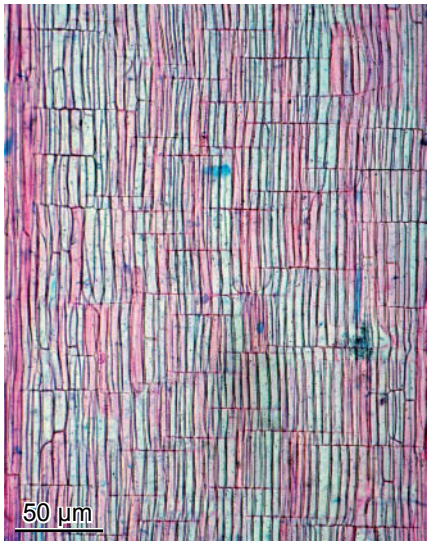



**Fig. 10.** Ray with thin-walled upright cells. Stem of a 1 m-high 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper methysticum*, radial section.

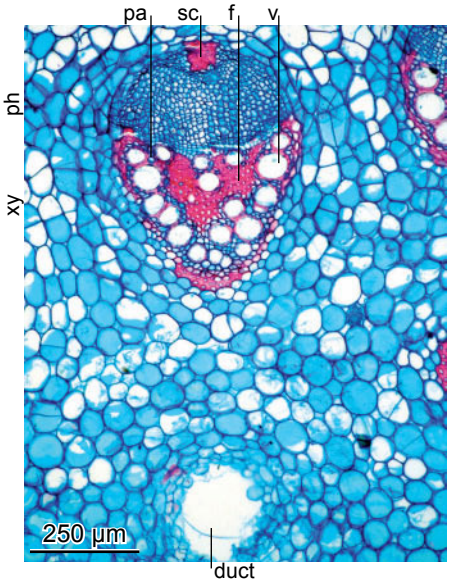



**Fig. 11.** Pith with medullary vascular bundles and shizogneous secretory canals. Stem of an 80 cm-high 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper nigrum*, transverse section.

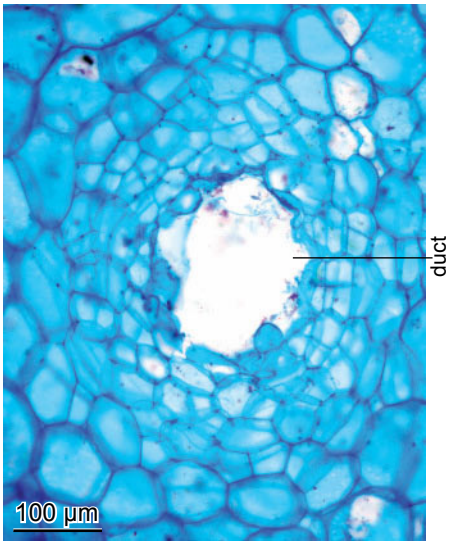



**Fig. 12.** Medullary shizogneous secretory canal in the center of the pith. Stem of a 1 m-high 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper methysticum*, transverse section.

### Taxa characteristic features

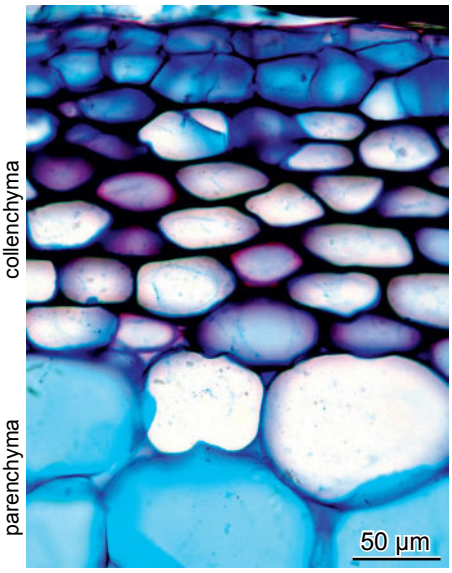
Characteristic of *Peperomia caperata* is the absence of secondary growth (**Fig. 1**).

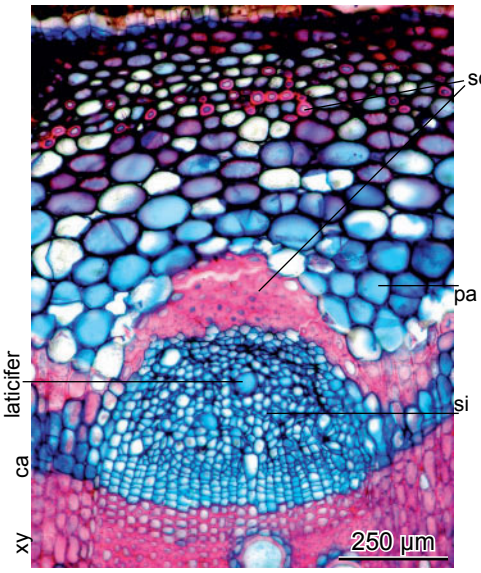
### Ecological trends and relations to life forms

Since all analyzed species are from the tropical zone, no ecological trends could be detected.

### Characteristics of the phloem and the cortex

Tangentially enlarged parenchyma cells are characteristic of the cortex of all species (**Fig. 13**). Cell walls are often thickened like collenchyma (**Fig. 13**). The cortex of *Piper nigrum* contains a few lignified fibers and *Piper methysticum* contains a belt of smaller cells between the phloem and the cortex (**Fig. 15**). Half moon-shaped parenchyma/sieve tube groups stand outside the vessel/fiber strips of the xylem of both *Piper* species (**Fig. 14**). Between them are partially dilated parenchyma cells (**Fig. 15**). All species contain crystal sand (**Fig. 16**). Characteristic of *Peperomia caperata* are raphides (**Fig. 17**). Laticifers were found in the phloem of *Piper nigrum* (**Fig. 14**).




**Left Fig. 13.** Collenchyma-like parenchyma cells of the cortex. Stem of a 100 cm-long, hanging, 2-4-year-old shoot, tropical greenhouse, Botanical Garden Basel, Switzerland. *Peperomia caperata*, transverse section.

**Right Fig. 14.** Vascular bundle. Phloem with small sieve tubes, medium-sized parenchyma cells and few larger laticifers. The bundle is laterally linked with others by an intervascular cambium and externally delimitated from the cortex by a belt of thick-walled sclerenchyma cells. The cortex contains some thick-walled, lignified fibers. Stem of an 80 cm-high, 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper nigrum*, transverse section.

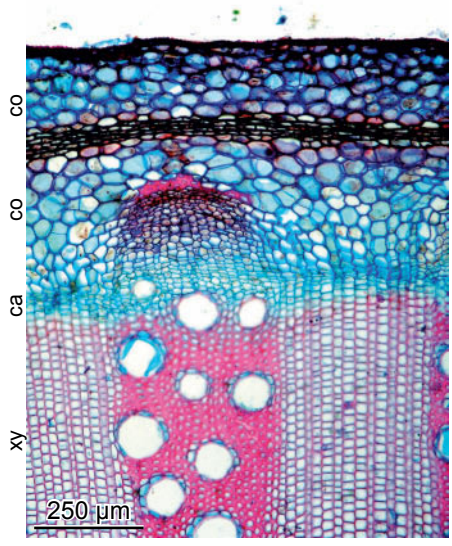



**Fig. 15.** The vascular bundle is laterally linked with others by an intervascular cambium. A belt of small cells devides the cortex. Stem of an 80 cm-high, 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper nigrum*, transverse section.

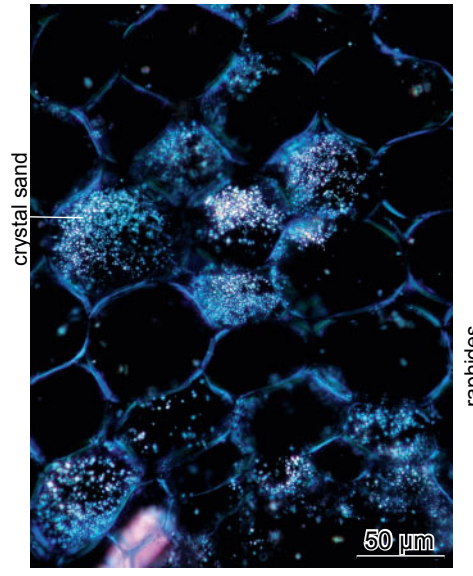



**Fig. 16.** Crystal sand in parenchymatic cortex cells. Stem of an 80 cm-high, 3-year-old shrub, tropical greenhouse, Botanical Garden Basel, Switzerland. *Piper nigrum*, transverse section, polarized light.

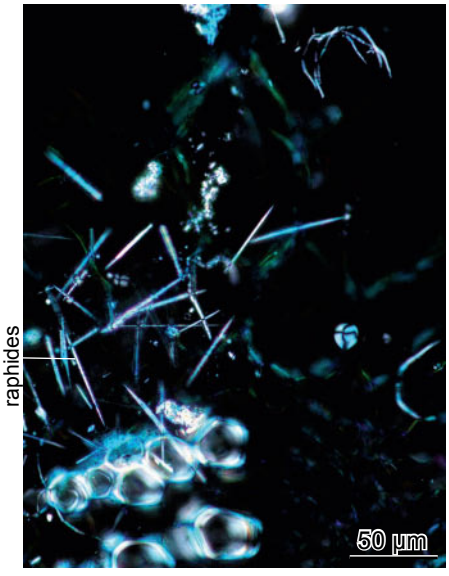



**Fig. 17.** Rhaphides in parenchymatic cells of the pith. Stem of a 100 cm-long, hanging, 2-4-year-old shoot, tropical greenhouse, Botanical Garden Basel, Switzerland. *Peperomia caperata*, transverse section, polarized light.

**Discussion in relation to previous studies**

Metcalfe and Chalk (1957) characterised the wood structure of the genera *Piper* and *Peperomia*, including *Piper nigrum* and *P. methysticum*. Many authors described the wood of some genera of *Piper* and *Macropiper* (Gregory 1994).

The results of the present study agree with those of previous authors. The description of *Peperomia caperata* is new.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **3** |
| 2 | growth rings absent | 3 |
| 9 | vessels predominantly solitary | 2 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 3 |
| 14 | vessels with scalariform perforation plates | 1 |
| 20 | intervessel pits scalariform | 2 |
| 20.1 | intervessel pits pseudoscariform to reticulate | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 1 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 1 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 1 |
| 50 | <100 vessels per mm$^2$ in earlywood | 2 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 1 |
| 56 | tylosis with thin walls | 1 |
| 60.1 | fibers absent | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 1 |
| 65 | septate fibers present | 1 |
| 70 | fibers thin- to thick-walled | 1 |
| 79.1 | parenchyma pervasive | 1 |
| 99 | rays commonly >10-seriate | 2 |
| 99.1 | vascular-bundle form remaining | 3 |
| 103 | rays of two distinct sizes (tangential section) | 2 |
| 105 | ray: all cells upright or square | 2 |
| 110 | rays with sheet cells tangential section | 1 |
| 117 | rayless | 1 |
| 120 | storied axial tissue (parenchyma, fibers, vessels, tangential section) | 1 |
| 136 | prismatic crystals present | 1 |
| 149 | rhaphides present | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R7 | with prismatic crystals | 2 |
| R7.1 | with acicular crystals | 1 |
| R9 | with crystal sand | 3 |
| R11 | with rhaphides | 2 |
| P1 | with medullary phloem or vascular bundles | 3 |
| P2 | with laticifers or intercellular canals | 2 |

# Platanaceae

**Number of species, worldwide and in Europe**

The Platanaceae family includes 1 genus with 9 species in tropical to temperate regions in North America and Eurasia. The trees often grow along rivers. Two species occur in Europe (*Platanus orientalis* and *Platanus x hybrida*).

**Analyzed material**

The xylem and phloem of 3 Platanaceae species were analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | 3 | ca. 3 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 1 | |
| Mediterranean | 1 | |
| Arid | 1 | |

**Analyzed species:**

*Platanus x hispanica* Münchh.
*Platanus orientalis* L.
*Platanus wrightii* S. Watson

*Platanus x hispanica*

*Platanus orientalis*

*Platanus orientalis*

### Characteristics of the xylem

Annual rings occur in the analyzed material of all species (**Figs. 1** and **2**). Ring boundaries are defined by a slight semi-ring porosity and a few rows of radially flat marginal fibers (**Fig. 3**). Vessels are solitary or in groups (**Fig. 3**). Earlywood vessel diameter varies from 50-100 µm and vessel density from 100-200/mm$^2$. Vessel perforations are simple and scalariform with 10-20 bars. (**Figs. 4-6**). Small inter-vessel pits occur in opposite arrangement (**Fig. 6**). Transitions from pits to scalariform perforations occur (**Fig. 6**). Vessel-ray pits are round or have horizontally enlarged apertures. Radial walls of fibers are perforated by bordered, round to scalariform pits (<2-4 µm) with slit-like apertures (libriform fibers and fiber tracheids). Fibers are thin- to thick-walled (**Fig. 3**). Axial parenchyma is apotracheal diffuse, diffuse in aggregates or paratracheal (**Fig. 7**). Ray width varies between 5-14 cells (**Fig. 8**). Rays are homocellular with procumbent cells.

### Characteristic features of taxa

The xylem and phloem of the analyzed species cannot be differentiated.

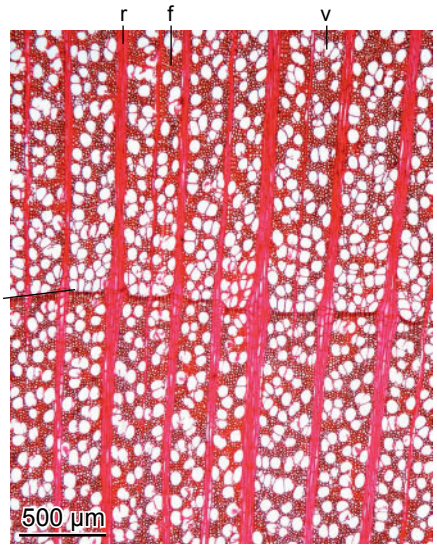



**Fig. 1.** Diffuse-porous wood with distinct annual rings. Stem of a 10 m-high tree located in a riverbed, Mediterranean zone, Meteora, Greece. *Platanus orientalis*, transverse section.

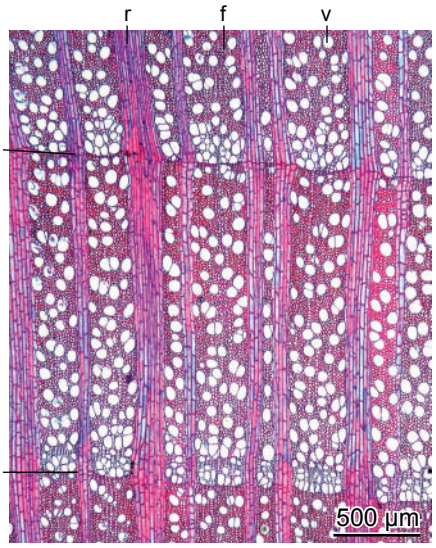



**Fig. 2.** Diffuse-porous to slightly semi-ring-porous wood with distinct annual rings. Stem of a 6 m-high tree in a canyon, arid zone, Bakersfield, Arizona, USA. *Platanus wrightii*, transverse section.

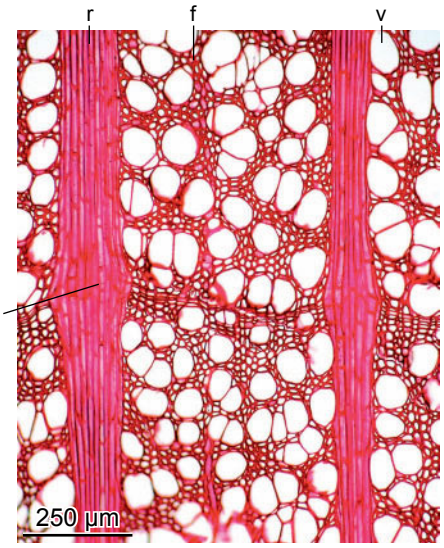



**Fig. 3.** Diffuse-porous wood with a distinct ring boundary. It is defined by a few radial flat fibers and enlarged large rays. Stem of a 12 m-high tree, cultivated at the road side, hill zone, Zürich, Switzerland. *Platanus x hispanica*, radial section.

**Fig. 4.** Scalariform perforations with 10-20 bars. Stem of a 12 m-high tree, cultivated at the road side, hill zone, Zürich, Switzerland. *Platanus x hispanica*, radial section.

**Fig. 5.** A simple perforation and a scalariform perforation with three bars. Stem of a 10 m-high tree located in a riverbed, Mediterranean, Meteora, Greece. *Platanus orientalis*, radial section.

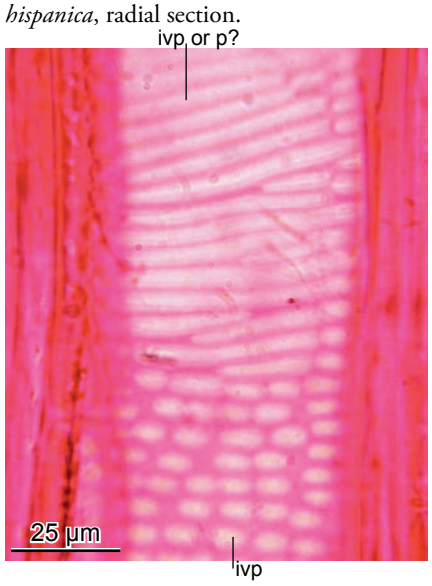
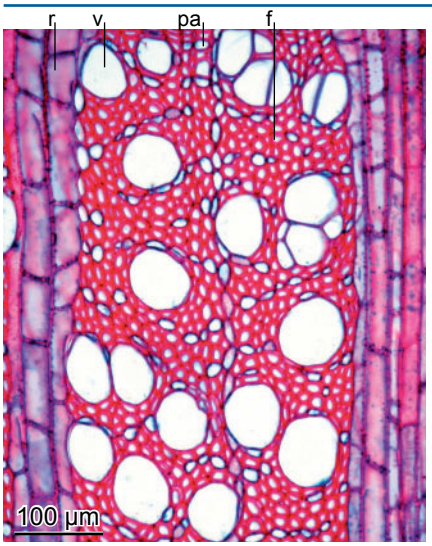
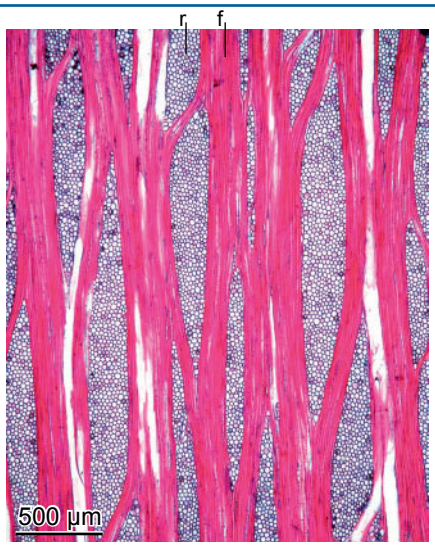



**Fig. 6.** Transition between round, bordered horizontally arranged pits and scalariform pits. Stem of a 10 m-high tree in a riverbed, Mediterranean zone, Meteora, Greece. *Platanus orientalis*, radial section.



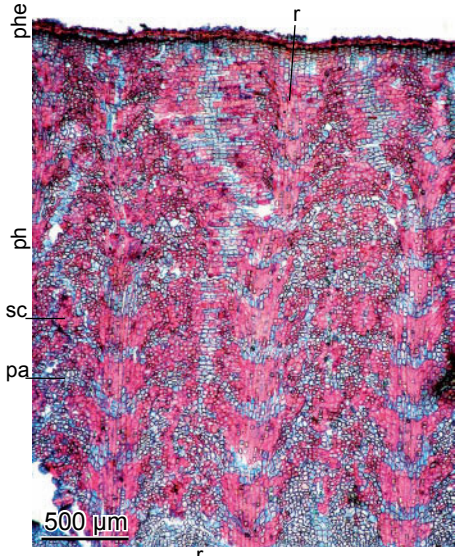

**Left Fig. 7.** Different types of axial parenchyma: diffuse, diffuse in aggregates and paratracheal (blue cells). Stem of a 6 m-high tree located in a canyon, arid zone, Bakersfield, Arizona, USA. *Platanus wrightii*, radial section.

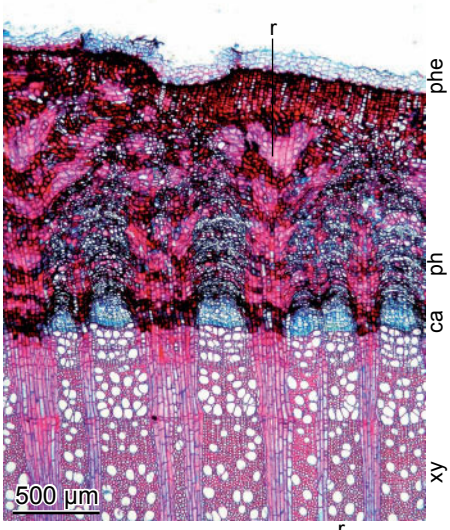
**Right Fig. 8.** Large, homocellular rays with 6-12 cells width. Stem of a 6 m-high tree located in a canyon, arid zone, Bakersfield, Arizona, USA. *Platanus wrightii*, tangential section.



### Characteristics of the phloem and the cortex

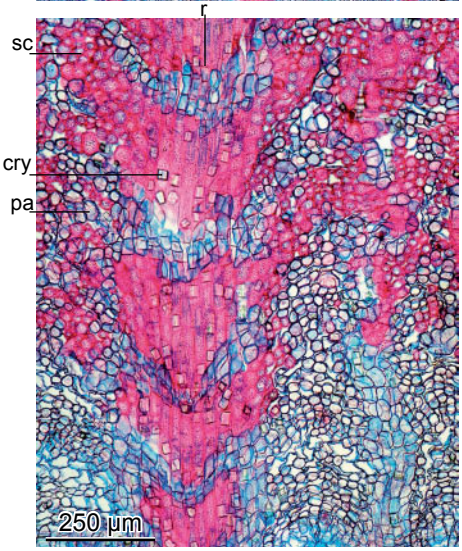
Characteristic of all species is the presence of tangential arc-like arranged bands of thick-walled fibers, ray dilatations and the presence of large prismatic crystals (**Figs. 9-12**). Parts of the phellem in contact with the phloem are always small because older parts become detached (**Figs. 9** and **10**).

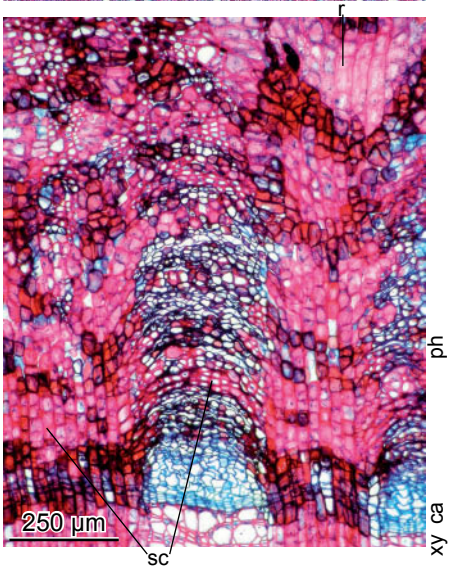



**Left Fig. 9.** Bark with a small band of phellem. The phloem mainly consists of sclereids (red). Stem of a 12 m-high tree, cultivated on a road side, hill zone, Zürich, Switzerland. *Platanus x hispanica*, transverse section.

**Right Fig. 10.** Bark with a small band of phellem. Rays are intensively sclerotized. Stem of a 6 m-high tree in a canyon, arid zone, Bakersfield, Arizona, USA. *Platanus wrightii*, transverse section.




**Left Fig. 11.** Phloem with intensively sclerotized rays. Unlignified tissue occurring near the cambium indicates that sclerotisation between the rays is delayed. Large prismatic crystals occupy lignified ray cells. Stem of a 12 m-high tree, cultivated on a road side, hill zone, Zürich, Switzerland. *Platanus x hispanica*, transverse section.

**Right Fig. 12.** The parenchyma/sieve tube zone occurring between two intensively lignified rays is partially compressed. Only the cells near the cambium seem to be active. Stem of a 6 m-high tree located in a canyon, arid zone, Bakersfield, Arizona, USA. *Platanus wrightii*, transverse section.

## Ecological trends and relations to life forms

No ecological trends were found.

## Discussion in relation to previous studies

Gregory (1994) refers to 33 studies of the xylem anatomy of the genus *Platanus*. Descriptions and photographs are found in atlases by Fahn et al. (1986), Greguss (1945), Grosser (1977), Jaquiot et al. (1893), Panshin and Zeeuw (1980) and Schweingruber (1990). Holdheide (1951) described the bark.

The present study confirms observations from earlier studies. *Platanus wrightii* is characterized for the first time in this study.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **3** |
| 1 | growth rings distinct and recognizable | 3 |
| 4 | semi-ring-porous | 3 |
| 5 | diffuse-porous | 3 |
| 9 | vessels predominantly solitary | 3 |
| 11 | vessels predominantly in clusters | 3 |
| 13 | vessels with simple perforation plates | 3 |
| 14 | vessels with scalariform perforation plates | 3 |
| 20 | intervessel pits scalariform | 3 |
| 21 | intervessel pits opposite | 3 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 3 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 3 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 3 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 3 |
| 70 | fibers thin- to thick-walled | 3 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 3 |
| 79 | parenchyma paratracheal | 3 |
| 98 | rays commonly 4-10-seriate | 3 |
| 99 | rays commonly >10-seriate | 3 |
| 103 | rays of two distinct sizes (tangential section) | 3 |
| 104 | ray: all cells procumbent (radial section) | 3 |
| 136 | prismatic crystals present | 3 |
| R1 | groups of sieve tubes present | 1 |
| R2 | groups of sieve tubes in tangential rows | 1 |
| R3 | distinct ray dilatations | 2 |
| R4 | sclereids in phloem and cortex | 2 |
| R6.1 | sclereids in tangential rows | 2 |
| R7 | with prismatic crystals | 2 |

# Plumbaginaceae



**Number of species, worldwide and in Europe**

The cosmopolitan Plumbaginaceae family includes 27 genera with 650 species. In Europe there are 8 genera with 117 species. The majority of the species are members of the genera *Limonium* (87 species) and *Armeria* (43 species; Tutin et al. 1964-1980). 22 species are endemic to the Canary Islands (Hohenester and Wells 1993).

**Analyzed material**

The xylem and phloem of 10 Plumbaginaceae species were analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 1 | |
| Woody chamaephytes | 1 | 11 |
| Semi-woody chamaephytes | 8 | 1 |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 1 | |
| Boreal | 1 | |
| Hill and mountain | 2 | |
| Mediterranean | 2 | |
| Arid | 4 | |

**Analyzed species:**

*Armeria alpina* Willd.
*Armeria arctica* Sternb.
*Armeria arenaria* Schultes
*Armeria maritima* (Miller) Willd.
*Dyerophytum indicum* Kuntze
*Limoniastrum monopetalum* Boiss.
*Limoniastrum guyonianum* Duc.
*Limonium insigne* Kuntze
*Limonium pectinatum* Kuntze
*Plumbago zeylanica* L.

**Right:** *Limonium vulgare* (photo: Stützel)

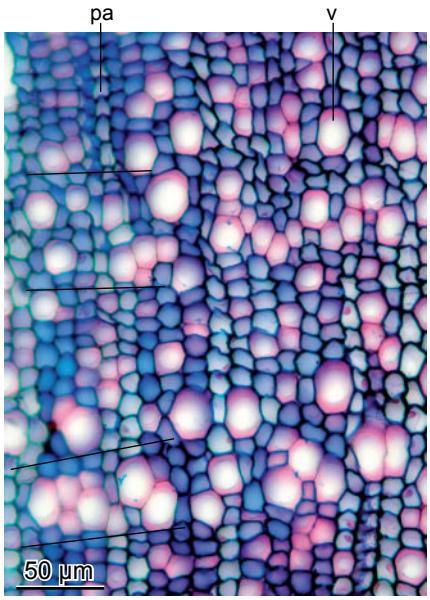
*Armeria maritima*

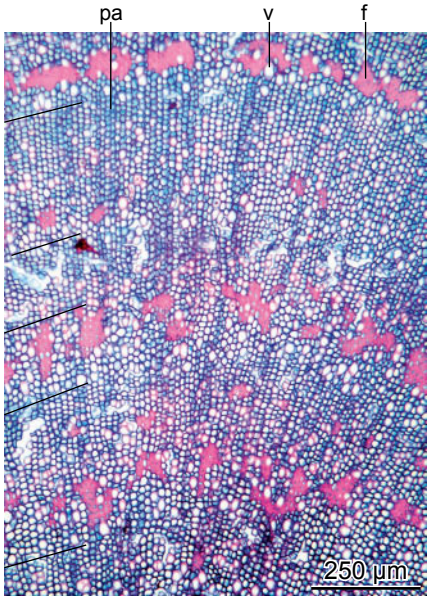
*Armeria alpina* (photo: Landolt)

**Characteristics of the xylem**

Annual rings occur in the present material in all *Armeria* species of the temperate zone (**Figs. 1** and **2**). Rings are often absent or indistinct in species growing in the Mediterranean and subtropical climate (*Dyerophytum*, *Limonium* and *Plumbago*; **Fig. 3**). Ring boundaries of the four *Armeria* species are defined by semi-ring porosity (**Fig. 1**). Diffuse porosity is characteristic for all other species (**Fig. 3**). Vessels of the genera *Armeria*, *Limonium* and *Limoniastrum* are predominantly solitary (**Figs. 1** and **3**). Radial multiples are characteritic of *Dyerophytum indicum* (**Fig. 9**) and *Plumbago zeylanica* (**Fig. 14**). Vessel diameter is <20 µm in all *Armeria* species (**Fig. 1**) and *Limonium pectinatum*. Vessel density varies mostly between 300-500/mm$^2$. Vessels of most species are thick-walled (**Figs. 1** and **3**), except in *Dyerophytum indicum* and *Plumbago zeylanica*. Vessels contain exclusively simple perforations. Inter-vessel pits are predominantly scalariform and pseudoscalariform in *Armeria* (**Fig. 4**), and small and round in all other species (**Fig. 5**). Spiral thickenings are absent from the present material. Dark-staining substances were observed in few cells of *Limonium pectinatum*.

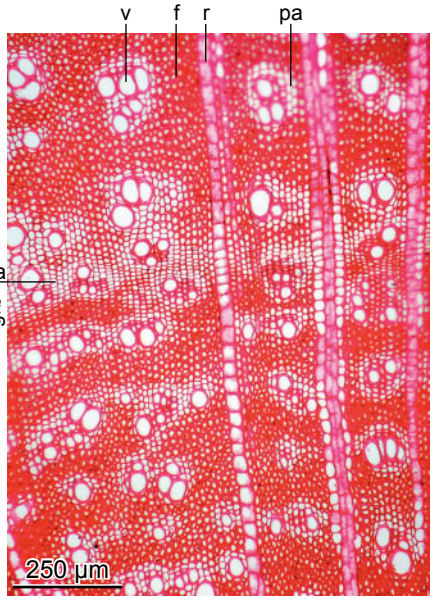
The radial walls of fibers are perforated by very small (<2 µm) slit-like or round pits in all species. Septate fibers occur only in *Dyerophytum indicum* (**Fig. 6**). Fibers are either thin- or thin- to thick-walled in *Armeria*, *Dyerophytum* and *Limoniastum monopetalum*. They are thick-walled in *Limoniastrum guyonianum* and both *Limonium* species (**Fig. 7**). Fibers are absent from *Armeria alpina* and *A. arenaria* (**Fig. 1**). Living, thick-walled fibers with nuclei are found in *Limonium pectinatum* (**Fig. 8**). Paratracheal parenchyma occurs in all species (**Fig. 9**) except *Armeria*, where parenchyma is pervasive (**Figs. 1** and **2**). Marginal parenchyma bands are distinct in *Limonium pectinatum*. Storied structures tend to be absent or indistinct. Rays are absent from




**Left Fig. 1.** Semi-ring-porous xylem with a distinct annual ring boundary. The thick-walled solitary vessels are surrounded by a pervasive parenchyma. Fibers are absent. Root collar of a 15 cm-high chamaephyte, meadow, subalpine zone, Pyrenees, Spain. *Armeria alpina*, transverse section.

**Right Fig. 2.** Slightly semi-ring-porous xylem. The thick-walled fiber groups (red) are surrounded by a pervasive parenchyma. Root collar of a 15 cm-high chamaephyte, meadow, coastal zone, Devon, Great Britain. *Armeria maritima*, transverse section.



**Left Fig. 3.** Diffuse-porous xylem with an indistinct ring boundary. Thick-walled vessels are solitary or in small groups and are surrounded by vasicentric, paratracheal parenchyma. Stem of a 50 cm-high dwarf shrub, sand dune, Mediterranean, coastal zone, Cadiz, Spain. *Limoniastrum monopetalum*, transverse section.

**Right Fig. 4.** Imperforate and scalariform vessel pitting. Root collar of a 15 cm-high chamaephyte, dry meadow, mountain zone, France. *Armeria arenaria*, radial section.

*Armeria maritima* (**Fig. 2**). A few large rays divide rayless parts in the other *Armeria* species (**Fig. 12**). All other species have 3-6-seriate rays (**Fig. 11**). Ray cells are thin-walled and unlignified in *Limonium pectinatum* and primarely square or upright. Successive cambia occur in *Dyerophytum indicum* (**Fig. 13**) and in *Plumbago zeylanica* (**Fig. 14**), but are absent from all other species analyzed. Crystals are very rare. Prismatic crystals occur only in *Limoniastrum guyonianum*.

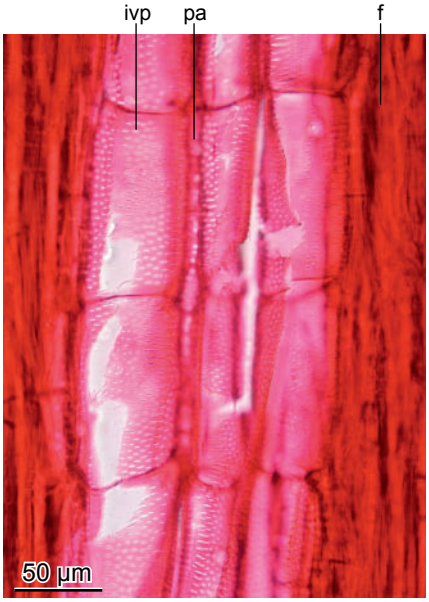
**Ecological trends and relations to life forms**

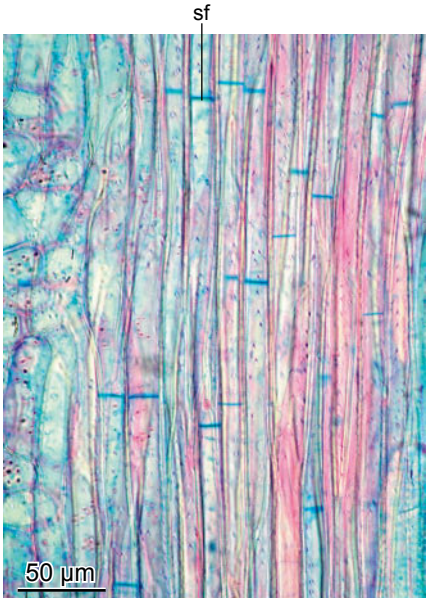
Ring boundaries in plants of the subtropical climateare absent or at least less distinct than in species of the temperate zone. No relations to growth forms could be found.

**Characteristic features of the taxa**

Some features are characteristic of single species or of groups of species: The xylem of all *Armeria* species differs from the other taxa in the Plumbaginaceae in that it shows distinct semi-ring porosity, reticulate vessel pitting and pervasive parenchyma. Only *Dyerophytum indicum* and *Plumbago zeylanica* contain successive cambia. The presence of crystals characterizes *Limoniastrum guyonianum*. The vessel number is relatively low (<200) in *Limonium* and *Limoniastrum*. Overall, the family of Plumbaginaceae is a heterogeneous group.

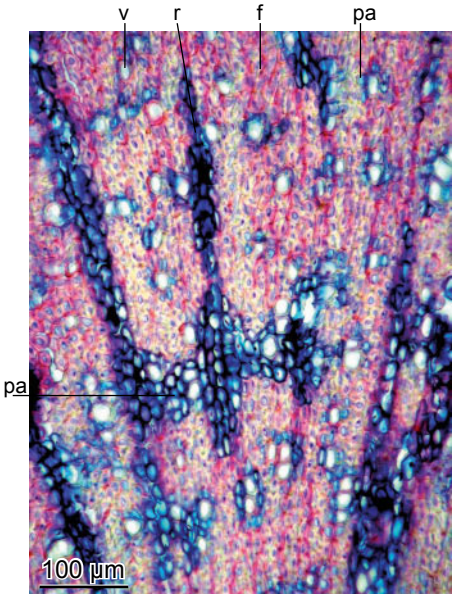





**Left Fig. 5.** Vessels with small pits and a simple perforation. Stem of a 1 m-high shrub, on rock, subtropical climate, Dhofar, Oman. *Plumbago zeylanica*, radial section.

**Right Fig. 6.** Septate fibers with unlignified, horizontal cell walls. Stem of a 1.5 m-high shrub, on rock, subtropical climate, Dhofar, Oman. *Dyerophytum indicum*, radial section.



**Left Fig. 7.** Solitary vessels are surrounded by paratracheal parenchyma and thick-walled fibers. Root collar of a 20 cm-high chamaephyte, subtropical climate, coast, Gran Canaria, Canary Islands. *Limonium pectinatum*, transverse section.

**Right Fig. 8.** Living, thick-walled fibers with nuclei. Root collar of a 20 cm-high chamaephyte, subtropical climate, coast, Gran Canaria, Canary Islands. *Limonium pectinatum*, radial section.

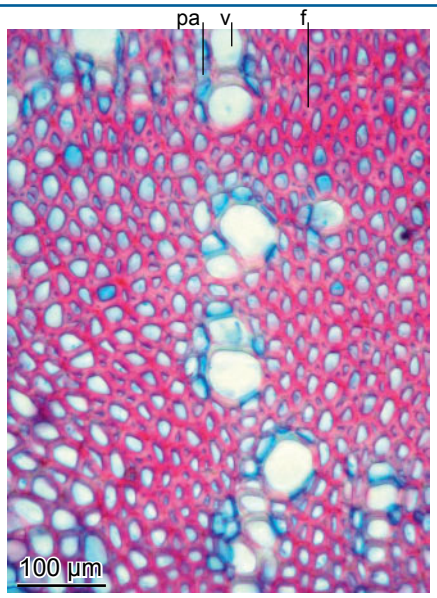



**Fig. 9.** Paratracheal parenchyma around solitary vessels and radial vessel groups. Stem of a 1.5 m-high shrub, on rock, subtropical climate, Dhofar, Oman. *Dyerophytum indicum*, transverse section.

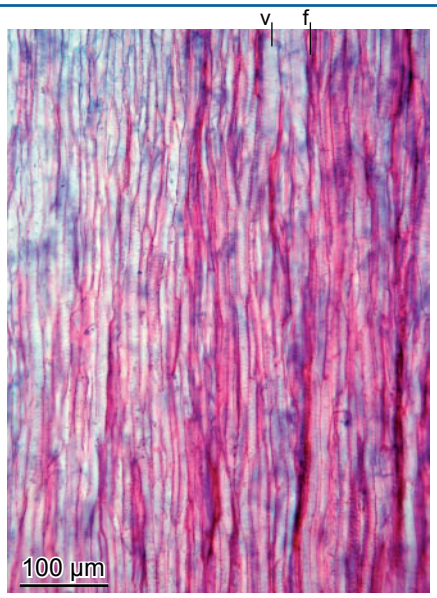



**Fig. 10.** Absent rays. Root collar of a 15 cm-high chamaephyte, meadow, coastal zone, Devon, Great Britain. *Armeria maritima*, tangential section.

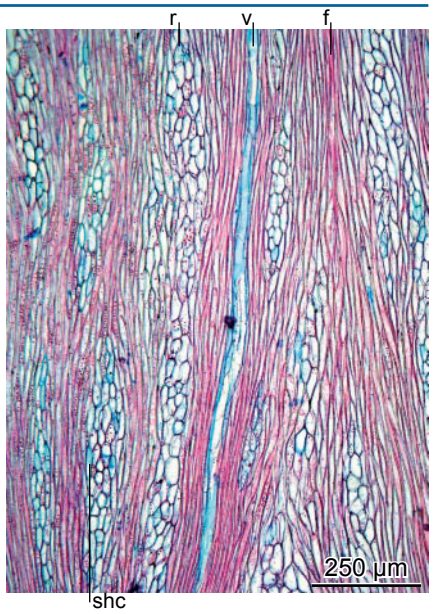



**Fig. 11.** 3-6-seriate rays, partially with sheet cells. Stem of a 1.5 m-high shrub, on rock, subtropical climate, Dhofar, Oman. *Dyerophytum indicum*, tangential section.

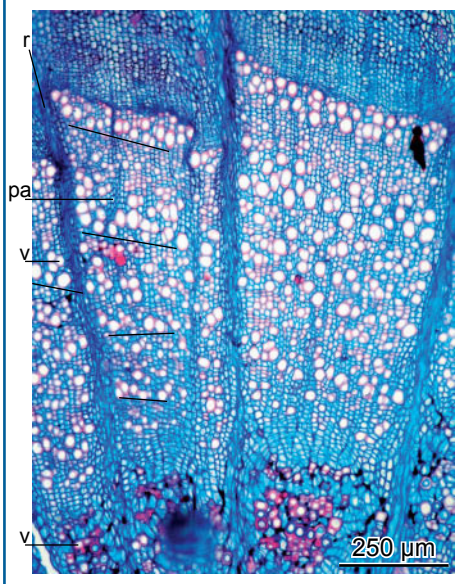



**Fig. 12.** A few large rays occur between rayless compartments. Root collar of a 15 cm-high chamaephyte, dry meadow, mountain zone, France. *Armeria arenaria*, transverse section.

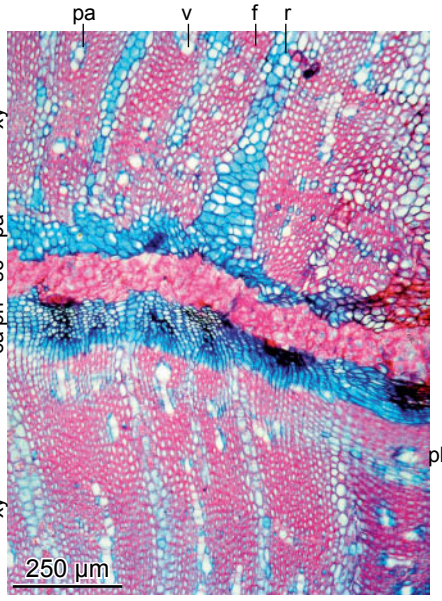



**Fig. 13.** Products of a successive cambium. A band of thick-walled lignified fibers occurs outside the phloem with dilatations. The new xylem formation starts with a band of unlignified, thin-walled parenchyma cells (blue). Stem of a 1.5 m-high shrub, on rock, subtropical climate, Dhofar, Oman. *Dyerophytum indicum*, transverse section.

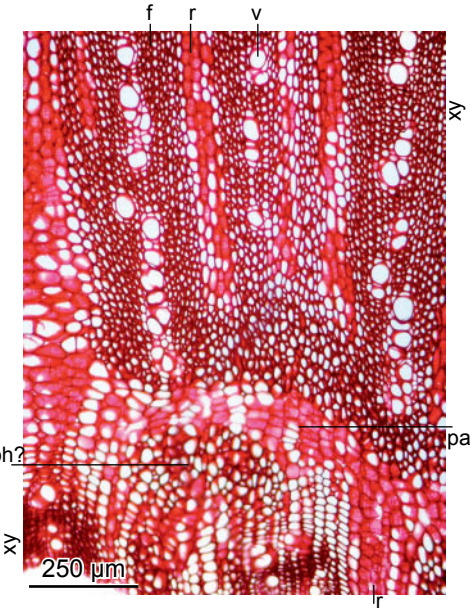



**Fig. 14.** Products of a successive cambium. A zone of unlignified, thin-walled parenchyma occurs between the phloem of the previous new band. Vessels are grouped in radial multiples. 60 cm-high hemicryptophyte, subtropical climate, coast, Dhofar, Oman. *Plumbago zeylanica*, transverse section.

**Characteristics of the phloem and the cortex**

The anatomy of the bark of the Plumbaginaceae is heterogeneous. All species are characterized by the absence of crystals. The phloem and the cortex are simply structured in most species (**Fig. 15**). Distinct groups of sieve tubes are present only in *Armeria arctica*. Sclereids occur sporadically and are clustered in small, tangentially oriented groups (*Armeria arenaria*; **Fig. 16**) and in irregular groups (*Limonium insigne* and *L. pectinatum*; **Fig. 17**). Ray dilatations were only observed in *Armeria arenaria* (**Fig. 16**).

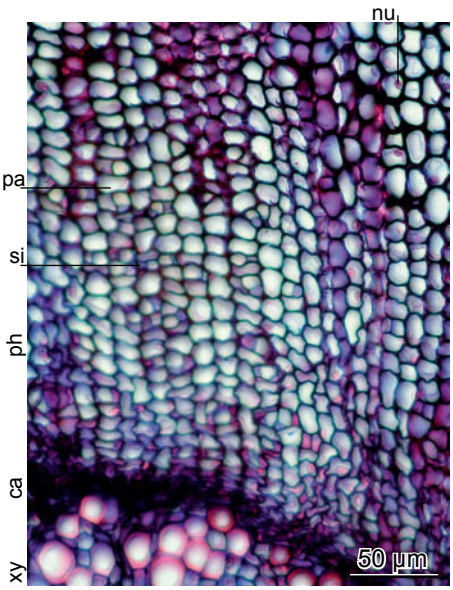



**Fig. 15.** Simple construction of the phloem. Sieve tubes are smaller than parenchyma cells. Root collar of a 15 cm-high chamaephyte, meadow, subalpine zone, Pyrenees, Spain. *Armeria alpina*, transverse section.

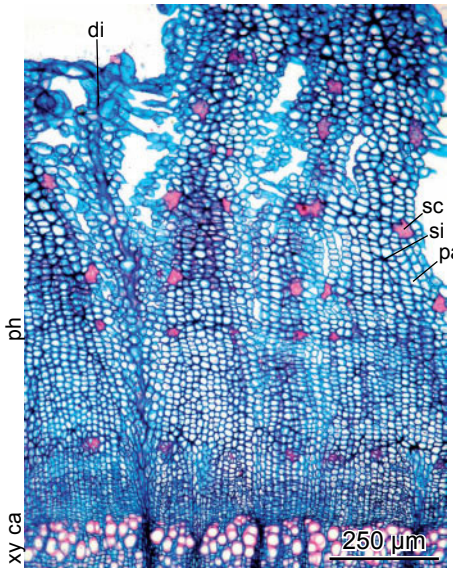



**Fig. 16.** Phloem with small groups of fibers embedded in a tissue of parenchyma and sieve tubes. Characteristic of all species are dilatations. Root collar of a 15 cm-high chamaephyte, dry meadow, mountain zone, France. *Armeria arenaria*, transverse section.

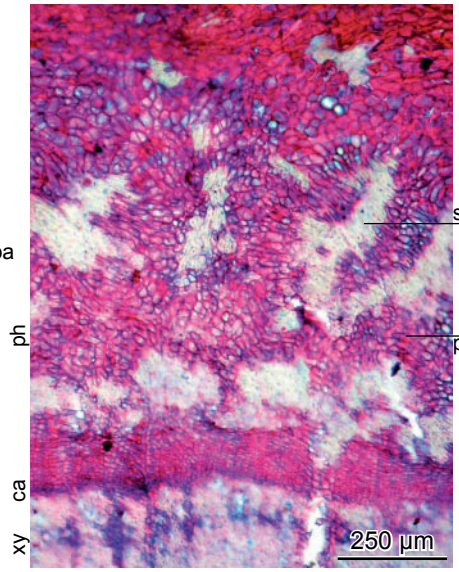



**Fig. 17.** Irregular, sclerenchymatic groups surrounded by a uniform parenchymatic tissue. Root collar of a 20 cm-high chamaephyte, subtropical climate, coast, Gran Canaria, Canary Islands. *Limonium pectinatum*, transverse section.



## Discussion in relation to previous studies

The only existing comprehensive wood anatomical survey is that of Carlquist and Boggs (1996). It is based on 12 woody species. Metcalfe and Chalk (1957) describe *Plumbago capensis*. A few authors characterized several woody species (Gregory 1994). The present study is comparable to the earlier analysis of *Limoniastrum guyonianum* (Neumann et al. 2001), *Armeria maritima* (Carlquist 2003), *Limonium insigne* and *Limoniastrum monopetalum* (Schweingruber 1990). As Carlquist and Boggs (1996) recognized, the anatomy within the family of Plumbaginaceae varies significantly. Within the genus *Armeria* the anatomy is relatively homogeneous. Species with successive cambia form another group (*Plumbago* and *Dyerophytum*). There is insufficient material in this study to classify all species into groups. Characteristics common to the family could not be found.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **10** |
| 1 | growth rings distinct and recognizable | 8 |
| 2 | growth rings absent | 2 |
| 4 | semi-ring-porous | 4 |
| 5 | diffuse-porous | 5 |
| 9 | vessels predominantly solitary | 8 |
| 9.1 | vessels in radial multiples of 2-4 common | 2 |
| 10 | vessels in radial multiples of 4 or more common | 1 |
| 11 | vessels predominantly in clusters | 7 |
| 13 | vessels with simple perforation plates | 9 |
| 20 | intervessel pits scalariform | 3 |
| 20.1 | intervessel pits pseudoscalariform to reticulate | 4 |
| 39.1 | vessel cell-wall thickness >2 µm | 8 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 5 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 6 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 4 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 5 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 10 |
| 65 | septate fibers present | 1 |
| 69 | fibers thick-walled | 3 |
| 70 | fibers thin- to thick-walled | 6 |
| 75 | parenchyma absent or unrecognizable | 1 |
| 79 | parenchyma paratracheal | 6 |
| 79.1 | parenchyma pervasive | 4 |
| 89 | parenchyma marginal | 2 |
| 97 | ray width predominantly 1-3 cells | 1 |
| 98 | rays commonly 4-10-seriate | 8 |
| 105 | ray: all cells upright or square | 4 |
| 106 | ray: heterocellular 1 upright cell row (radial section) | 0 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 3 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 3 |
| 110 | rays with sheet cells (tangential section) | 1 |
| 117 | rayless | 1 |
| 120 | storied axial tissue (parenchyma, fibers, vessels, tangential section) | 1 |
| 135 | interxylary phloem present | 2 |
| 136 | prismatic crystals present | 1 |
| R1 | groups of sieve tubes present | 1 |
| R2 | groups of sieve tubes in tangential rows | 1 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 4 |
| R10 | phloem not well structured | 7 |

# Polygalaceae



**Number of species, worldwide and in Europe**

The cosmopolitan Polygalaceae family includes 17 genera with 850 species. In Europe there is one genus with 33 species (*Polygala*). There are no endemic species on the Canary Islands.

**Analyzed material**

The xylem and phloem of 1 genus with 7 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes >4 m | | 11 genera |
| Nanophanerophytes 0.5-4 m | 1 | |
| Semi-woody chamaephytes | 1 | 1 |
| Hemicryptophytes and geophytes | 5 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 1 | |
| Boreal | 1 | |
| Hill and mountain | 5 | |

**Analyzed species:**

*Polygala alpestris* Hegetschw.
*Polygala chamaebuxus* L.
*Polygala comosa* Schk.
*Polygala myrtifolia* L.
*Polygala pedemontana* Perr. et Verlot
*Polygala tenuifolia* Link
*Polygala transcaucasica* Tamamsch

*Polygala vulgaris* (photo: Zinnert)

*Polygala amarella*

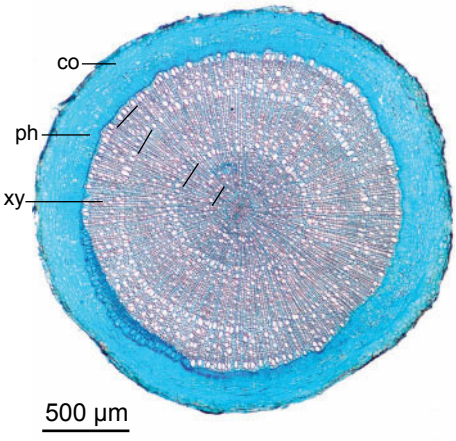
*Polygala comosa* (photo: Zinnert)

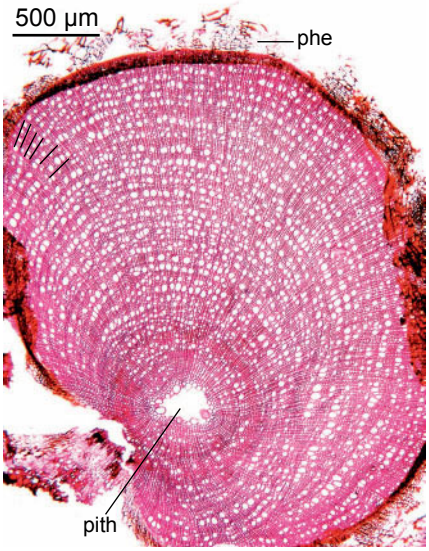
*Polygala chamaebuxus* (photo: Zinnert)

### Characteristics of the xylem

Annual rings are present in most species (**Figs. 1** and **2**) but are indistinct in *Polygala myrtifolia* (**Fig. 3**). Rings are very small in *Polygala chamaebuxus* (**Fig. 2**) at natural sites. Ring boundaries are marked by semi-ring-porosity; vessels are arranged mostly solitary (**Figs. 1-3**, **6** and **7**). The earlywood vessel diameter of the majority of species varies from 30-40 µm. Vessel density varies mostly from 200-300/mm$^2$, but it is below 100/mm$^2$ in *Polygala myrtifolia* (**Fig. 3**). Vessels contain exclusively simple perforations (**Fig. 4**). Inter-vessel pits are mostly round and large (3 µm) in alternating position (**Fig. 5**). They are vestured in *Polygala chamaebuxus*. Distinct helical thickenings occur in *Polygala chamaebuxus* (**Fig. 4**). Vessels of a few species contain dark-staining substances, e.g. *Polygala tenuifolia*.

Fibers are mostly thin- to thick-walled (**Figs. 6** and **7**), but are thick-walled in *Polygala myrtifolia* (**Fig. 3**) and thin-walled in *Polygala alpestris*. Parenchyma is absent or apotracheal in aggregates (**Figs. 6** and **7**). Rays are absent or difficult to recognize in *Polygala chamaebuxus*, and are uni- to biseriate in all other species (**Figs. 8-10**). Rays are mostly homocellular with square and upright cells (**Fig. 11**) but are occasionally heterocellular with a few square or procumbent cells (*Polygala myrtifolia*; **Fig. 12**). Crystals are absent in all species.




**Left Fig. 1.** Distinct rings of a semi-ring-porous xylem. Root collar of a 5 cm-high hemicryptophyte, meadow, alpine zone, Grisons, Switzerland. *Polygala alpestris*, transverse section.

**Right Fig. 2.** Distinct rings of a semi-ring-porous xylem containing more than 30 rings. Root collar of a 8 cm-high chamaephyte, on rock, subalpine zone, Grisons, Switzerland. *Polygala chamaebuxus*, transverse section.

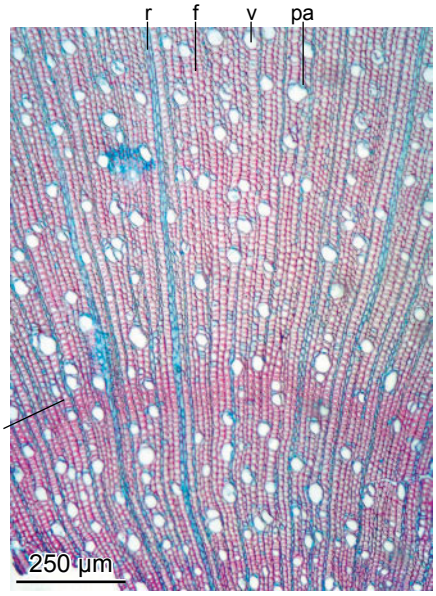



**Fig. 3.** Indistinct rings in a diffuse-porous wood. Stem of a 1 m-high shrub, cultivated, Botanical Garden, Ticino, Switzerland. *Polygala myrtifolia*, transverse section.

**Fig. 4.** Vessel with a simple perforation, large, round intervessel pits and thick helical thickenings. Root collar of an 8 cm-high chamaephyte, on rock, subalpine zone, Grisons, Switzerland. *Polygala chamaebuxus*, radial section.

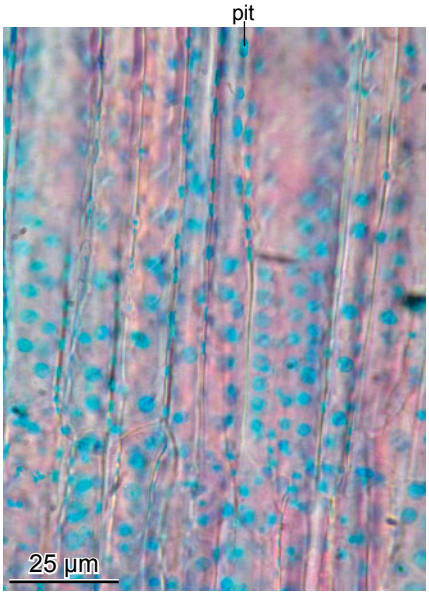
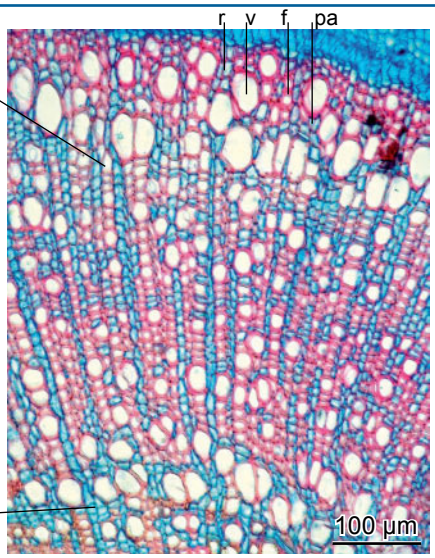
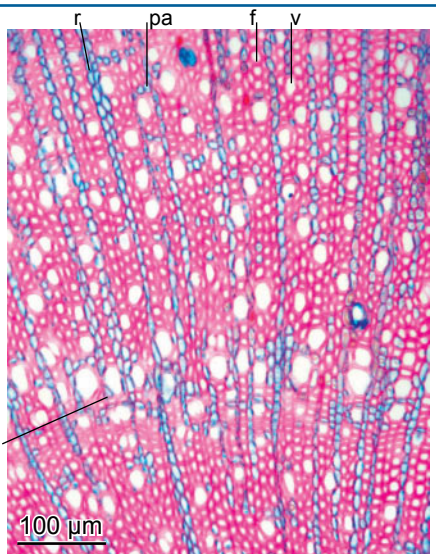


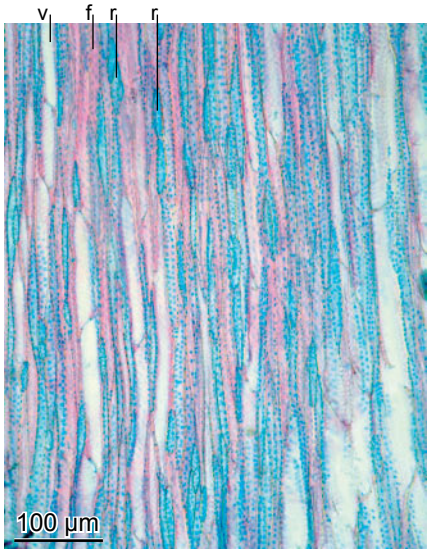

**Fig. 5.** Large, round pits on vessels and fibers. Root collar of a 10 cm-high hemicryptophyte, dry meadow, mountain zone, Grisons, Switzerland. *Polygala pedemontana*, radial section.

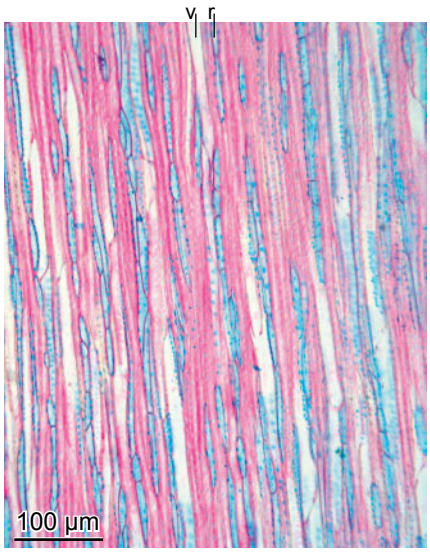



**Left Fig. 6.** Apotracheal parenchyma in aggregates in a semi-ring-porous xylem. Root collar of a 10 cm-high hemicryptophyte, dry meadow, mountain zone, Grisons, Switzerland. *Polygala pedemontana*, transverse section.

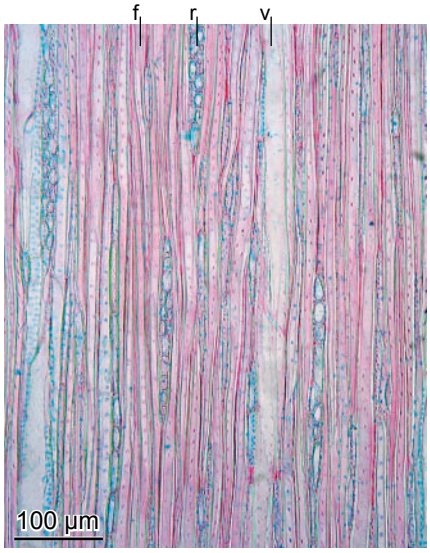
**Right Fig. 7.** Apotracheal parenchyma in a semi-ring-porous xylem. Root collar of a 15 cm-high hemicryptophyte, dry meadow, mountain zone, Caucasus, Georgia. *Polygala transcaucasica*, transverse section.

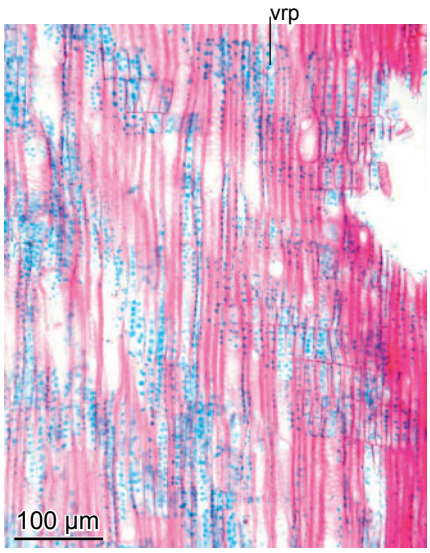



**Left Fig. 8.** Exclusively uniseriate, unlignified rays. Root collar of a 10 cm-high hemicryptophyte, dry meadow, mountain zone, Grisons, Switerland. *Polygala pedemontana*, transverse section.

**Right Fig. 9.** Uniseriate, unlignified rays. Root collar of a 15 cm-high hemicryptophyte, dry meadow, mountain zone, Caucasus, Georgia. *Polygala transcaucasica*, tangential section.



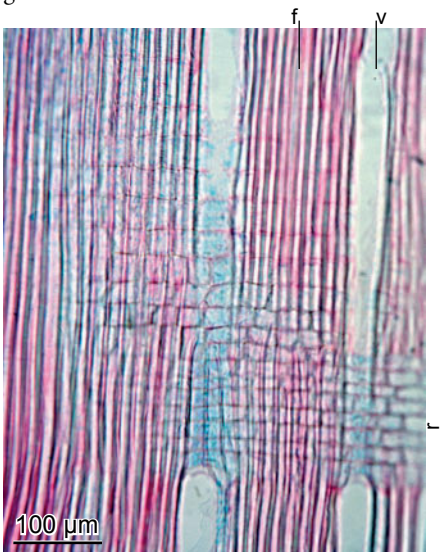




**Fig. 10.** Biseriate rays. Stem of a 1 m-high shrub, cultivated, hill zone, Botanical Garden, Ticino, Switzerland. *Polygala myrtifolia*, tangential section.

**Fig. 11.** Homocellular rays with upright cells. Root collar of a 15 cm-high hemicryptophyte, dry meadow, mountain zone, Caucasus, Georgia. *Polygala transcaucasica*, radial section.

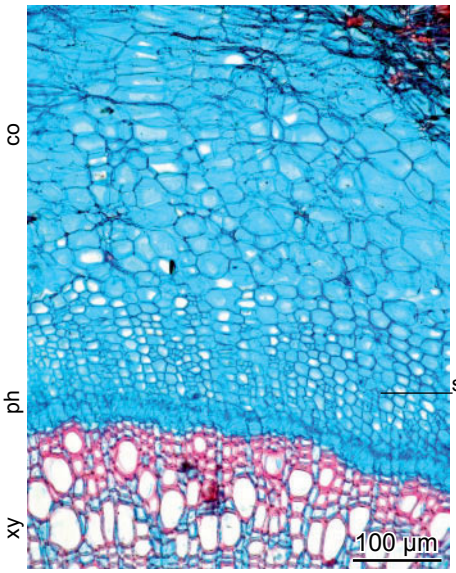
**Fig. 12.** Heterocellular ray with some procumbent cells in the center and many square and upright marginal cells. Stem of a 1 m-high shrub, cultivated, hill zone, Botanical Garden, Ticino, Switzerland. *Polygala myrtifolia*, radial section.

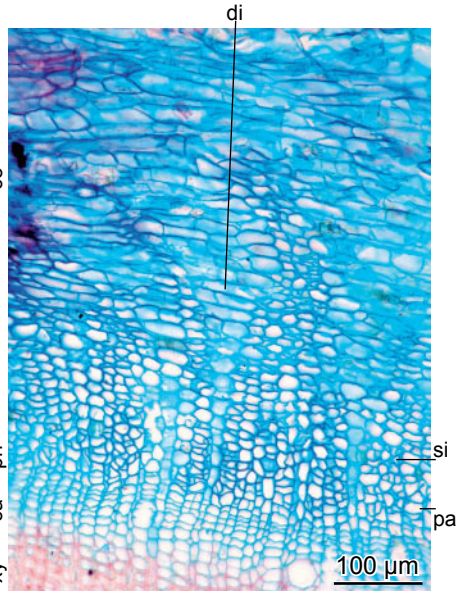
## Characteristics of the phloem

The phloem of all species consists mainly of parenchyma in which small groups of sieve-tubes are embedded (**Figs. 13** and **14**).

## Ecological trends and relations to life forms

Ecological trends in relation to vegetation zones are not recognizable. The shrubby species display some distinct characteristics: *Polygala chamaebuxus* reaches a relatively old age (>30 rings) and vessels have helical thickenings. Rings are indistinct and vessel density is low in the Australian shrub *Polygala myrtifolia* (cultivated in Europe).




**Left Fig. 13.** Phloem with small groups of small sieve-tubes surrounded by larger parenchyma cells. Root collar of a 10 cm-high hemicryptophyte, dry meadow, mountain zone, Grisons, Switzerland. *Polygala pedemontana*, transverse section.

**Right Fig. 14.** Phloem with small sieve tubes surrounded by larger parenchyma cells and ray dilatations. Stem of a 1 m-high shrub, cultivated, hill zone, Botanical Garden, Ticino, Switzerland. *Polygala myrtifolia*, transverse section.

## Discussion in relation to previous studies

The xylem of tree-like genera is well-known, especially the genus *Xanthophyllum*. Gregory (1994) cited 22 articles with anatomical descriptions of Polygalaceae. From the species characterised here only the genus *Polygala* is different from many tree-like species: crystals and successive cambia are absent (Carlquist 2001). *Polygala chamaebuxus* was described before (Greguss 1945) and our findings are in accordance with the earlier study. All other species have not been described before.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **7** |
| 1 | growth rings distinct and recognizable | 7 |
| 4 | semi-ring-porous | 6 |
| 9 | vessels predominantly solitary | 7 |
| 13 | vessels with simple perforation plates | 7 |
| 22 | intervessel pits alternate | 7 |
| 29 | vestured pits | 1 |
| 36 | helical thickenings present | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 7 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 7 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 1 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 6 |
| 68 | fibers thin-walled | 1 |
| 69 | fibers thick-walled | 1 |
| 70 | fibers thin- to thick-walled | 5 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 7 |
| 96 | rays uniseriate | 4 |
| 97 | ray width predominantly 1-3 cells | 3 |
| 105 | ray: all cells upright or square | 4 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 3 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 4 |
| 110 | rays with sheet cells (tangential section) | 3 |
| R1 | groups of sieve tubes present | 7 |
| R3 | distinct ray dilatations | 1 |

# Polygonaceae



**Number of species, worldwide and in Europe**

The cosmopolitean Polygonaceae family includes 43 genera with 1100 species. The genus *Eriogonum* with 250 species is native to North America. Represantives are common in northern temperate regions. In Europe there are 12 genera with 104 species. The majority belong to *Rumex* (50 species) and *Polygonum* (36 species).

**Analyzed material**

The xylem and phloem of 41 Polygonaceae species were analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | 3 | 30 |
| Semi-woody chamaephytes | 7 | |
| Lianas | 2 | |
| Hemicryptophytes and geophytes | 22 | |
| Therophytes | 7 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 7 | |
| Hill and mountain | 26 | |
| Mediterranean | 1 | |
| Arid | 5 | |
| Subtropical | 2 | |

*Rumex scutatus*

**Analyzed species:**

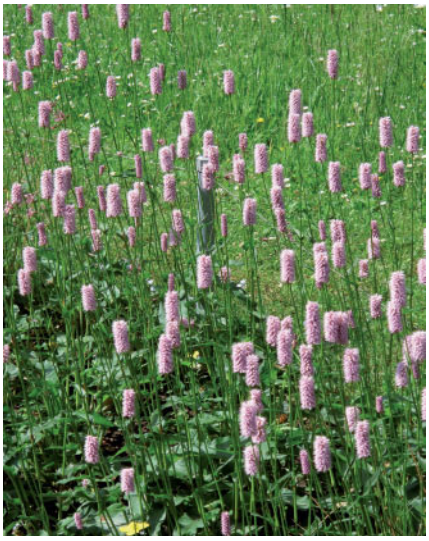
Subfamily Eriogonidae, Eriogonae (endemic to North America)
- *Eriogonum fendlerianum* (Benth.) Small
- *Eriogonum inflatum* Torr. & Frem.
- *Eriogonum jamesii* Benthan
- *Eriogonum longifolium* Nutt.
- *Eriogonum ovalifolium* Nutt.
- *Eriogonum pyrifolium* Hook
- *Eriogonum trichopes* Torr.

Subfamily Polygonoideae, tribe Polygoneae
- *Calligonum crinitum* Boiss.
- *Calligonum comosum* L. Hér.
- *Fallopia convolvulus* (L.) Holub.
- *Fallopia dumetorum* (L.) Holub.
- *Oxyria digyna* (L.) Hill
- *Polygonum aviculare* L.
- *Polygonum bistorta* L.
- *Polygonum bistortoides* Pursh.
- *Polygonum equisetiforme* Siebth. et Sm.
- *Polygonum hydropiper* L.
- *Polygonum minus* Huds.
- *Polygonum mite* Schrank
- *Polygonum paronychia* Cham. & Shildt. (endemic to N. America)
- *Polygonum persicaria* L.
- *Polygonum polystachyum* Meissner (naturalized in Europe)
- *Polygonum viviparum* L.
- *Reynoutria japonica* Houtt. (naturalized in Europe)
- *Rumex acetosa* L.
- *Rumex acetosella* L.
- *Rumex alpinus* L.
- *Rumex alpestris* Jacq.
- *Rumex conglomeratus* Murray
- *Rumex crispus* L.
- *Rumex hydrolapathum* Huds.
- *Rumex lunaria* L. (endemic to the Canary Islands)
- *Rumex maderensis* Lowe (endemic to the Canary Islands)
- *Rumex nivalis* Hegetschw.
- *Rumex obtusifolius* L.
- *Rumex scutatus* L.
- *Rumex thyrsiflorus* Fingerh.
- *Rumex uthaensis* Rech. f. (endemic to North America)
- *Rumex vesicarius* L. (endemic to the Canary Islands)

Subfamily Polygonoideae, tribe Persicariae
- *Fagopyrum esculentum* Moench
- *Fagopyrum tataricum* (L.) Gaertn.

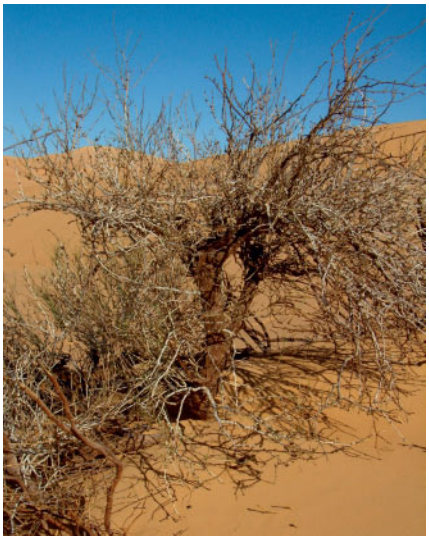
*Polygonum viviparum* (photo: Zinnert)

*Oxyria digyna*



*Polygonum bistorta*

*Fagopyrum esculentum* (photo: Zinnert)



*Calligonum azel*

*Calligonum comosum*

*Rumex alpinus*

*Polygonum amphibium*

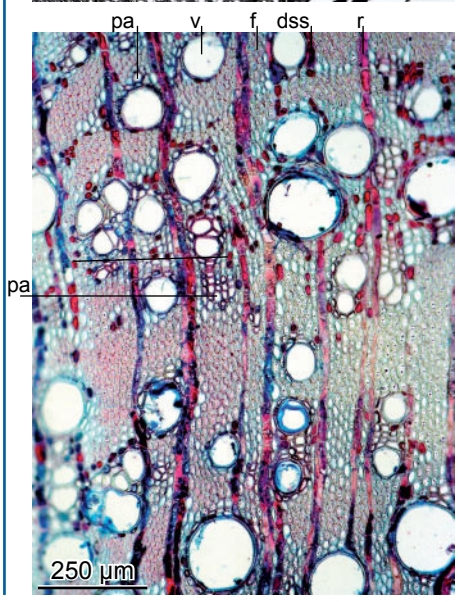
**Characteristics of the xylem**

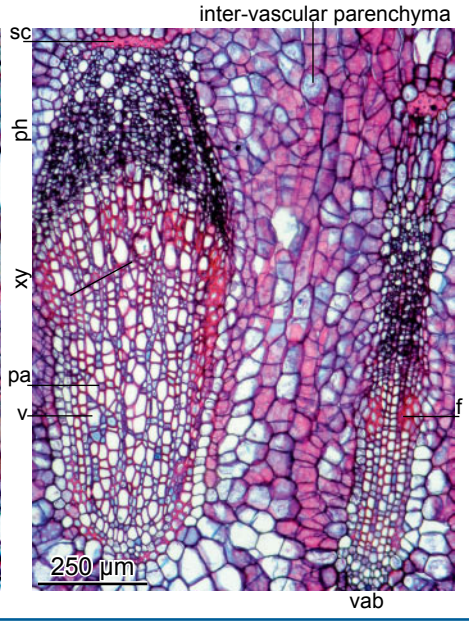
Annual rings occur in the present material in most perennial species of all vegetation zones. Ring boundaries of most species are defined by semi-ring porosity (16 out of 34 species) or diffuse porosity (**Figs. 1** and **2**). Only the two *Calligonum* species are ring-porous (**Fig. 3**). Rings are indistinct or absent in the bulbs of *Polygonum bistorta* (**Fig. 4**) and *P. viviparum* (**Fig. 5**), and indistinct in the rhizome of *Rumex acetosa* and the stem of *Oxyria digyna* (**Fig. 12**). Vessels are solitary or arranged in short radial multiples (2-4 vessels; **Figs. 6** and **7**) or groups (**Figs. 10** and **13**). Vessels of 7 species of the genera *Eriogonum* and *Polygonum* are arranged in tangential rows (**Fig. 7**). Vessel diameter varies greatly. Vessels are smaller than 20 µm in the bulb of the tiny alpine herb *Polygonum viviparum* (**Fig. 5**). The earlywood vessel diameter of the majority of species varies between 30-60 µm (e.g. **Fig. 1**). Diameter exceeds 100 µm in *Calligonum*, *Reynoutria* and *Fallopia convolvulus*. Vessel density varies in the majority of the analyzed species between 200-500/mm$^2$ (**Fig. 1**). It is lower only in *Calligonum* and *Reynoutria* (<100; **Fig. 3**) and it is very high in many subalpine species (**Figs. 1** and **12**). Vessels contain exclusively simple perforations (**Fig. 8**). Intervessel pits are predominantly small and round (**Fig. 8**). Pits can be slightly scalariform at the axial ends of perforations, e.g. in some *Eriogonum* and *Polygonum* species. Vestured pits are clearly visible with the light microscope on material stained only with safranin. They were observed on *Rumex lunaria* and *R. scutatus*.

13 species of several genera contain dark-staining substances in the center of the stem (heartwood; **Fig. 9**). *Polygonum polystachyum* produces small thin-walled, unlignified tylosis (**Fig. 10**). The radial walls of fibers in all species are perforated by very small slit-like or round pits (<2 µm). Septate fibers were found only in *Reynoutria japonica* (**Fig. 11**). Fibers are in the majority of analyzed species thin- or thin- to thick-walled (36 species; **Figs. 6** and **10**). They are thick-walled in both species

**Left Fig. 1.** Twenty distinct rings in a fluted stem of a semi-ring-porous wood. Stem of a 30 cm-long, slightly creeping chamaephyte, meadow, mountain zone, Colorado, USA. *Eriogonum jamesii*, transverse section.

**Right Fig. 2.** Stem with indistinct rings and large rays with thin-walled cells. Vessels are solitary or are in short radial groups. Stem of a 1 m-high shrub on volcanic rocks, thermophile zone, Gomera, Canary Islands. *Rumex lunaria*, transverse section.




**Left Fig. 3.** Ring-porous with distinct rings. Vessels with a diameter >100 µm are surrounded by paratracheal parenchyma. Fibers are thick-walled. Stem of a 1.5 m-high shrub on dunes, arid zone, Oman. *Calligonum comosum*, transverse section.

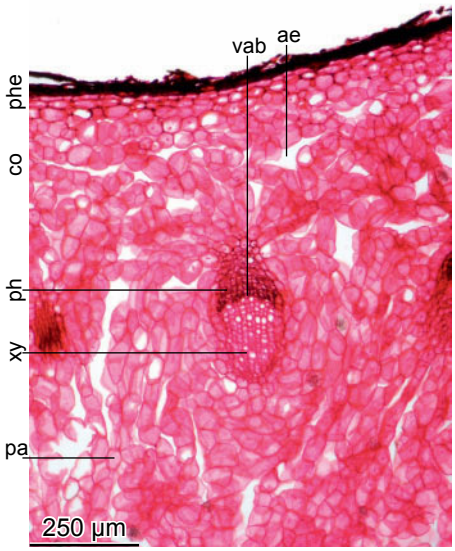
**Right Fig. 4.** Vascular bundle with two indistinct rings. Vessels are surrounded by pervasive parenchyma. A few fibers are located on the lateral sides of the bundles. Between the bundles are very large primary rays. Bulb of a 40 cm-high hemicryptophyte, moist meadow, mountain zone, Switzerland. *Polygonum bistorta*, transverse section.

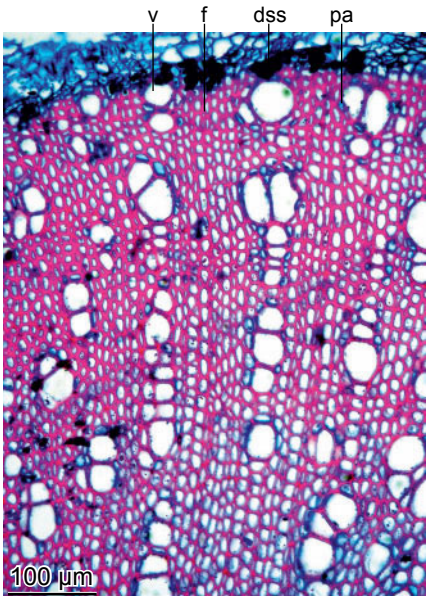
of *Calligonum* (**Fig. 3**). Fibers are missing in two alpine species (*Oxyria digyna*, *Rumex nivalis*; **Fig. 12**). The distribution of axial parenchyma is often difficult to determine, especially on slides stained only with safranin. There is a predominance of paratracheal parenchyma (28 species; **Figs. 6** and **10**), but apotracheal parenchyma was also found in 6 species (*Calligonum*, 3 *Eriogonum* species and 1 *Rumex* species). Pervasive parenchyma is characteristic of 12 of the 15 analysed *Rumex* (**Fig. 13**) species and *Oxyria digyna* (**Fig. 12**) and one *Eriogonum* species (**Fig. 14**). In some *Rumex* species and in *Eriogonum longifolium*, parenchyma cells form a marginal band (**Fig. 15**). Axial parenchyma cells and fibers are storied only in *Calligonum* (**Fig. 16**).

Ray diversity is high. Rays are absent in *Eriogonum jamesii*, *Polygonum mite* and *P. minus*, as well as in both *Fallopia* species (**Fig. 17**). Four *Eriogonum* species have uniseriate rays. Ten species of different genera have rays 1-3 cells in width (**Fig. 16**) and 22 species have rays 3-10 cells in width (**Figs. 2** and **18**). The primary vascular bundle form is found in 19 species (**Figs. 4**, **5**, **12**, **13** and **22**). In such cases ray width exceeds 10 cells. Ray cells are square or upright in most species (**Fig. 20**). Procumbent ray cells were observed only in *Calligonum*, *Eriogonum ovalifolium* and *E. pyrifolium*.

Included phloem was mentioned by Pfeiffer (1926) for *Rumex crispus* and *R. obtusifolius*. The present material does not have such inclusions. We found it only in the North American species *Polygonum bistortoides* (**Fig. 21**). This species is also unique in having medullary vascular bundles (**Fig. 22**).

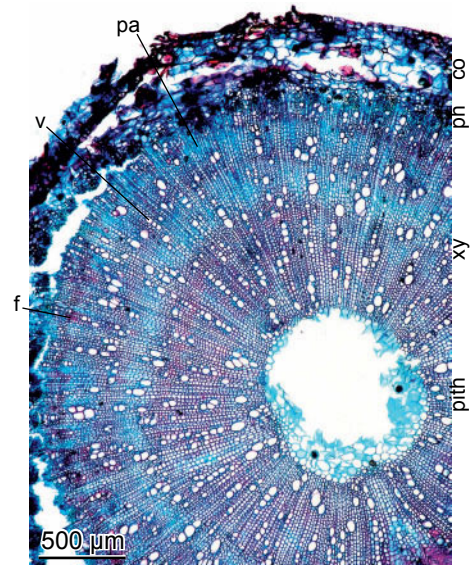
Crystals are rare. Druses are present in the parenchymatic cells of *Calligonum*, *Rumex acetosa*, *R. acetosella*, in *Fagopyrum* and *Polygonum hydropiper*.

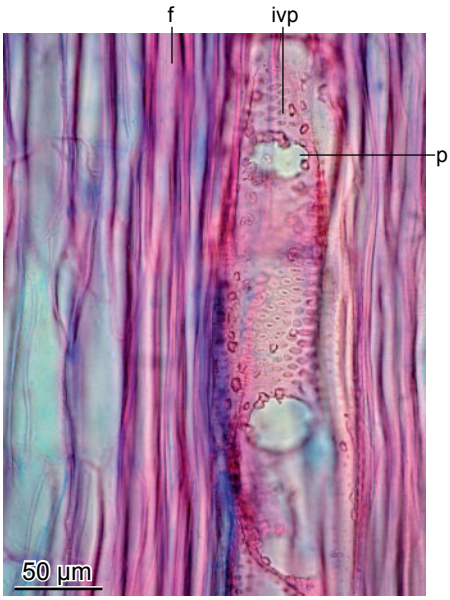



**Left Fig. 5.** Vascular bundle of a perennial plant without rings. Vessel diameter is <20 µm. The small bundles are embedded in an aerenchyma-like parenchymatic tissue. Bulb of an 8 cm-high geophyte, alpine zone, Switzerland. *Polygonum viviparum*, transverse section.

**Right Fig. 6.** Vessels in radial multiples are surrounded by paratracheal parenchyma. The fibers are thin- to thick-walled. Rays are absent. Root collar of an annual plant (therophyte), ruderal site, hill zone, Switzerland. *Polygonum mite*, transverse section.



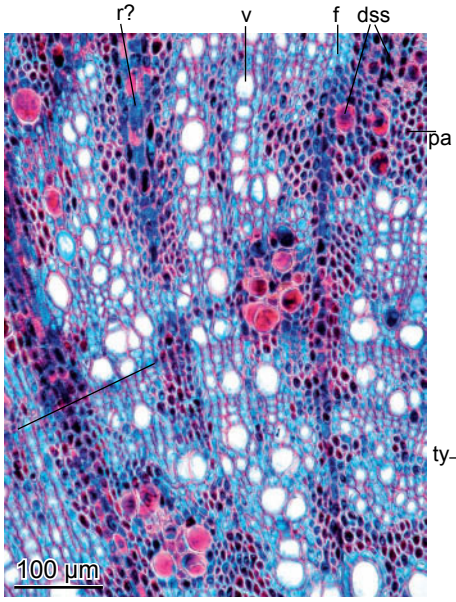

**Left Fig. 7.** Vessels in radial multiples arranged in tangential rows. Lignification of fibers runs parallel to the tangential vessel bands. Root collar of an annual plant (therophyte), ruderal site, hill zone, Switzerland. *Fagopyrum esculentum*, transverse section.

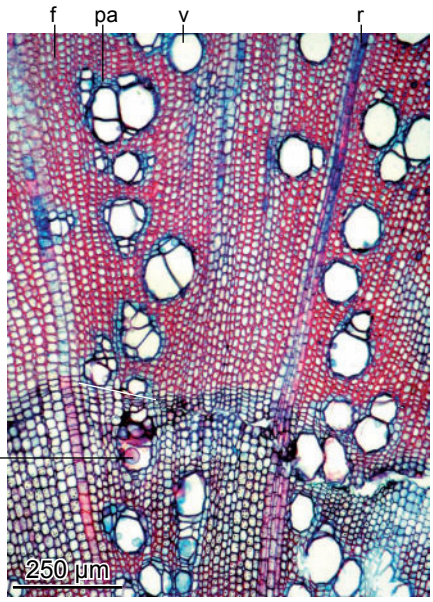
**Right Fig. 8.** Vessels with simple perforations and small, round-bordered pits. Root collar of an annual plant (therophyte), ruderal site, hill zone, Switzerland. *Fagopyrum tataricum*, radial section.

**Characteristic features of taxa**

Some features characterize single species or groups of species: Relatively high plant ages are typical of some *Eriogonum* species (*Eriogonum jamesii* 38 years, **Fig. 1**). The age of all species in other genera varies from 1-9 years.

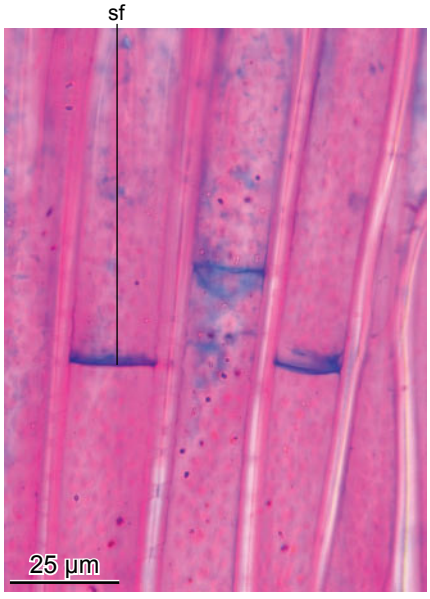
The absence of annuals (therophytes) is typical for the genera *Calligonum*, *Eriogonum*, *Oxyria* and *Reynoutria*. *Calligonum comosum* and *C. crinitum* are distingushed from all other species in the family of Polygonaceae by their ring-porosity (**Fig. 2**), storied fibers and parenchyma cells, very thick-walled fibers and tangential strands of sclereids in the bark. Dark-staining substances are missing in the genera *Polygonum*, *Fagopyrum* and *Fallopia*. Tangential rows of vessels are typical for most annual *Polygonum* and *Fagopyrum* species (**Fig. 7**). Fibers are absent in the alpine species *Oxyria digyna* and *Rumex nivalis* (**Fig. 12**). Septate fibers were found only in *Reynoutria japonica* (**Fig. 11**). Pervasive parenchyma is concentrated in the genus *Rumex* (**Fig. 13**). It also occurs in *Oxyria digyna* and in a different form in the alpine American species *Eriogonum fendlerianum* (**Fig. 14**). Interxylary phloem is present only in the American species *Polygonum bistortoides* (**Fig. 22**). Aerenchyma exists only in the genera *Polygonum* and *Rumex*.

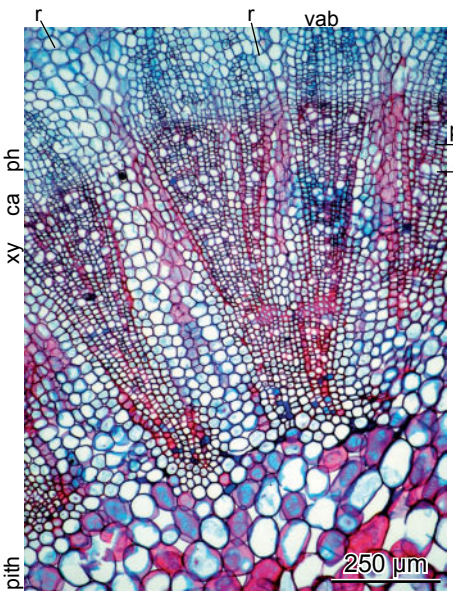



**Left Fig. 9.** Red-staining substances in vessels and parenchyma cells. Root collar of a chamaephyte, volcanic rock, subalpine zone, Washington DC, USA. *Eriogonum ovalifolium*, transverse section.

**Right Fig. 10.** Vessels in small groups with paratracheal parenchyma. Vessels in the lower part of the picture have thin-walled, unlignified tylosis. The ring boundary is marked by a marginal band of parenchyma cells. Root collar of a 1 m-high hemicryptophyte, ruderal site, hill zone, Switzerland. *Polygonum polystachyum*, transverse section.



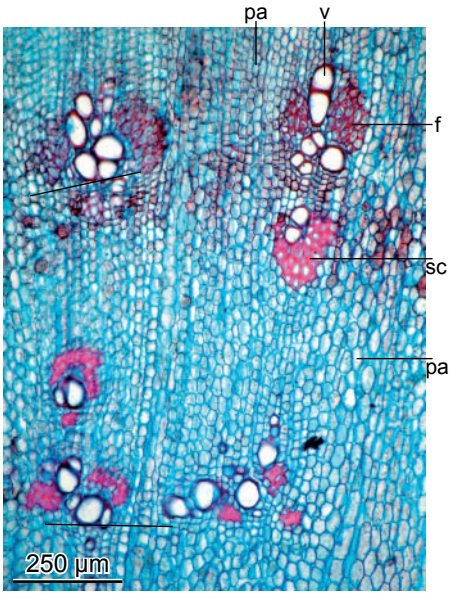




**Fig. 11.** Xylem with septate fibers. The horizontal walls are unlignified. Rhizome of a 1 m-high hemicryptophyte, ruderal site, hill zone, Switzerland. *Reynoutria japonica*, radial section.

**Fig. 12.** Vascular bundles with indistinct rings. Small vessels (20 µm) are surrounded by pervasive parenchyma. Root collar of a 8 cm-high, hemicryptophyte, snow bed, alpine zone, Switzerland. *Oxyria digyna*, transverse section.

**Fig. 13.** Groups of vessels, surrounded by axial parenchyma and fibers, are embedded in an extensive thin-walled parenchyma. 4 cm-thick, fleshy root collar of a 1 m-high hemicryptophyte, moist meadow, mountain zone, Alps, France. *Rumex hydrolapathum*, transverse section.

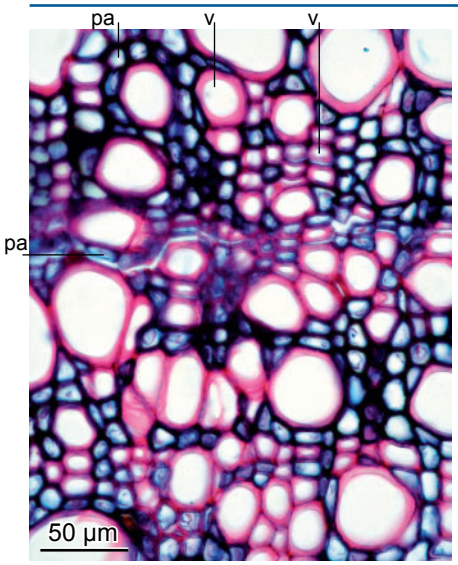



**Fig. 14.** Thick-walled vessels are surrounded by a pervasive parenchyma. Root collar of a 10 cm-high, approx. 20-year-old chamaephyte, dry meadow at lower timberline, Colorado, USA. *Eriogonum fendlerianum*, transverse section.

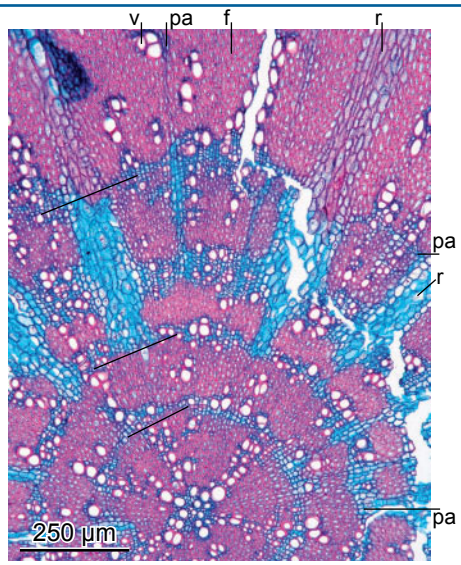



**Fig. 15.** Marginal parenchyma in the latewood of a 5-year-old herb. Vessel density is below 200/mm$^2$. Root collar of a 10 cm-high hemicryptophyte, dry ruderal site, hill zone, Alps, France. *Rumex acetosella* ssp. *angiocarpus*, transverse section.

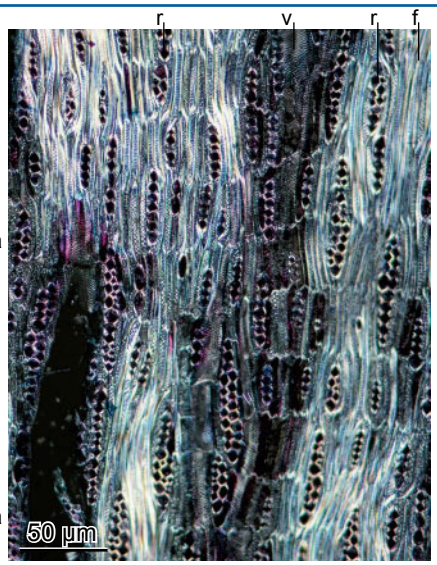
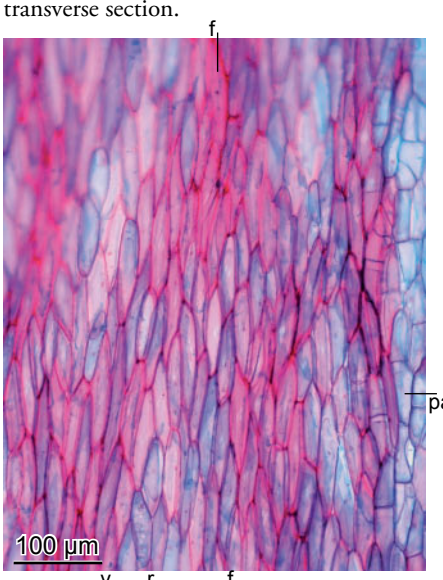
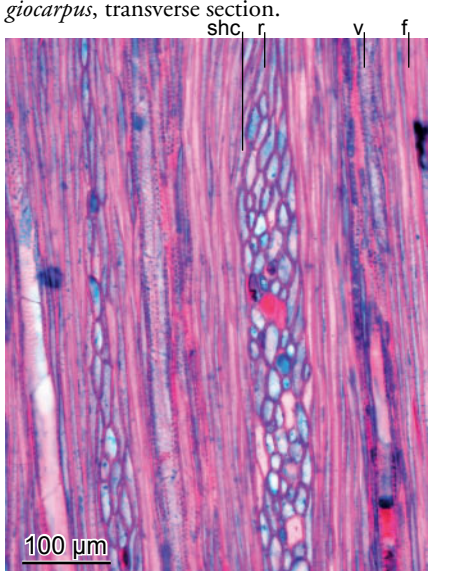


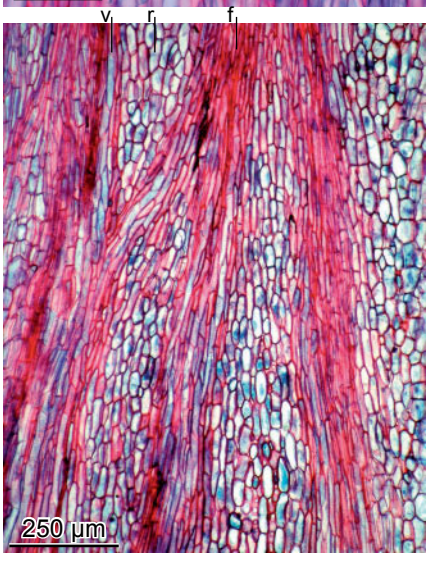

**Fig. 16.** Storied fibers and axial parenchyma cells in the xylem. Rays are 1-2 cells wide. Stem of a 1.5 m-high shrub on dunes, arid zone, Oman. *Calligonum comosum*, tangential section, polarized light.

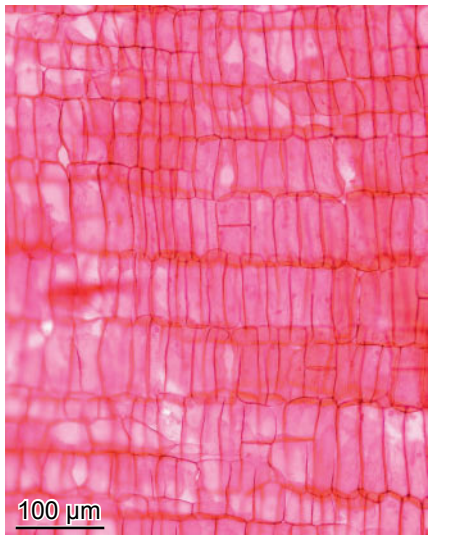



**Left Fig. 17.** Rayless xylem. Length of the axial fiber cells is approximately 100 µm. Stem of a 30 cm-long slightly creeping chamaephyte, meadow, mountain zone, Colorado, USA. *Eriogonum jamesii*, tangential section.

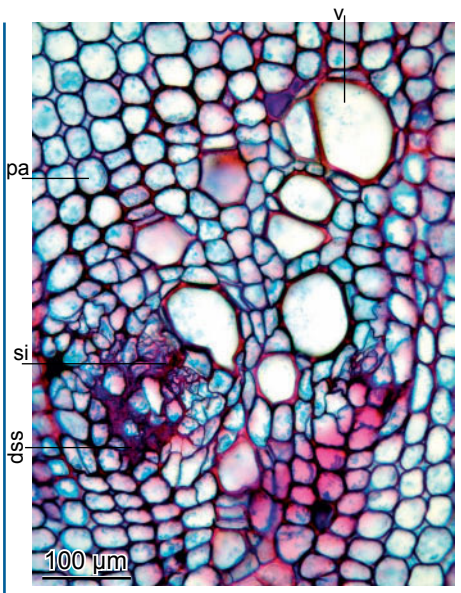
**Right Fig. 18.** Ray width 2-5 cells. Sheet cells are indistinct. Root collar of a 20 cm-high hemicryptophyte, sea shore, Astoria, Oregon, USA. *Polygonum paronychia*, tangential section.

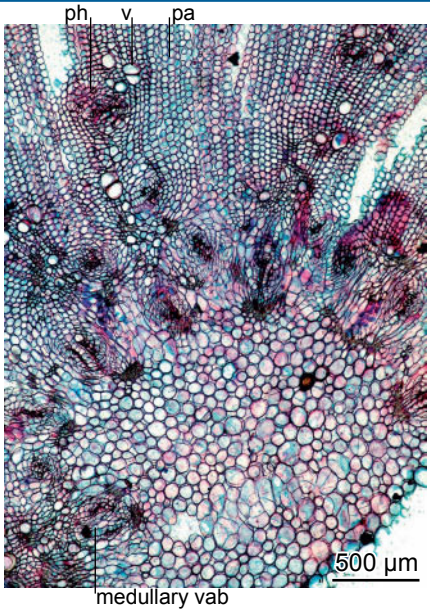



**Left Fig. 19.** Very large rays (>10 cells) with thin cell walls. Rays are often not properly delimitated from the vessel/fiber tissue. The rays represent primary parenchymatic tissue beween vascular bundles (see **Fig. 12**). Stem of an 8 cm-high hemicryptophyte, snow bed, alpine zone, Switzerland. *Oxyria digyna*, tangential section.

**Right Fig. 20.** Rays with exclusively upright cells. Root collar of a chamaephyte, limestone rock field, hill zone, Alps, Italy. *Rumex scutatus*, radial section.




**Left Fig. 21.** Groups of included sieve tubes near vessels (included phloem) in the xylem. Sieve-cell groups exist only in the center of the stem. 2 cm-thick, fleshy rhizome of a hemicryptophytic herb. Meadow, subalpine zone, Colorado, USA. *Polygonum bistortoides*, transverse section.

**Right Fig. 22.** Medullary vascular bundle at the periphery of the pith. 2 cm-thick, fleshy rhizome of a hemicryptophytic herb. Meadow, subalpine zone, Colorado, USA. *Polygonum bistortoides*, transverse section.

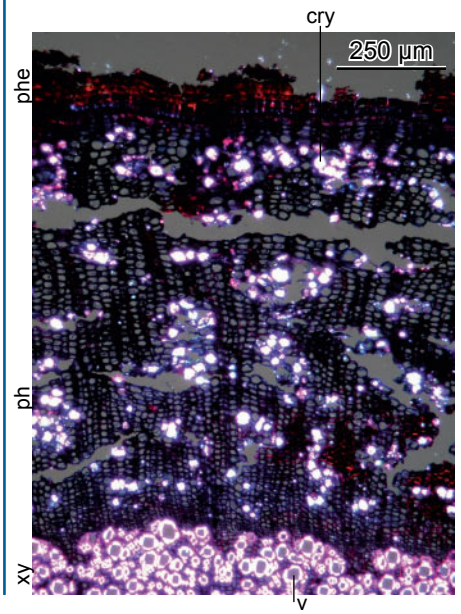
### Ecological trends and relations to life forms

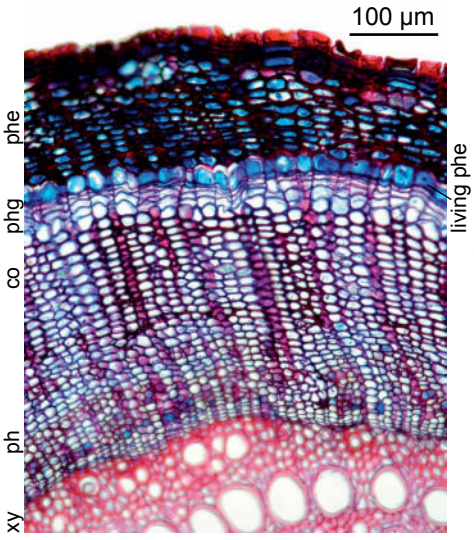
Ecological trends were found in vessel frequency and to some extent in vessel diameter. High numbers (>200/mm$^2$) and small vessels (approximately 15-25 µm) occur mainly in species growing in the subalpine and alpine zones while species in the hill zone of the temperate zone and in subtropical climates have larger and fewer vessels.

The large earlywood vessel diameters (often >100 µm) are characteristic of the annual shoots of the lianas *Fallopia convolvulus* (**Fig. 30**) and *F. dumetorum*, and of the desert shrub *Calligonum* (**Fig. 3**). Annual species and shrubs contain no pervasive parenchyma.

### Characteristics of the phloem and the cortex

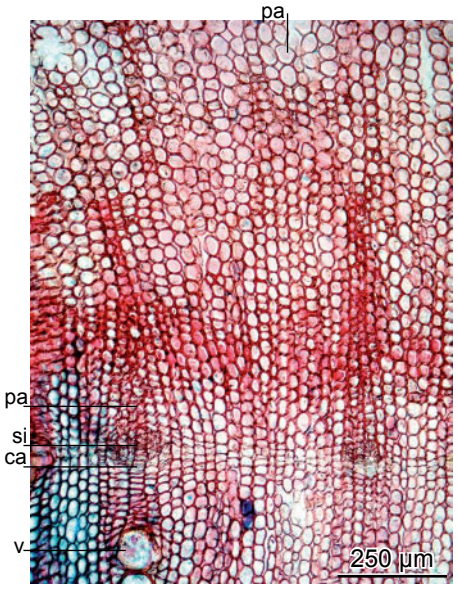
The anatomy of the bark of the Polygonaceae is very heterogeneous. Characteristic of most species is the presence of crystal druses (**Figs. 23**, **29** and **30**). They are absent in only a few *Polygonum* and *Rumex* species. The presence of silica bodies in *Eriogonum jamesii* is unique. The phloem and the cortex are simply structured in most *Eriogonum* species (**Figs. 24** and **25**). Distinct groups of sieve tubes are present sporadically in all generea (**Figs. 26-28**) except *Calligonum*. Sclereids also occur sporadically in all genera. They are clustered in small groups (*Rumex hydrolapathum*, *Reynoutria japonica*, *Fallopia convolvulus* (**Figs. 28-30**), in radially oriented groups (*Rumex acetosella*; **Fig. 31**), or in dense tangentially oriented strands such as those found in *Calligonum* (**Fig. 32**). 23 species have ray dilatations (**Figs. 27-29** and **31**). The presence of aerenchyma is special in *Rumex conglomeratus*, *R. obtusifolius*, *R. thyrsiflorus*, *R. alpinus*, *Polygonum bistorta* and *P. viviparum* (**Figs. 5** and **29**).

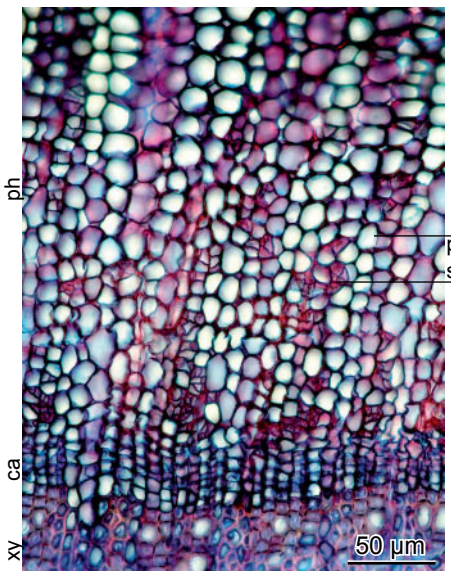



**Left Fig. 23.** Irregularly distributed crystal druses in the phloem and the cortex. Root collar of a 10 cm-high, approximately 20-year-old chamaephyte, dry meadow at lower timberline, Colorado, USA. *Eriogonum fendlerianum*, transverse section, polarized light.

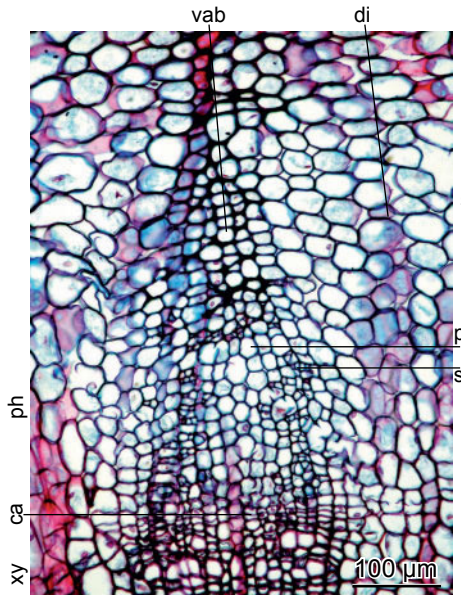
**Right Fig. 24.** Simple phloem anatomy. Parenchyma and sieve tubes cannot be distinguished. Sclereids are absent. The younger and the older bark are divided by a few rows of thin-walled phellogen cells and a row of large, living phellem cells. Stem of a 30 cm-long, slightly creeping chamaephyte, meadow, mountain zone, Colorado, USA. *Eriogonum jamesii*, transverse section.

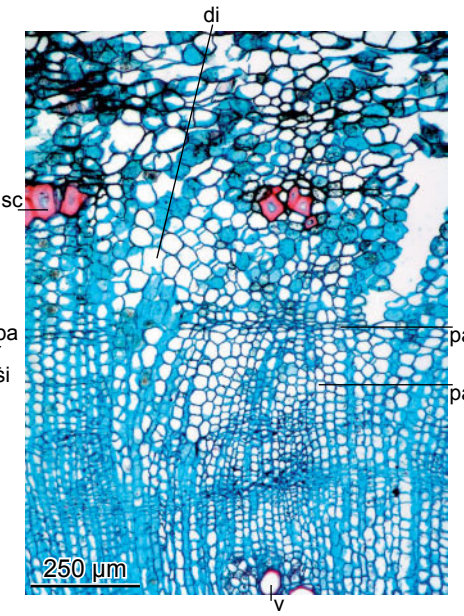



**Left Fig. 25.** Simple phloem anatomy. Parenchyma and sieve tubes are only recognizable in the continuation of the vessel/fiber strips of the xylem. 2 cm-thick, fleshy rhizome of 40 cm-high hemicryptophyte, meadow, subalpine zone, Colorado, USA. *Polygonum bistortoides*, transverse section.

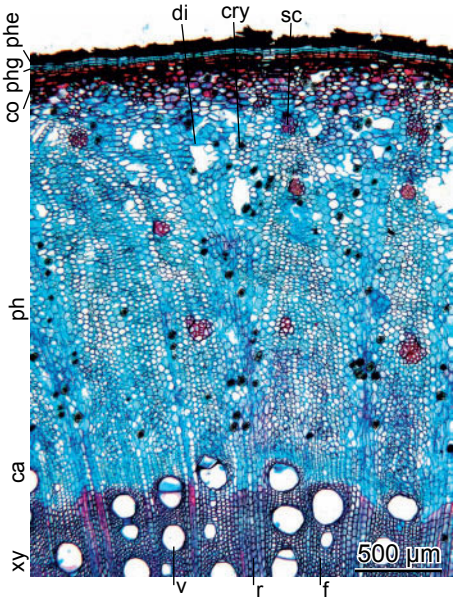
**Right Fig. 26.** Phloem with small sieve-cell groups. Sclereids are absent. Root collar of a chamaephyte, steppe, arid zone, Utah, USA. *Eriogonum inflatum*, transverse section.

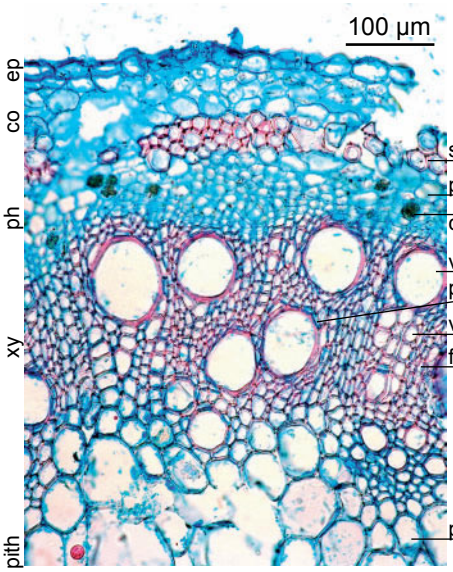



**Left Fig. 27.** Simple phloem anatomy. Small sieve-cell groups fit in the radial rows of parenchyma cells. Sclereids are absent. Ray dilatations divide the parenchyma/sieve-tube strips laterally. Root collar of an 8 cm-high hemicryptophyte, snow bed, alpine zone, Switzerland. *Oxyria digyna*, transverse section.

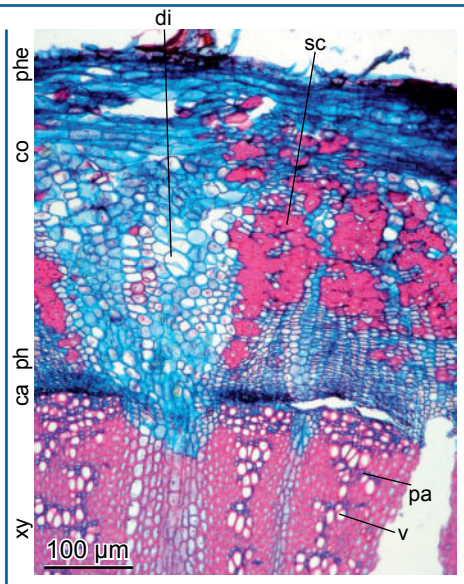
**Right Fig. 28.** A few sclereids are located in the border zone of the phloem and the cortex. Annual phloem layers are indicated by small, radially flat parenchyma cells. 4 cm-thick, fleshy root collar of a 1 m-high hemicryptophyte, moist meadow, mountain zone, Alps, France. *Rumex hydrolapathum*, transverse section.

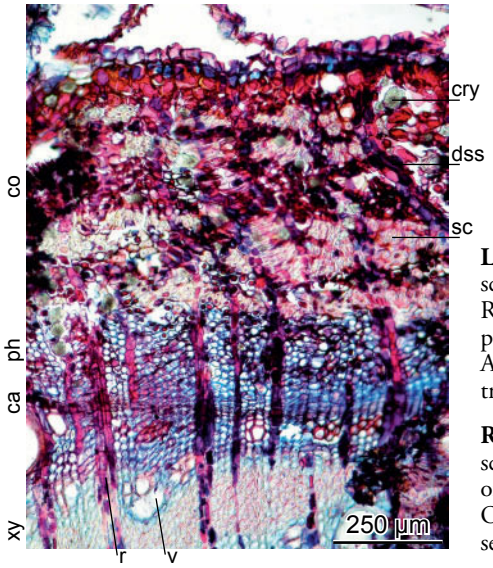



**Left Fig. 29.** Small groups of sclereids occur throughout the phloem. Crystal druses (black dots) are mainly in indistinct dilated rays. The outer part of the cortex is aerenchyma-like. Rhizome of a 1.5 m-high hemicryptophyte, ruderal site, hill zone, Switzerland. *Reynoutria japonica*, transverse section.

**Right Fig. 30.** Group of sclereids and crystal druses in the thin, not well structured bark. The large vessels in the xylem are characteristic of the species. 2 m-long, liana-like annual shoot, ruderal site, hill zone, Switzerland. *Fallopia convolvulus*, transverse section.




**Left Fig. 31.** Radially oriented groups of sclereids on both sides of a ray dilatation. Root collar of a 10 cm-high hemicryptophyte, dry ruderal site, hill zone, French Alps. *Rumex acetosella* ssp. *angiocarpus*, transverse section.

**Right Fig. 32.** Thick-walled strands of sclereids outside the living phloem. Stem of a 1.5 m-high shrub on dunes, arid zone, Oman. *Calligonum comosum*, transverse section.

**Discussion in relation to previous studies**

The only comprehensive wood anatomical study to date was performed by Carlquist (2003) on the basis of 30 woody species. Datta and Deb (1968) characterize the xylem of six *Rumex* species occuring in India. Pfeiffer (1926) describes two herbaceous species with interxylary phloem (*Rumex*) and successive cambia (*Antigonum leptopus*). Metcalfe and Chalk (1957) mention 10 genera, but the text is very condensed. Many authors have characterized just a few woody species (Gregory 1994). Comparable with the present study are *Calligonum comosum* (Neumann et al. 2001, Carlquist 2003 and Ma et al. 1994), *Rumex lunaria* (Carlquist 2003), *Rumex vesicarius* (Datta and Deb 1968) and *Polygonum equisetiforme* (Schweingruber 1990).

Most previous authors concentrated on the xylem of shrubs and dwarf shrubs. This study includes several growth forms of annual and perennial herbaceous species of different vegetation zones. Carlquist (2003) and the present analysis demonstrate the wide anatomical spectrum. All species have simple perforations but the distribution, diameter and frequency of vessels, the presence and absence of thin- and thick-walled fibers indicate the heterogeneity within the family. The material is not sufficient for a classification within the family.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **41** |
| 1 | growth rings distinct and recognizable | 31 |
| 2 | growth rings absent | 3 |
| 2.1 | only one ring | 7 |
| 3 | ring-porous | 2 |
| 4 | semi-ring-porous | 17 |
| 5 | diffuse-porous | 14 |
| 6 | vessels in intra-annual tangential rows | 5 |
| 9 | vessels predominantly solitary | 25 |
| 9.1 | vessels in radial multiples of 2-4 common | 24 |
| 10 | vessels in radial multiples of 4 or more common | 3 |
| 11 | vessels predominantly in clusters | 11 |
| 13 | vessels with simple perforation plates | 41 |
| 20 | intervessel pits scalariform | 6 |
| 29 | vestured pits | 2 |
| 39.1 | vessel cell-wall thickness >2 µm | 1 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 33 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 6 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 5 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 17 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 24 |
| 56 | tylosis with thin walls | 1 |
| 58 | dark-staining substances in vessels and/or fibers | 13 |
| 60.1 | fibers absent | 1 |
| 61 | fiber-pits small (<3 µm = libriform fibers) | 39 |
| 65 | septate fibers present | 1 |
| 68 | fibers thin-walled | 14 |
| 69 | fibers thick-walled | 2 |
| 70 | fibers thin- to thick-walled | 25 |
| 75 | parenchyma absent or unrecognizable | 2 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 5 |
| 79 | parenchyma paratracheal | 28 |
| 79.1 | parenchyma pervasive | 14 |
| 89 | parenchyma marginal | 4 |
| 96 | rays uniseriate | 4 |
| 97 | ray width predominantly 1-3 cells | 11 |
| 98 | rays commonly 4-10-seriate | 10 |
| 99 | rays commonly >10-seriate | 13 |
| 99.1 | vascular-bundle form remaining | 19 |
| 99.2 | stem lobed | 1 |
| 104 | ray: all cells procumbent (radial section) | 4 |
| 105 | ray: all cells upright or square | 28 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 4 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 1 |
| 110 | rays with sheet cells (tangential section) | 1 |
| 117 | rayless | 5 |
| 120 | storied axial tissue (parenchyma, fibers, vessels, tang. section) | 2 |
| 135 | interxylary phloem present | 1 |
| R1 | groups of sieve tubes present | 19 |
| R3 | distinct ray dilatations | 23 |
| R4 | sclereids in phloem and cortex | 24 |
| R6 | sclereids in radial rows | 2 |
| R7.1 | with acicular crystals | 2 |
| R8 | with crystal druses | 29 |
| R9 | with crystal sand | 1 |
| R10 | phloem not well structured | 7 |
| R13 | tannins in parenchyma cells | 2 |
| R14 | cortex with aerenchyma | 6 |
| P1 | with medullary phloem or vascular bundles | 1 |

# Portulacaceae

**Number of species, worldwide and in Europe**

The cosmopolitan Portulacaceae family includes 29 genera with 450 species. Many species occur in Western North America. In Europe there are 2 herbaceous genera (*Portulaca* and *Montia*) with 4 species.

**Analyzed species:**

*Cistanthe salsoloides* (Barnéod) Carolin ex Hersk.
*Claytonia megarhiza* Kuntze
*Portulaca oleracea* L.

**Analyzed material**

The xylem and phloem of 3 Portulacaceae species were analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes 0.5-4 m | | 16 |
| Woody chamaephytes | 1 | |
| Hemicryptophytes and geophytes | 2 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 1 | |
| Hill and mountain | 2 | |

**Right:** *Portulaca orientalis*

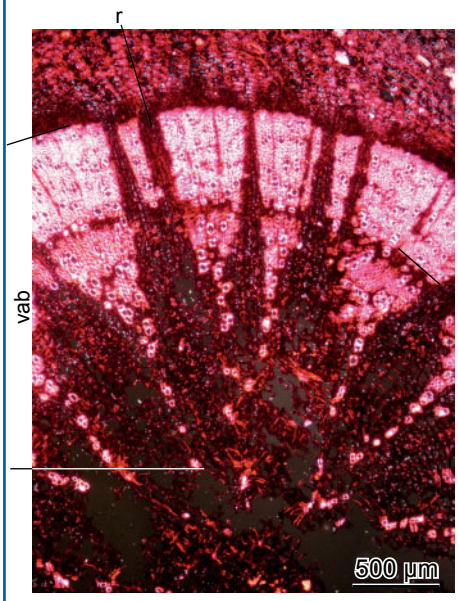
*Portulaca oleracea*

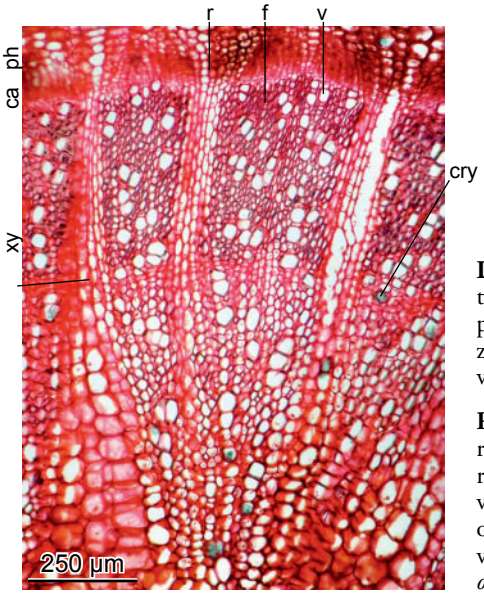
### Characteristics of the xylem

The anatomy varies greatly in the limited material available. Annual rings are distinct (**Figs. 1-3**) or indistinct (**Fig. 4**) in perennial plants. The xylem is diffuse (**Fig. 2**) or semi-ring-porous (**Fig. 3**). Vessels are small, arranged in small groups or in radial multiples (**Fig. 3**). Perforations are simple. Inter-vessel pits are scalariform to reticulate (*Claytonia*; **Fig. 5**). Carlquist (2001) mentions similar types in *Anacampseros marlothii*. Inter-vessel pits are small and round in *Portulaca* and *Cistanthe*. Fibers are absent in *Claytonia* and thin- to thick-walled in the other species. Parenchyma is pervasive in *Claytonia* (**Fig. 4**), paratracheal in *Portulaca* and paratracheal and marginal in *Cistanthe* (**Fig. 3**). Rays are absent in *Claytonia*, 1-3-seriate in *Cistanthe salsoloides* (**Fig. 6**) and 5-8-seriate in *Portulaca oleracea* (**Fig. 7**). Crystals are absent in *Claytonia*. A few vessels of *Portulaca* and *Cistanthe* contain crystal druses, composed of large prismatic crystals.

### Characteristics of the phloem

The anatomy of the bark of the Portulacaceae is also very heterogeneous. See legends to **Figs. 8** and **9**.




**Left Fig. 1.** Biannual plant with two distinct rings. Root collar of a 20 cm-high prostrate hemicryptophyte, vineyard, hill zone, Switzerland. *Portulaca oleracea*, transverse section, polarized light.

**Right Fig. 2.** Diffuse-porous xylem. The ring boundary is defined by a few rows of radial flat parenchyma cells. Grey spots in vessels represent crystal druses. Root collar of a 20 cm-high prostrate hemicryptophyte, vineyard, hill zone, Switzerland. *Portulaca oleracea*, transverse section, polarized light.

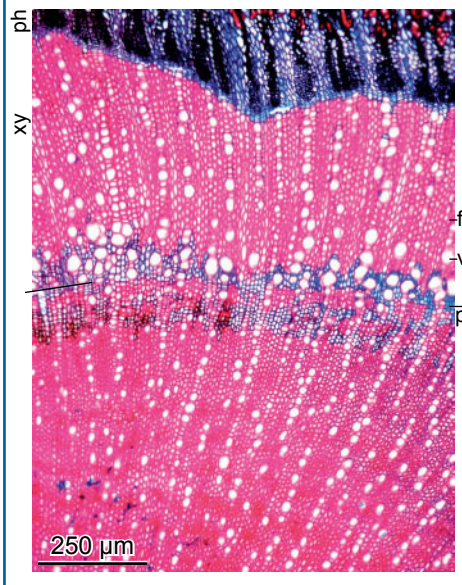



**Fig. 3.** Semi-ring-porous xylem with distinct marginal parenchyma in the earlywood and the latewood. Vessels are arranged in radial rows. Fibers are fairly thick-walled. Root collar of a 20 cm-high dwarf shrub, on a rock, hyperarid, Athacama desert, Chile. *Cistanthe salsoloides*, transverse section.

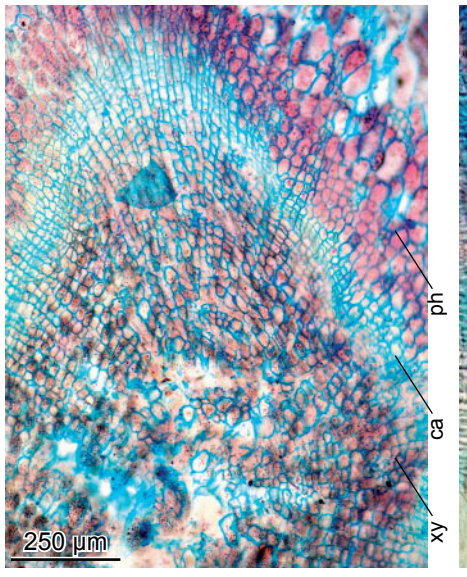



**Fig. 4.** Simple structure of the rayless xylem and phloem. Vessels and parenchyma cells have almost the same diameter. The parenchyma seems to be pervasive. Thick vertical rhizome of a 10 cm-high hemicryptophyte, meadow, alpine zone, Colorado, USA. *Claytonia megarhiza*, transverse section.

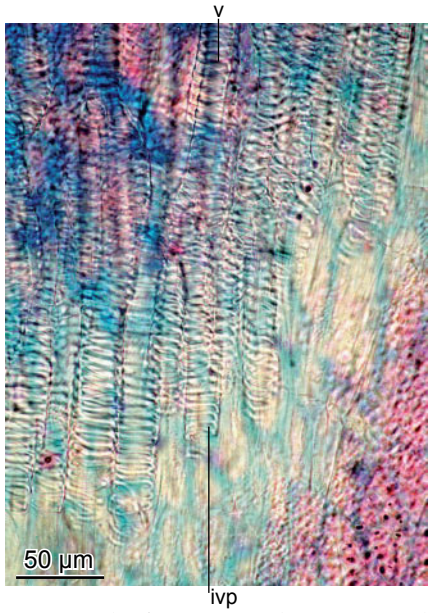
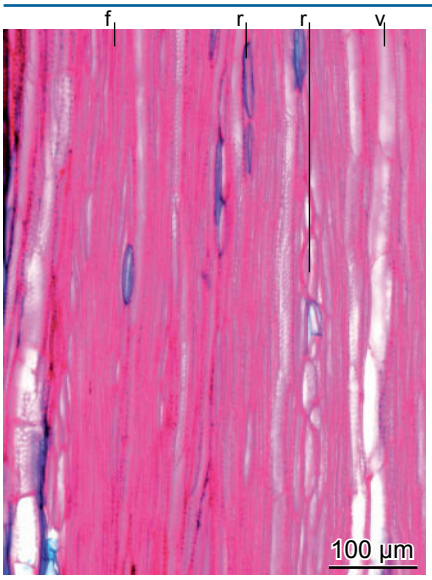
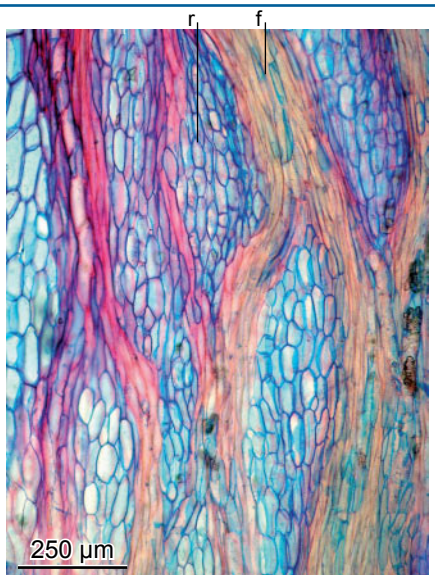


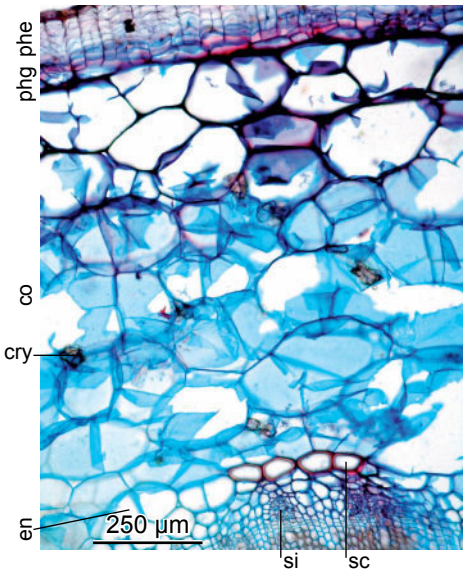

**Fig. 5.** Scalariform to reticulate inter-vessel pits. Thick vertical rhizome of a10 cm-high hemicryptophyte, meadow, alpine zone, Colorado, USA. *Claytonia megarhiza*, radial section.

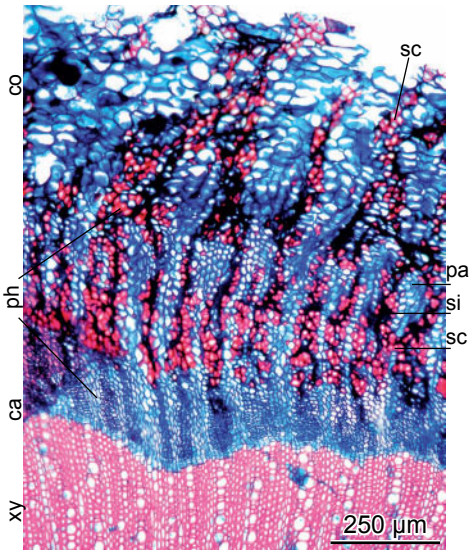



**Left Fig. 6.** 1-3-seriate rays. Some uniseriate rays are unlignified (blue). Root collar of a 20 cm-high dwarf shrub, on rock, hyperarid, Athacama desert, Chile. *Cistanthe salsoloides*, tangential section.

**Right Fig. 7.** 4-8-seriate rays. The ray cells are partially irregularly formed and their walls are unlignified. Root collar of a 20 cm-high prostrate hemicryptophyte, vineyard, hill zone, Switzerland. *Portulaca oleracea*, tangential section.




**Left Fig. 8.** A small phloem with a unicellular external border of lignified sclerenchyma cells is in contact with the xylem. The lateral discontinuous phloem is embedded in the primary bark, which consists of large water storing parenchyma cells. Characteristic is the presence of some crystal druses. Root collar of a 20 cm-high prostrate hemicryptophyte, vineyard, hill zone, Switzerland. *Portulaca oleracea*, transverse section.

**Right Fig. 9.** Phloem with radial groups of sclereids and compressed sieve tubes (dark) between parenchyma cells. Root collar of a 20 cm-high dwarf shrub, on rock, hyperarid, Athacama desert, Chile. *Cistanthe salsoloides*, tangential section.

## Discussion in relation to previous studies

Prabhakar and Ramayya (1979) described the xylem of the Indian woody genera *Portulaca* and *Talinum*. Carlquist (1998) studied 16 woody species (*Anacampseros*, *Calyptrotheca*, *Cerasia*, *Cistanthe*, *Lewisia*, *Petiveria*, *Portulacaria*, *Rivinia*, *Stegnosperma*, *Talinella*, *Talinopsis*, *Talinum*). Carlquist (2000) and the present study demonstrate the intra-familial heterogeneity, especially with the inclusion of herbaceous species. *Portulaca oleracea* and *Claytonia* sp. have not been described before.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **3** |
| 1 | growth rings distinct and recognizable | 2 |
| 2 | growth rings absent | 1 |
| 4 | semi-ring-porous | 1 |
| 5 | diffuse-porous | 1 |
| 9 | vessels predominantly solitary | 1 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 10 | vessels in radial multiples of 4 or more common | 1 |
| 13 | vessels with simple perforation plates | 3 |
| 20 | intervessel pits scalariform | 1 |
| 20.1 | intervessel pits pseudoscariform to reticulate | 1 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 2 |
| 50.2 | 200-1000 vessels per mm² in earlywood | 3 |
| 60.1 | fibers absent | 1 |
| 61 | fiber pits small (<3 µm = libriform fibers) | 2 |
| 69 | fibers thick-walled | 1 |
| 70 | fibers thin- to thick-walled | 1 |
| 79 | parenchyma paratracheal | 2 |
| 79.1 | parenchyma pervasive | 1 |
| 89.1 | parenchyma marginal thin walled, dark in polarized light | 1 |
| 97 | ray width predominantly 1-3 cells | 1 |
| 98 | rays commonly 4-10-seriate | 1 |
| 105 | ray: all cells upright or square | 2 |
| 117 | rayless | 1 |
| 136 | prismatic crystals present | 1 |
| 144 | druses present | 1 |
| R1 | groups of sieve tubes present | 2 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 2 |
| R6 | sclereids in radial rows | 1 |
| R10 | phloem not well structured | 1 |

# Primulaceae



**Number of species, worldwide and in Europe**

The northern hemispheric Primulaceae family includes 20 genera with 1000 species. In Europe, there are 14 genera with 98 species.

**Analyzed material**

The xylem and phloem of 9 genera with 30 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Hemicryptophytes | 26 | 1 |
| Therophytes | 2 | |
| Helophytes | 1 | |
| Hydrophytes | 1 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 19 | |
| Hill and mountain | 10 | |
| Mediterranean | 1 | |

**Analyzed species:**

*Anagallis arvensis* L.
*Anagallis foemina* Miller
*Anagallis monelli* L.
*Androsace alpina* (L.) Lam
*Androsace helvetica* (L.) All.
*Androsace lactea* L.
*Androsace obtusifolia* All.
*Androsace septentrionalis* L.
*Androsace villosa* L.
*Androsace vitaliana* (L.) Lapeyr
*Cyclamen purpurascens* Mill.
*Dionysia aretioides* Boiss.
*Hottonia palustris* L.
*Lysimachia nemorum* L.
*Lysimachia nummularium* L.
*Lysimachia punctata* L.
*Lysimachia thyrsiflora* L.
*Lysimachia vulgaris* L.
*Primula auricula* L.
*Primula elatior* (L.) L.
*Primula farinosa* L.
*Primula hirsuta* L.
*Primula integrifolia* L.
*Primula latifolia* L.
*Primula parry* Gray
*Primula veris* L.
*Primula woronowi* Losina-Losinks
*Samolus valerandi* L.
*Soldanella alpina* L.
*Soldanella pusilla* L.

*Primula farinosa* (photo: Landolt)

*Primula elatior* (photo: Zinnert)

*Anagallis arvensis*

*Lysimachia vulgaris* (photo: Zinnert)

*Androsace chamaejasme* (photo: Zinnert)

*Androsace helvetica*

*Androsace vitaliana* (photo: Landolt)

*Soldanella alpina* (photo: Landolt)

**Characteristics**

Common to all species are small vessel diameters, simple perforations, pervasive or absent parenchyma, and absent rays. Most species have scalariform intervessel pits. Hydrophytes and helophytes have an aerenchymatic cortex. The following groups exist within the family:

**Types without secondary growth**

Terrestrial plants: *Soldanella* sp. and *Primula* sp.

*Soldanella* sp.: A small xylem is surrounded by a small phloem and a large cortex. The pith is filled with sclerenchyma cells (**Fig. 1**). Intervessel pits are scalariform (**Fig. 2**). There is no phellem.

*Primula* sp.: Anastomosing concentric vascular bundles (**Figs. 3** and **4**) occupy a parenchymatic stem (**Figs. 5** and **6**) or surround a pith (**Fig. 7**). A few rows of rectangular cells form the phellem (**Fig. 8**).

Hydrophyte: *Hottonia palustris*

A central cylinder (**Fig. 9**) is surrounded by a large aerenchymatic parenchymatic tissue (**Fig. 10**). The central cylinder consists of vessels with scalariform intervessel pits and parenchyma cells (**Fig. 11**). There is no phellem (**Fig. 10**).

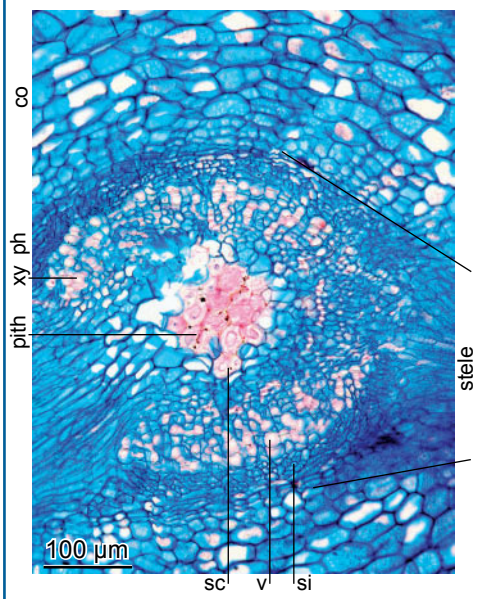



**Fig. 1.** Central cylinder with sclereids located in the center of a rhizome. Rhizome of a 4 cm-high hemicryptophyte, snow bed, alpine zone, Davos, Grisons, Switzerland. *Soldanella pusilla*, transverse section.

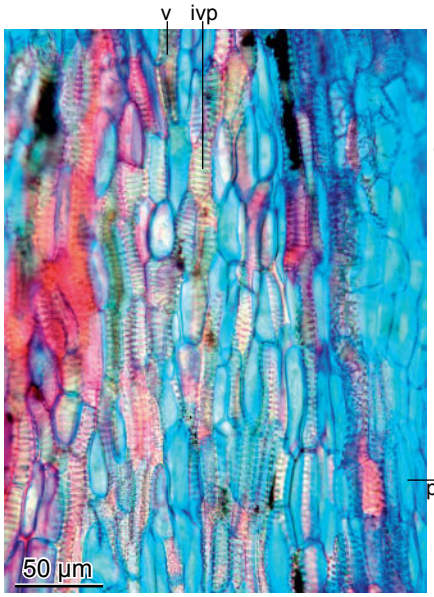



**Fig. 2.** Short vessels with scalariform intervessel pits. Rhizome of a 4 cm-high hemicryptophyte, snow bed, alpine zone, Davos, Grisons, Switzerland. *Soldanella pusilla*, transverse section.

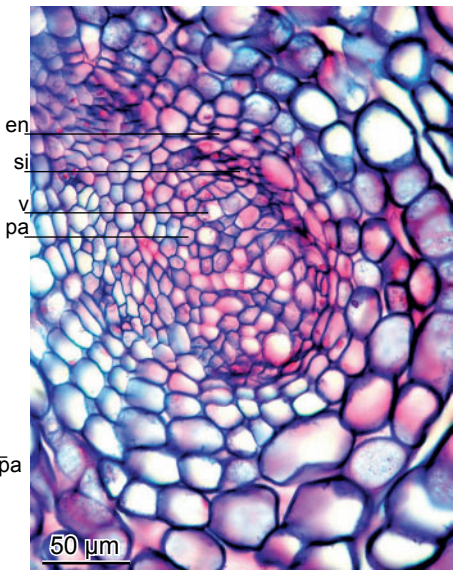
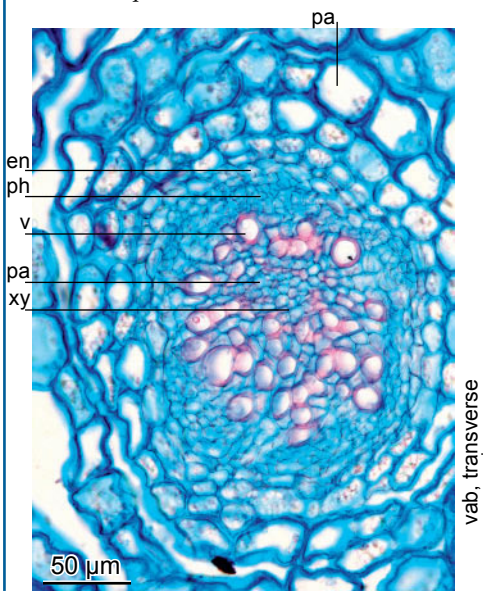
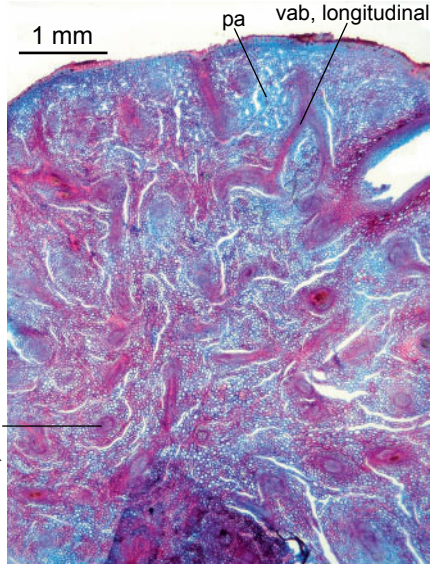


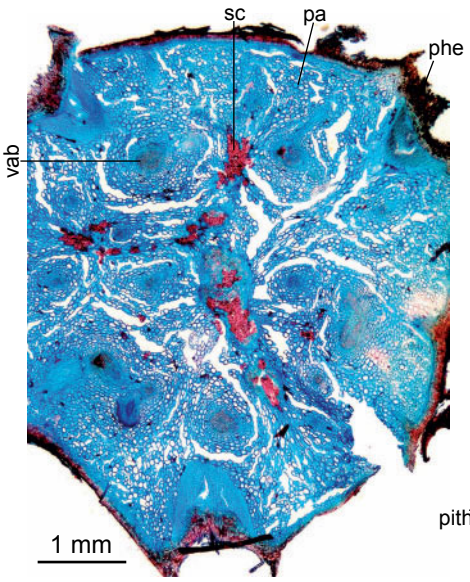

**Fig. 3.** Concentric vascular bundle. Vessels are surrounded by parenchyma. Rhizome of a 10 cm-high hemicryptophyte, on rock, subalpine zone, Stoos, Schwyz, Switzerland. *Primula auricula*, transverse section.

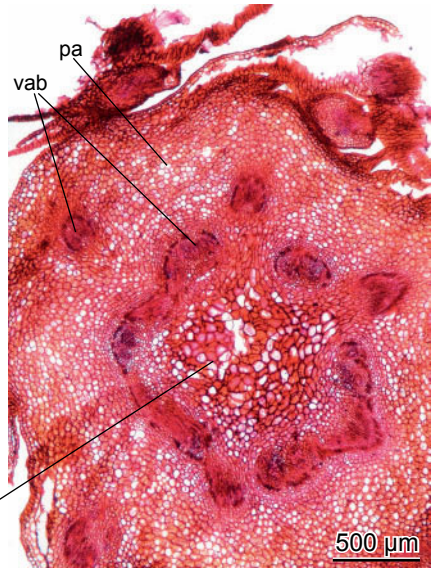



**Left Fig. 4.** Concentric vascular bundle. Vessels are surrounded by a pervasive parenchyma. Rhizome of a 4 cm-high hemicryptophyte, on rock, alpine zone, Pizol, Grisons, Switzerland. *Primula integrifolia*, transverse section.



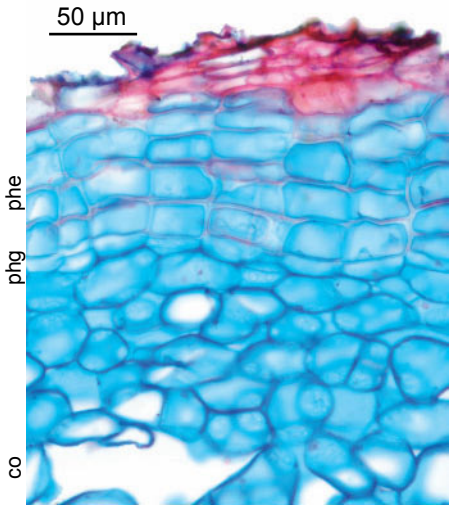

**Right Fig. 5.** Anastomosing concentric vascular bundles located within a parenchymatic tissue. Rhizome of a 10 cm-high hemicryptophyte, on rock, subalpine zone, Stoos, Schwyz, Switzerland. *Primula auricula*, transverse section.

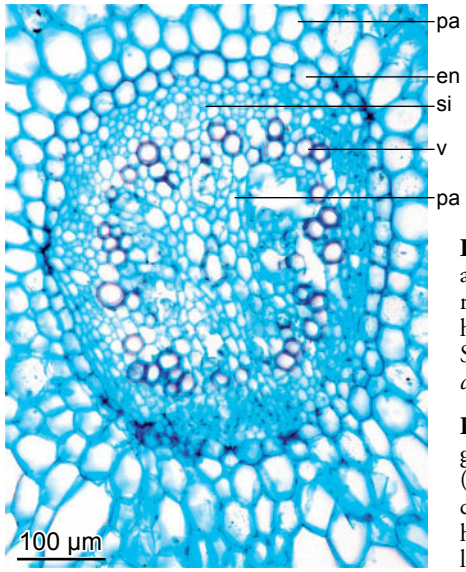



**Left Fig. 6.** Concentric vascular bundles located within a parenchymatic tissue with groups of sclerenchyma. Rhizome of a 5 cm-high hemicryptophyte, on rock, alpine zone, San Bernardino, Ticino, Switzerland. *Primula hirsuta*, transverse section.

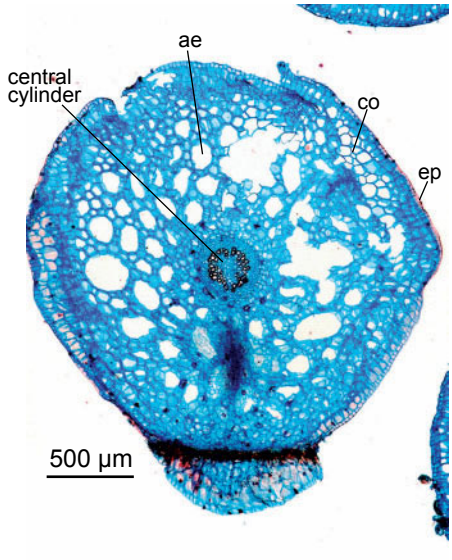
**Right Fig. 7.** Vascular bundles located in a circle around the pith and isolated in the cortex. Rhizome of a 5 cm-high hemicryptophyte, meadow, subalpine zone, Stoos, Schwyz, Switzerland. *Primula farinosa*, transverse section.

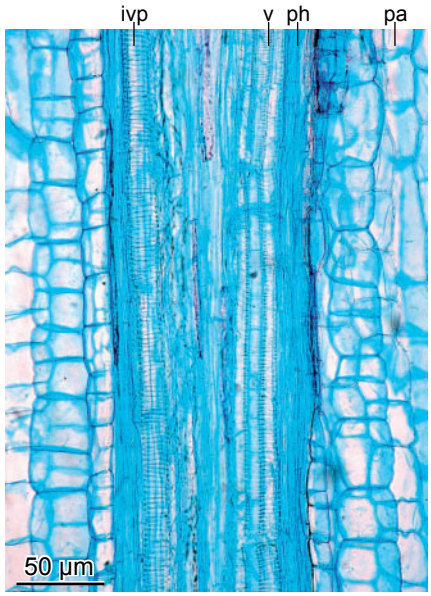



**Left Fig. 8.** Transition between the cortex and the phellem. The phellem consists of rectangular cells. Rhizome of a 10 cm-high hemicryptophyte, on rock, subalpine zone, Stoos, Schwyz, Switzerland. *Primula auricula*, transverse section.

**Right Fig. 9.** Plant without secondary growth. An endodermis surrounds a stele (central cylinder) with vessels and parenchyma cells. Rhizome of a 30 cm-high hydrophyte, pond, hill zone, Bern, Switzerland. *Hottonia palustris*, transverse section.




**Left Fig. 10.** A small stele is surrounded by a large aerenchymatic cortex. Rhizome of a 30 cm-high hydrophyte, pond, hill zone, Bern, Switzerland. *Hottonia palustris*, transverse section.

**Right Fig. 11.** Longitudinal section through a stele (central cylinder) surrounded by thin-walled parenchyma cells. The stele contains vessels with scalariform intervessel pits. Rhizome of a 30 cm-high hydrophyte, pond, hill zone, Bern, Switzerland. *Hottonia palustris*, radial section.

**Types with secondary growth**

Plants with remaining vascular bundles: *Androsace* sp. and *Cyclamen sp.*

Plants with recognizable (**Figs. 12** and **13**) or absent annual rings (**Fig. 14**). Thick-walled vessels are embedded in a thin-walled parenchymatic tissue (**Fig. 15**). Intervessel pits are scalariform or round (**Figs. 16-18**).

Plants with a continuous cambial ring: *Dionysia* sp., *Lysimachia* sp. and *Samolus valerandi*

Collateral vascular bundles are arranged around a large pith (**Figs. 19-22**) and are often connected by a ring of fibers. Intervessel pits are small and round (**Figs. 23** and **24**).

Plants with fibers: *Anagallis* sp. and *Lysimachia vulgaris*

Annual plants with a xylem ring and biannual plants with a semi-ring-porous xylem (**Figs. 25-27**). Vessel pits are small and round (**Fig. 28**).

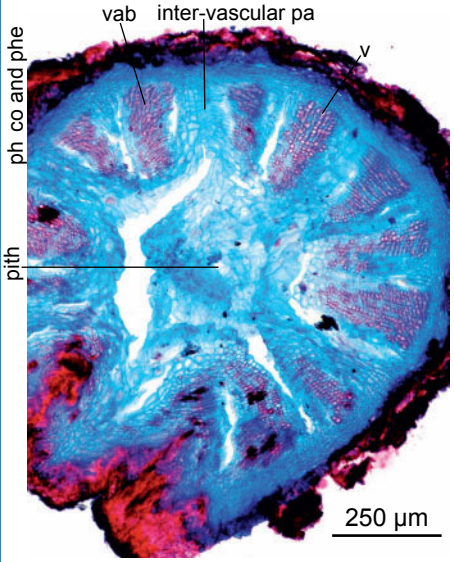



**Fig. 12.** Vascular bundles are separated by large unlignified rays. Rhizome of a 4 cm-high hemicryptophyte, on rock, alpine zone, Pizol, Grisons, Switzerland. *Androsace alpina*, transverse section.

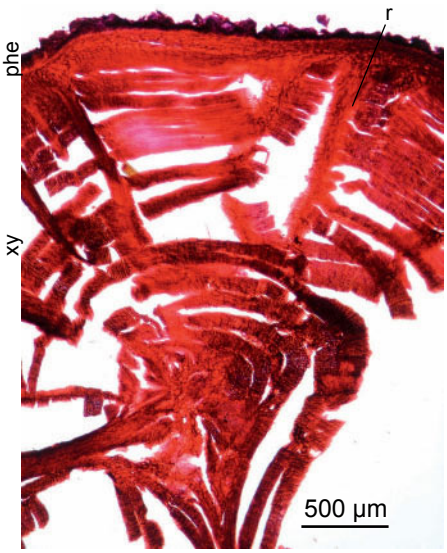



**Fig. 13.** Tangentially separated annual ring-like layers (ring shake). Rhizome of a 4 cm-high hemicryptophyte, on rock, alpine zone, Pizol, Grisons, Switzerland. *Androsace helvetica*, transverse section.

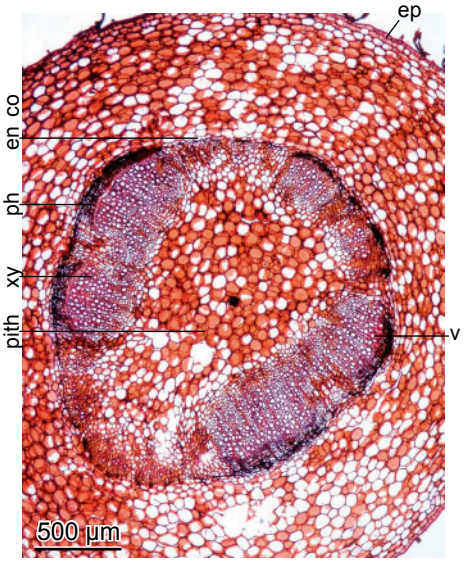



**Fig. 14.** A small phloem and a xylem without annual rings is located within a large parenchymatic cortex. Rhizome of a 15 cm-high hemicryptophyte, beech forest, montane zone, Masun, Slovenia. *Cyclamen purpurascens*, transverse section.

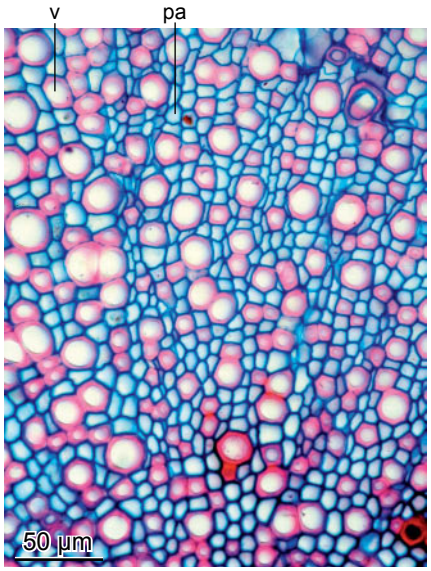



**Fig. 15.** Rayless xylem. Thick-walled vessels are surrounded by pervasive parenchyma. Rhizome of a 4 cm-high hemicryptophyte, on rock, alpine zone, Mt. Ventoux, Provence, France. *Androsace villosa*, transverse section.

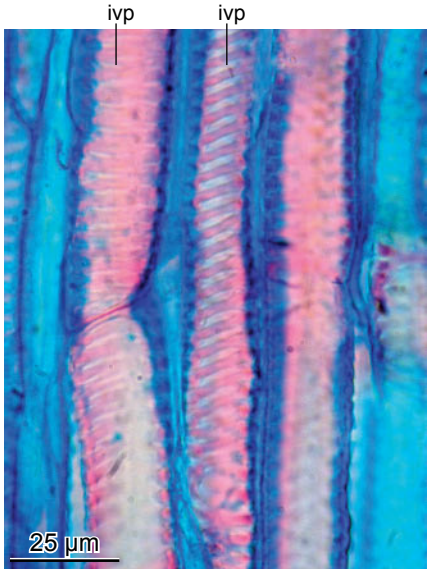
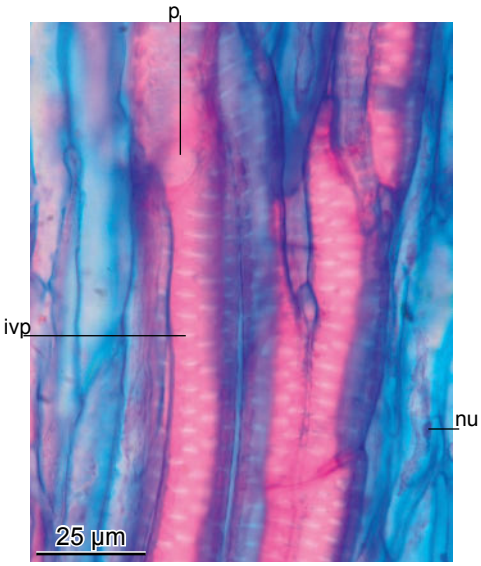
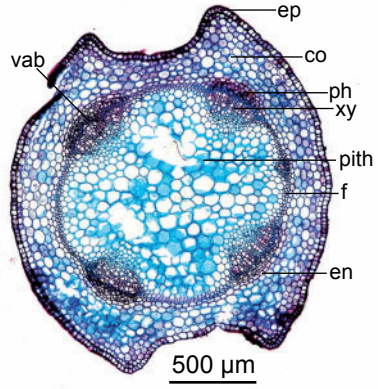



**Fig. 16.** Vessels with scalariform intervessel pits. Rhizome of a 4 cm-high hemicryptophyte, on rock, alpine zone, Mt. Ventoux, Provence, France. *Androsace villosa*, radial section.

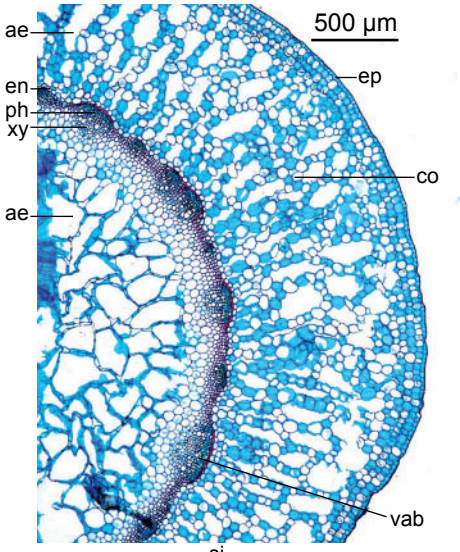
**Fig. 17.** Vessels with scalariform intervessel pits. Rhizome of a 15 cm-high hemicryptophyte, beech forest, montane zone, Masun, Slovenia. *Cyclamen purpurascens*, radial section.

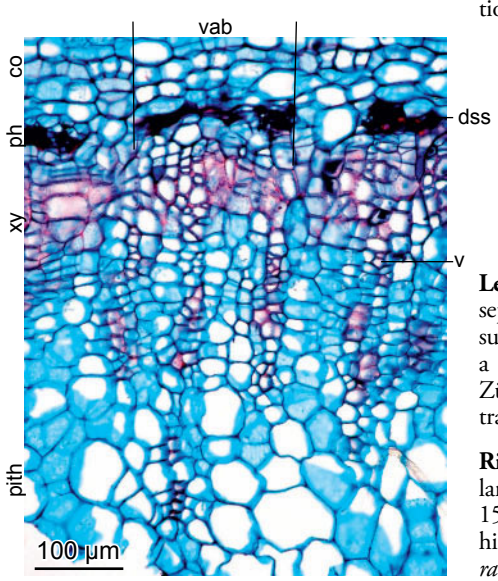



**Left Fig. 18.** Vessels with simple perforations and intervessel pits with distinct borders and slit-like apertures. Rhizome of a 5 cm-high hemicryptophyte, meadow, steppe, Monte Vista, Colorado, USA. *Androsace septentrionalis*, radial section.

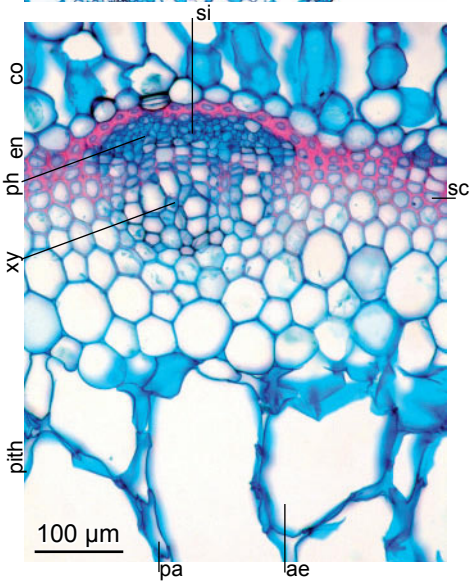
**Right Fig. 19.** Four vascular bundles are linked by a small band of fibers. There is no phellem. Rhizome of a 15 cm-high therophyte, meadow, hill zone, Zürich, Switzerland. *Lysimachia nemorum*, transverse section.

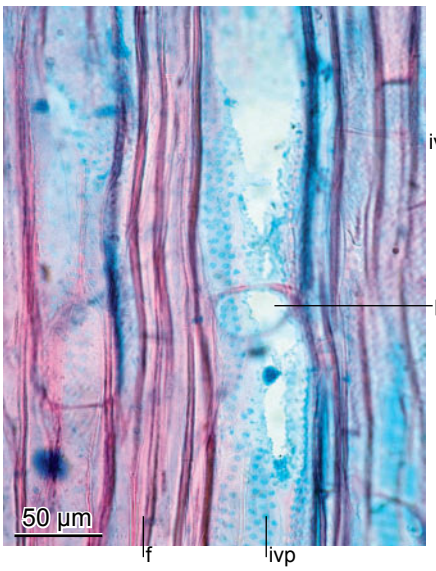



**Left Fig. 20.** A circle of vascular bundles separates aerenchymatic parenchymatic tissues of the pith and the cortex. Rhizome of a 30 cm-high helophyte, pond, hill zone, Zürich, Switzerland. *Lysimachia thyrsiflora*, transverse section.

**Right Fig. 21.** Radially oriented, irregularly formed vascular bundles. Rhizome of a 15 cm-high hemicryptophyte, wet meadow, hill zone, Bern, Switzerland. *Samolus valerandi*, transverse section.



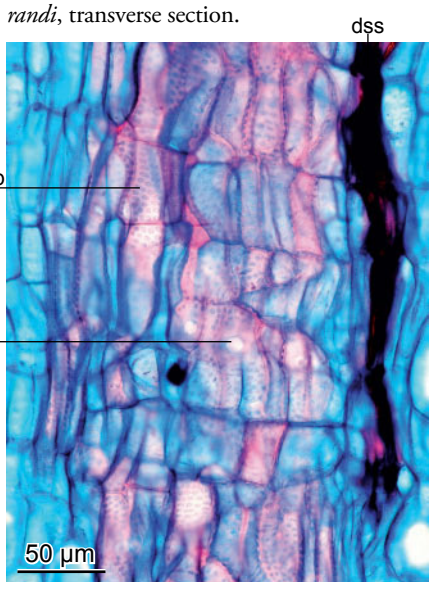
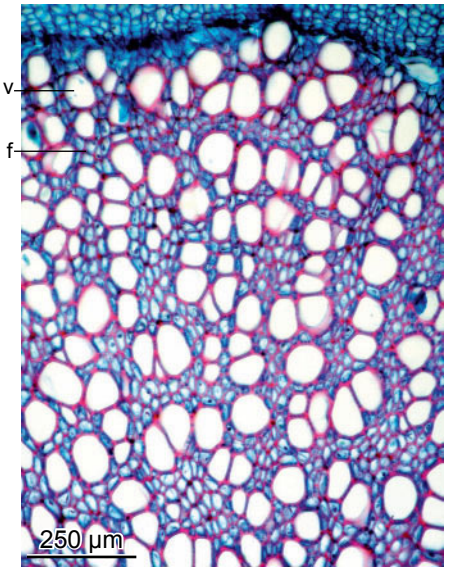
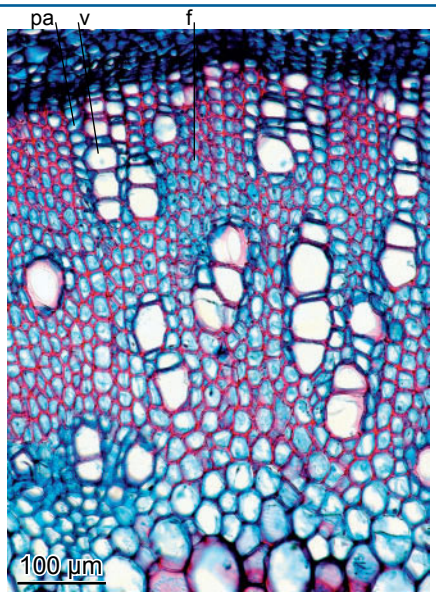




**Fig. 22.** The peripheral zone of a collateral vascular bundle consisting of a band of lignified fibers. Rhizome of a 30 cm-high helophyte, pond, hill zone, Zürich, Switzerland. *Lysimachia thyrsiflora*, transverse section.

**Fig. 23.** Vessels with simple perforations and small round intervessel pits. Rhizome of a 40 cm-high hemicryptophyte, wet meadow, montane zone, Schwyz, Switzerland. *Lysimachia vulgaris*, radial section.

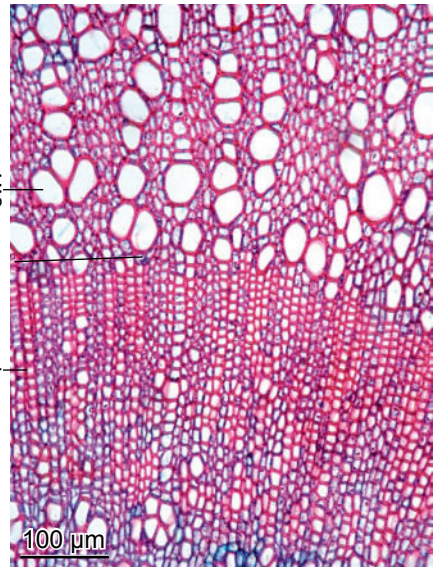
**Fig. 24.** Short vessels with small round intervessel pits. One vessel has a small, round, simple perforation. Rhizome of a 15 cm-high therophyte, ruderal site, hill zone, Bern, Switzerland. *Samolus valerandi*, radial section.

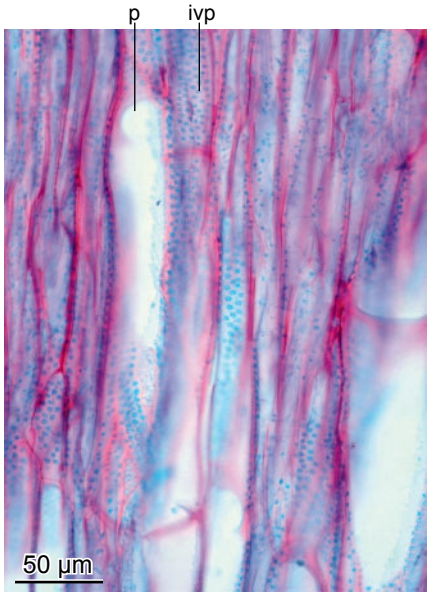



**Left Fig. 25.** Rayless xylem with many vessels and thin-walled fibers. Root collar of a 10 cm-high hemicryptophyte, ruderal site, hill zone, Zürich, Switzerland. *Anagallis arvensis*, transverse section.

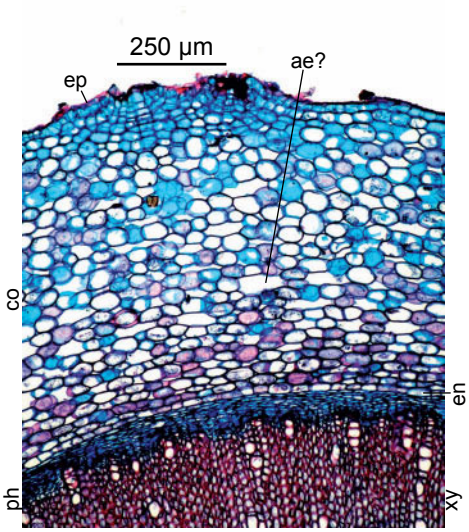
**Right Fig. 26.** One ring of a rayless xylem containing vessels in radial multiples that are surrounded by lignified fibers. Rhizome of a 40 cm-high hemicryptophyte, wet meadow, montane zone, Schwyz, Switzerland. *Lysimachia vulgaris*, transverse section

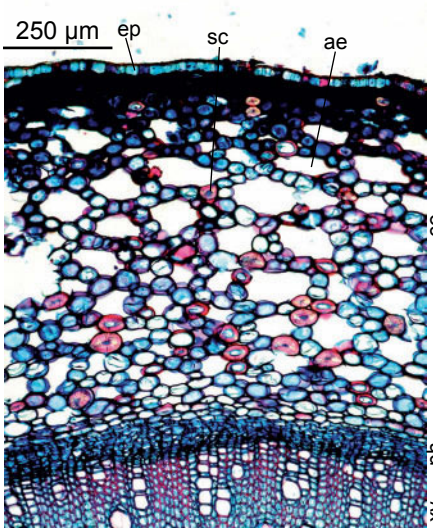



**Left Fig. 27.** Rayless semi-ring-porous xylem. Root collar of a 15 cm-high hemicryptophyte, ruderal site, Mediterranean zone, El Bosque, Andalusia, Spain. *Anagallis monelli*, transverse section.

**Right Fig. 28.** Vessels with simple perforations and small round intervessel pits. Fiber pits have the same form as vessel-pits. Root collar of a 10 cm-high hemicryptophyte, ruderal site, hill zone, Zürich, Switzerland. *Anagallis arvensis*, radial section.




**Left Fig. 29.** The cortex is composed of thin-walled, round parenchyma cells. There is no phellem. Rhizome of a 40 cm-high hemicryptophyte, dry meadow, hill zone, Ticino, Switzerland. *Lysimachia vulgaris*, transverse section.

**Right Fig. 30.** The cortex is composed of thin-walled aerenchymatic unlignified tissue containing thick-walled, isolated, lignified fibers. Rhizome of a 40 cm-high hemicryptophyte, wet meadow, montane zone, Schwyz, Switzerland. *Lysimachia vulgaris*, transverse section.

## Ecological trends and relations to life forms

The arrangement of vascular bundles varies within the family from a protostele where a central cylinder exists within a large cortex (*Hottonia palustris*; **Fig. 9**), to an actinostele where many vascular bundles are embedded in a parenchymatic tissue (*Primula* sp.; **Figs. 5** and **6**), to a siphonostele where rings of xylem and phloem form a tube around the pith (*Lysimachia* sp.; **Fig. 20**).

The presence of aerenchyma in *Lysimachia vulgaris* is site-specific. The cortex of plants on dry sites is composed of thin-walled round parenchyma cells (**Fig. 29**). In contrast, plants on wet sites have a typical aerenchyma (**Fig. 30**).

## Discussion in relation to previous studies

Most species analyzed here were not analyzed before. Metcalfe and Chalk (1957) and Douglas (1936) mentioned the anatomical diversity within the family but their limited material did not allow a classification. More material might show that the grouping given above might not be complete.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **30** |
| 1 | growth rings distinct and recognizable | 6 |
| 2 | growth rings absent | 5 |
| 2.1 | only one ring | 7 |
| 2.2 | without secondary growth | 12 |
| 4 | semi-ring-porous. | 2 |
| 5 | diffuse-porous | 4 |
| 9 | vessels predominantly solitary | 26 |
| 9.1 | vessels in radial multiples of 2-4 common | 6 |
| 10 | vessels in radial multiples of 4 or more common | 2 |
| 13 | vessels with simple perforation plates | 30 |
| 20 | intervessel pits scalariform | 12 |
| 20.1 | intervessel pits pseudoscalariform to reticulate | 9 |
| 22 | intervessel pits alternate | 11 |
| 39.1 | vessel cell-wall thickness >2 µm | 8 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 25 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 6 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 21 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 9 |
| 60.1 | fibers absent | 25 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 5 |
| 65 | septate fibers present | 1 |
| 68 | fibers thin-walled | 1 |
| 70 | fibers thin- to thick-walled | 2 |
| 75 | parenchyma absent or unrecognizable | 7 |
| 79 | parenchyma paratracheal | 1 |
| 79.1 | parenchyma pervasive | 22 |
| 89.2 | ring shake, *Saxifraga* type | 6 |
| 99 | rays commonly >10-seriate | 5 |
| 99.1 | vascular bundle form remaining | 14 |
| 105 | ray: all cells upright or square | 5 |
| 117 | rayless | 30 |
| 133 | successive cambia, Caryophyllaceae type | 2 |
| R1 | groups of sieve tubes present | 18 |
| R4 | sclereids in phloem and cortex | 1 |
| R10 | phloem not well structured | 18 |
| R12 | with laticifers, oil ducts or mucilage ducts | 1 |
| R14 | cortex with aerenchyma | 4 |

# Ranunculaceae



**Number of species, worldwide and in Europe**

The Ranunculaceae family includes 47 genera with 2000 species. Major genera are *Ranunculus* (200), *Aconitum* (250), *Clematis* (250), *Delphinium* (250), *Anemone* (150) and *Thalictrum* (100). Representatives are common in temperate and boreals regions of the northern hemisphere. In Europe there are 21 genera with 95 species. The majority belongs to *Ranunculus* (131).

**Analyzed material**

The xylem and phloem of 17 genera with 63 Ranunculaceae species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Semi-woody chamaephytes | 3 | 1 |
| Lianas | 10 | 138 |
| Hemicryptophytes and geophytes | 44 | 3 |
| Therophytes | 4 | |
| Hydrophytes and helophytes | 2 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 14 | |
| Hill and mountain | 45 | |
| Mediterranean | 2 | |
| Subtropical | 1 | |
| Arid | 1 | |

*Anemone nemorosa* (photo: Nüske)

**Analyzed species:**

*Aconitum lycoctonum* ssp. *vulparia* Nyman
*Aconitum napellus* ssp. *lusitanicum* Rouy
*Aconitum variegatum* ssp. *paniculatum* (Arcang.) Negodi
*Actaea spicata* L.
*Adonis flammea* Jacq.
*Adonis vernalis* L.
*Anemone coronaria* L.
*Anemone narcissiflora* L.
*Anemone nemorosa* L.
*Anemone ranunculoides* L.
*Aquilegia coerulea* James
*Aquilegia vulgaris* L.
*Caltha palustris* L.
*Clematis alpina* ssp. *alpina* (L.) Miller
*Clematis alpina* ssp. *sibirica* (L.) O. Kunze
*Clematis campaniflora* Brot.
*Clematis columbiana* (Nutall), T. &.G.
*Clematis cirrhosa* L.
*Clematis drumondi* Torr. et Grey
*Clematis flammula* L.
*Clematis hirsutissima* Pursh.
*Clematis montevidensis* Spreng
*Clematis recta* L.
*Clematis vitalba* L.
*Clematis viticella* L.
*Consolida regalis* Gray.
*Eranthis hyemalis* (L.) Salisb.
*Helleborus foetidus* L.
*Helleborus niger* ssp. *niger* L.
*Helleborus viridis* L.
*Hepatica nobilis* Schreb.
*Nigella arvensis* L.
*Nigella damascena* L.
*Pulsatilla alpina* ssp. *alpina* (L.) Delabre
*Pulsatilla alpina* ssp. *millefoliata* (Bertol.) D.M. Moser
*Pulsatilla alpina* ssp. *apiifolia* (Scop.) Nyman
*Pulsatilla montana* (Hoppe) Rchb.
*Pulsatilla multifida* (E.Pritz.) Juz.
*Pulsatilla patens* (L.) Mill.
*Pulsatilla vernalis* (L.) Mill.
*Pulsatilla vulgaris* ssp. *vulgaris* Mill.
*Ranunculus aconitifolius* L.
*Ranunculus acris* L.
*Ranunculus alismifolius* Geyer
*Ranunculus alpestris* L.
*Ranunculus bulbosus* L.
*Ranunculus circinatus* Sibth.
*Ranunculus cortusifolius* Willd.
*Ranunculus ficaria* L.
*Ranunculus flammula* L.
*Ranunculus glacialis* L.
*Ranunculus kuepferi* Greuter et Burdet
*Ranunculus lanuginosus* L.
*Ranunculus montanus* Willd.
*Ranunculus repens* L.
*Ranunculus serpens* Schrank
*Ranunculus trichophyllus* Chaix
*Thalictrum alpinum* L.
*Thalictrum aquilegifolium* L.
*Thalictrum foetidum* L.
*Thalictrum minus* L.
*Trollius albiflorus* L.
*Trollius europaeus* L.

*Trollius europaeus* (photo: Landolt)

*Aquilegia vulgaris* (photo: Landolt)

*Ranunculus nemorosus*

*Helleborus niger* (photo: Landolt)

*Adonis aestivalis* (photo: Landolt)

*Clematis alpina* (photo: Landolt)

*Thalictrum aquilegifolium* (photo: Landolt)

*Consolida regalis* (photo: Landolt)

*Eranthis hyemalis*

*Adonis vernalis*

*Pulsatilla vulgaris*

**Characteristic groups within the family of Ranunculaceae**

All Ranunculaceae species analyzed have two features in common: the presence of simple perforations (**Figs. 1** and **2**), and the rare occurrence of crystals and phellem (*Clematis* and partially in *Aquilegia* and *Thalictrum*). A few groups have very similar anatomical structures:

*1. Type with collateral vascular bundles:*

1.1 Without annual rings: *Aconitum*, *Anemonastrum*, *Anemone* div. species, *Caltha*, *Eranthis*, *Ranunculus*, *Trollius*. All species analyzed (28) are herbaceous, geophytes, hemicryptophytes or hydrophytes. 11 grow in the hill and mountain zone, 10 in the mountain and subalpine zone and 6 in the subalpine and alpine zone.

1.2 With annual rings: *Actaea*, *Anemone narcissiflora*, *Aquilegia*, *Pulsatilla*, *Thalictum*. All species analyzed (15) are herbaceous geophytes or hemicryptophytes. 7 grow in the hill and mountain zone and 7 in the subalpine and alpine zone. The number of rings counted varies between 2 and 16.

*2. Type with a closed xylem-ring:*

2.1 Annual herbs (therophytes): *Consolida*, *Adonis flammea*, *Nigella*. All species analyzed (4) are herbaceous and grow in the hill zone.

2.2 Perennial hemicryptophytes: *Hepatica nobilis*, the species grows in forests from the hill to the subalpine zone.

2.3 Perennial chamaephyte: *Helleborus*. All species analyzed (3) are woody at the basis. All grow in the hill and mountain zone. The number of rings counted varies between 2 and 10.

2.4 Perennial climbers (lianas) and chamaephytes: *Clematis*. All species analyzed (12) are woody, at least at the basis. 5 grow in the hill zone, 2 in the Mediterranean zone and 4 in the mountain and subalpine zone. The number of counted rings varies between 2 and 19.

Ecological trends could not be observed in any group.

**1.1 Type with collateral bundles but without annual rings: *Aconitum*, *Anemonastrum*, *Anemone* div. species, *Caltha*, *Eranthis*, *Ranunculus*, *Trollius***

**Characteristics of the xylem**

There are some common features within this group despite the different forms of rhizomes (bulbs , horizontal thin or thick rhizomes). In the present material annual rings are absent. Vascular bundles are arranged circular around the pith (**Figs. 3-6**). They are small and rare in parenchymatic rhizomes, e.g. *Eranthis hyemalis*, *Anemone nemorosa* (**Fig. 4**) and *Anemone coronaria* and form almost a ring in the horizontal rhizome of large plants as *Aconitum lycoctonum* (**Fig. 5**) or *Ranunculus lanuginosus* (**Fig. 6**). A fascicular cambium was observed in all *Aconitum* species.

The form of vascular bundles varies within plants and between species. Sclerenchymatic groups or belts are absent in many rhizomes (**Figs. 7** and **8**) or in stems of hydrophytes (*Ranunculus circinatus*, *R. trichophyllus*; **Fig. 9**). Vascular bundles are completely surrounded by a belt of sclerenchymatic cells as in the annual stems of hemicryptic *Ranunculus* species (**Fig. 10**) or they have groups of sclerenchymatic cells externally and internally or just externally (**Figs. 11** and **18**):

-Vascular bundles are collaterally closed, without any signs of a cambium, in hemicryptophytic *Ranunculus* stems.

-Vascular bundles of *Ranunculus trichophyllus* are bi-collateral (**Fig. 9**).

-A cambium-like zone is characteristic of many vascular bundles in rhizomes, but a secondary growth seems to be absent. Vascular bundles pervade the rhizomes in an irregular way. Characteristic transverse and longitudinal features appear therefor on transverse sections.

Vessels are solitary (**Fig. 11**) or in small groups (**Figs. 7-10**). Vessels are rather small with an earlywood vessel diameter of 15-40 µm. Vessel density is high in the zones between the parenchymatic zones (>200/mm$^2$). The form of inter-vessel pits varies for two reasons: a) because cross-sections contain mostly longitudinal parts of the metaxylem with annular and spiral vessel-wall thickenings and the secondary xylem with predominantly round and slit-like pits and b) because it is typical of the secondary xylem. Some species have predominantly helical intervessel pits (**Figs. 12** and **13**), others have slit-like pits (**Figs. 14** and **15**), and a few *Ranunculus* species have predominantly round pits (**Fig. 1**). Vessel walls are hardly lignified in hydrophytes such as *Ranunculus trichophyllus* (**Fig. 9**) and *R. circinatus* (**Fig. 16**). Lacunae occur in the protoxylem zone of *Ranunculus trichophyllus* (**Fig. 9**).

Fibers are missing wheras axial parenchyma is pervasive in all species (**Figs. 11** and **17**). The large rays between the vascular bundles represent medullary unlignified parenchyma without secondary walls (cells do not stain with safranin and appear black in polarized light). Rays are absent within vascular bundles (**Figs. 7-11** and **18**). The pith of some *Aconitum* individuals sometimes contains a few medullary sieve-tube groups.

**Characteristics of the phloem and the cortex**

The phloem of all species is simply structured. Sieve tubes and parenchyma are not easily distinguishable in cross sections (**Fig. 18**). The cortex of most species consists of round parenchyma cells (**Figs. 19** and **20**). Distinct sieve-tube groups exist in the cortex of *Aconitum napellus* and *A. variegatum* (**Figs. 21** and **22**). Sclerenchymatic cells occur only in the cortex of *Aconitum lycoctonum*. Intercellulares (**Figs. 23** and **24**) and aerenchyma (**Fig. 25**) in the cortex are characteristic of heolphytes and hydrophytes. Only *Aconitum napellus* has a small phellem (**Fig. 21**).

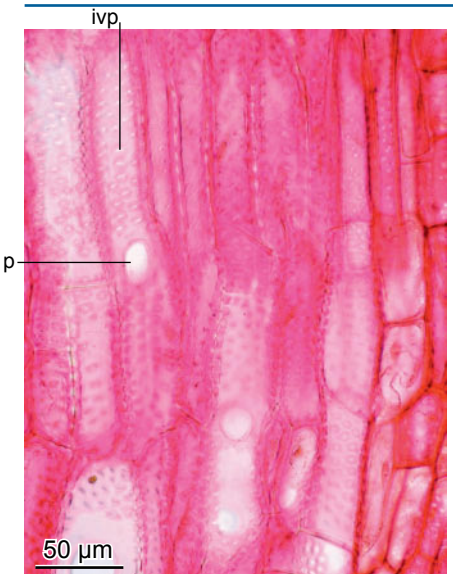



**Fig. 1.** Vessels with simple perforations. Rhizome of an 80 cm-high hemicryptophyte, rock field, mountain zone, Piemont, Italy. *Aconitum lycoctonum*, radial section.

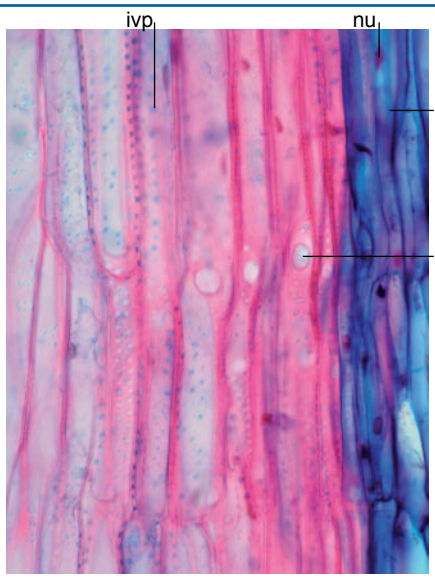



**Fig. 2.** Vessels with simple perforations. Root collar of a 20 cm-high annual plant, field, Mediterranean zone, Provence, France. *Adonis flammea*, radial section.

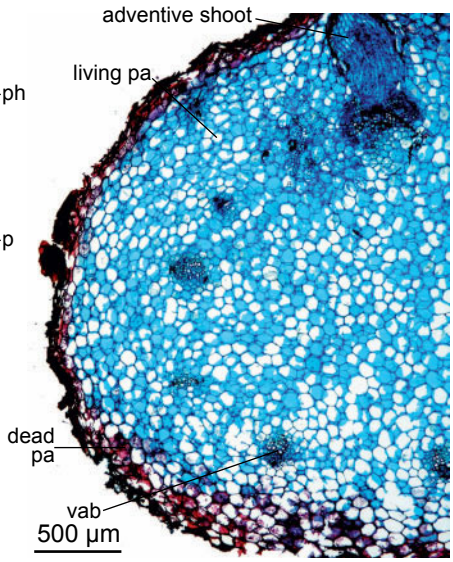
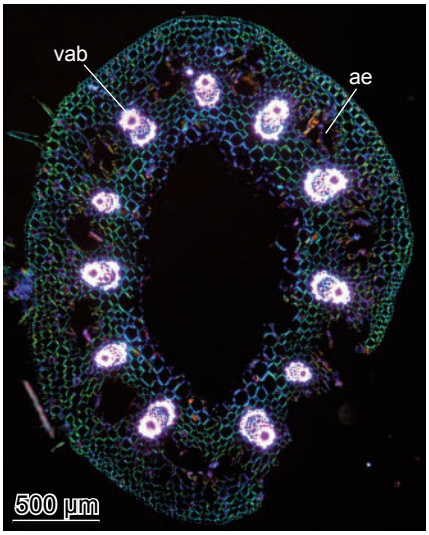
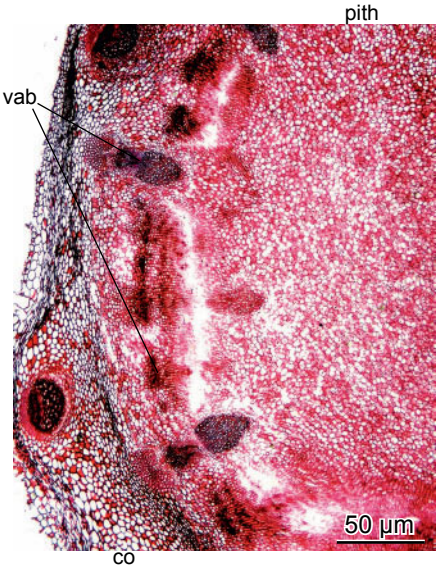


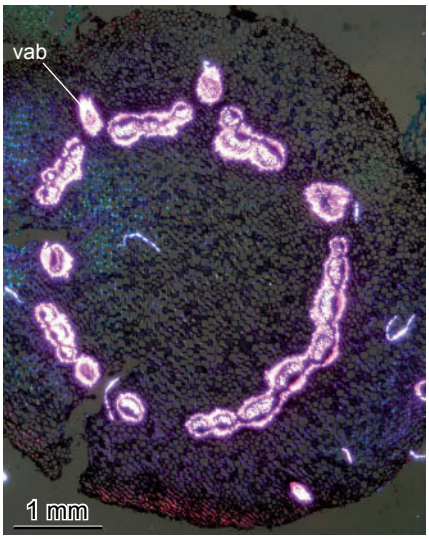

**Fig. 3.** Circular arranged vascular bundles in a parenchymatic tissue. Horizontal rhizome of a 15 cm-high geophyte, beech forest, hill zone, Switzerland. *Anemone nemorosa*, transverse section.

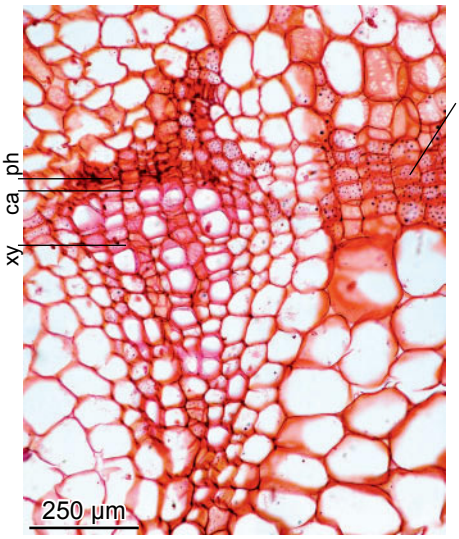



**Left Fig. 4.** Circular arranged vascular bundles in a thin-walled parenchymatic tissue of a helophyte. Stem of a 10 cm-high helophyte, wet meadow, mountain zone, Switzerland. *Ranunculus flammula*, transverse section, polarized light.

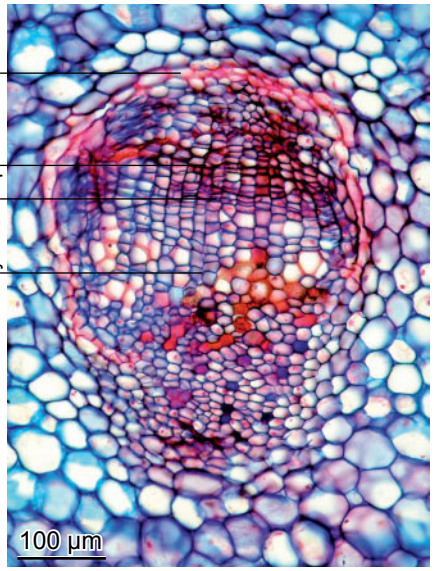
**Right Fig. 5.** Circular arranged vascular bundles around the pith. Rhizome of an 80 cm-high hemicryptophyte, rock field, mountain zone, Piemont, Italy. *Aconitum lycoctonum*, transverse section.

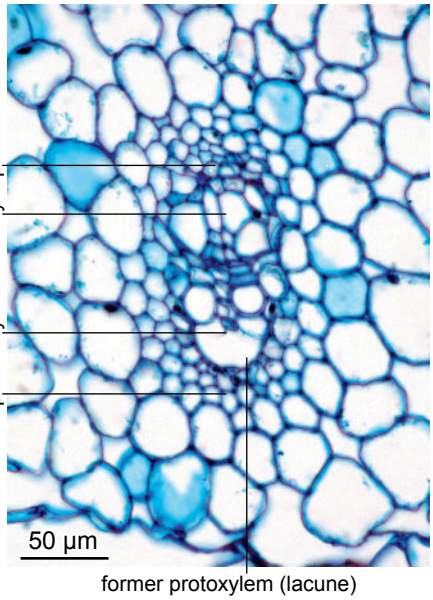



**Left Fig. 6.** Circular arranged vascular bundles around the pith. The bundles form an almost closed ring. Rhizome of an 80 cm-high hemicryptophyte, wet meadow, mountain zone, Switzerland. *Ranunculus lanuginosus*, transverse section, polarized light.

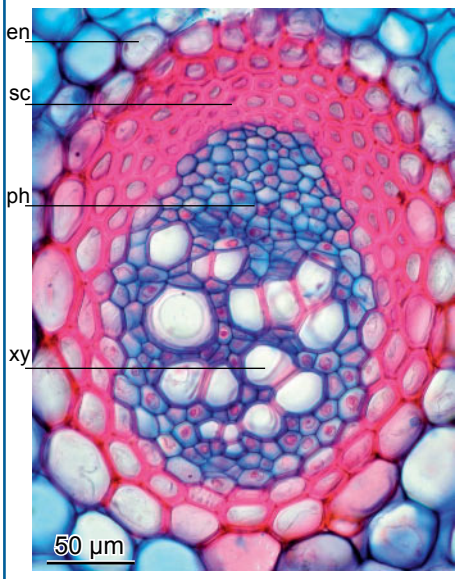
**Right Fig. 7.** Vascular bundle without any sclerenchymatic groups. The bundles are laterally connected with an interfascicular meristem. Rhizome of a 60 cm-high hemicryptophyte, wet meadow, subalpine zone, Switzerland. *Aconitum napellus*, transverse section.

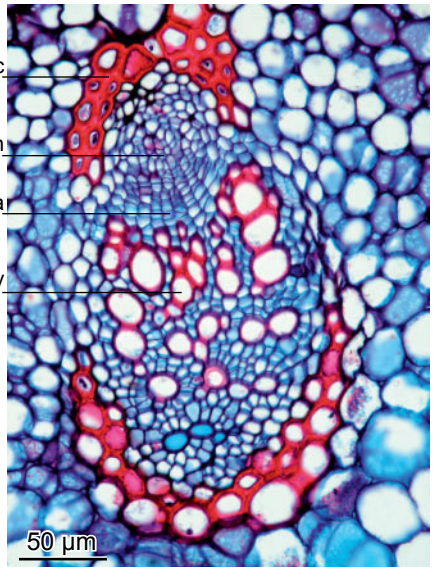



**Left Fig. 8.** A row of thin-walled, lignified parenchyma cells surrounds the vascular bundle (endodermis). The bundle is not laterally connected with an interfascicular meristem. Rhizome of a 30 cm-high hemicryptophyte, wet meadow, mountain zone, Switzerland. *Ranunculus aconitifolius*, transverse section.

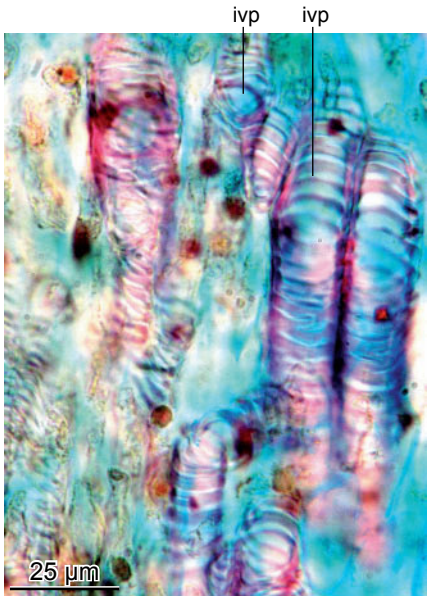
**Right Fig. 9.** Bi-collateral vascular bundle of a hydrophyte. Vessel walls are unlignified. The crushed protoxylem is replaced by a lacune. Stem of a 1 m-long floating hydrophyte, almost stagnating river, hill zone, Switzerland. *Ranunculus trichophyllus*, transverse section.

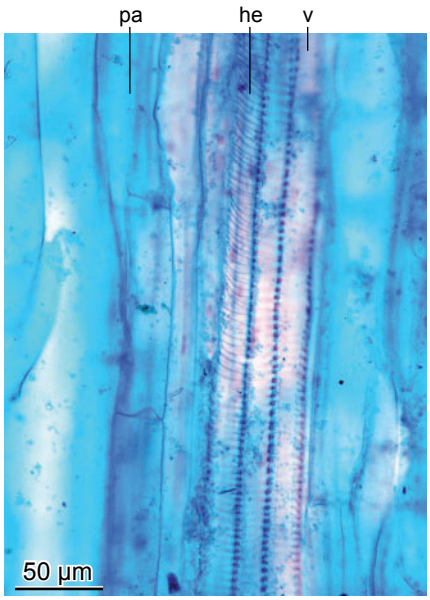



**Left Fig. 10.** A belt of thick-walled sclerenchyma fibers surrounds a collateral vascular bundle. Stem of a 30 cm-high hemicryptophyte, wet meadow, mountain zone, Switzerland. *Ranunculus aconitifolius*, transverse section.

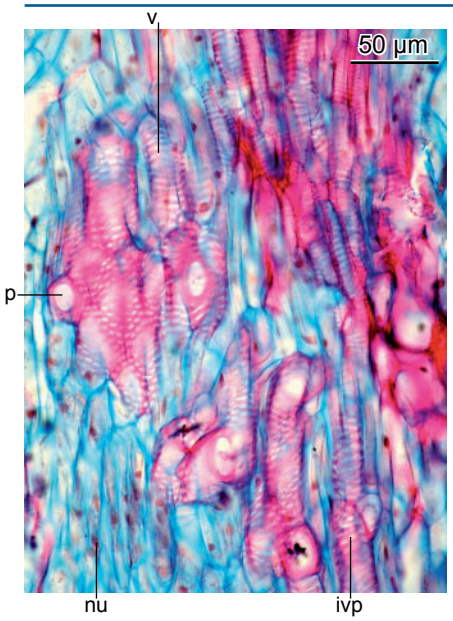
**Right Fig. 11.** Centrifugal and centripetal ends of the collateral vascular bundles contain arc-shaped zones of intensively lignified sclerenchyma fibers. Bulb-like rhizome of a 10 cm-high plant, dry meadow, hill zone, Switzerland. *Ranunculus bulbosus*, transverse section.

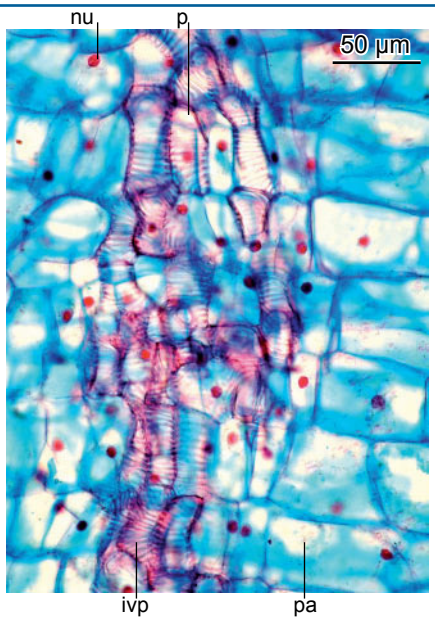



**Left Fig. 12.** Annular to scalariform intervessel pits. Rhizome of a 20 cm-high hemicryptophyte, volcanic rock, subtropical climate, mountain zone, Tenerife, Canary Islands. *Ranunculus cortusifolius*, radial section.

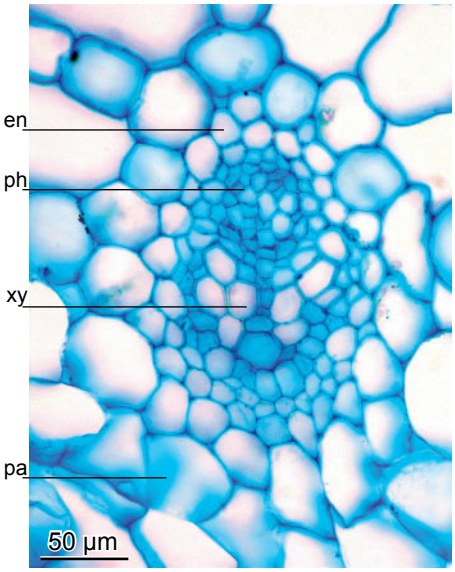
**Right Fig. 13.** Very fine helical vessel-wall thickening. Stem of a 1 m-long floating hydrophyte, almost stagnating river, hill zone, Switzerland. *Ranunculus trichophyllus*, radial section.

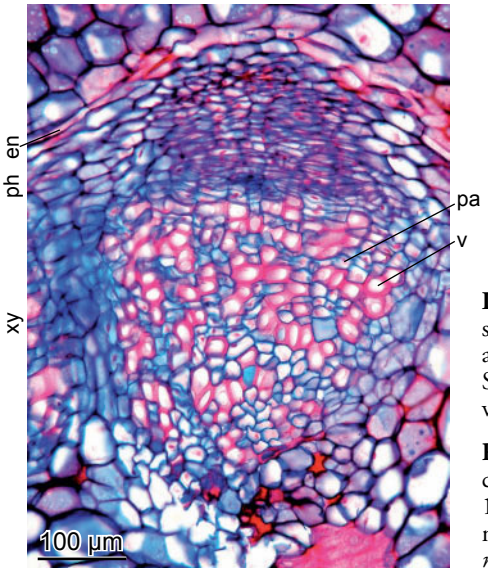



**Left Fig. 14.** Vessels with round to slit-like intervessel pits and simple perforations. Stem of a 30 cm-high hemicryptophyte, wet meadow, mountain zone, Switzerland. *Ranunculus aconitifolius*, radial section.

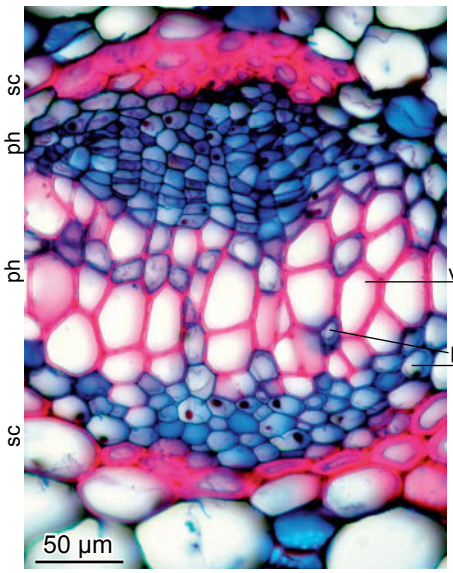
**Right Fig. 15.** Vessels with scalariform to slit-like vessel pits and simple perforations. Bulb of a 10 cm-high hemicryptophyte, cultivated in a garden, hill zone, Switzerland. *Eranthis hyemalis*, radial section.

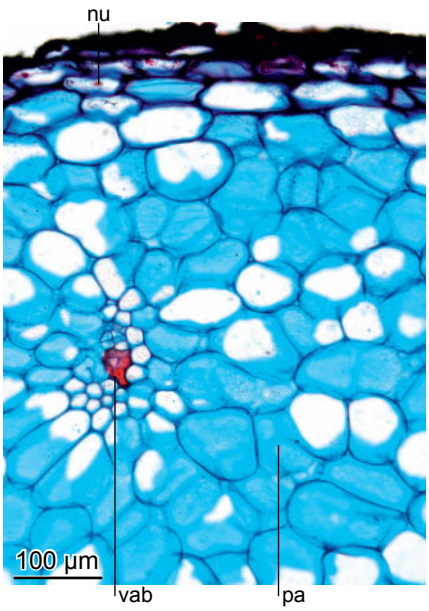



**Left Fig. 16.** Unlignified thin-walled vessels in a collateral vascular bundle. Stem of a 15 cm-high hydrophyte, pond, hill zone, Switzerland. *Ranunculus circinatus*, transverse section.

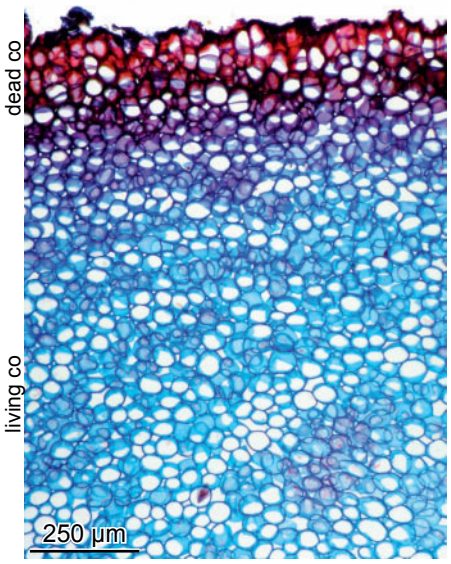
**Right Fig. 17.** Pervasive parenchyma in a collateral vascular bundle. Rhizome of a 10 cm-high hemicryptophyte, meadow, mountain zone, Switzerland. *Ranunculus montanus*, transverse section.

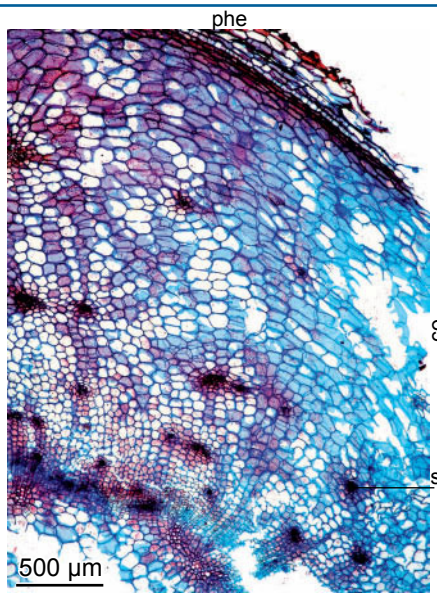



**Left Fig. 18.** Simply structured phloem in a collateral vascular bundle. Sieve tubes and parenchyma cells have almost the same shape in cross sections. Rhizome of a 50 cm-high hemicryptophyte, wet meadow, mountain zone, Switzerland. *Ranunculus lanuginosus*, transverse section.

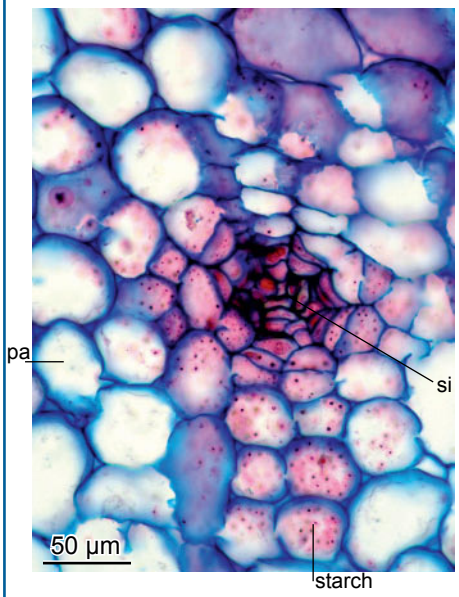
**Right Fig. 19.** Small vascular bundle in a cortex with large, thin-walled parenchyma cells. A phellem is absent. Horizontal rhizome of a 15 cm-high geophyte, beech forest, hill zone, Switzerland. *Anemone ranunculoides*, transverse section.

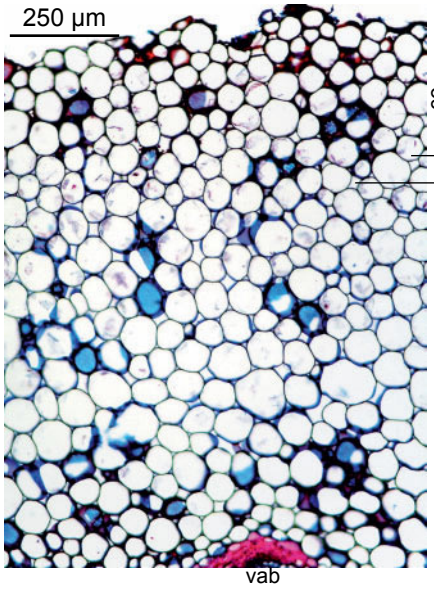



**Left Fig. 20.** Cortex with large, thin-walled parenchyma cells. A phellem is absent. The starch-containing cells (blue) are protected by a compartimentalized zone (brown). Rhizome of a 25 cm-high hemicryptophyte, wet meadow, hill zone, Switzerland. *Caltha palustris*, transverse section.

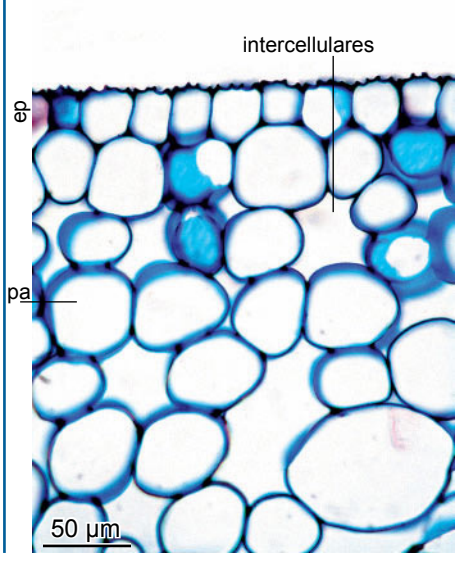
**Right Fig. 21.** Sieve-cell groups in the cortex. The cortex is surrounded by a small phellem. Rhizome of a 60 cm-high hemicryptophyte, wet meadow, subalpine zone, Switzerland. *Aconitum napellus*, transverse section.

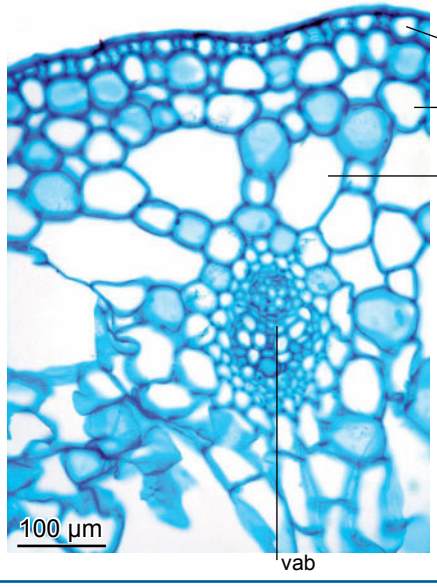



**Left Fig. 22.** A sieve-tube group with circular arranged sieve tubes. The group is embedded in parenchyma cells that contain starch. Rhizome of a 60 cm-high hemicryptophyte, wet meadow, subalpine zone, Switzerland. *Aconitum napellus*, transverse section.

**Right Fig. 23.** Cortex with thin-walled parenchyma cells and distinct intercellulares. Rhizome of a 50 cm-high hemicryptophyte, wet meadow, mountain zone, Switzerland. *Ranunculus lanuginosus*, transverse section.




**Left Fig. 24.** Intercellulares between large, unlignified, thin-walled parenchyma cells in the cortex. The external cell wall of the epidermis is dentate. Bulb of a 15 cm-high helophyte, wet meadow, mountain zone, Switzerland. *Ranunculus flammula*, transverse section.

**Right Fig. 25.** A cortex with aerenchyma between unlignified parenchyma cells surrounds a vascular bundle. Stem of a 15 cm-high hydrophyte, pond, hill zone, Switzerland. *Ranunculus circinatus*, transverse section.

**1.2 Type with open collateral bundles with annual rings and large radial strips of medullary parenchyma (= very large ray): *Actaea, Adonis vernalis, Aquilegia, Pulsatilla, Thalictrum***

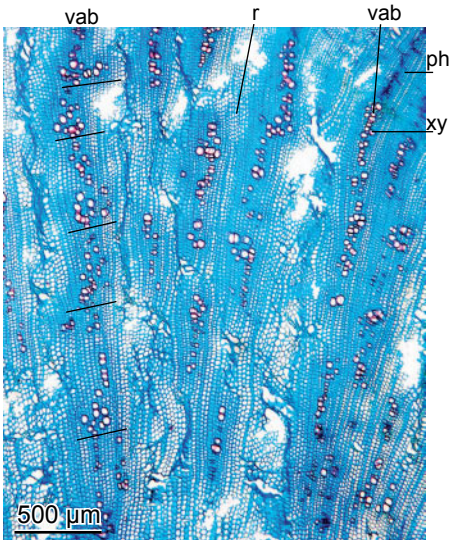
**Characteristics of the xylem**

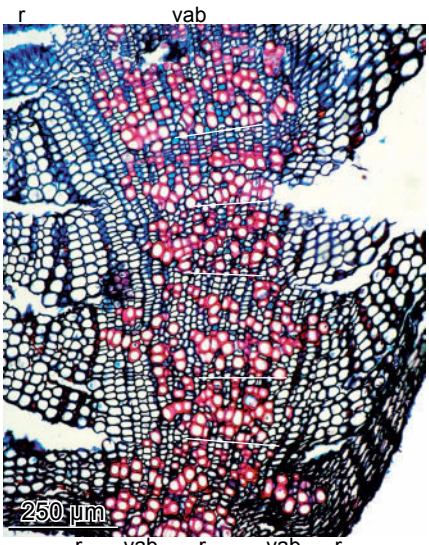
All species are herbaceous hemicryptophytes with rhizomes. Annual rings occur in the present material in all species but they are more-or-less distinct. Ring boundaries of most species are defined by a slight semi-ring porosity (**Figs. 26-29**). Vessels are solitary or in small groups except in *Actaea spicata* and *Thalictrum alpinum*, where they are in radial multiples (**Figs. 28** and **29**). Vessels are rather small with an earlywood vessel diameter that varies from 20-50 µm. Vessel density is high in the zones between the large rays (>200/mm$^2$). Characteristic of *Pulsatilla* species are thick-walled vessels (**Fig. 30**). Vessels of the other genera are not thick-walled. Inter-vessel pits are predominantly small and round but the apertures are sporadically slit-like (**Figs. 31-33**). Fibers are missing in all *Pulsatilla* (**Fig. 30**) and *Aquilegia* (**Fig. 26**) species as well as in *Thalictrum alpinum* (**Fig. 34**). Thin- to thick-walled fibers are present in *Actaea spicata* (**Fig. 28**) and most *Thalictrum* species. Septate fibers were observed in *Thalictrum aquilegifolium*. Axial parenchyma is pervasive in *Adonis vernalis*, *Aquilegia* (**Fig. 26**), *Pulsatilla* (**Fig. 30**) and *Thalictrum alpinum* (**Fig. 34**), paratracheal in the other *Thalictrum* species and hardly recognizeable in *Actaea spicata* (**Fig. 28**). The large rays between the vascular bundles represent medullary unlignified parenchyma without secondary walls (**Figs. 26-29**). Rays are absent within vascular bundles. Vessels and vasicentric tracheids are not storied or at least indistinct. A large number of crystal druses occur in *Thalictrum minus* (**Fig. 35**). Stems of *Pulsatilla* are mostly fluted in young states. With increasing growth the lobes separate to form independent stems (**Fig. 27**).

**Taxonomical note:** The wood anatomical structures of *Thalictrum alpinum* and *Adonis vernalis* are similar to those of *Pulsatilla*.

**Characteristics of the phloem and the cortex**

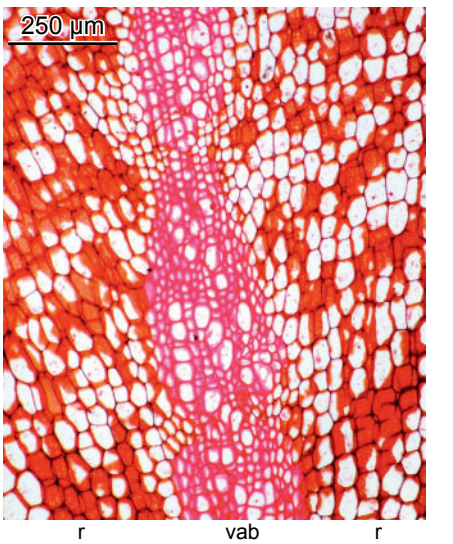
All species have sieve-tube groups (**Figs. 36-38**). They are arranged in more-or-less distinct tangential rows in all specimens with distinct xylem rings. Sclerenchymatic cell groups occur only in *Thalictrum aquilegifolium* (**Fig. 39**). Phellem was observed only in *Aquilegia vulgaris* (**Fig. 40**), *Thalictrum alpinum* (**Fig. 41**) and *T. aquilegifolium*.

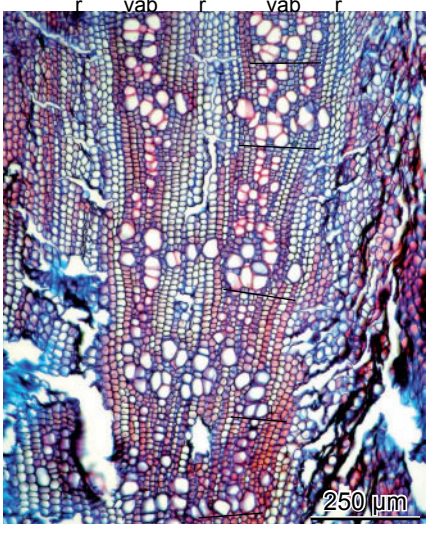



**Left Fig. 26.** Radial strips of vessels/parenchyma between large, indistinct rays. Semi-ring-porous arranged vessels indicate ring boundaries. Only vessel walls are lignified. Rhizome of a 40 cm-high hemicryptophyte, *Pinus mugo* forest, mountain zone, Switzerland. *Aquilegia vulgaris*, transverse section.

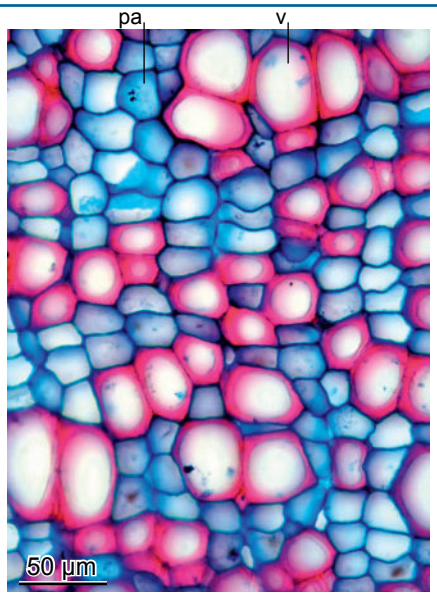
**Right Fig. 27.** Radial strip (lobe) of vessels/parenchyma between large rays. Slightly semi-ring-porous arranged radial multiple vessels indicate ring boundaries. Rhizome of a 10 cm-high hemicryptophyte, alpine meadow, Colorado, USA. *Pulsatilla patens*, transverse section.

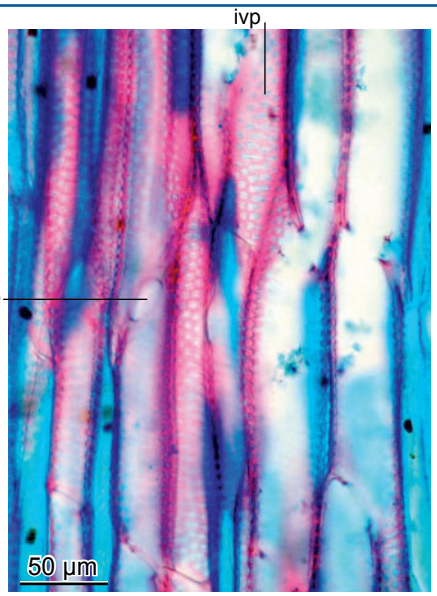



**Left Fig. 28.** Radial strip of vessels/fiber (vascular bundle) between large rays. Semi-ring-porous arranged vessels indicate ring boundaries. Rhizome of a 10 cm-high hemicryptophyte, spruce forest, mountain zone, Piemont, Italy. *Actaea spicata*, transverse section.

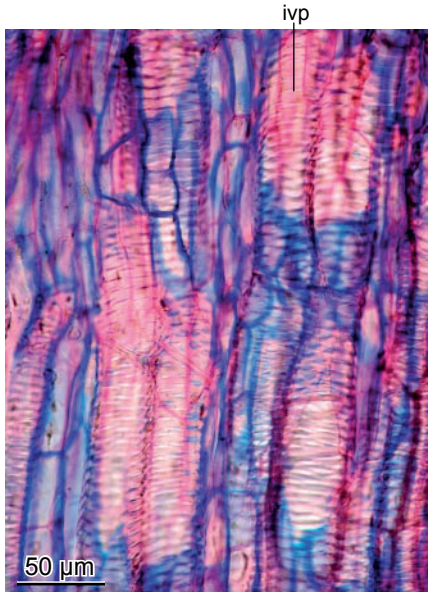
**Right Fig. 29.** Radial strip of vessels/parenchyma between large rays. Semi-ring-porous arranged radial multiple vessels indicate ring boundaries. Rhizome of a 10 cm-high hemicryptophyte, volcanic rock, alpine zone, Colorado, USA. *Thalictrum alpinum*, transverse section.



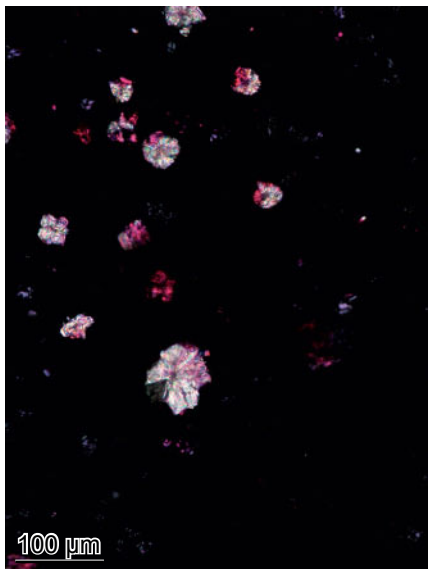

**Left Fig. 30.** Thick-walled vessels are surrounded by unlignified pervasive parenchyma. Fibers are absent. Rhizome of a 10 cm-high hemicryptophyte, dry meadow, hill zone, Burgenland, Austria. *Pulsatilla vulgaris*, transverse section.

**Right Fig. 31.** Round intervessel pits. Rhizome of a 10 cm-high hemicryptophyte, dry meadow, hill zone, Burgenland, Austria. *Pulsatilla vulgaris*, radial section.



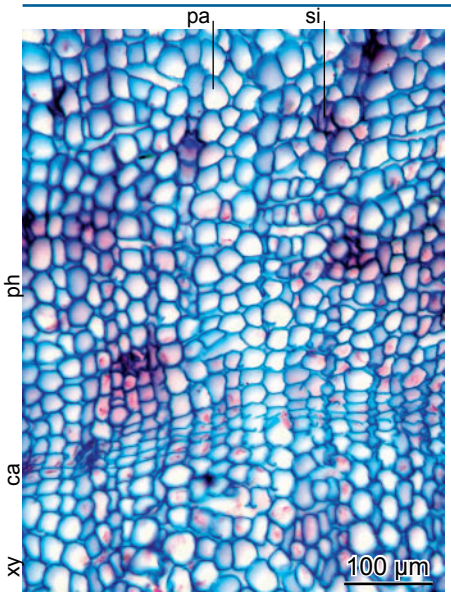

**Left Fig. 32.** Slit-like intervessel pits. Rhizome of a 10 cm-high hemicryptophyte, alpine meadow, alpine zone, Ht. Savoy, France. *Pulsatilla alpina* ssp. *millefoliata*, radial section.

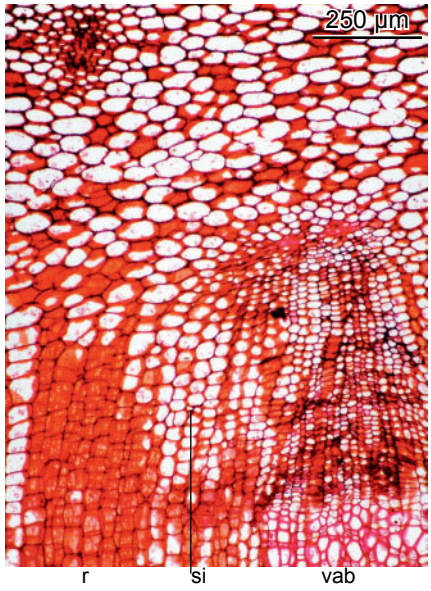
**Right Fig. 33.** Slit-like to scalariform intervessel pits. Rhizome of a 10 cm-high hemicryptophyte, volcanic rock, alpine zone, Colorado, USA. *Thalictrum alpinum*, radial section.




**Left Fig. 34.** Solitary and radial, multiple, lignified vessels are surrounded by unlignified pervasive parenchyma. Fibers are absent. Rhizome of a 10 cm-high hemicryptophyte, volcanic rock, alpine zone, Colorado, USA. *Thalictrum alpinum*, transverse section.

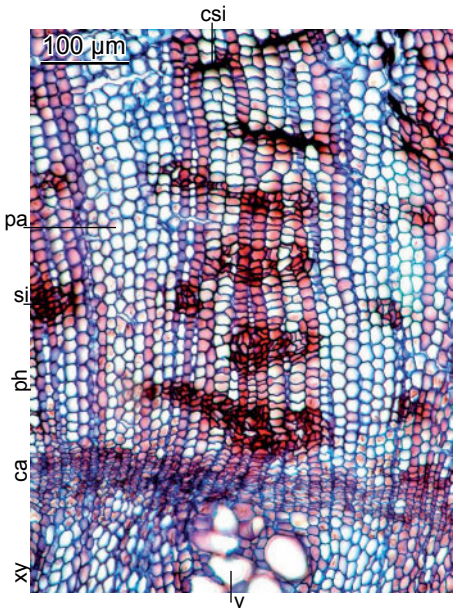
**Right Fig. 35.** Crystal druses in ray cells. Rhizome of a 10 cm-high hemicryptophyte, meadow, subalpine zone, Grisons, Switzerland. *Thalictrum minus*, tangential section, polarized light.

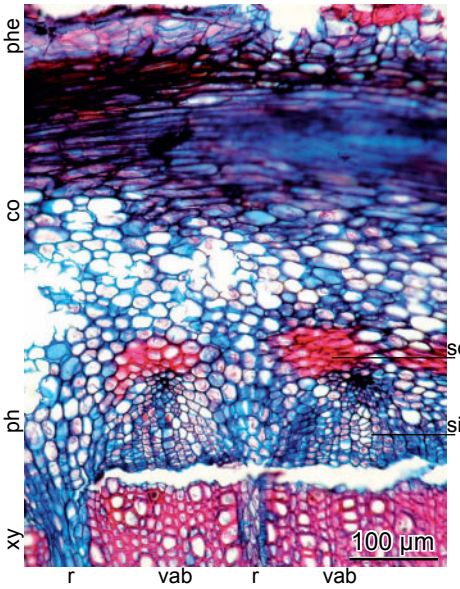



**Left Fig. 36.** Small groups of sieve tubes in the ray zone of the phloem. Rhizome of a 40 cm-high hemicryptophyte, *Pinus mugo* forest, mountain zone, Switzerland. *Aquilegia vulgaris*, transverse section.

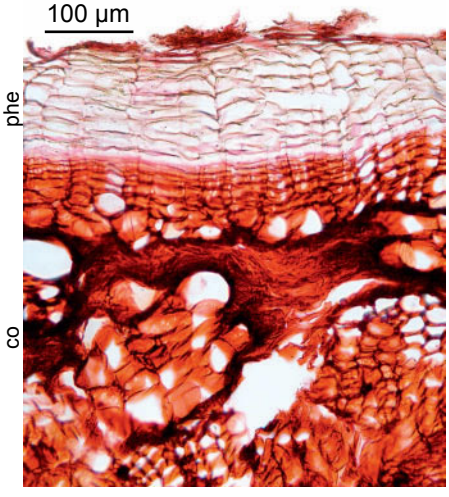
**Right Fig. 37.** Groups of more-or-less tangentially arranged sieve tubes in the phloem. Rhizome of a 10 cm-high hemicryptophyte, spruce forest, mountain zone, Piemont, Italy. *Actaea spicata*, transverse section.

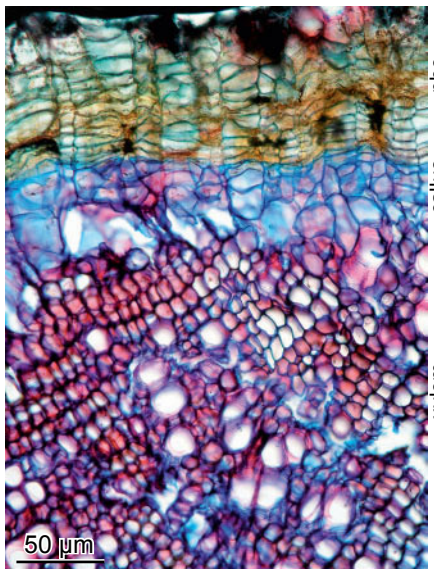



**Left Fig. 38.** Tangentially arranged groups of sieve tubes in the phloem. Rhizome of a 10 cm-high hemicryptophyte, Switzerland. *Thalictrum alpinum*, transverse section.

**Right Fig. 39.** Groups of sclerenchymatic cells at the external side of the phloem between the rays. The cortex is covered by a phellem. Rhizome of a 10 cm-high hemicryptophyte, on volcanic rock, alpine zone, Colorado, USA. *Thalictrum alpinum*, transverse section.




**Left Fig. 40.** The cortex is covered by a phellem. Rhizome of a 40 cm-high hemicryptophyte, *Pinus mugo* forest, mountain zone, Switzerland. *Aquilegia vulgaris*, transverse section.

**Right Fig. 41.** A phellem covers a zone of callus cells above the xylem. Rhizome of a 10 cm-high hemicryptophyte, on volcanic rock, alpine zone, Colorado, USA. *Thalictrum alpinum*, transverse section.

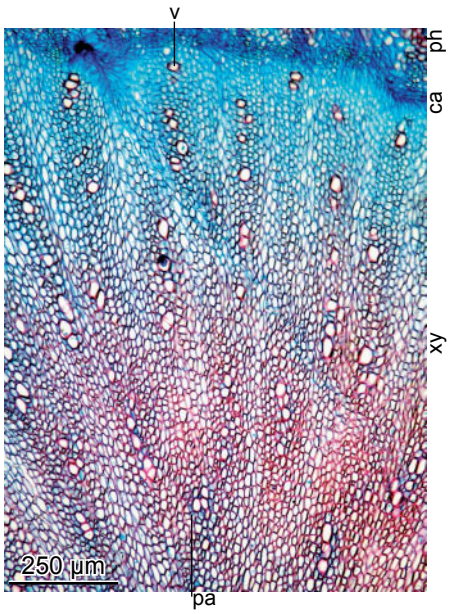
**2. Type with a closed xylem-ring:**
**2.1 Annual herbs (therophytes): *Consolida*, *Adonis flammea*, *Nigella***

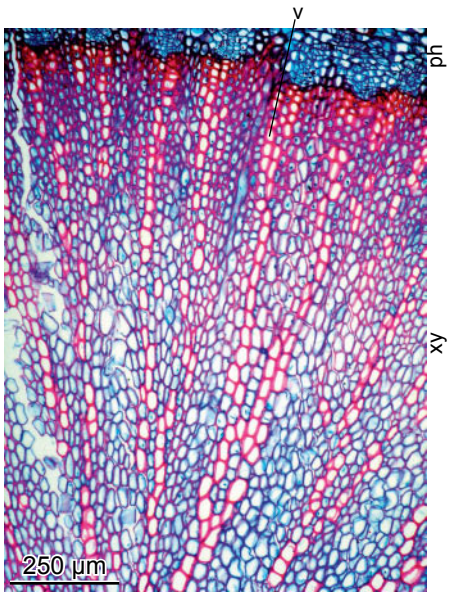
**Characteristics of the xylem**

All species are herbaceous therophytes with tap roots. All species have only one ring. Vessels are solitary or in short radial multiples (*Consolida regalis*; **Fig. 42**) or in long radial multiples (*Adonis flammea* and *Nigella* sp.; **Figs. 43-45**). Vessels are very small and hard to distinguish from the fiber tissue in *Adonis flammea* (**Fig. 43**) and rather small in all other species. Vessel diameter varies from 20-40 µm. Vessel density is high (>200/mm$^2$). Vessels have distinct simple perforations and small, round intervessel pits (**Fig. 46**). Fibers have small pits and are predominantly thin-walled (**Fig. 47**). Axial parenchyma is paratracheal in *Consolida regalis* and *Nigella* sp. (**Fig. 45**) and hardly recognizable in *Adonis flammea* (**Fig. 43**). Rays are absent in *Nigella* sp. (**Fig. 48**), up to 4 rows in width but confluent to the fiber tissue in *Adonis flammea* and *Consolida regalis* (**Figs. 49** and **50**).

**Characteristics of the phloem and the cortex**

All species have sieve-tube groups (**Figs. 51-54**). Sclerenchyma is absent in *Nigella* sp. (**Figs. 51** and **52**). *Adonis flammea* has small and *Consolida regalis* large sclerenchymatic cell groups (**Fig. 44**). Phellem is absent (**Fig. 53**).




**Left Fig. 42.** Vessels are solitary or in short radial multiples. They are surrounded by thin-walled fibers. Paratracheal parenchyma can be recognized at the inner part of the stem. Root collar of a 15 cm-high therophyte, field, hill zone, Piemont, Italy. *Consolida regalis*, transverse section.

**Right Fig. 43.** Small vessels with intensively lignified walls (red) stand in long radial multiples. Parenchyma and fibers cannot be distinguished on cross sections. Root collar of a 20 cm-high therophyte, meadow, hill zone, Provence, France. *Adonis flammea*, transverse section.

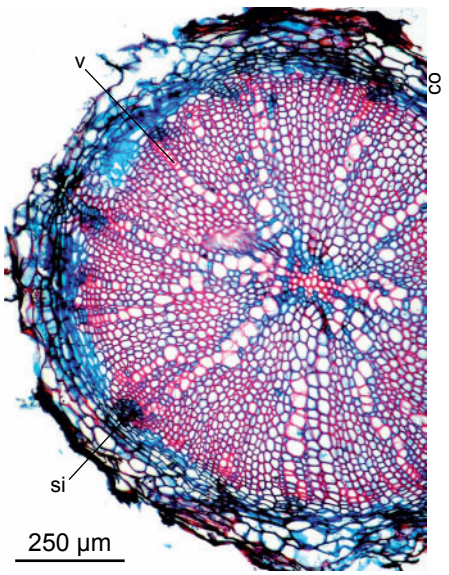



**Fig. 44.** Small vessels stay in long radial multiples. Parenchyma is paratracheal. Root collar of a 15 cm-high therophyte, field, hill zone, Provence, France. *Nigella arvensis*, transverse section.

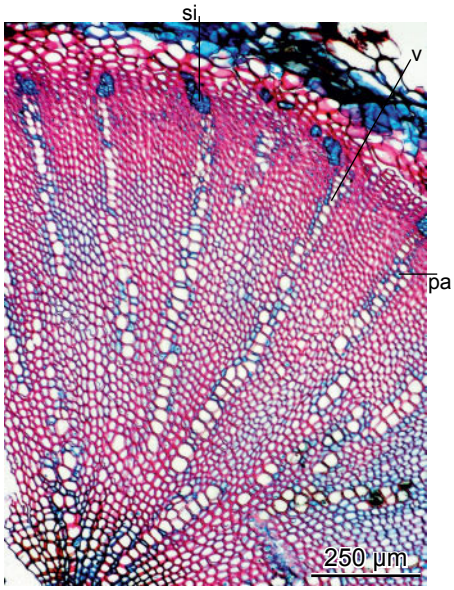



**Fig. 45.** Small vessels stay in long radial multiples. Parenchyma is paratracheal. Root collar of a 25 cm-high therophyte, garden, hill zone, Switzerland. *Nigella damascena*, transverse section.

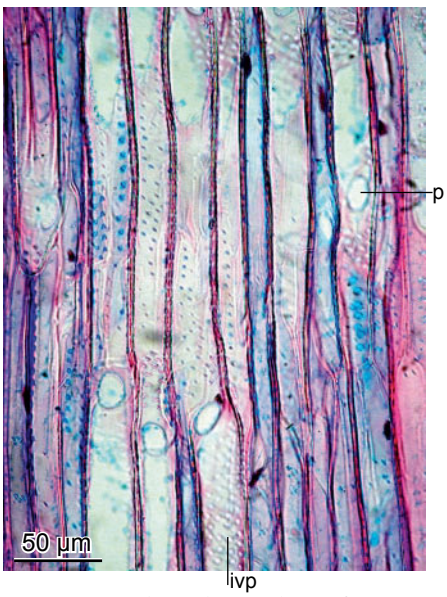
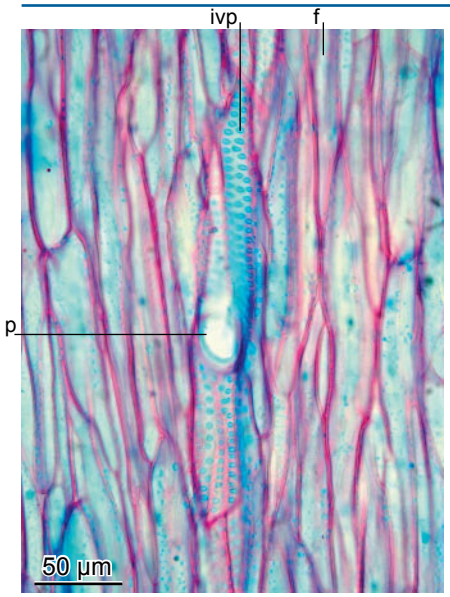
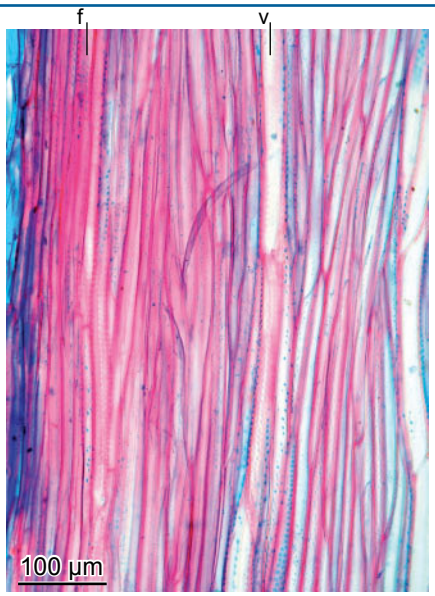


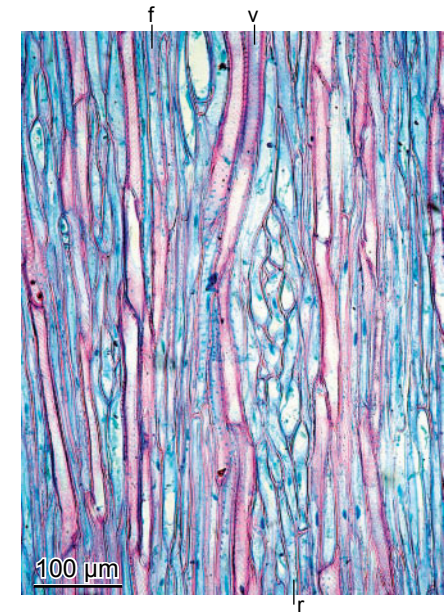

**Fig. 46.** Vessels with simple perforations and small, round inter-vessel pits. Root collar of a 20 cm-high therophyte, meadow, hill zone, Switzerland. *Nigella damascena*, radial section.

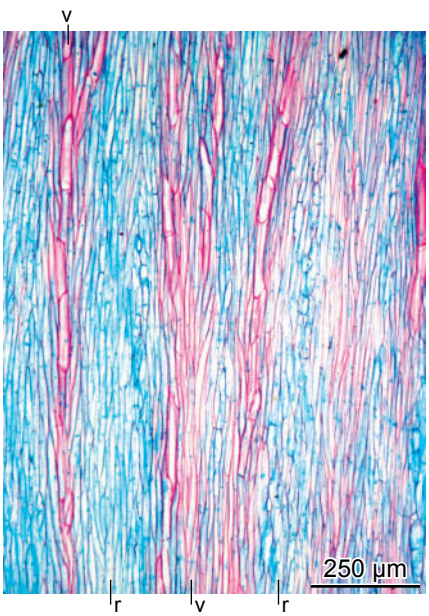



**Left Fig. 47.** Vessels with simple perforations and small, round intervessel pits. Fibers are short and thin-walled. Root collar of a 15 cm-high therophyte, field, hill zone, Piemont, Italy. *Consolida regalis*, radial section.

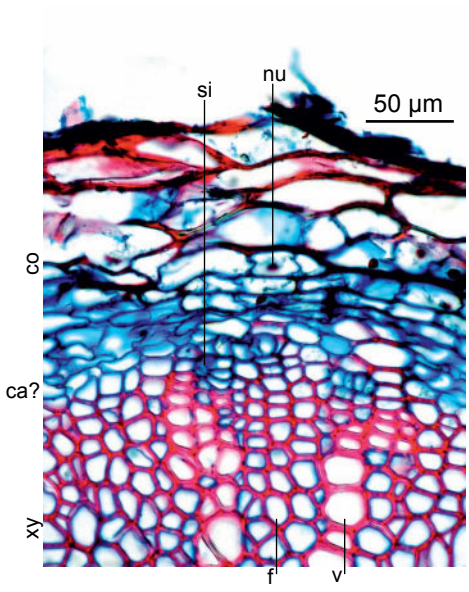
**Right Fig. 48.** Absent rays. Root collar of a 15 cm-high therophyte, field, hill zone, Provence, France. *Nigella arvensis*, tangential section.

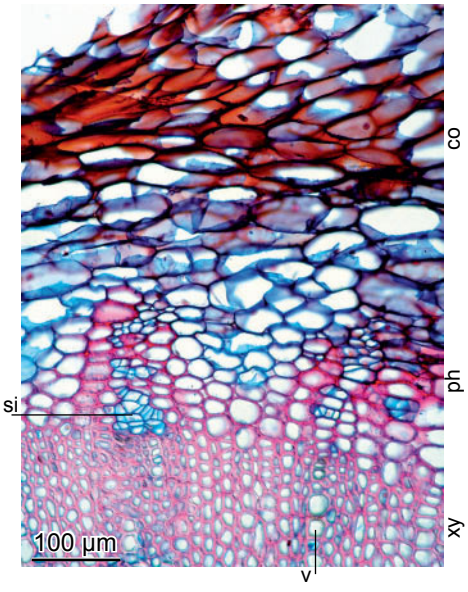



**Left Fig. 49.** Confluent rays with irregular cells. Root collar of a 20 cm-high therophyte, meadow, hill zone, Provence, France. *Adonis flammea*, tangential section.

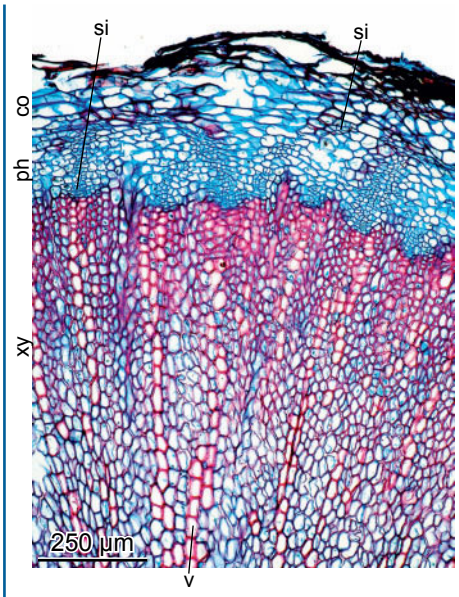
**Right Fig. 50.** Confluent rays with unlignified cell walls. Root collar of a 15 cm-high therophyte, field, hill zone, Piemont, Italy. *Consolida regalis*, tangential section.

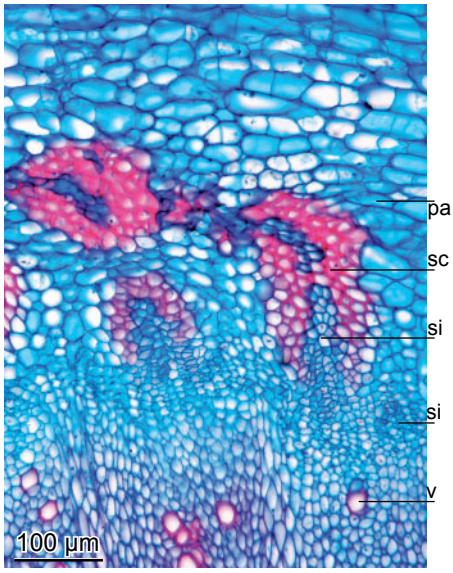



**Left Fig. 51.** Parenchyma cells are hard to distinguish from sieve tubes in the phloem. Cortex cells are much larger than those in the phloem. A phellem is absent. Root collar of a 15 cm-high therophyte, field, hill zone, Provence, France. *Nigella arvensis*, transverse section.

**Right Fig. 52.** Sieve-tube groups are surrounded by parenchyma cells with lignified (red) walls in the phloem. Cortex cells are much larger than those in the phloem. A phellem and the cambium are absent. Root collar of a 20 cm-high therophyte, meadow, hill zone, Switzerland. *Nigella damascena*, transverse section.




**Left Fig. 53.** Radial groups of small sieve tubes stand between larger parenchyma cells in the phloem. A phellem is absent. Root collar of a 20 cm-high therophyte, meadow, hill zone, Provence, France. *Adonis flammea*, transverse section.

**Right Fig. 54.** Sieve-tube groups are surrounded by thick-walled, lignified fibers (red) and thin-walled, unlignified parenchyma cells (blue). Root collar of a 15 cm-high therophyte, field, hill zone, Piemont, Italy. *Consolida regalis*, transverse section.

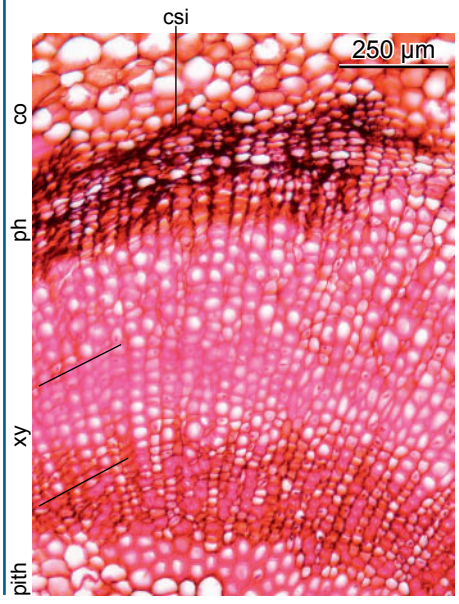
### 2.2 Perennial hemicryptophytes: *Hepatica*

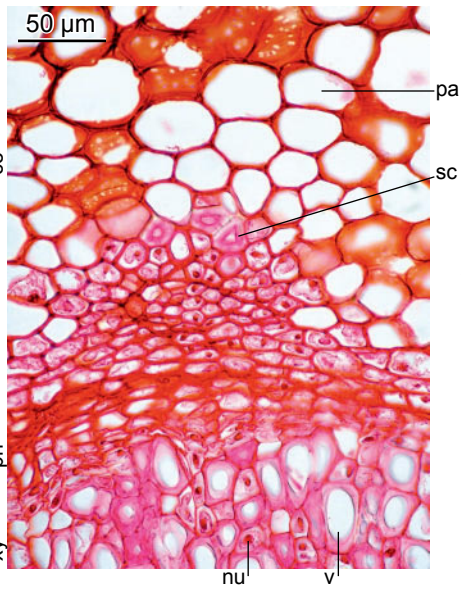
#### Characteristics of the xylem

*Hepatica nobilis* is a herbaceous hemicryptophyte with rhizomes. Annual rings can be recognized as an indistinct semi-ring porosity (**Fig. 55**). The fairly thick-walled (<20 µm), small vessels are solitary (**Fig. 56**). Vessel density is high in the zones between the parenchymatic zones (>200/mm$^2$). Intervessel pits are mostly round and sometimes slit-like. Fibers and rays are absent. Axial parenchyma is pervasive. Around the pith are thick-walled sclerenchyma cells in the form of a belt or in groups.

#### Characteristics of the phloem and the cortex

The phloem is simply structured. Sieve tubes and parenchyma cannot be distinguished. On the outside the phloem consists of groups of sclerenchyma (**Fig. 56**). The cortex contains large, thin-walled unlignified cells. The phellem is absent.




**Left Fig. 55.** Ring boundaries of the 2-3-year-old plant are indicated by a slight semi-ring porosity. Vessels are very small. Rhizome of an 8 cm-high hemicryptophyte, beech forest, mountain zone, Switzerland. *Hepatica nobilis*, transverse section.

**Right Fig. 56.** A group of sclerenchyma cells remains on the external side of the simply structured phloem. Rhizome of an 8 cm-high hemicryptophyte, beech forest, mountain zone, Switzerland. *Hepatica nobilis*, transverse section.

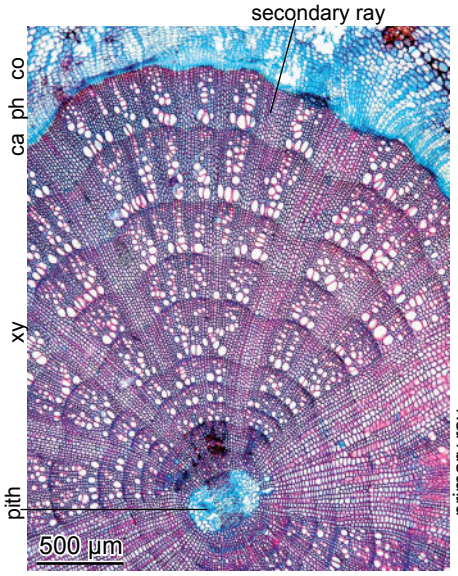
### 2.3 Perennial chamaephyte: *Helleborus*

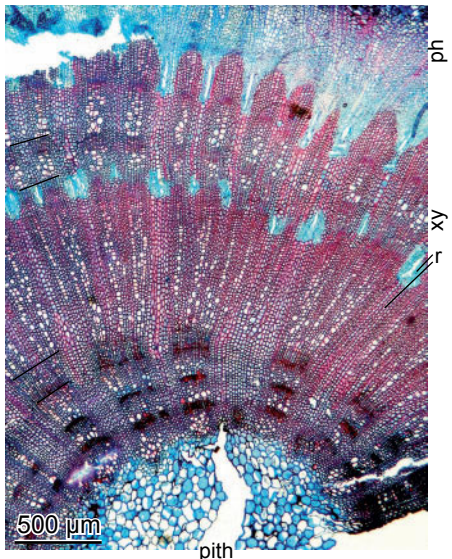
#### Characteristics of the xylem

Annual rings are distinct in both species (*Helleborus foetidus* and *H. viridis*; **Figs. 57** and **58**). Ring boundaries are defined by a semi-ring porosity and radially flat latewood fibers (**Figs. 59** and **60**). The tracheid groups at the ring boundaries of juvenile plants are rather special (**Fig. 59**). Vessels are solitary or in radial multiples (**Figs. 59** and **60**). Vessel diameter varies from 20-50 µm and vessel density is high in the zones between the large rays (>200/mm$^2$). Vessels have simple perforations (**Fig. 61**), thin-walled helical thickenings and round intervessel pits (**Fig. 62**). Fibers occur in two forms: most of them have very small pits with slit-like apertures, but those at the ring boundaries are tracheids with large, round pits (**Fig. 63**). Axial parenchyma is paratracheal (**Fig. 59**). Rays are very large and often confluent to fiber tissue (**Fig. 64**). All ray cells are upright (**Fig. 65**) and often unlignified at the ring boundaries on *Helleborus foetidus* (**Fig. 60**).

#### Characteristics of the phloem and the cortex

Both species have sieve-tube groups, often arranged in short radial rows (**Figs. 66** and **67**). Ray dilatations are distinct (**Figs. 66** and **67**). Phellem is absent (**Fig. 66**).




**Left Fig. 57.** Semi-ring-porous xylem with distinct rings and very large rays. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, France. *Helleborus viridis*, transverse section.

**Right Fig. 58.** Semi-ring-porous xylem with distinct rings. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, Piemont, Italy. *Helleborus foetidus*, transverse section.

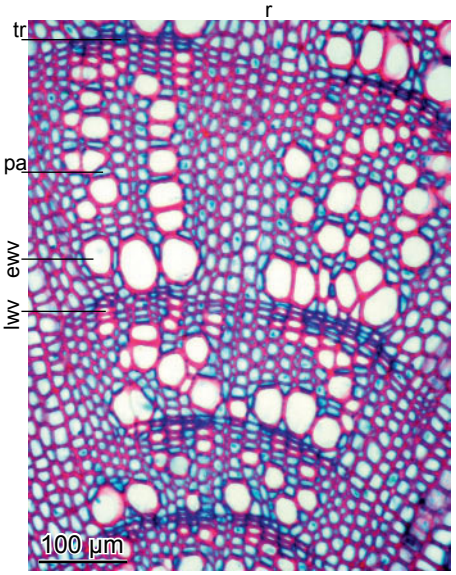



**Fig. 59.** Semi-ring-porous xylem with radial multiples. Axial parenchyma is paratracheal. See **Fig. 57**. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, France. *Helleborus viridis*, transverse section.

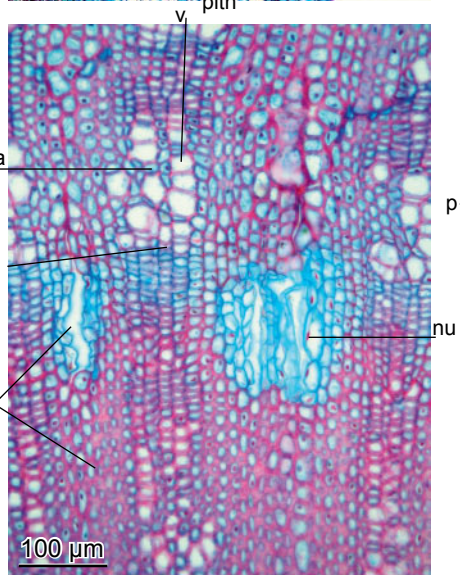



**Fig. 60.** Semi-ring-porous xylem with radial multiples. Ray cells at ring boundaries are unlignified. Axial parenchyma is paratracheal. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, Piemont, Italy. *Helleborus foetidus*, transverse section.

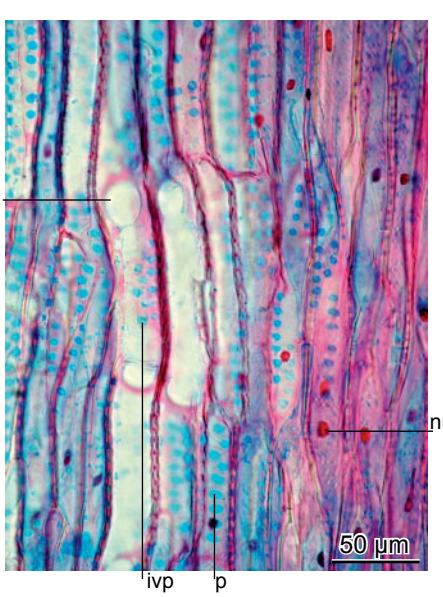
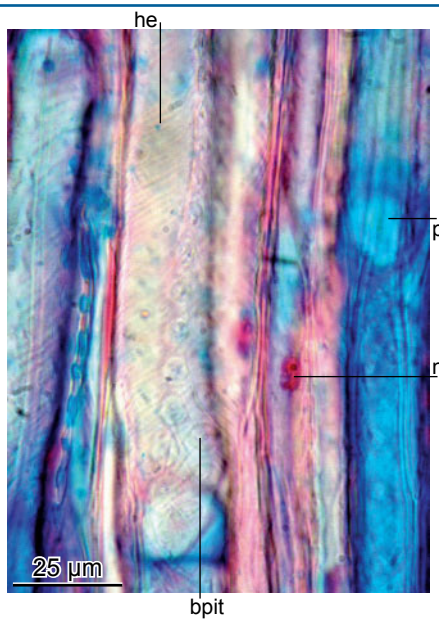
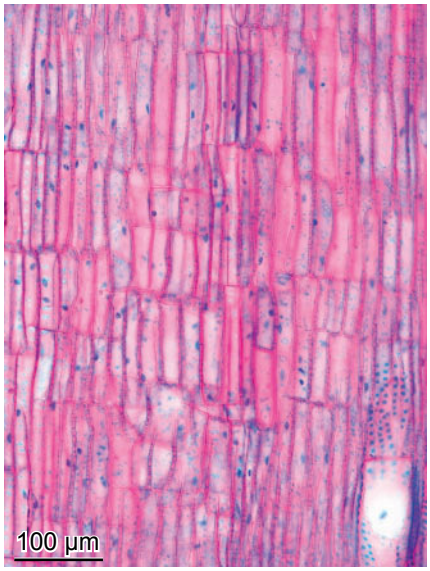



**Fig. 61.** Vessels with simple perforations and round inter-vessel pits. Fibers contain nuclei. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, Piemont, Italy. *Helleborus foetidus*, radial section.



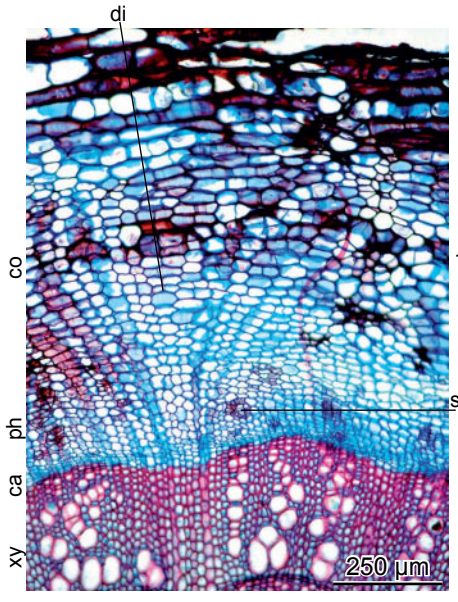
**Left Fig. 62.** Vessels with very fine helical thickenings. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, Piemont, Italy. *Helleborus foetidus*, radial section.

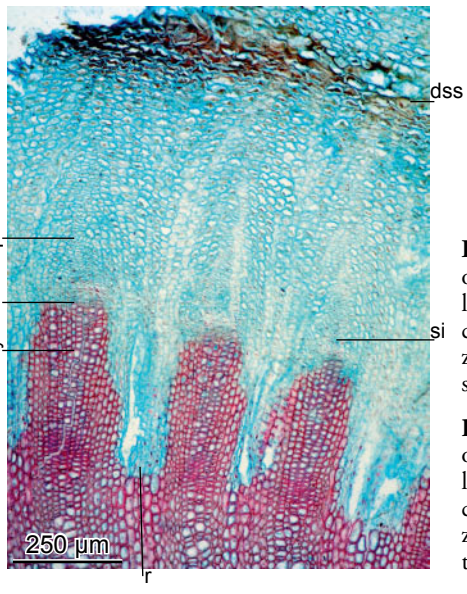
**Right Fig. 63.** Fibers with small and tracheids with large pits in the latewood. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, France. *Helleborus viridis*, radial section.




**Left Fig. 64.** Confluent large ray. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, France. *Helleborus viridis*, tangential section.

**Right Fig. 65.** Upright ray cells. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, France. Helleborus *viridis*, radial section.




**Left Fig. 66.** Phloem with small groups of sieve tubes and ray dilatations. A phellem is absent. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, France. *Helleborus viridis*, transverse section.

**Right Fig. 67.** Phloem with small groups of sieve tubes and ray dilatations. A phellem is absent. Stem basis of a 40 cm-high chamaephyte, limestone rock, mountain zone, Piemont, Italy. *Helleborus foetidus*, transverse section.

### 2.4 Perennial lianas and chamaephytes: *Clematis*

#### Characteristics of the xylem

Annual rings occur in the present material more-or-less distinct in all species. Ring boundaries of most species are defined by ring-porosity (**Figs. 68**, **69** and **74**) or semi-ring porosity (**Figs. 70-72**). Distinctly ring-porous are *C. campaniflora*, *C. cirrhosa*, *C. vitalba* (**Fig. 68**) and *C. viticella* (**Fig. 69**). All the others are more-or-less semi-ring-porous, never diffuse-porous. Vessels are solitary or in small groups, especially in the latewood (vessel dimorphism). Vessel diameter varies greatly and is approximately 50 µm on the small upright *C. columbiana* (**Fig. 73**), 50-100 µm on upright chamaephytes and smaller lianas and 100-300 µm on larger lianas e.g. *C. vitalba* (**Fig. 68**). Vessel density is normally much higher in the latewood than in the earlywood. High vessel density occurs e.g. in *C. alpina* (earlywood <700/mm$^2$, latewood >1000/mm$^2$; **Fig. 70**) and low vessel density in *C. vitalba* (earlywood 150/mm$^2$, latewood 250/mm$^2$; **Fig. 68**). Since vessel density varies between individuals as well, a classification is difficult. Intervessel pits are large (5-7 µm), predominantly round but the apertures are sporadically slit-like (**Fig. 75**). Helical thickenings were observed primarly in fiber-like cells with large pits (tracheids or vascular tracheids) in *C. alpina* ssp. *sibirica*, *C. flammula*, *C. hirsutissima* and *C. vitalba* (**Fig. 76**). Two distinct types of fibers occur: fibers with small, often slit-like pits (libriform fibers) and pits fibers with large, bordered pits (fiber tracheids, tracheids or vascular tracheids; **Fig. 77**). Since these types cannot be distinguished with certainty we summarize them under "fibers with large, bordered pits". All species contain fibers with large, bordered pits; fibers with small pits were observed only in *C. campaniflora*, *C. flammula* (**Fig. 80**), *C. montevidensis*, *C. hirsutissima* and *C. viticella*. All fibers are thin-walled (*C. alpina* ssp. *alpina*; **Fig. 78**) or thin- to thick-walled (all other species).

All species have apotracheal and paratracheal axial and some marginal parenchyma (**Figs. 78** and **79**). On slides stained only with safranin it is difficult to locate parenchyma cells on cross-sections. The primary form of vascular bundles is maintained by large rays (>10 cells; **Fig. 74**). Rays are lignified in *C. cirrhosa*, *C. montevidensis* (**Fig. 80**), *C. viticella* and *C. vitalba*. All the other species have thin-walled, unlignified ray cells (**Figs. 81** and **82**). Interfascicular cambia make rays larger and wedge-like in *Clematis alpina* (**Fig. 70**). Secondary rays begin abruptly and occur in *C. cirrhosa*, *C. flammula* (**Fig. 74**), *C. montevidensis*, *C. vitalba* and *C. viticella*. Ray cells are mostly square. Rays are extremely high (e.g. >10 cm in *C. vitalba*) and some have distinct sheet cells (**Figs. 80** and **81**). More-or-less distinct storying of vessels and fibers occurs primarely in older individuals. They contain no crystals.

#### Characteristics of the phloem and the cortex

Thin-walled, unlignified sieve tubes and parenchyma are annually layered (**Fig. 83**), but these cell types cannot be distinguished. Sclerenchyma cells form an arc outside an annual layer (**Fig. 84**), and are laterally present in groups (**Figs. 85** and **86**) or are missing (**Fig. 83**). Ray dilatations are distinct (**Figs. 84** and **85**). A phellem is present in all species. In most cases it forms annual layers consisting of large square, thin-walled cork cells and thicker-walled small phloem cells (**Fig. 87**). Rhytidioms (dead phloem and phellem) do not last long on the bark (**Fig. 88**).

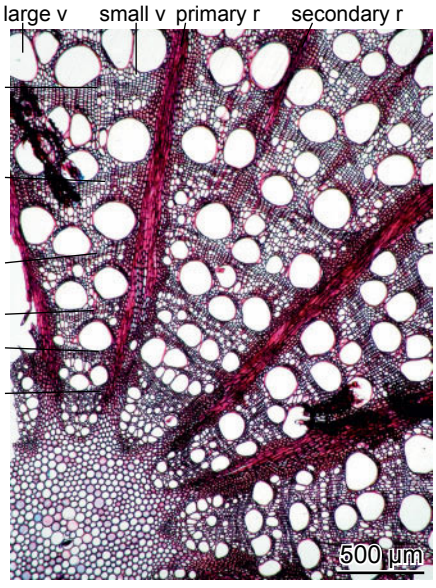



**Fig. 68.** Ring-porous wood with distinct annual rings. Stem of a climber (liana), hedge, hill zone, Trentino, Italy. *Clematis vitalba*, transverse section.

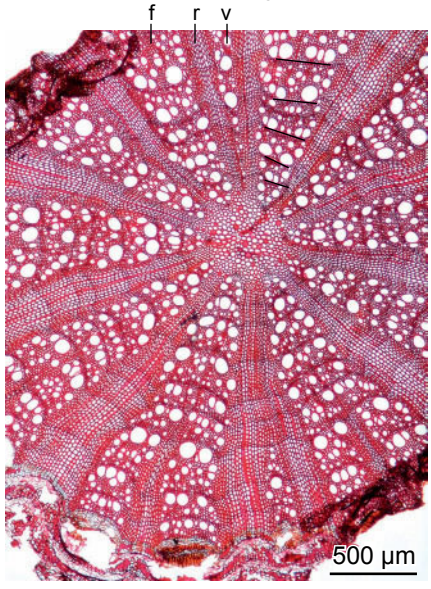



**Fig. 69.** Ring-porous wood with distinct annual rings with many primary and a few secondary rays. Ray width increases with increasing stem diameter. A few secondary rays are initiated. Stem of a climber (liana), on a wall, Mediterranean zone, Samos, Greece. *Clematis viticella*, transverse section.

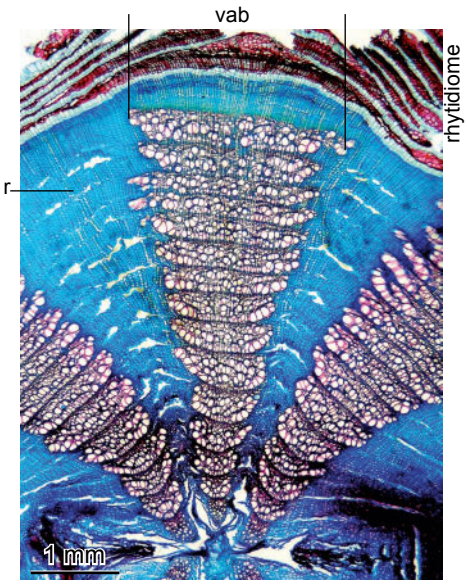
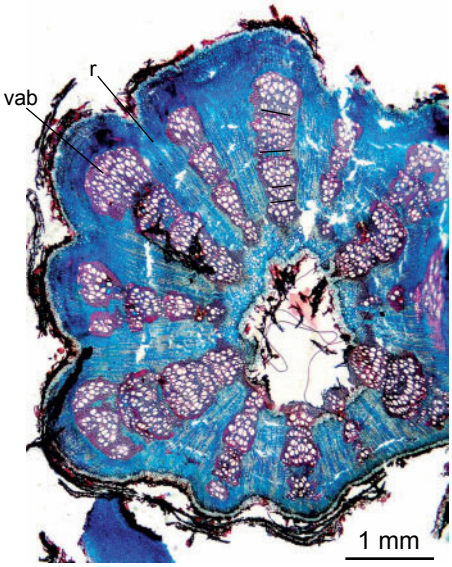
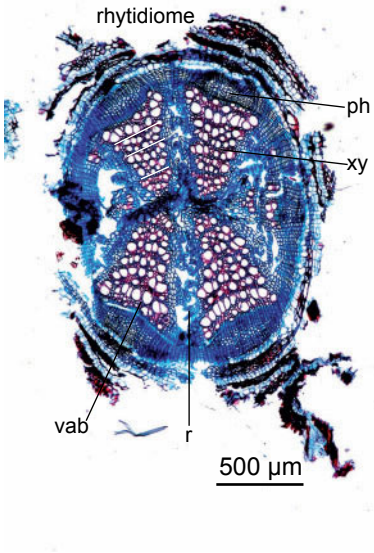


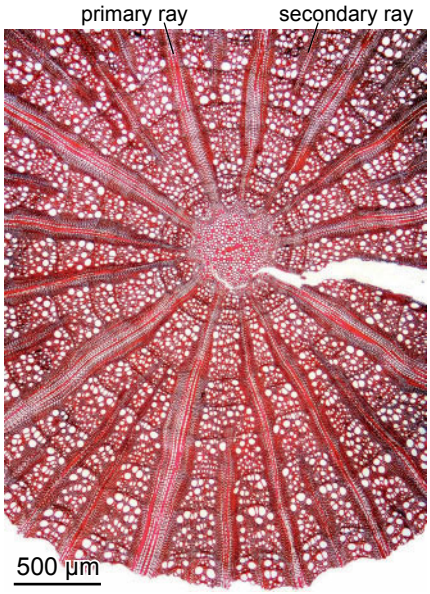

**Fig. 70.** Semi-ring-porous wood with distinct annual rings. Ray width and vessel fiber zones increase with increasing stem diameter. Ray cells are unlignified (blue). Stem of a climber (liana), spruce forest, subalpine zone, Grisons, Switzerland. *Clematis alpina* ssp. *alpina*, transverse section.




**Left Fig. 71.** Semi-ring-porous wood with distinct annual rings. Ray cells are unlignified. Stem of an 80 cm-high chamaphyte, *Ostrya* forest, hill zone, Ticino, Switzerland. *Clematis recta*, transverse section.

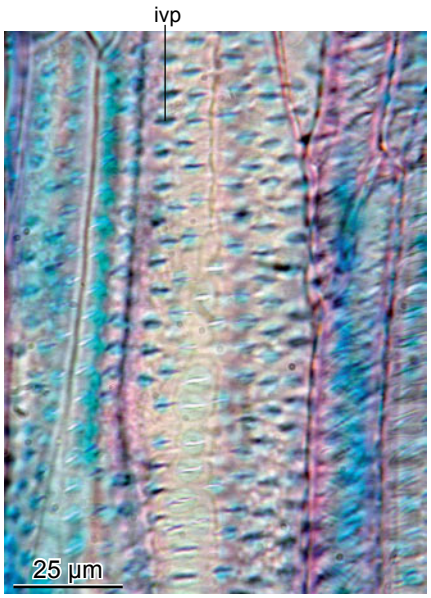
**Right Fig. 72.** Semi-ring-porous wood with distinct annual rings. Ray width increases slightly with increasing stem diameter. Ray cells are unlignified. Stem of a chamephyte, *Pinus ponderosa* forest, mountain zone, Colorado, USA. *Clematis hirsutissima*, transverse section.

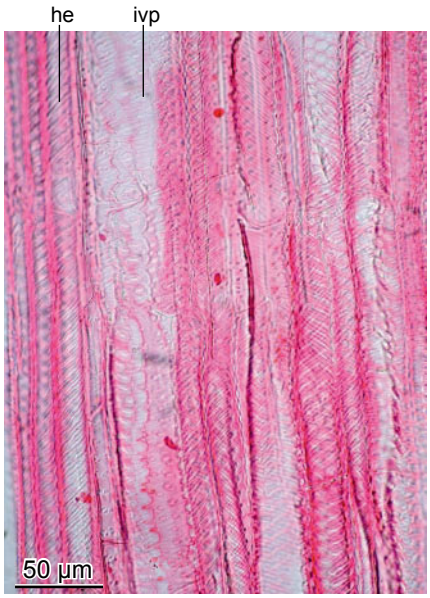



**Left Fig. 73.** Semi-ring-porous wood with distinct annual rings, ray width increases with increasing stem diameter. Ray cells are unlignified. Stem of a climber, dry meadow, mountain zone, Colorado, USA. *Clematis columbiana*, transverse section.

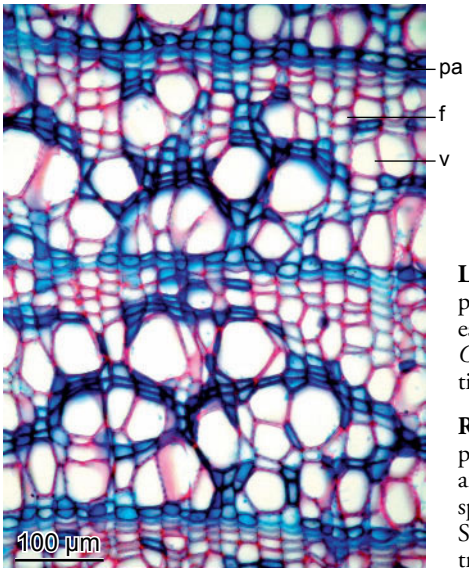
**Right Fig. 74.** Ring-porous wood with distinct annual rings. With increasing diameter more and more secondary rays are initiated. Stem of a climber (liana), hedge, Mediterranean zone, Provence, France. *Clematis flammula*, transverse section.



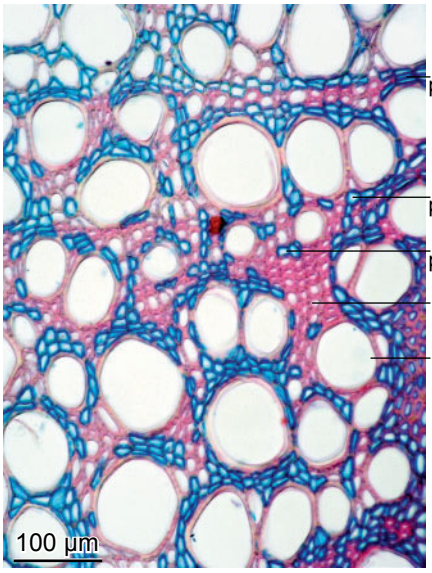

**Left Fig. 75.** Large intervessel pits with horizontally enlarged apertures. Stem of a climber (liana), *Ostrya* forest, hill zone, Ticino, Switzerland. *Clematis recta*, radial section.

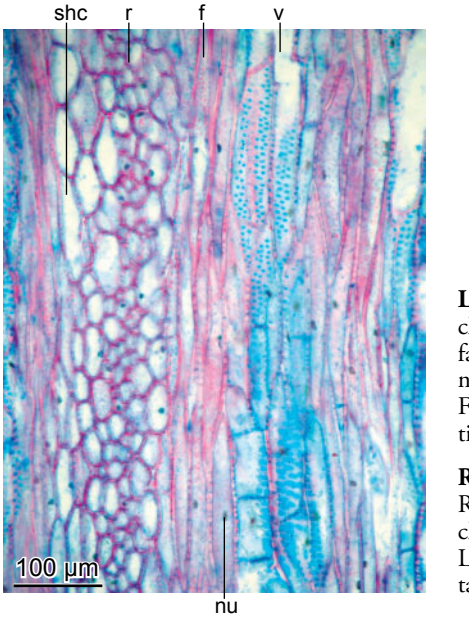
**Right Fig. 76.** Helical thickenings in vessels and vasicentric tracheids. Stem of a climber (liana), hedge, hill zone, Trentino, Italy. *Clematis vitalba*, radial section.




**Left Fig. 77.** Fibers with large bordered pits. Stem of a climber (liana), spruce forest, subalpine zone, Grisons, Switzerland. *Clematis alpina* ssp. *alpina*, tangential section.

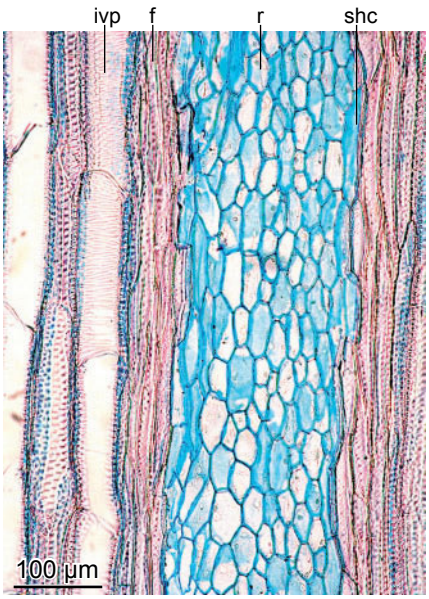
**Right Fig. 78.** Parenchyma is paratracheal, pervasive and marginal. Fibers and vessels are thin-walled. Stem of a climber (liana), spruce forest, subalpine zone, Grisons, Switzerland. *Clematis alpina* ssp. *alpina*, transverse section.

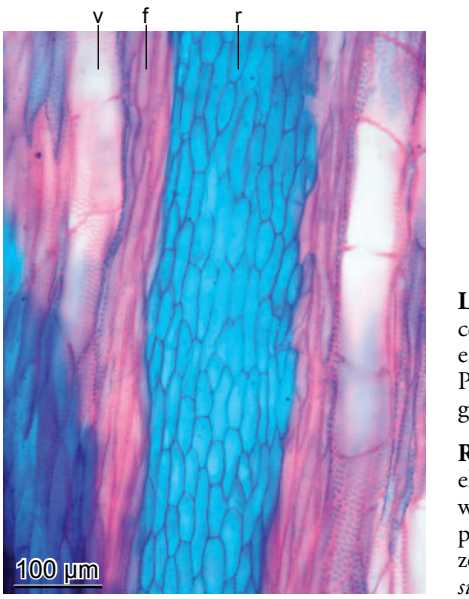



**Left Fig. 79.** Parenchyma arranged paratracheal and pervasive. Fibers and vessels are fairly thick-walled. Stem of a climber (liana), hedge, Mediterranean zone, Provence, France. *Clematis flammula*, transverse section.

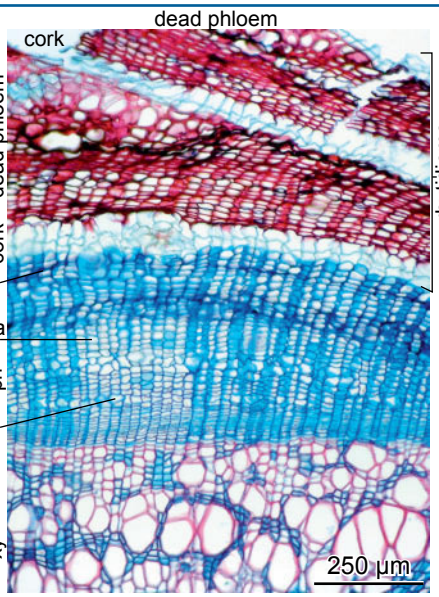
**Right Fig. 80.** Large ray with sheet cells. Ray cell walls are lignified. Stem of a climber (liana), hedge, arid zone, Valle della Luna, Argentina. *Clematis montevidensis*, tangential section.

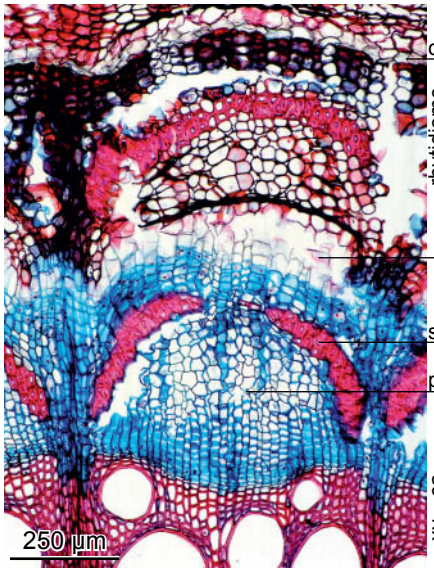



**Left Fig. 81.** Large ray with sheet cells. Ray cell walls are unlignified. Stem of a climber (liana), hedge, Mediterranean zone, Provence, France. *Clematis flammula*, tangential section.

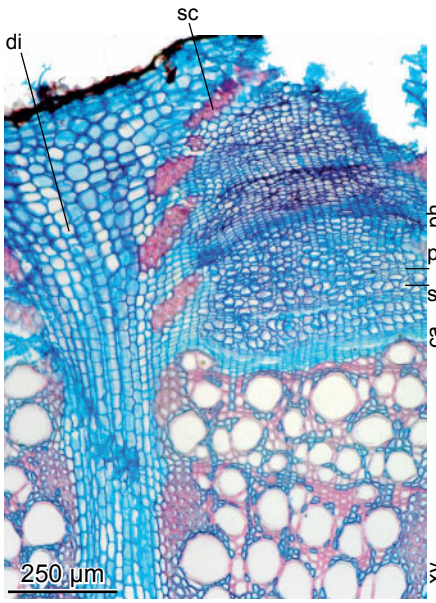
**Right Fig. 82.** Large ray with vertically elongated cells. Ray cell walls are thin-walled and unlignified. Stem of a chamephyte, *Pinus ponderosa* forest, mountain zone, Colorado, USA. *Clematis hirsutissima*, tangential section.

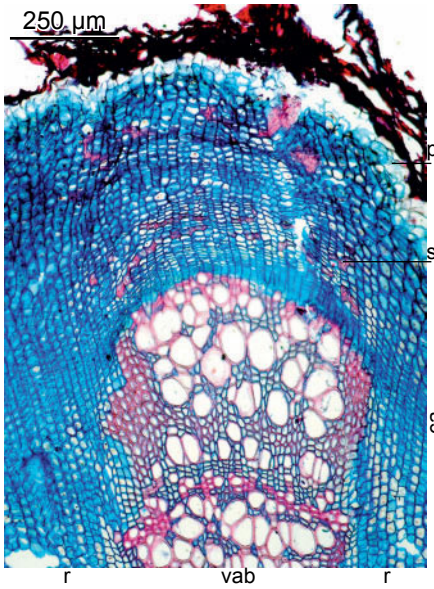



**Left Fig. 83.** Phloem with annual small rectangular sieve tube and round parenchyma layers. Sieve tubes collapse after the second year (dark blue tangential zones). Stem of a climber (liana), spruce forest, subalpine zone, Grisons, Switzerland. *Clematis alpina* ssp. *alpina*, transverse section.

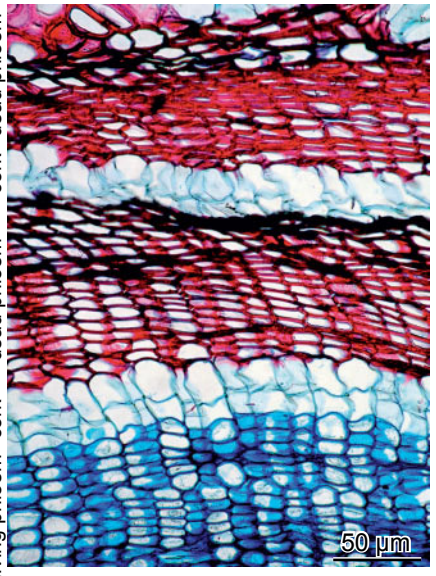
**Right Fig. 84.** The living phloem consists of small sieve tubes, larger parenchyma cells and an arc of thick-walled sclerenchyma cells (red). The phellogen produces cork cells (unstained rectangular cells outside the blue zone) after one year and was active after approximately 5 years. Stem of a climber (liana), hedge, hill zone, Trentino, Italy. *Clematis vitalba*, transverse section.

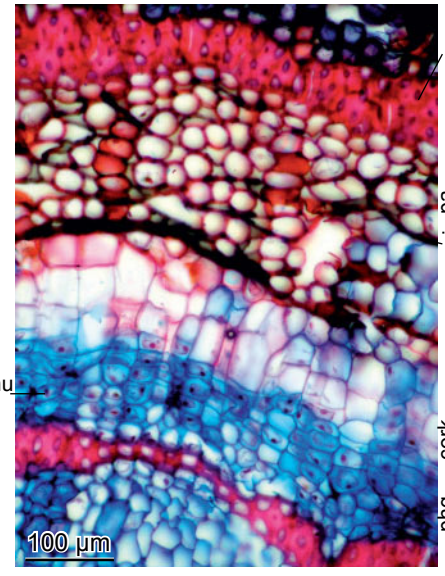



**Left Fig. 85.** The phloem consist of small sieve tubes, larger parenchyma cells and few groups sclerenchyma cells adjacent to the ray. Stem of a climber (liana), hedge, Mediterranean zone, Provence, France. *Clematis flammula*, transverse section.

**Right Fig. 86.** The living phloem consists of small sieve tubes, larger parenchyma cells and a few small groups of sclerenchyma cells. The phellogen becomes active after approximately 5 years. Stem of a chamephyte, *Pinus ponderosa* forest, mountain zone, Colorado, USA. *Clematis hirsutissima*, transverse section.




**Left Fig. 87.** Two phellem (cork) layers outside the phloem. The phellem consist of two rows of large, thin-walled cork cells and several rows of fairly thick-walled dead phloem cells. Stem of a climber (liana), spruce forest, subalpine zone, Grisons, Switzerland. *Clematis alpina* ssp. *alpina*, transverse section.

**Right Fig. 88.** Rhytidiome (cork and dead phloem) outside the phellogen with nuclei in the cells. The phellem consist of two rows of large, thin-walled cork cells. Outside the collapsed sieve tubes (dark line) are dead round parenchyma cells and a band of sclerenchyma cells. Stem of a climber (liana), hedge, hill zone, Trentino, Italy. *Clematis vitalba*, radial section.

**Discussion in relation to previous studies**

The xylem of the genera *Clematis* was the subject of 14 articles (Gregory 1994). The study of Smith (1979) concentrates on the stem construction (stele of 138 *Clematis* species). Sieber and Kutschera (1980) analysed *Clematis vitalba* and added a critical review of previous studies. Carlquist (1995) analysed 19 woody species (14 *Clematis*, 1 *Delphinium*, 1 *Helleborus*, 1 *Hydrastis*, 1 *Thalictrum*, 1 *Xanthorriza*). Bergmann (1944) studied the anatomy of annual flower stems and a few rhizomes of 23 *Ranunculus* species. In addition, Metcalfe and Chalk (1957) describe briefly cross-sections of 9 rhizomes of herbaceous species. Holdheide (1951) described the bark of *Clematis vitalba*.

Previous studies are based on a few woody species and are mainly concentrating on the genus *Clematis*. In contrast, the present study includes many annual and perennial herbaceous species of different life forms from different vegetation zones and relates them to *Clematis*. The anatomy within the family of Ranunculaceae is very diverse. The present large material basis enables the formation of anatomical groups.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **63** |
| 1 | growth rings distinct and recognizable | 32 |
| 2 | growth rings absent | 27 |
| 2.1 | only one ring | 4 |
| 2.2 | without secondary growth | 16 |
| 3 | ring-porous | 8 |
| 4 | semi-ring-porous | 28 |
| 5 | diffuse-porous | 6 |
| 7 | vessels in diagonal and/or radial patterns | 1 |
| 9 | vessels predominantly solitary | 23 |
| 9.1 | vessels in radial multiples of 2-4 common | 2 |
| 10 | vessels in radial multiples of 4 or more common | 2 |
| 11 | vessels predominantly in clusters | 58 |
| 13 | vessels with simple perforation plates | 63 |
| 20 | intervessel pits scalariform | 5 |
| 20.1 | intervessel pits pseudoscalariform to reticulate | 2 |
| 21 | intervessel pits opposite | 2 |
| 36 | helical thickenings present | 29 |
| 39.1 | vessel cell-wall thickness >2 µm | 15 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 26 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 28 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 8 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 7 |
| 50 | <100 vessels per mm$^2$ in earlywood | 21 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 37 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 5 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 2 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 11 |
| 60.1 | fibers absent | 41 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 16 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 14 |
| 65 | septate fibers present | 1 |
| 68 | fibers thin-walled | 5 |
| 69 | fibers thick-walled | 3 |
| 70 | fibers thin- to thick-walled | 13 |
| 75 | parenchyma absent or unrecognizable | 4 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 13 |
| 79 | parenchyma paratracheal | 19 |
| 79.1 | parenchyma pervasive | 41 |
| 89 | parenchyma marginal | 9 |
| 97 | ray width predominantly 1-3 cells | 2 |
| 98 | rays commonly 4-10-seriate | 2 |
| 99 | rays commonly >10-seriate | 59 |
| 99.1 | vascular-bundle form remaining | 54 |
| 99.2 | stem lobed | 1 |
| 100.1 | rays confluent with ground tissue | 13 |
| 100.2 | rays not visible in polarized light | 53 |
| 105 | ray: all cells upright or square | 57 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 3 |
| 110 | rays with sheet cells (tangential section) | 8 |
| 117 | rayless | 40 |
| 120 | storied axial tissue (parenchyma, fibers, vessels, tangential section) | 11 |
| R1 | groups of sieve tubes present | 35 |
| R2 | groups of sieve tubes in tangential rows | 25 |
| R3 | distinct ray dilatations | 12 |
| R4 | sclereids in phloem and cortex | 14 |
| R6 | sclereids in radial rows | 2 |
| R6.1 | sclereids in tangential rows | 5 |
| R8 | with crystal druses | 1 |
| R10 | phloem not well structured | 25 |
| R14 | cortex with aerenchyma | 3 |
| P1 | with medullary phloem or vascular bundles | 2 |

# Resedaceae



**Number of species, worldwide and in Europe**

The Resedaceae family includes 6 genera and 70 species. All species occur in the northern hemisphere.

**Analyzed material**

Analyzed are the xylem of 9 and the phloem of 5 Resedaceae.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes (0.5-4 m) | 3 | 2 |
| Hemicryptophytes and geophytes | 5 | 6 |
| Therophytes | 1 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 2 | |
| Mediterranean | 2 | |
| Arid | 5 | |

**Analyzed species:**

*Caylusea hexagyna* (Frosk.) Green
*Ochradenus baccatus* Del.
*Randonia africana* Coss.
*Reseda lutea* L.
*Reseda luteola* L.
*Reseda phyteuma* L.
*Reseda scoparia* Brouss.
*Reseda suffruticosa* Loeff.
*Reseda villosa* Coss.

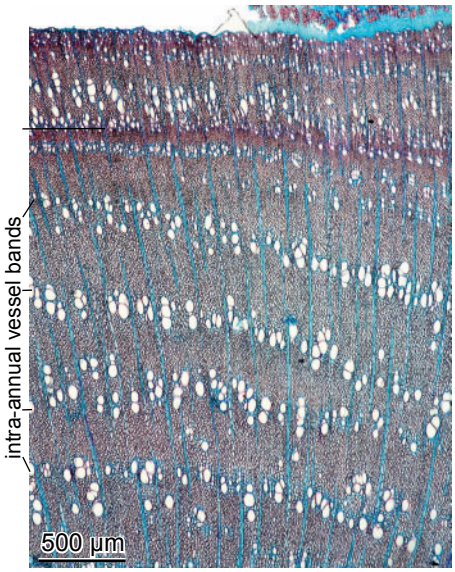
**Right:** *Reseda odorata* (photo: Hendriksma)

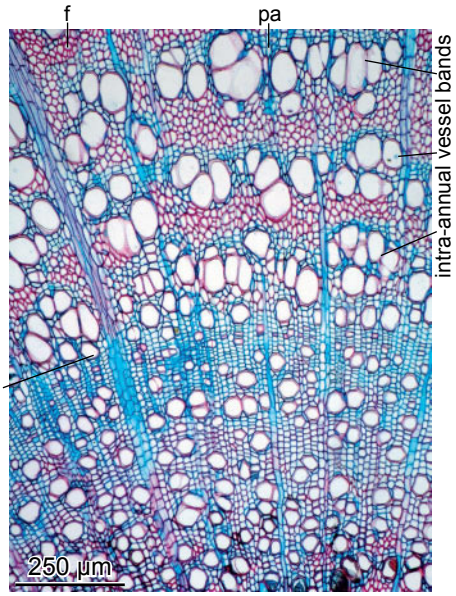
*Reseda luteola* (photo: Thor)

*Ochradenus baccatus*

### Characteristics of the xylem

Perennial species from temperate regions have annual rings. Characteristic of the genus *Reseda* are the intra-annual tangential rows of vessels (**Figs. 1** and **2**) and a slight semi-ring porosity (**Fig. 1**). The desert species *Randonia africana* and *Caylusea hexagyna* are diffuse-porous (**Fig. 3**). Vessel diameter varies between 50-100 µm. Helical thickenings are absent. All species have simple vessel perforations (**Fig. 5**). The intervessel pits are primarely round (**Fig. 4**), but *Reseda lutea* (**Fig. 5**) and *Ochradenus baccatus* have scalariform vessel pitting. Vestured pits are absent except in *Reseda suffruticosa* (**Fig. 4**). All species have paratracheal axial parenchyma (**Fig. 6**). Some species have marginal parenchyma (*Reseda luteola*, **Fig. 1** and *Randonia africana*, **Fig. 9**). All species contain fibers with reduced pit borders (<3 µm) and round to slit-like apertures on radial and tangential walls (libriform fibers). Tension wood (**Fig. 7**) is unique to *Reseda suffruticosa* while included sieve-tube groups occur only in *Reseda scoparia* (**Fig. 8**). Ray width varies from uniseriate (*Reseda suffruticosa*), to 3-seriate (**Fig. 10**). Rays are predominantly heterocellular (**Fig. 11**). Only *Reseda suffruticosa* and *Ochradenus baccata* have rays with exclusively upright and square cells. Crystals are absent.




**Left Fig. 1.** Xylem with tangential vessel bands. 70 cm-high, fast growing plant on a ruderal site, submediterranean zone, southwestern Alps. *Reseda lutea*, transverse section.

**Right Fig. 2.** Semi-ring-porous xylem with tangential vessel bands, paratracheal parenchyma and rays with a width of 1-4 cell rows. 30 cm-high plant, gravel place, the hill zone, southern Alps. *Reseda luteola*, transverse section.

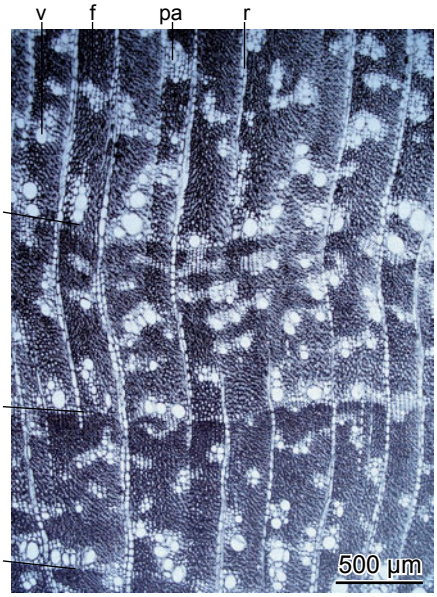



**Fig. 3.** Semi-ring-porous xylem with paratracheal parenchyma and thick-walled fibers. 1 m-high desert shrub in northern Africa. *Randonia africana*, transverse section. See Neumann et al. (2001).

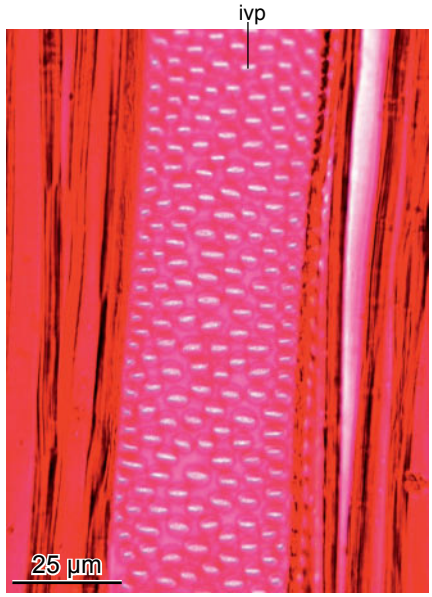
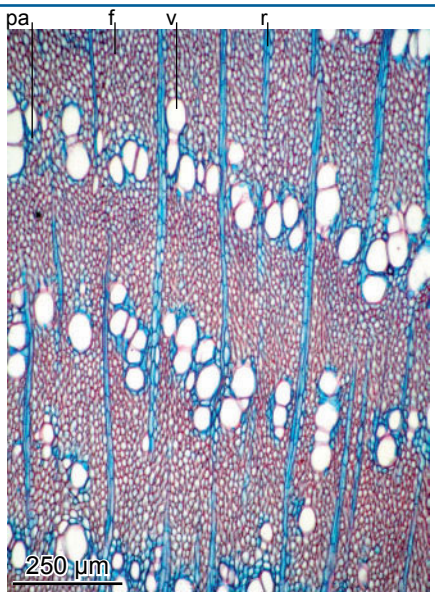
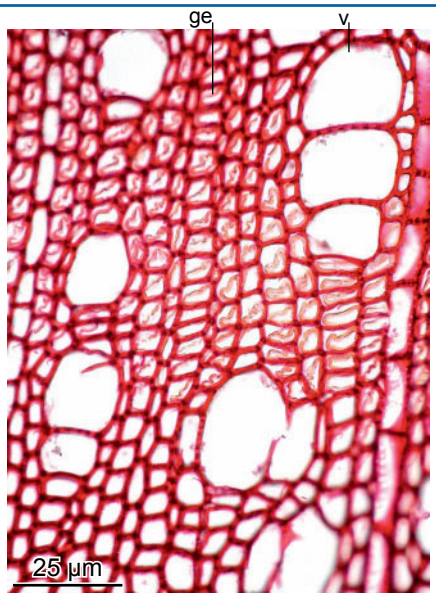



**Fig. 4.** Vestured pits on a vessel-cell wall of a 50 cm-high plant with a woody basis, ruderal site, Central Spain. *Reseda suffruticosa*, radial section.

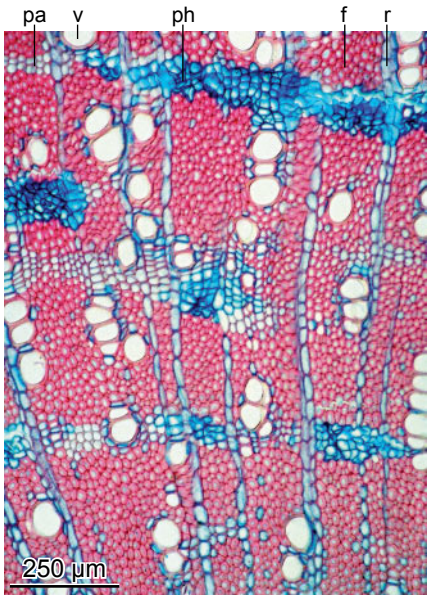
**Fig. 5.** Simple vessel perforation and vessel pits with elongated openings (scalariform vessel pits). 30 cm-high plant, gravel place, hill zone, southern Alps. *Reseda luteola*, radial section.

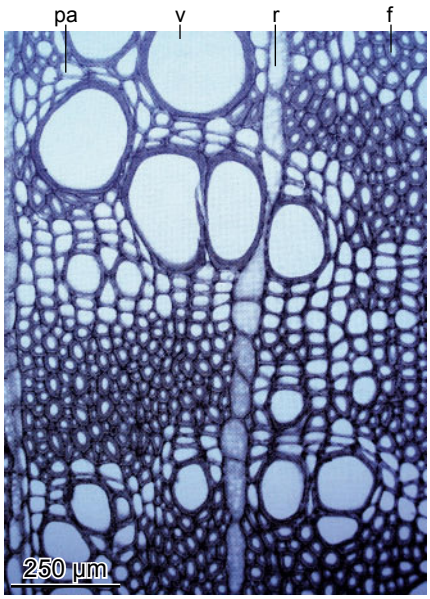



**Left Fig. 6.** Paratracheal parenchyma surround vessel clusters orientated in intra-annual tangential bands. 70 cm-high, fast growing plant, ruderal site, submediterranean zone, southwestern Alps. *Reseda lutea*, transverse section.

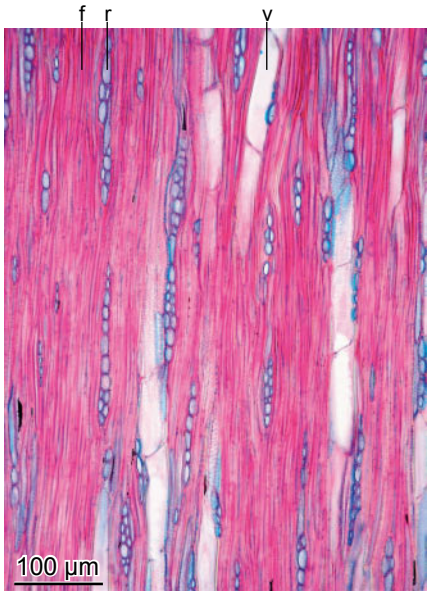
**Right Fig. 7.** Gelatinous fibers (tension wood) in fibers of the annual shoot of a 50 cm-high biannual plant, dry ruderal site, arid zone, Marokko. *Reseda villosa*, transverse section.

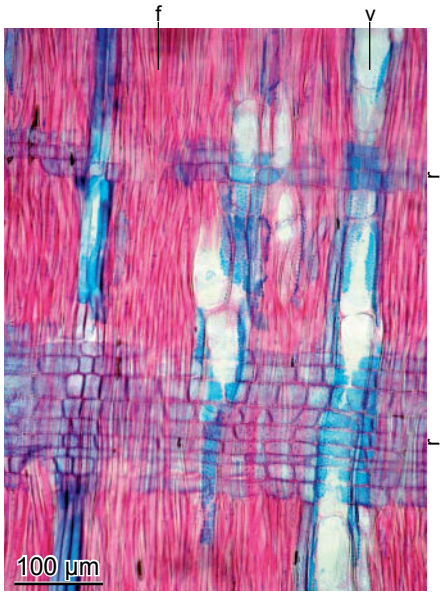



**Left Fig. 8.** Included groups of sieve tubes (included phloem) in a tissue with thick-walled fibers and parenchyma arranged in tangential groups. Parenchyma is primarely paratracheal but can also be apotracheal. 50 cm-high plant, ruderal site, thermophuile zone, subtropical climate, Gomera, Canary Islands. *Reseda scoparia*, transverse section.

**Right Fig. 9.** Semi-ring-porous wood with parenchyma arranged in tangential and marginal groups. 1 m-high shrub, desert of northern Algeria. *Randonia africana*, transverse section. See Neumann et al. (2001).




**Left Fig. 10.** Homocellular and heterocellular rays with 1-3 cells. 50 cm-high plant, ruderal site, thermophile zone, subtropical climate, Gomera, Canary Islands. *Reseda scoparia*, tangential section.

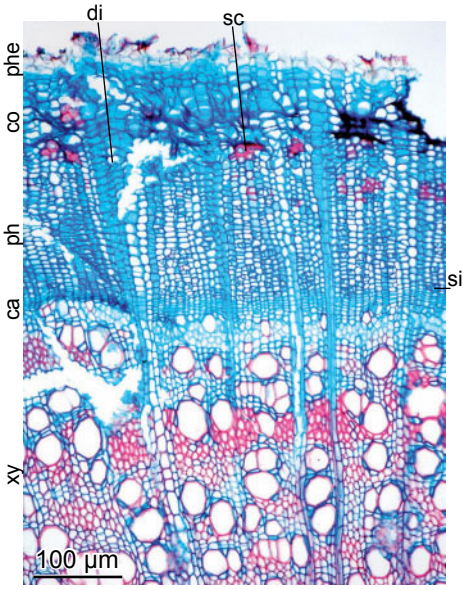
**Right Fig. 11.** Slightly heterocellular ray (lower part in the picuture) with some rows of procumbent and square cells. 50 cm-high plant, ruderal site, thermophile zone, subtropical climate, Gomera, Canary Islands. *Reseda scoparia*, radial section.

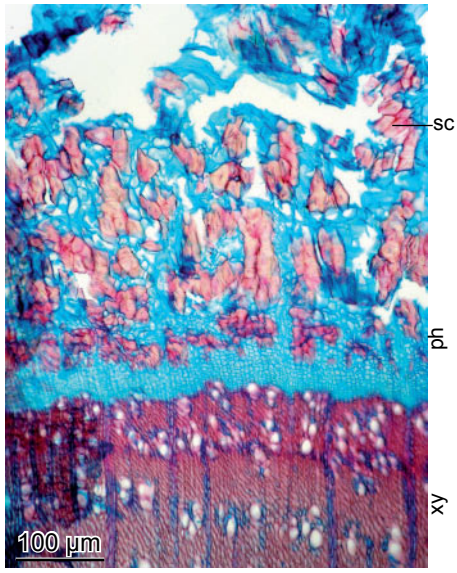
### Characteristics of the phloem and the cortex

The phloem and the cortex are in the majority of analyzed species simply structured by the radial arrangement of parenchyma and sieve tubes. Groups of sclereids occur in all species and are small (**Fig. 12**) except in *Reseda luteola* where they occupy the major part of the bark (**Fig. 13**).

### Ecological trends in the xylem and phloem

Ecological trends could not be recognized in the limited amount of sample material analyzed.




**Left Fig. 12.** Bark with radially oriented rows of parenchyma cells, groups of small sieve tubes and a few sclerenchyma cells (red), located in the outer part of the phloem. Rays are slightly dilated. 30 cm-high plant on a gravel place in the hill zone of the southern Alps. *Reseda luteola*, transverse section.

**Right Fig. 13.** Intensively sclerotized bark. Sclerenchyma cells have extremely thick cell walls. 70 cm-high, fast growing plant on a ruderal site in the submediterranean zone of the southwestern Alps. *Reseda lutea*, transverse section.

### Discussion in relation to previous studies

Carlquist (1998) analyzed the xylem of 7 Resedaceae species (*Caylusea hexagyna*, *Ochradenus baccatus*, *Oligomeris linifolia*, *Reseda alba*, *R. crystallina*, *R. lutea* and *R. luteola*). Neumann et al. (2004) studied 3 shrubs from the arid Sahara (*Randonia africana*, *Ochradenuns baccatus*, *Reseda villosa*); Fahn *et al.* (1986) recorded the wood anatomy of the desert shrub *Ochradenus baccatus*. Schweingruber (1990) studied the dwarf shrub *Reseda suffruticosa* and the hemicryptophyte *Reseda luteola* from Central and southern Europe.

The present study confirms the findings of all previous analyses. New is the detection of included phloem in the genus *Reseda* (*Reseda scoparia*).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **9** |
| 1 | growth rings distinct and recognizable | 5 |
| 2 | growth rings absent | 3 |
| 4 | semi-ring-porous | 4 |
| 5 | diffuse-porous | 4 |
| 6 | vessels in intra-annual tangential rows | 7 |
| 9 | vessels predominantly solitary | 2 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 11 | vessels predominantly in clusters | 8 |
| 13 | vessels with simple perforation plates | 9 |
| 20 | intervessel pits scalariform | 4 |
| 29 | vestured pits | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 9 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 9 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 2 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 9 |
| 68 | fibers thin-walled | 4 |
| 69 | fibers thick-walled | 2 |
| 70 | fibers thin- to thick-walled | 3 |
| 70.2 | tension wood present | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 79 | parenchyma paratracheal | 9 |
| 96 | rays exclusively uniseriate | 2 |
| 97 | ray width predominantly 1-3 cells | 7 |
| 98 | rays commonly 4-10-seriate | 1 |
| 105 | ray: all cells upright or square | 3 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 5 |
| 120 | storied axial tissue (parenchyma and vessels) | 1 |
| 134 | successive cambia, diffuse = foraminate | 1 |
| R6 | sclereids in radial rows | 6 |
| R6.1 | sclereids in tangential rows | 1 |
| R10 | phloem not well structured | 4 |

# Rhamnaceae



**Number of species, worldwide and in Europe**

The cosmopolitan Rhamnaceae family includes 45 genera with 850 species. In Europe, there are 4 genera (*Frangula*, *Paliurus*, *Rhamnus*, *Ziziphus*) with 19 species.

**Analyzed material**

Analyzed are the xylem and phloem of 7 genera with 28 species.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes (0.5-4 m) | 24 | numerous |
| Woody chamaephytes | 4 | 5 |
| **Plants analyzed from different vegetation zones:** | | |
| Boreal | 2 | |
| Hill and mountain | 9 | |
| Mediterranean | 9 | |
| Arid | 5 | |
| Subtropical | 3 | |

**Analyzed species:**

*Ceanothus arborescens* Greene
*Ceanothus fendleris* A. Grey
*Ceanothus hearstiorum* Hoover et Roof
*Ceanothus integerrimus* Hook et Arn
*Ceanothus velutinus* Dougl.
*Chrysothamnus nauseosus* Britton
*Chrysothamnus parryi* (A Grey) Greene
*Chrysothamnus viscidiflorus* (Hook.) Nutt.
*Colubrina californica* J.M. Johnst.
*Frangula alnus* Mill.
*Frangula azorica* Tutin
*Paliurus spina-christi* Mill.
*Rhamnus alaternus* L.
*Rhamnus alnifolia* Pursh.
*Rhamnus alpina* L.
*Rhamnus cathartica* L.
*Rhamnus crenulata* Ait.
*Rhamnus davurica* Pall.
*Rhamnus fallax* Boiss.
*Rhamnus glandulosa* Ait.
*Rhamnus myrtifolius* Willk.
*Rhamnus oleoides* L.
*Rhamnus pallasii* C.A. May
*Rhamnus pumila* Turra
*Rhamnus saxatilis* Jacq.
*Ziziphus jujuba* Miller
*Ziziphus oblongifolius* S. Moore
*Ziziphus spina-christi* (L.) Willd.

*Paliurus spina-christi* (photo: Zinnert)

*Rhamnus alaternus* (photo: Zinnert)

*Rhamnus pumila*

*Frangula alnus*

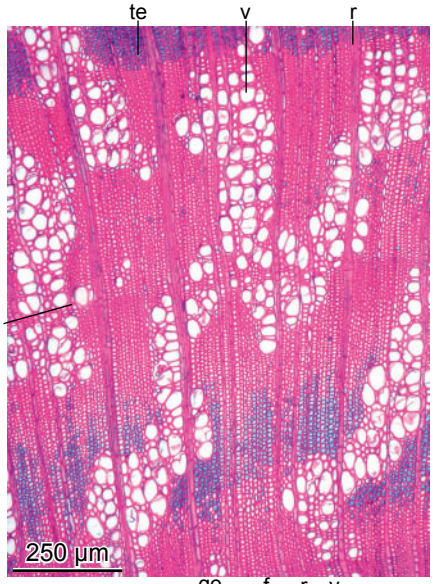
*Paliurus spina-christi*

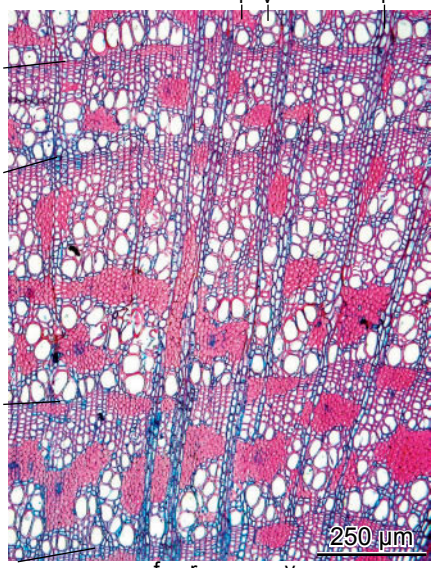
*Ziziphus spina-christi*

**Characteristics of the xylem**

Ring boundaries are distinct (**Figs. 1**, **2** and **4**) or at least recognizable (**Figs. 3** and **5**). Diffuse- to semi-ring-porosity is the dominant vessel distribution pattern within the family (e.g. **Figs. 1-8**). Characteristic of the genera *Ceanothus*, *Chrysothamnus* and *Rhamnus* are the diagonal to dendritic vessel distribution patterns (**Figs. 1-3** and **6**). Vessels are arranged solitary or in radial multiples in *Frangula*, *Paliurus* and *Ziziphus* (**Figs. 4**, **5** and **8**). Earlywood vessels with a diameter of 30-70 µm and a density of 150-200/mm$^2$ are characteristic of all species of the genera *Ceanothus*, *Chrysothamnus*, *Frangula* and *Rhamnus*. Vessel diameter is much larger and vessel density is lower (<50/mm$^2$) in *Paliurus* and *Ziziphus* (**Figs. 5** and **8**). Vessels of all species have simple perforations. Intervessel pits are round and arranged in alternating position. Helical thickenings occur in all genera (**Fig. 16**) except *Paliurus* and *Ziziphus*. Vessels of some species contain dark-staining substances (**Fig. 8**). In most species fibers with small pits with slit-like apertures are thin- and thin- to thick-walled (**Fig. 4**) or thick-walled (**Figs. 1-3**, **5** and **8-10**). Transitions between both features occur within individuals. The occurrence of tension wood is a genus-specific feature for all species analyzed (**Figs. 6** and **7**).

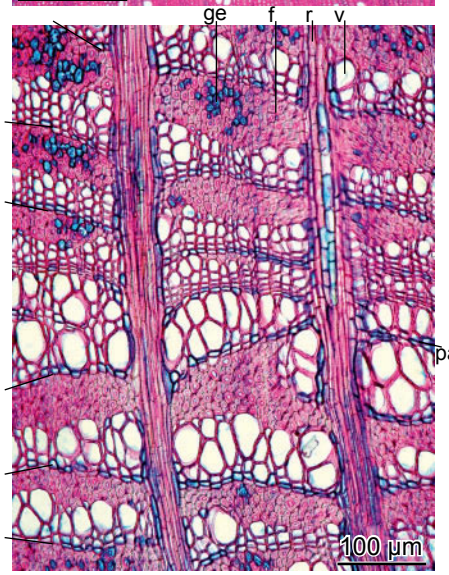
The distribution of axial parenchyma is often difficult to determine (**Figs. 1**, **4**, **6** and **7**), especially on slides stained only with safranin. Paratracheal parenchyma cells were observed in a few species of all genera. Paratracheal parenchyma is very distinct in *Paliurus* and *Ziziphus* (**Figs. 5**, **8** and **10**). A unicellular row of marginal (terminal) parenchyma was observed on a few species in the genera of *Colubrina*, *Paliurus*, *Rhamnus* (**Fig. 10**) and *Ziziphus* (**Fig. 8**). Ray width is variable. Uniseriate rays occur mainly in *Ziziphus* (**Fig. 11**), biseriate rays are present in most species (**Figs. 12** and **13**), 3-5-seriate rays occur in a few *Rhamnus* species (**Fig. 14**) and very large rays with sheet cells occur only in *Chrysothamnus viscidiflorus* (**Fig. 15**). Most species are characterized by either homocellular rays with procumbent cells or heterocellular rays with one to a few rows of square and upright cells (**Fig. 16**). Transitions between different types are frequent. Homocellular rays with exlusively upright cells were observed only in twigs (juvenile wood; **Fig. 17**) and in *Ziziphus spina-christi*.

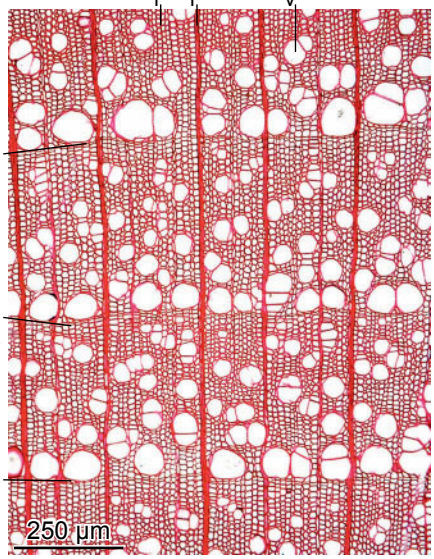



**Left Fig. 1.** Diffuse-porous xylem with a distinct annual ring boundary. Vessels are arranged in diagonal dendritic patterns. Stem of a 3 m-high shrub, hedge, Mediterranean, El Bosque, Andalusia, Spain. *Rhamnus alaternus*, transverse section.

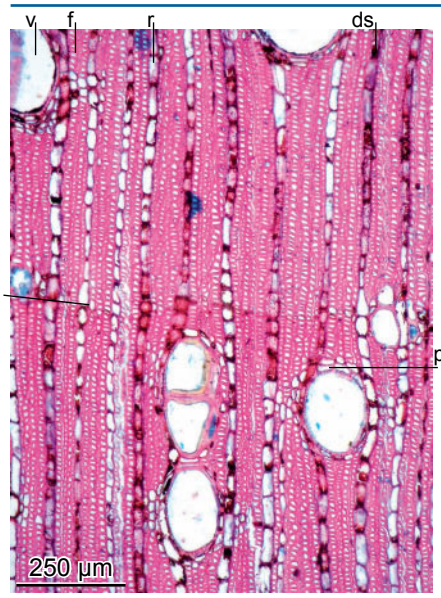
**Right Fig. 2.** Semi-ring-porous xylem. Most vessels are arranged in dendritic patterns. Fibers are thick-walled and located in groups. Stem of a 1 m-high shrub, *Pinus ponderosa* forest, semi-arid zone, Flagstaff, Arizona, USA. *Chrysothamnus nauseosus*, transverse section.

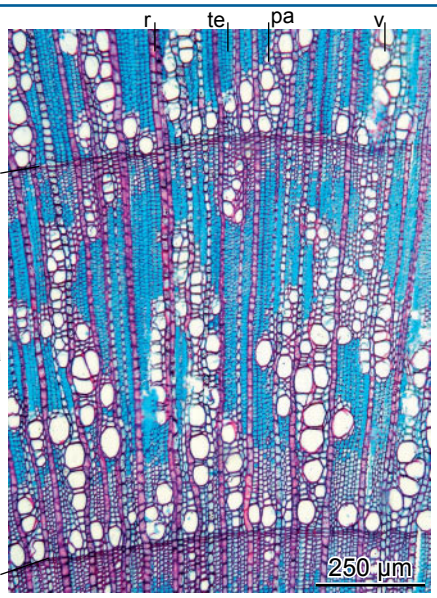



**Left Fig. 3.** Semi-ring-porous xylem. Intra-annual vessel groups are arranged in oblique, tangential patterns. Uniseriate rows of parenchyma cells surround the vessel groups. Stem of a 1 m-high shrub, Pinyon, dry lower timberline zone, Monte Vista, Colorado, USA. *Chrysothamnus viscidiflorus*, transverse section.

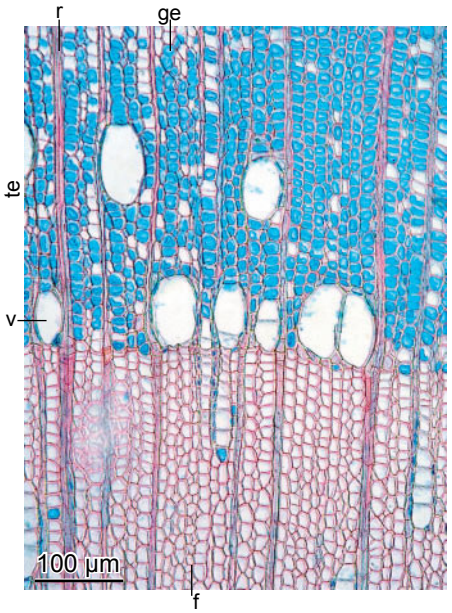
**Right Fig. 4.** Semi-ring-porous xylem. Vessels are arranged solitary and in short radial multiples. Parenchma cells are not recognizable. Stem of a 3 m-high shrub, beech forest, hill zone, Zürich, Switzerland. *Frangula alnus*, transverse section.

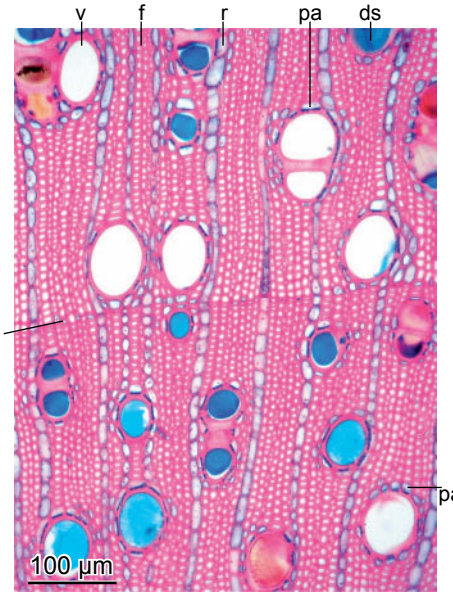



**Left Fig. 5.** Diffuse-porous xylem with a few thick-walled vessels (<50/mm²), thick-walled fibers and paratracheal parenchyma. Stem of a 2 m-high shrub, riparian, arid zone, Nizwa, Oman. *Ziziphus spina-christi*, transverse section.

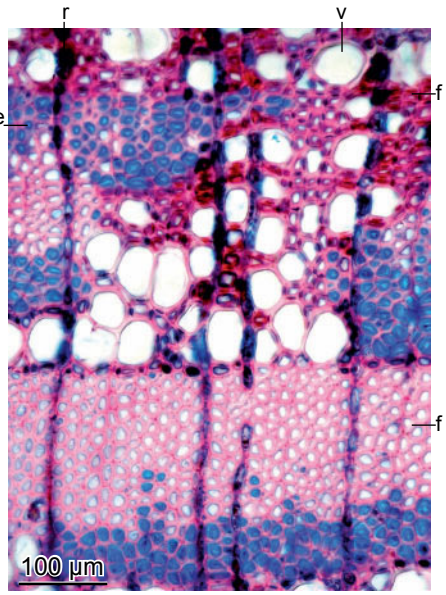
**Right Fig. 6.** Semi-ring-porous xylem with much tension wood. Stem of a 1 m-high shrub, Pinyon, dry lower timberline zone, Dinosaur, Colorado, USA. *Ceanothus velutinus*, transverse section.



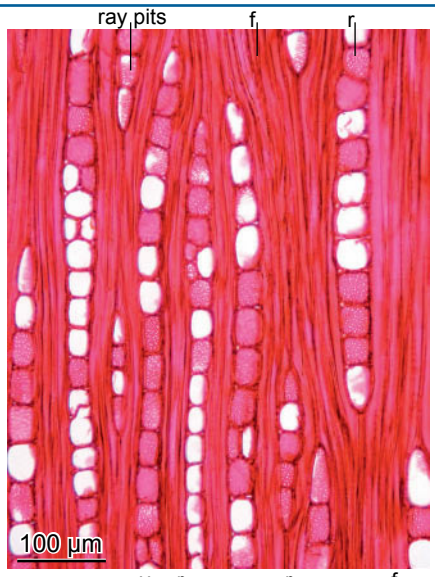

**Left Fig. 7.** Semi-ring-porous xylem with much tension wood in the earlwood. Stem of a 3 m-high shrub, beech forest, hill zone, Zürich, Switzerland. *Frangula alnus*, transverse section.

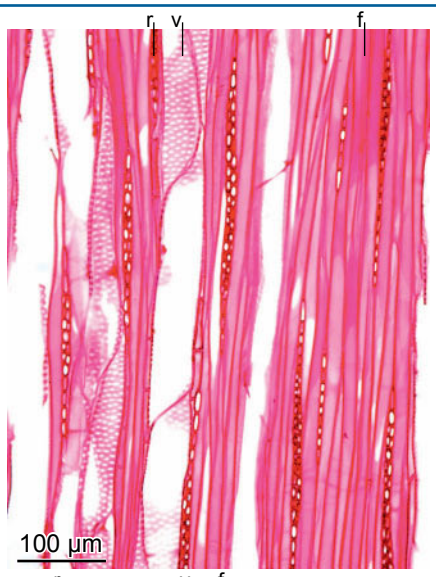
**Right Fig. 8.** Semi-ring-porous xylem. The thick-walled vessels are arranged solitary and are surrounded by paratracheal parenchyma and filled with a blue-stained substance. Stem of a 1.5 m-high shrub, dry meadow, hill zone, Tbilisi, Georgia. *Paliurus spina-christi*, transverse section.




**Left Fig. 9.** Thick-walled vessels surrounded by paratracheal parenchyma cells. Stem of a 1.5 cm-high shrub, shrub desert, arid zone, Mamoth, Arizona, USA. *Ziziphus oblongifolius*, transverse section.

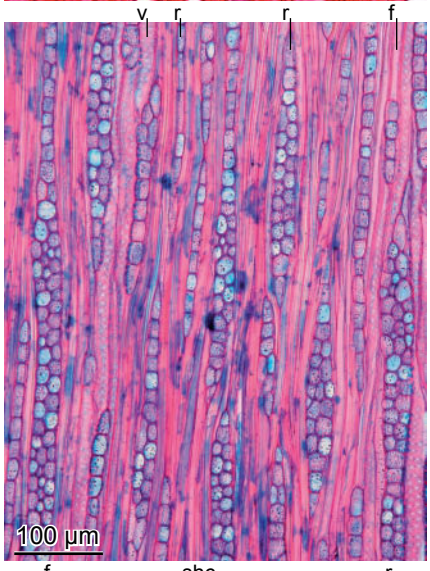
**Right Fig. 10.** Paratracheal and marginal parenchyma in a semi-ring-porous xylem with tension wood. Stem of a 30 cm-high dwarf shrub, dry rock field, submediterranean, Florence, Tuscany, Italy. *Rhamnus saxatilis*, transverse section.

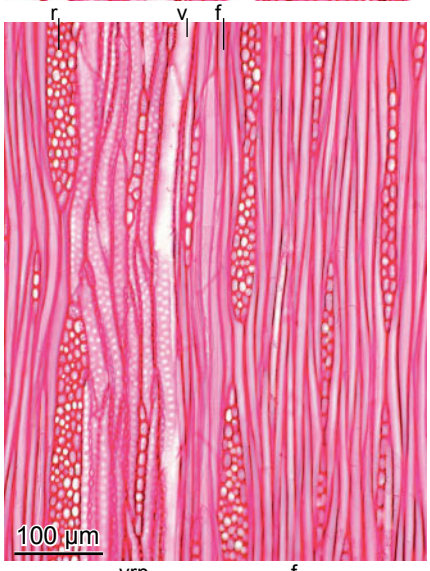



**Left Fig. 11.** Uniseriate rays consisting of large, round cells. Stem of a 2 m-high shrub, ruderal site, Mediterranean, Limasol, Cyprus, Greece. *Ziziphus jujuba*, tangential section.

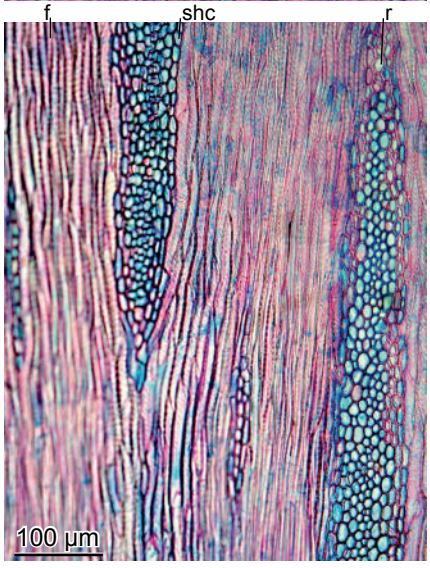
**Right Fig. 12.** Uni- and biseriate rays consisting of small, axially slightly elongated cells. Stem of a 3 m-high shrub, beech forest, hill zone, Zürich, Switzerland. *Frangula alnus*, tangential section.

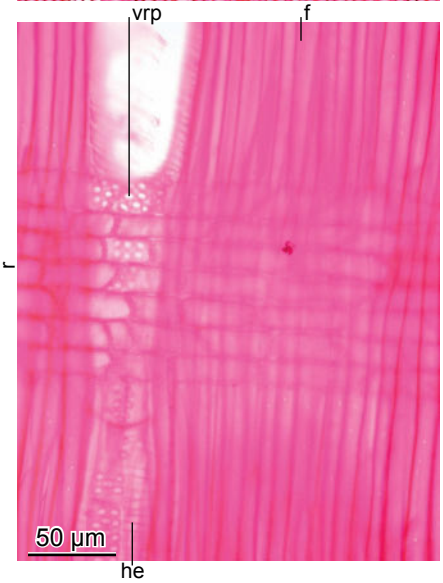



**Left Fig. 13.** 1-3-seriate rays consisting of round cells. Stem of a 1 m-high shrub, Pinyon, dry lower timberline zone, Dinosaur, Colorado, USA. *Ceanothus velutinus*, tangential section.

**Right Fig. 14.** 1-5-seriate rays consisting of small, round cells. Stem of a 2 m-high shrub, hedge, Mediterranean, Postojna, Bosnia. *Rhamnus fallax*, tangential section.



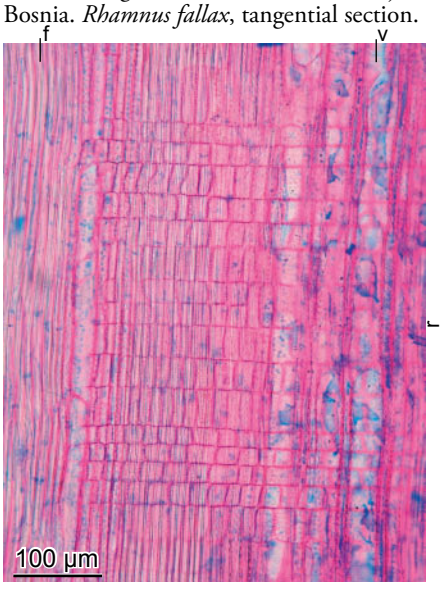




**Fig. 15.** Large rays with 9-11 cells in width, with lateral sheet cells. Stem of a 1 m-high shrub, Pinyon, dry lower timberline zone, Monte Vista, Colorado, USA. *Chrysothamnus viscidiflorus*, tangential section.

**Fig. 16.** Homocellular ray consisting of procumbent cells. Stem of a 3 m-high shrub, beech forest, hill zone, Zürich, Switzerland. *Frangula alnus*, radial section.

**Fig. 17.** Homocellular ray consisting of square and upright cells. Stem of a 50 cm-high dwarf shrub, Mediterranean, Botanical Garden Santa Barbara, California, USA. *Ceanothus hearstiorum*, radial section.

### Characteristics of the phloem and the cortex

Characteristic of well-grown individuals are the more-or-less tangentially arranged layers or groups of sclerenchyma. Continuous bands of sclerenchyma occur in *Paliurus* and *Ziziphus* (**Fig. 18**). Irregular bands were observed in *Ceanothus* (**Fig. 19**). Unique to *Chrysothamnus parryi* are the rectangular blocks of sclerenchyma (**Fig. 20**). Round, large to small lens-like groups occur in all genera except for *Paliurus* and *Ziziphus* (**Figs. 21-25**). The groups are surrounded by thin-walled parenchyma cells (**Figs. 23-25**). Alternating sieve-tubes/parenchyma layers of variable distinctness (**Fig. 19**) occur in all genera (**Figs. 21**) but are irregular in a few species (**Figs. 22-25**). Sieve-tube bands are often collapsed (**Fig. 23-25**). Prismatic crystals, if present, are integrated into or surround the sclerenchyma groups (**Fig. 26**). Crystal druses occur mostly in axial parenchyma cells or in rays (**Fig. 26**).

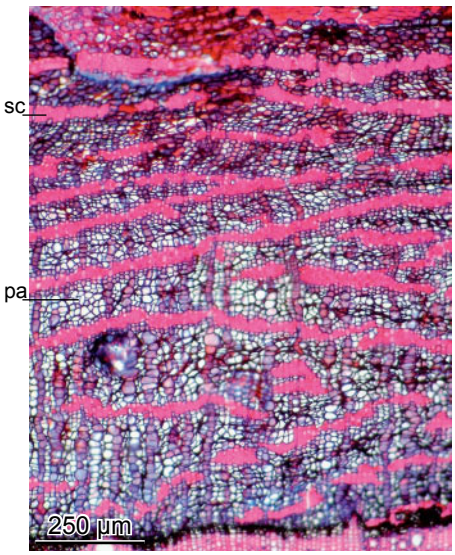



**Fig. 18.** Phloem with tangential bands of sclerenchyma cells. Stem of a 1.5 m-high shrub, hedge, Mediterranean, Provence, France. *Paliurus spina-christi*, transverse section.

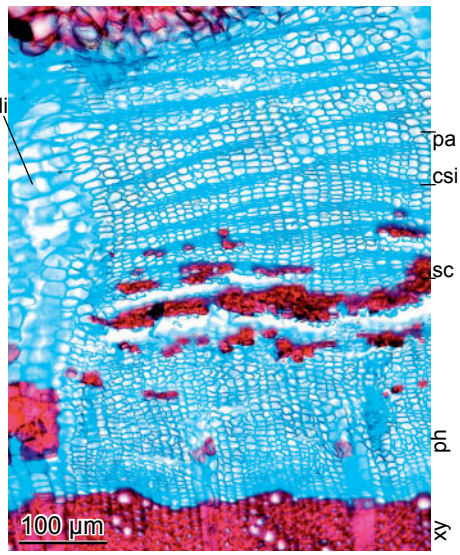



**Fig. 19.** Irregular bands of sclerenchymatic cells arranged lateral to a dilatation. Stem of a 50 cm-high dwarf shrub, Mediterranean, Botanical Garden Santa Barbara, California, USA. *Ceanothus arborescens*, transverse section.

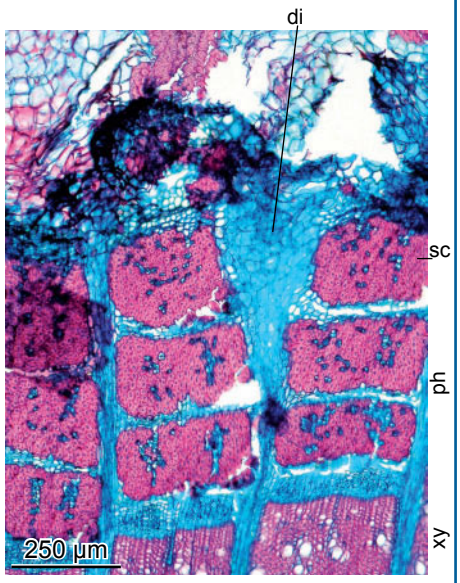



**Fig. 20.** Rectangular blocks of sclerenchyma cells located between unlignified dilated rays. Stem of a 50 cm-high dwarf shrub, shrub steppe, arid zone, Kingman, Arizona, USA. *Chrysothamnus parryi*, transverse section.

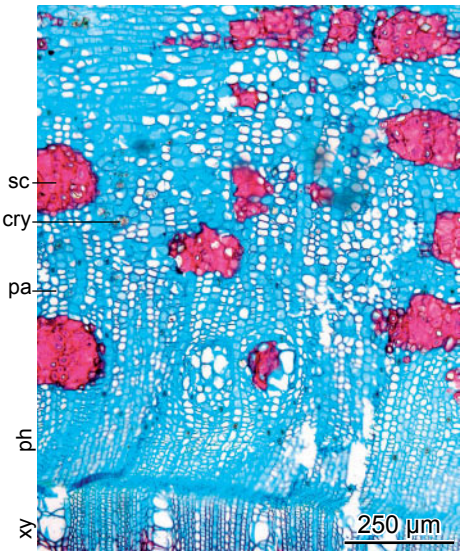



**Fig. 21.** Round groups of sclerenchyma in a tissue of unlignified sieve-tubes and parenchyma cells. Stem of a 1 m-high shrub, Pinyon, dry lower timberline zone, Dinosaur, Colorado, USA. *Ceanothus velutinus*, transverse section.

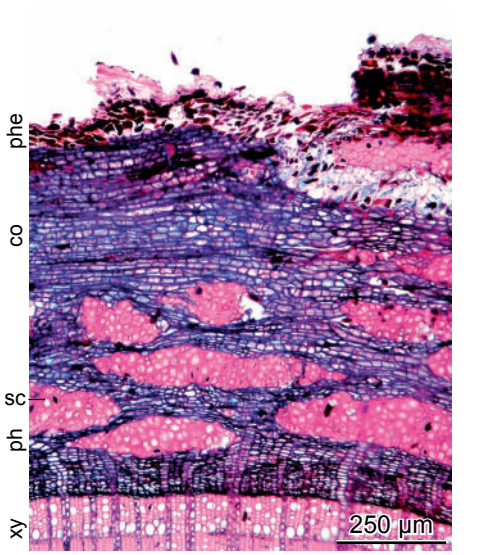



**Fig. 22.** Large lenses of sclerenchyma cells in a tissue of unlignified sieve-tubes and parenchyma cells. Stem of a 50 cm-high dwarf shrub, shrub steppe, arid zone, Kingman, Arizona, USA. *Chrysothamnus parryi*, transverse section.

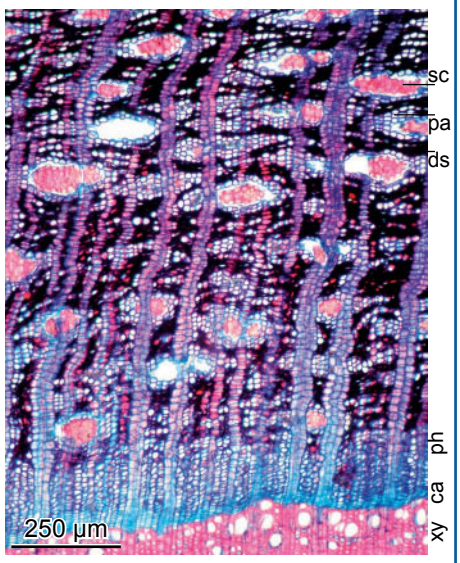



**Fig. 23.** Oval lenses of sclerenchyma cells are surrounded by thin-walled, unlignified parenchyma cells. Stem of a 2 m-high shrub, Laurel forest, subtropical, Tenerife, Canary Islands. *Rhamnus crenulata*, transverse section.

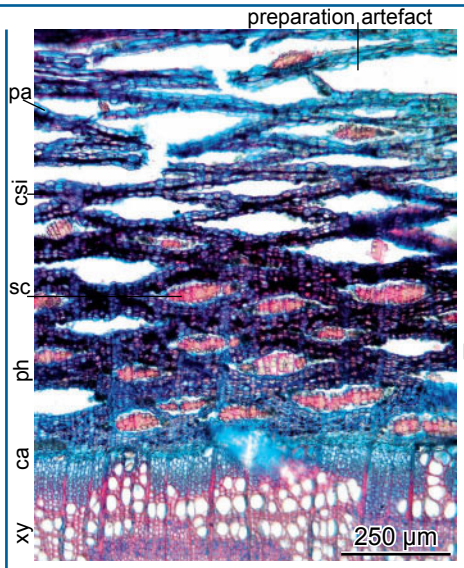



**Fig. 24.** Small lenses of sclerenchyma cells are surrounded by thin-walled, unlignified parenchyma cells. Empty spaces are artifacts of blunt microtome knives. Stem of a 30 cm-high dwarf shrub, dry rock field, submediterranean, Florence, Tuscany, Italy. *Rhamnus saxatilis*, transverse section.

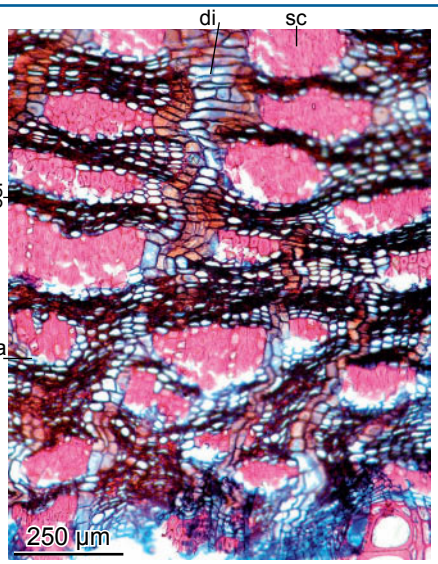



**Fig. 25.** Densely packed round to oval groups of sclerenchyma cells located between partially dilated rays. Stem of a 1 m-high shrub, shrub desert, arid zone, Mamoth, Arizona, USA. *Ziziphus oblongifolius*, transverse section.

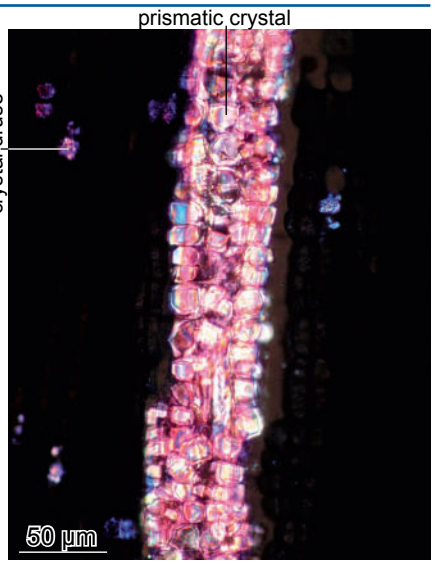



**Fig. 26.** Prismatic crystals and crystal druses in the phloem. Crystals are located mainly around the sclerenchyma groups. Stem of a 2 m-high shrub, Laurel forest, subtropical, Tenerife, Canary Islands. *Rhamnus crenulata*, radial section, polarized light.

## Discussion in relation to previous studies

The xylem of all genera analyzed here (shrubs and dwarf shrubs), except for *Chrysothamnus*, have been characterized before. Gregory (1994) mentioned 105 references on 25 genera. The xylem of dwarf shrubs (*Rhamnus*) has been described only by Schweingruber (1990) and Akkemik et al. (2007). Holdheide (1951) described the bark of *Frangula alnus* and *Rhamnus cathartica* in detail. The bark of 16 species is described here for the first time. As previous authors realized, the family is anatomically divided into three groups. *Paliurus* and *Ziziphus* are diffuse-porous and have a few large, solitary vessels, whereas *Frangula* is semi-ring-porous with uniformly distributed vessels. Vessels of all other genera are diagonal or even dendritically arranged. Within the genus of *Rhamnus*, some species can be differentiated by ray width. Anatomical differences between life forms (shrubs and dwarf shrubs) from different vegetation belts, e.g. hill zone versus alpine zone, seem to be absent.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **28** |
| 1 | growth rings distinct and recognizable | 28 |
| 4 | semi-ring-porous | 22 |
| 5 | diffuse-porous | 11 |
| 6 | vessels in intra-annual tangential rows | 1 |
| 7 | vessels in diagonal and/or radial patterns | 19 |
| 8 | vessels in dendritic patterns | 21 |
| 9 | vessels predominantly solitary | 3 |
| 9.1 | vessels in radial multiples of 2-4 common | 6 |
| 10 | vessels in radial multiples of 4 or more common | 1 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 28 |
| 22 | intervessel pits alternate | 28 |
| 36 | helical thickenings present | 22 |
| 39.1 | vessel cell-wall thickness >2 µm | 4 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 21 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 8 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 3 |
| 50 | <100 vessels per mm² in earlywood | 4 |
| 50.1 | 100-200 vessels per mm² in earlywood | 20 |
| 50.2 | 200-1000 vessels per mm² in earlywood | 4 |
| 56 | tylosis with thin walls common | 2 |
| 58 | dark staining substances in vessels and/or fibers | 9 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 11 |
| 61 | fiber pits small (<3 µm = libriform fibers) | 28 |
| 68 | fibers thin-walled | 3 |
| 69 | fibers thick-walled | 13 |
| 70 | fibers thin- to thick-walled | 16 |
| 70.2 | tension wood present | 17 |
| 75 | parenchyma absent or unrecognizable | 17 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 4 |
| 79 | parenchyma paratracheal | 8 |
| 89 | parenchyma marginal | 8 |
| 96 | rays uniseriate | 5 |
| 97 | ray width predominantly 1-3 cells | 18 |
| 98 | rays commonly 4-10-seriate | 8 |
| 100.2 | rays not visible in polarized light | 2 |
| 103 | rays of two distinct sizes (tangential section) | 2 |
| 104 | ray: all cells procumbent (radial section) | 6 |
| 105 | ray: all cells upright or square | 2 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 13 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 2 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 5 |
| 110 | rays with sheet cells (tangential section) | 2 |
| 136 | prismatic crystals present | 8 |
| 144 | druses present | 2 |
| R1 | groups of sieve tubes present | 2 |
| R2 | groups of sieve tubes in tangential rows | 15 |
| R3 | distinct ray dilatations | 7 |
| R4 | sclereids in phloem and cortex | 18 |
| R6 | sclereids in radial rows | 1 |
| R6.1 | sclereids in tangential rows | 10 |
| R6.2 | sclereids in tangential arranged groups, *Rhamnus* type | 11 |
| R7 | with prismatic crystals | 13 |
| R8 | with crystal druses | 7 |

# Rosaceae



**Number of species, worldwide and in Europe**

The cosmopolitean Rosaceae family includes 100 genera with 3000 species. In Europe, there are 43 genera with 460 species. The genus *Bencomia* is endemic to the Canary Islands.

**Analyzed material**

The xylem and phloem of 158 Rosaceae species is analyzed here, including 29 Maloideae, 23 Prunoideae, 94 Rosoideae and 12 Spiroideae.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | 26 | several authors >30 |
| Nanophanerophytes (0.5-4 m) | 66 | several authors >20 |
| Woody chamaephytes | 6 | Schweingruber (1990) 3 |
| Semi-woody chamaephytes | 6 | |
| Liana | 1 | |
| Hemicryptophytes and geophytes | 52 | Schweingruber (1990) 2 |
| Therophytes | 1 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 24 | |
| Boreal and arctic | 21 | |
| Hill and mountain | 89 | |
| Mediterranean | 14 | |
| Arid | 4 | |
| Subtropical | 6 | |

*Rosa pendulina*

**Analyzed species:**

Hemicryptophytes (herbs) appear underlined
Trees, shrubs, dwarf shrubs appear not unterlined

*Acaena splendens* Hook et Arn.
*Agrimonia eupatoria* L.
*Alchemilla alpina* L.
*Alchemilla decumbens* Buser
*Alchemilla fissa* Günther et Schumei
*Alchemilla hoppeana* Dalla Torre
*Alchemilla hybrida* L.
*Alchemilla pentaphyllea* L.
*Alchemilla sericea* Willd.
*Alchemilla vulgaris* L.
*Amelanchier florida* Lindl.
*Amelanchier laevis* Wiegand
*Amelanchier ovalis* L.
*Amelanchier sanguinea* DC
*Amelanchier utahensis* Koehne
*Aruncus dioicus* (Walther) Fernald.
*Bencomnia sphaerocarpa* Svent.
*Chamaerhodos altaica* Bunge
*Coleogyne ramosissima* Torr.
*Cotoneaster granatensis* Boiss.
*Cotoneaster horizontalis* Decne
*Cotoneaster integerrimus* Medicus
*Cotoneaster nebrodensis* (Guss.) C. Koch
*Cotoneaster niger* (Thunb.) Fries
*Cotoneaster nummularius* Lindl.
*Cotoneaster tomentosus* C.A. Mey
*Cowania mexicana* D. Don
*Crataegus calycina* Peterm.
*Crataegus curvisepala* Franco
*Crataegus laciniata* Ucria
*Crataegus monogyna* Jacq.
*Crataegus oxyacantha* L.
*Crataegus pinnatifida* Bunge
*Crataegus pycnoloba* Boiss. et Heldr.
*Crataegus sanguinea* Pall.
*Cydonia oblonga* Miller
*Dryas grandis* Juz.
*Dryas integrifolia* Vahl
*Dryas octopetala* L.
*Dryas sumneviczii* Sergievsk.
*Eriobotrya japonica* Lindley
*Exochorda racemosa* Rehder
*Filipendula ulmaria* Maxim
*Filipendula vulgaris* Moench
*Fragaria vesca* L.
*Fragaria viridis* Duchesne
*Geum glaciale* Fisch
*Geum macrophyllum* Hook
*Geum montanum* L.
*Geum reptans* L.
*Geum rivale* L.
*Geum triflorum* Pursh
*Geum urbanum* L.

*Hagenia abyssinica* J.F. Gmel.
*Holodiscus discolor* Maxim.
*Kerria japonica* (L.) DC
*Marcetella moquiniana* (Web) Svent.
*Mespilus germanica* L.
*Oemleria cerasiformis* Landon
*Petrophyton caespitosum* Rydb.
*Physocarpus amurensis* Maxim.
*Potentilla argentea* L.
*Potentilla aurea* L.
*Potentilla brauniana* Hoppe
*Potentilla caucasica* Juz.
*Potentilla caulescens* L.
*Potentilla crantzii* G. Beck ex Frisch
*Potentilla cinerea* Chaix ex Vill.
*Potentilla erecta* (L.) Räuschel
*Potentilla frigida* Vill.
*Potentilla fruticosa* L.
*Potentilla grandiflora* L.
*Potentilla hippiana* Lehm
*Potentilla lanuginosa* Juz
*Potentilla micrantha* Ramond
*Potentilla multifida* L.
*Potentilla neumanniana* Rchb.
*Potentilla nitida* L.
*Potentilla nivalis* Lapeyr.
*Potentilla palustris* L.
*Potentilla pennsylvanica* L.
*Potentilla pusilla* Host
*Potentilla recta* L.
*Potentilla reptans* L.
*Potentilla rubricaulis* Lehm
*Potentilla sterilis* (L.) Garke
*Potentilla supina* L.
*Potentilla thuringiaca* Bernh. ex Link
*Prunus amygdalus* Batsch.
*Prunus armeniaca* L.
*Prunus avium* L.
*Prunus brigantina* Vill.
*Prunus cerasifera* Erh.
*Prunus cerasus* L.
*Prunus domestica* L.
*Prunus dulcis* D.A. Webb
*Prunus fruticosa* Pallas
*Prunus ilicifolia* Nutt. ex Hook et Arn
*Prunus laurocerasus* L.
*Prunus lusitanica* L.
*Prunus mahaleb* L.
*Prunus padus* L.
*Prunus persica* (L.) Batsch
*Prunus prostrata* Labill
*Prunus ramburii* Boiss.
*Prunus sachalinensis* Koidzumi
*Prunus spinosa* L.
*Prunus tenella* Batsch.
*Prunus virginiana* L.
*Prunus webbii* (Spach) Vierh.
*Purshia tridentata* (Pursh) DC
*Pyracantha coccinea* M.J. Roemer
*Pyrus amygdaliformis* Vill.
*Pyrus communis* L.
*Pyrus malus* L.
*Pyrus orientalis* Pall.
*Rosa acicularis* Lindl.
*Rosa arkansana* Porter
*Rosa arvensis* Hudson
*Rosa canina* L.
*Rosa elliptica* Tausch
*Rosa pendulina* L.
*Rosa pomifera* J. Herrmann
*Rosa rugosa* Thunb
*Rosa sempervirens* L.
*Rubus caesius* L.
*Rubus chamaemorus* L.
*Rubus fruticosus* L.
*Rubus idaeus* L.
*Rubus saxatilis* L.
*Rubus spectabilis* Pursh
*Sanguisorba ancistroides* Desf.
*Sanguisorba minor* ssp. *minor* Scop.
*Sanguisorba minor* ssp. *magnolii* Scop.
*Sanguisorba officinalis* L.
*Sarcopoterium spinosum* (L.) Spach
*Sibbaldia parviflora* Willd.
*Sibbaldia procumbens* L.
*Sibiraea altaensis* Maxim.
*Sorbaria sorbifolia* (L.) A. Braun
*Sorbus aria* (L.) Crantz
*Sorbus aucuparia* L.
*Sorbus chamaemespilus* (L.) Crantz
*Sorbus decora* C.K. Schneid
*Sorbus domestica* L.
*Sorbus graeca* (Spach) Kotschy
*Sorbus sambucifolia* M. Roem.
*Sorbus sibirica* Hedl.
*Sorbus torminalis* (L.) Crantz
*Spiraea betulifolia* Pall.
*Spiraea dahurica* (Rupr.) Maxim
*Spiraea douglasii* Hook
*Spiraea hypericifolia* L.
*Spiraea latifolia* Bork.
*Spiraea media* F. Schmidt
*Spiraea salicifolia* L.
*Spiraea stevenii* (C.K. Schneid.) Rytb.
*Worownia speciosa* Juz.

*Potentilla reptans*

*Alchemilla alpina*

*Geum reptans*

*Dryas octopetala* (photo: Landolt)

*Prunus laurocerasus*

*Potentilla aurea*

*Pyrus malus*

*Sorbus aucuparia*

*Crataegus oxycantha* (photo: Landolt)

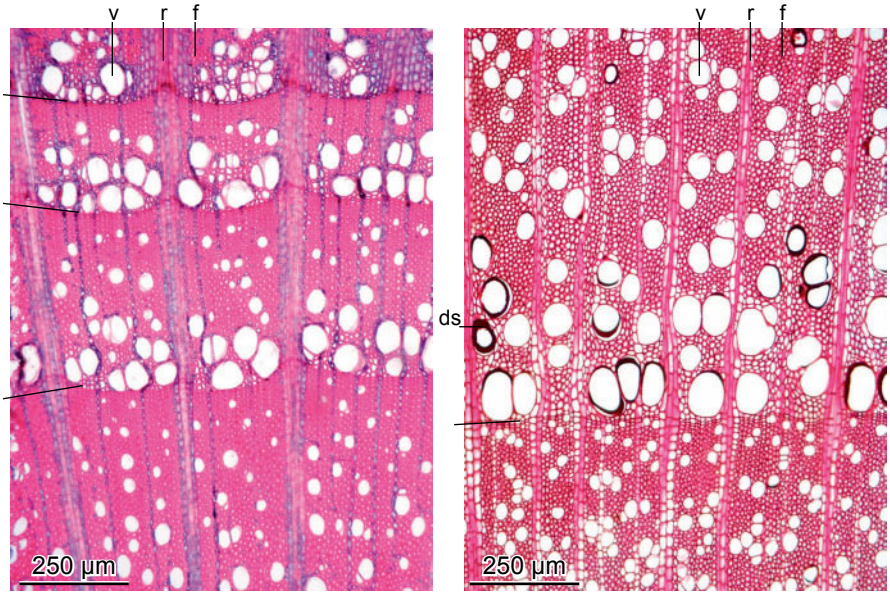
*Filipendula ulmaria* and *Sanguisorba officinalis*

**Characteristics of the xylem**

Characteristic of the family for most species in all vegetation zones is the absence of annual plants (therophytes), the presence of simple perforations, of fibers with large round pits (2 to >3 µm) and distinct or at least recognizable rings.

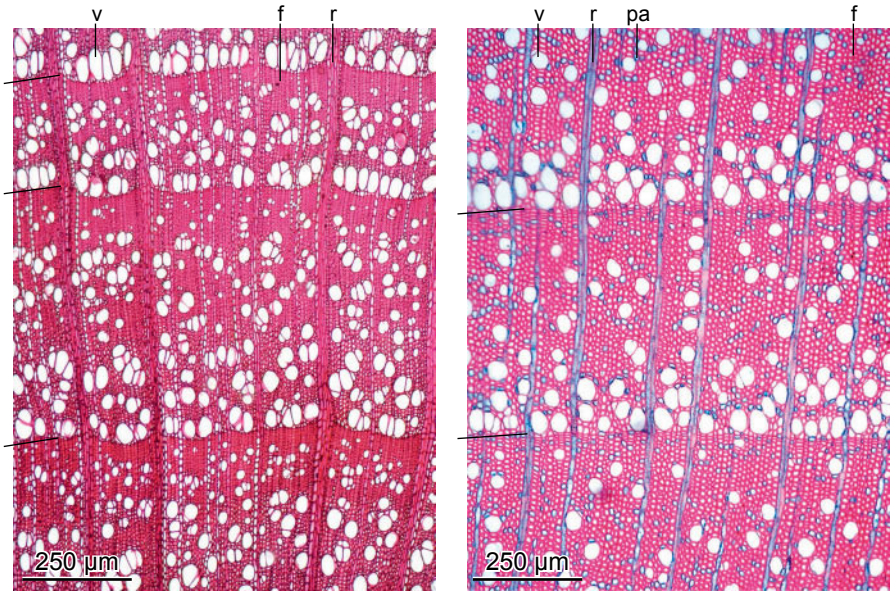
The family is divided into two groups: i) hemicryptophytes and chamaephytes (herbs); ii) trees, shrubs and dwarf shrubs (woody species).

Ring boundaries of a few *Prunus* and *Rosa* species are primarely ring-porous (**Figs. 1** and **2**). Semi-ring porosity is the dominant vessel distribution pattern within the family (**Figs. 3-5**) although diffuse porosity is frequent (**Figs. 6** and **7**). Transitions between diffuse- and semi-ring-porosity are very frequent. Vessels are arranged mostly solitary (**Figs. 1**, **2**, **4** and **6**). Selected species of the genera *Physocarpus*, *Bencomnia*, *Filipendula*, *Marcetella*, *Prunus* and *Potentilla* contain mostly radial multiples (2 to >4 vessels; **Figs. 8-10**) and *Prunus amygdalus* and *Rubus idaeus* contain distinct vessel groupings (**Fig. 11**).Vessels with a diameter <20 µm occur only in small dwarf shrubs, chamaephytes and hemicryptophytes (*Acaena*, *Alchemilla*, *Chamaerhodos*, *Fragaria*, *Geum*, *Petrophyton*, *Potentilla*, *Rubus chamaemorus*, *Sibbaldia*, *Woronowia*; **Fig. 12**). This feature is often associated with thick-walled vessels (<2.5 to >3 µm; **Fig. 13**). Earlywood vessels with a diameter between 20-40 µm are characteristic of the majority of species and large vessels with a diameter between 50-100 µm are only typical for the genera *Prunus* and *Rosa* (**Figs. 1** and **2**). Vessel diameter is slightly larger than 100 µm in some *Prunus* and *Rosa* species and in the tropical tree *Hagenia abyssinica*. Vessel density varies from 100-200/mm$^2$ in shrubs and trees (**Figs. 1-4**) and from 200-500/mm$^2$ in hemicryptophytes and chamaephytes (**Fig. 12**). Few vessels were observed only in *Hagenia abyssinica* (tropical tree ) and in the North American shrubs *Holodiscus discolor* and *Rubus spectabilis* (<100/mm$^2$).



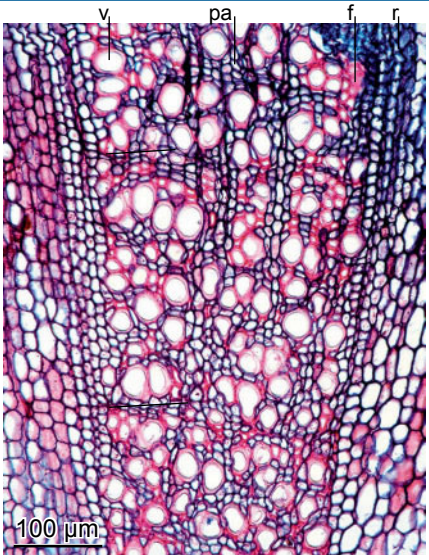

**Left Fig. 1.** Ring-porous-wood with solitary vessels in the latewood. Stem of a 1 m-high shrub, mountain zone, Grisons, Switzerland. *Rosa pomifera*, transverse section.

**Right Fig. 2.** Ring-porous-wood with mostly solitary vessels in the latewood. Some vessels contain dark substances. Stem of a 5 m-high tree, cultivated, hill zone, Zürich, Switzerland. *Prunus persica*, transverse section.



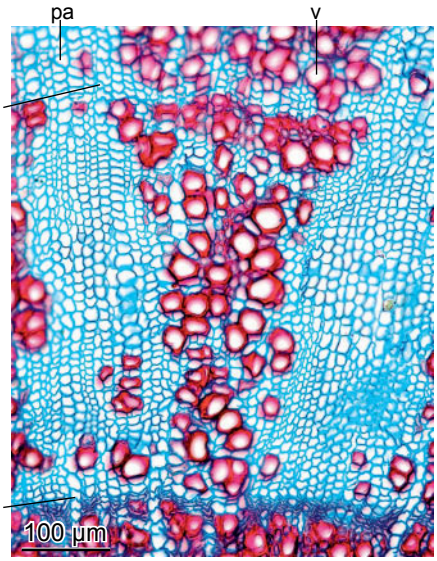

**Left Fig. 3.** Semi-ring-porous wood with grouped vessels in the latewood. Stem of a 1 m-high shrub, moist meadow, boreal zone, Magadan, Siberia, Russia. *Spiraea stevenii*, transverse section.

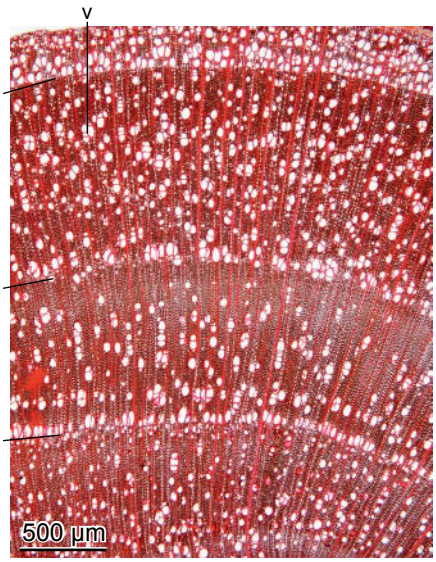
**Right Fig. 4.** Semi-ring-porous wood with solitary vessels in the latewood. Stem of a 1.5 m-high shrub, *Pinus cembra* forest, subalpine zone, Grisons, Switzerland. *Sorbus chamaemespilus*, transverse section.




**Left Fig. 5.** Semi-ring-porous wood. The rings are partially extremely small (<0.1 mm). Stem of a prostrate, 5 cm-high and 30 cm-long dwarf shrub, windy crest, subarctic zone, Banks Island, Canada. *Dryas integrifolia*, transverse section.

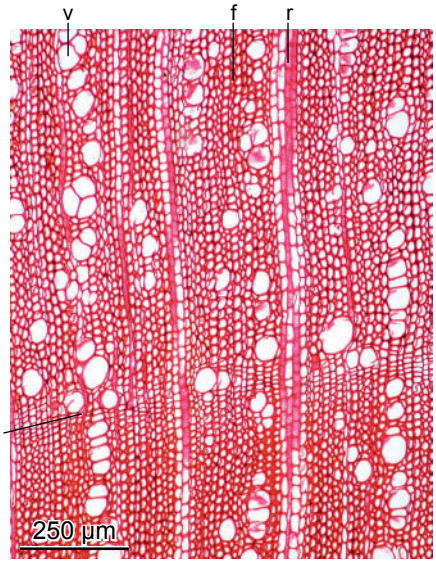
**Right Fig. 6.** Diffuse-porous wood. Fibers are almost absent. Root collar of a 20 cm-high hemicryptophyte, on limestone rock, mountain zone, Jura, Switzerland. *Sanguisorba minor*, transverse section.

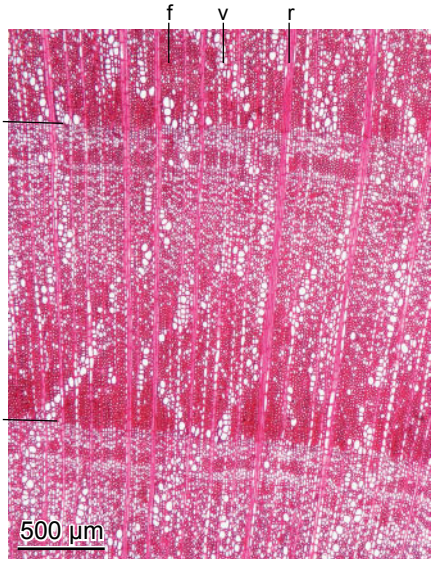



**Left Fig. 7.** Diffuse-porous wood. Fibers are absent. Root collar of a 20 cm-high hemicryptophyte, on loam, Mediterranean, Andalusia, Spain. *Sanguisorba ancistroides*, transverse section.

**Right Fig. 8.** Semi-ring-porous wood with short radial multiples in the latewood. Stem of a 1.5 m-high shrub, cultivated, moist site, boreal zone, Jakutsk, Siberia, Russia. *Physocarpus amurensis*, transverse section.



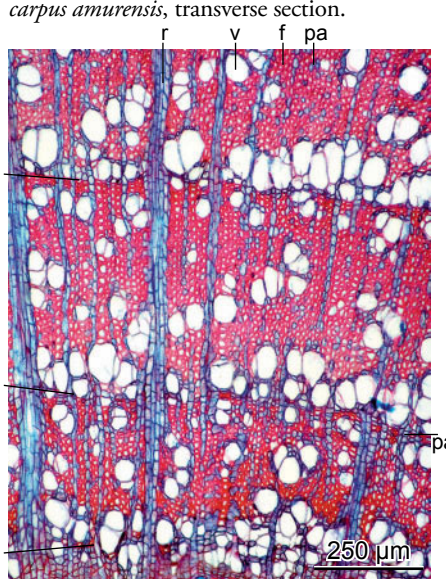



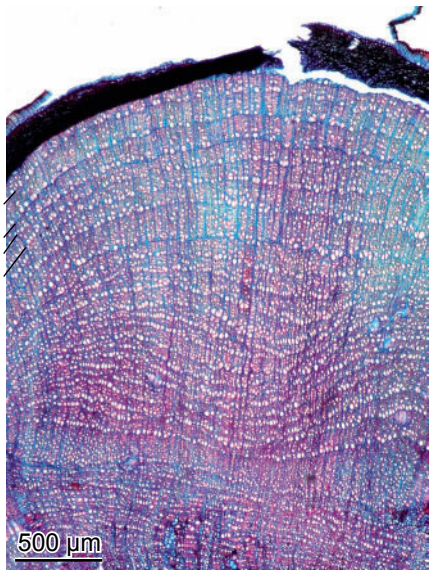

**Fig. 9.** Diffuse-porous wood with long radial multiples. Stem of a 1.5 m-high shrub, *Laurus* forest, Madeira, Macaronesia, Portugal. *Bencomnia sphaerocarpa*, transverse section.

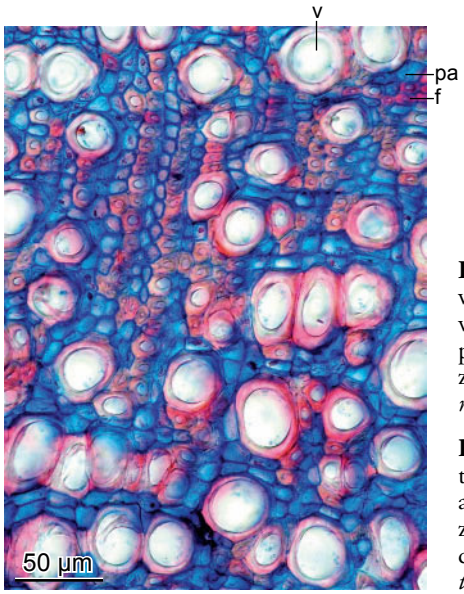
**Fig. 10.** Diffuse-porous wood with long radial multiples, often arranged in diagonal patterns. Stem of a 1.5 m-high shrub, *Castanea sativa* forest, hill zone, Ticino, Switzerland. *Prunus laurocerasus*, transverse section.

**Fig. 11.** Semi-ring-porous wood with vessel groups in the latewood. Parenchyma cells are partially marginal. Rhizome of a 1 m-high shrub, rock field, subalpine zone, Italy. *Rubus idaeus*, transverse section.

Vessels of all species have simple perforations. Simple scalariform perforations with a few bars were observed in *Kerria japonica*, *Potentilla palustris* and *Rubus chamaemorus* (**Fig. 14**). Intervessel pits are small and round and arranged in alternating position in all trees, shrubs and dwarf shrubs, while often scalariform to various degrees in hemicryptophytes (**Figs. 15** and **17**). Helical thickenings occur only in trees and shrubs , they are often fairly thick in all *Prunus* species (**Fig. 16**) and rather thin in all other genera (*Amelanchier*, *Cotoneaster*, *Cydonia*, *Eriobotrya*). They are absent from the genera *Holodiscus*, *Kerria*, *Marcetella*, *Exochorda*, *Oemleria*, *Physocarpus*, *Purshia* and *Rubus*. Dark-staining substances occur in the heartwood of all *Prunus* species as well in *Pyrus malus*, *Sorbaria sorbifolia* and *Sibiraea altaensis* (heartwood).

Fibers with large, round pits (**Fig. 18**) are thin-walled in dwarf shrubs, e.g. *Dryas* sp. (**Fig. 19**), *Potentilla palustris* and thin- to thick-walled or thick-walled (**Figs. 20** and **24**) in all trees and shrubs. Transitions between the two features vary from site to site. Unlignified fibers cannot be distinguished from parenchyma cells in transverse sections (**Fig. 21**). The occurrence of tension wood is unique for the genus *Prunus* (**Fig. 22**). Septate fibers were found in *Potentilla sterilis*, *Rubus spectabilis*, *Spiraea douglasii* and *Sorbus decora* (**Fig. 23**).




**Left Fig. 12.** Diffuse- to semi-ring-porous wood with very small vessels (<20 µm) and very small rings. Stem of a 10 cm-high prostrate dwarf shrub, dry meadow, boreal zone, Lake Baikal, Siberia, Russia. *Chamaerhodos altaica*, transverse section.

**Right Fig. 13.** Thick-walled vessels between many parenchyma cells (pervasive) and radial rows of thick-walled fibers. Rhizome of a 10 cm-high hemicryptophyte, dry meadow, Halle, Saale, Germany. *Potentilla cinerea*, transverse section.

**Fig. 14.** Simple and scalariform perforations with a few bars occurring together in individuals. Rhizome of a 10 cm-high chamaephyte, bog, Yamal penninsula, Siberia, Russia. *Potentilla palustris*, radial section.

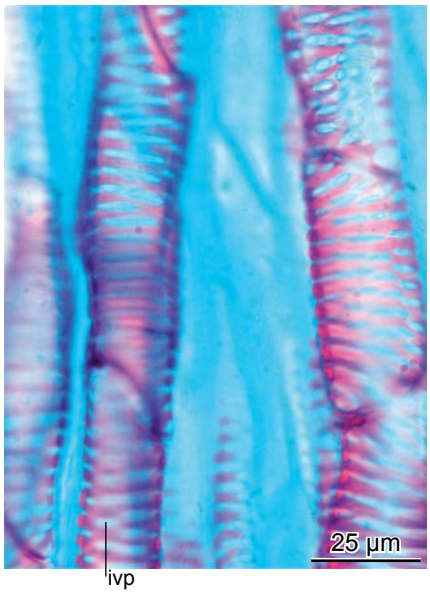



**Fig. 15.** Scalariform intervessel pits located in adult parts of rhizomes. Rhizome of a 10 cm-high hemicryptophyte, dry meadow, Putorana Mountains, Siberia, Russia. *Geum glaciale*, radial section.

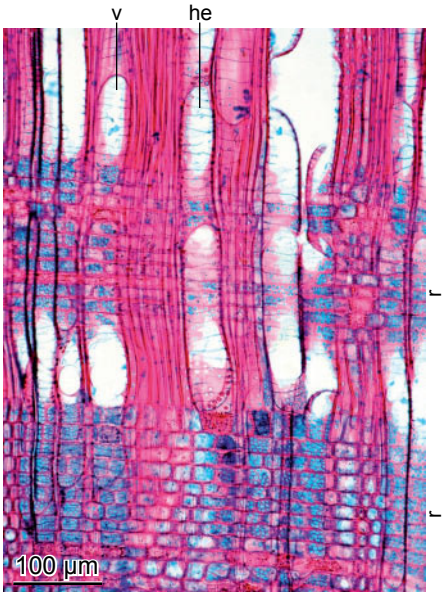
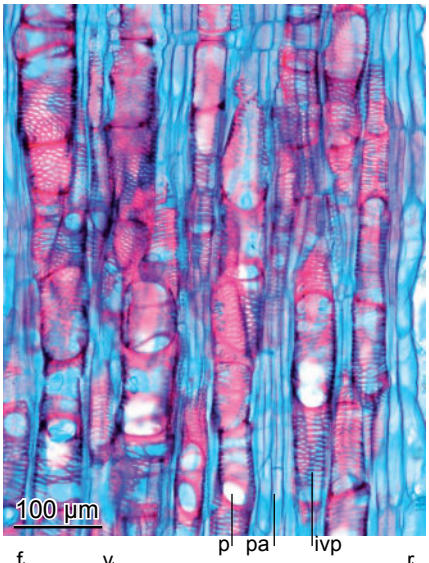
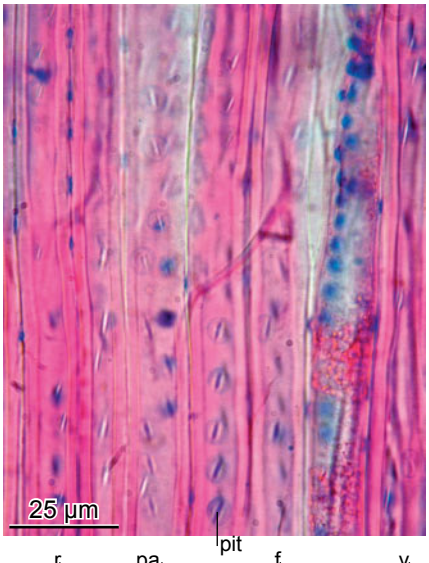


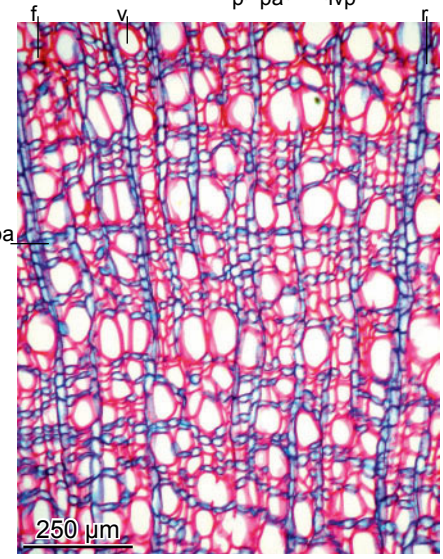

**Fig. 16.** Horizontally oriented, unlignified (blue), thick-walled helical thickenings in vessels with simple perforations. Stem of a 3 m-high tree, hedge in a dry meadow, submediterranean, Briançon, France. *Prunus brigantina*, radial section.

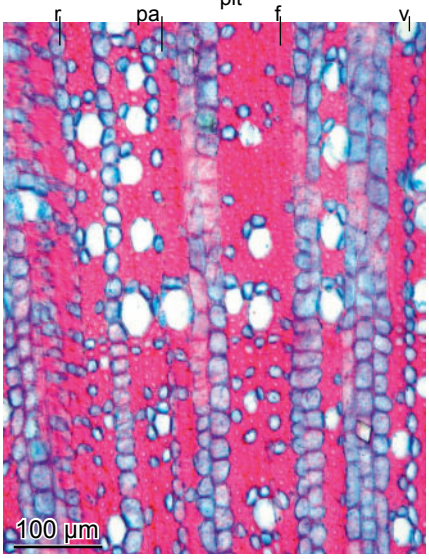



**Left Fig. 17.** Simple perforations in vessels with round and scalariform intervessel pits. Rhizome of a 20 cm-high hemicryptophyte, bog, Yamal Peninsula, Siberia, Russia. *Sanguisorba officinalis*, radial section.

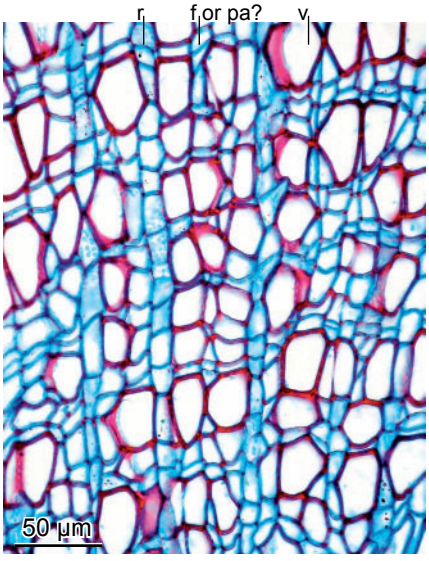
**Right Fig. 18.** Fibers with large, round pits with slit-like apertures. Stem of a 1.5, m-high shrub, dry rock, shrub desert, arid zone, Utah, USA. *Amelanchier utahensis*, radial section.

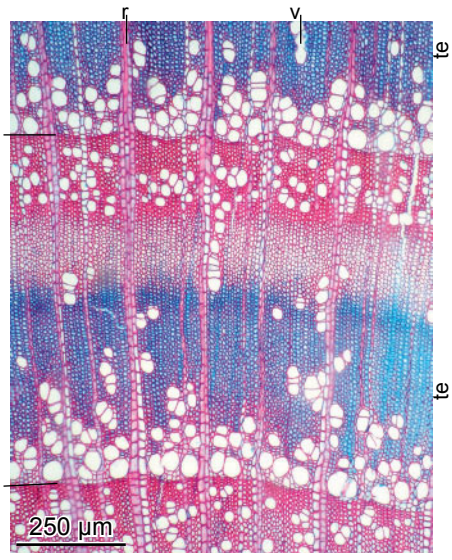



**Left Fig. 19.** Thin-walled fibers (red) and apotracheal parenchyma cells. Stem of a 5 cm-high prostrate dwarf shrub, on limestone rock, Grisons, Switzerland. *Dryas octopetala*, transverse section.

**Right Fig. 20.** Thick-walled fibers and apotracheal and partially paratracheal parenchyma. Stem of a 1.5 m-high shrub, cultivated, hill zone, Botanical Garden Munich, Germany. *Oemleria cerasiformis*, transverse section.



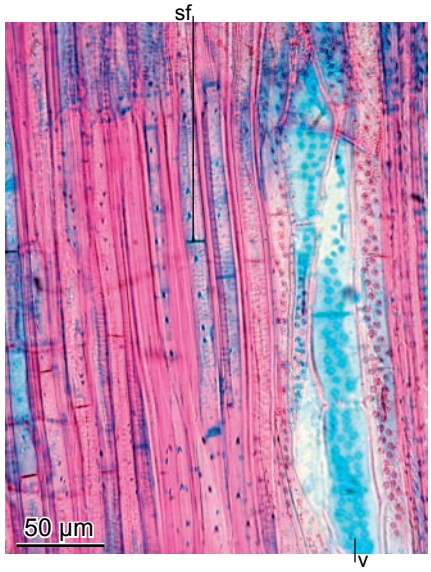




**Fig. 21.** Thin-walled unlignified fibers and parenchyma cells are surrounded by lignified vessels. Rhizome of a 10 cm-high chamaephyte, bog, Yamal Peninsula, Siberia, Russia. *Rubus chamaemorus*, transverse section.

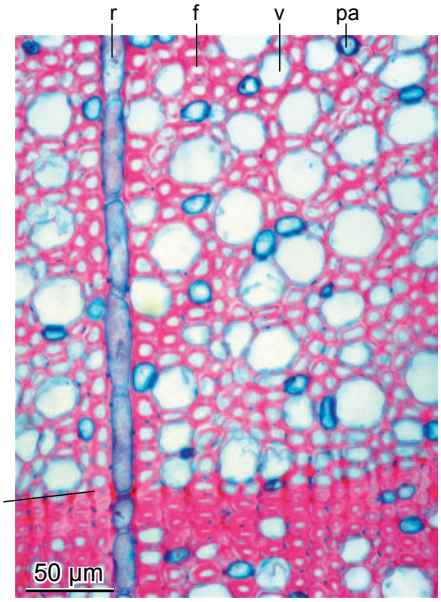
**Fig. 22.** Tension wood (blue) in the earlywood. Stem of a 15 m-high tree, riparian, hill zone, Aarau, Switzerland. *Prunus avium*, transverse section.

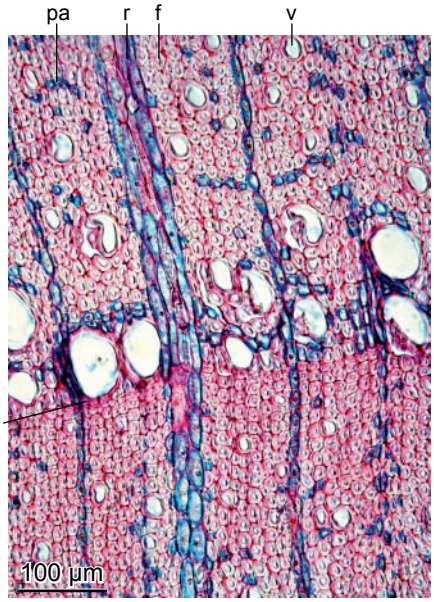
**Fig. 23.** Septate fibers with unlignified transverse walls (blue). Stem of a 1.5 m-high shrub, *Picea sitchensis* forest, hill zone, Oregon, USA. *Rubus spectabilis*, radial section.

The distribution of axial parenchyma is often difficult to determine, especially on slides stained only with safranin. There is a predominance of apotracheal parenchyma (**Figs. 24** and **25**), but in the same species it is combined with paratracheal parenchyma (**Fig. 20**). Pervasive parenchyma occurs in many hemicryptophytes (**Fig. 26**) but not in dwarf shrubs, shrubs or trees. Presence of marginal parenchyma is rare and usually discontinuous in the lateral direction.

Ray diversity is high. Exlusively uniseriate rays occur in all *Alchemilla* species and in *Potentilla palustris* (**Fig. 27**). Biseriate rays are characteristic for the genera *Amelanchier*, *Cotoneaster*, *Cowania*, *Crataegus*, *Sorbus*, *Pyrus*, *Pyracantha* and *Purshia* (**Fig. 28**). Ray dimorphism is very frequent: uniseriate rays are combined with multiseriate rays of 4-6 cells (**Fig. 29**) or more then 10 cells width, e.g. in some *Rosa* and *Rubus* species and *Sorbaria sorbifolia* (**Fig. 30**). Large rays exceed 2 mm in height in the genera *Holodiscus*, *Kerria*, *Rosa* and *Rubus* (**Fig. 30**). Species with exclusively very large rays are hemicryptophytes with remaining primary vascular bundles, e.g *Filipendula*, *Fragaria*, *Sanguisorba* and *Woronowia* (**Figs. 31-33**). The large rays are unlignified, parenchymateous separations between the bundles (**Figs. 32** and **33**). These types are normally rayless in the vessel/fiber zones. Sheet cells occur in a few species with large rays but the occurrence varies within species (**Fig. 34**). Rays of trees and shrubs are composed of many rows of procumbent cells. In some cases, rays also have a few marginal rows of square and/or upright cells (**Fig. 35**). Ray cells are square or upright in uniseriate rays of types with ray dimorphism expecially in species with remaining primary vascular bundles.

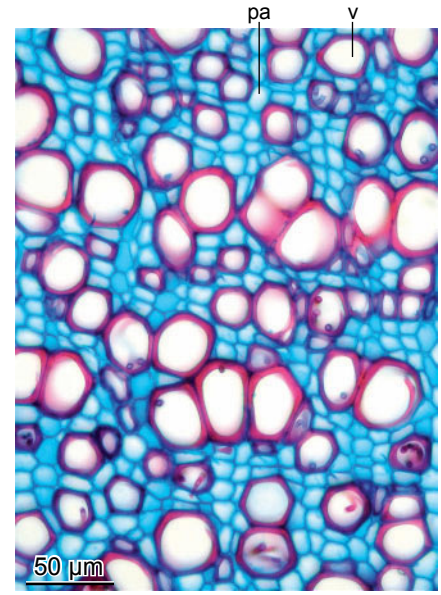
Prismatic crystals occur occasionally in rays of hemicryptophytes, e.g. in *Potentilla*, *Sanguisorba* and *Sarcopoterium*, and of shrubs, e.g. in *Prunus* and *Pyrus*. The occurrence is not constant within species. Crystal druses are very frequent in hemicryptophytes of the genera *Filipendula*, *Fragaria*, *Geum*, *Potentilla* and *Woronowia* but they also occur in trees of the genus *Prunus*, e.g. in *Prunus amygdalus*, *P. armeniaca* and *P. avium*.

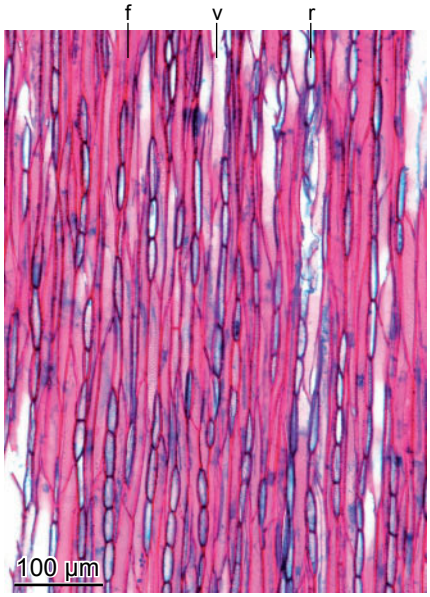



**Left Fig. 24.** Diffuse apotracheal parenchyma. Stem of a 1.5 m-high shrub, dry rock, shrub desert, arid zone, Utah, USA. *Amelanchier utahensis*, transverse section.

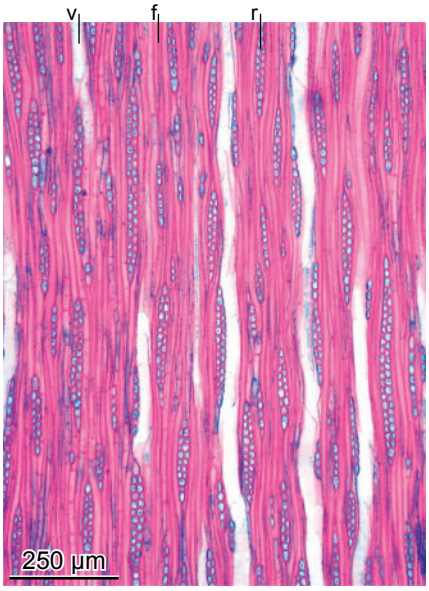
**Right Fig. 25.** Parenchyma, diffuse and partially diffuse in aggregates. Stem of a 1 m-high shrub, dry rock, shrub desert, arid zone, Utah, USA. *Coleogyne ramosissima*, transverse section.

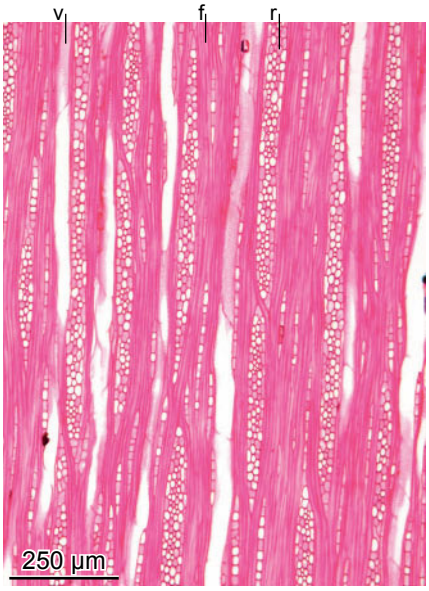



**Left Fig. 26.** Pervasive parenchyma between thick-walled, lignified vessels. Rhizome of a 5 cm-high prostrate hemicryptophyte, limestone gravel, subalpine zone, Grisons, Switzerland. *Geum reptans*, transverse section.

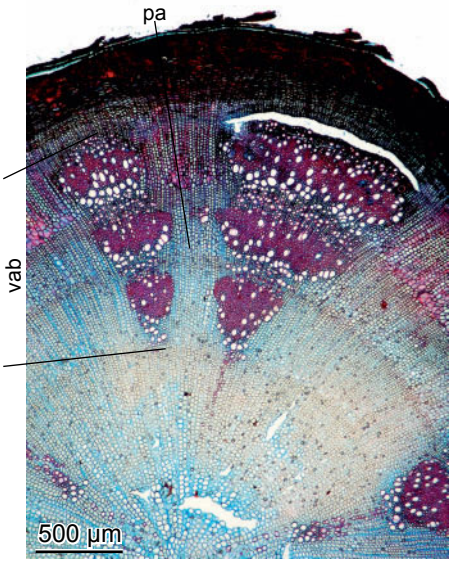
**Right Fig. 27.** Uniseriate rays with axially elongated cells. They are upright in the radial section. Rhizome of a 15 cm-high chamaephyte, bog, Yamal penninsula, Siberia, Russia. *Potentilla palustris*, tangential section.



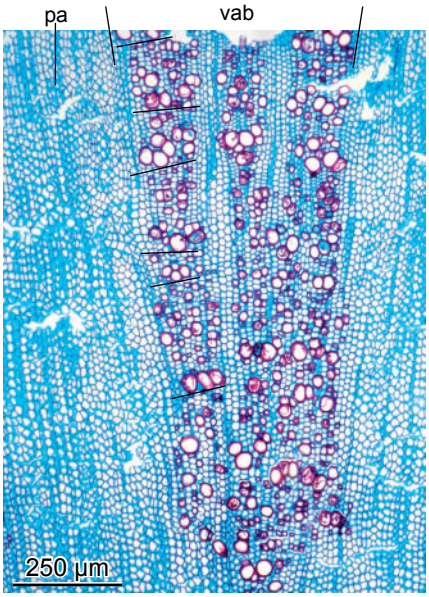

**Left Fig. 28.** Biseriate rays with round central cells and partially slightly elongated marginal cells. Stem of a 1.4 m-high shrub, *Pinus cembra* forest, subalpine zone, Grisons, Switzerland. *Sorbus chamaemespilus*, tangential section.

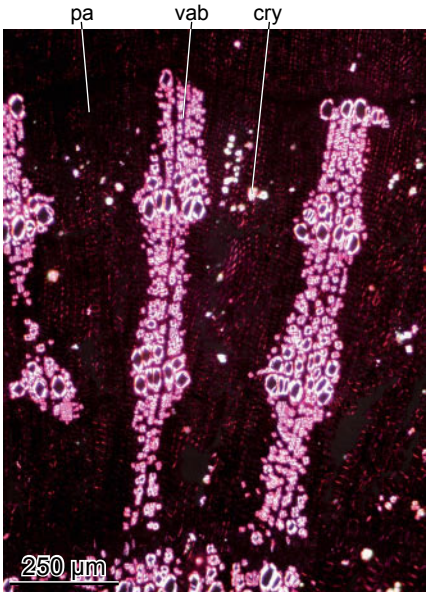
**Right Fig. 29.** Ray dimorphism: uniseriate and 3-4-seriate rays. Stem of a 5 m-high tree, cultivated, hill zone, Zürich, Switzerland. *Prunus persica*, tangential section.




**Left Fig. 30.** Ray dimorphism: uniseriate and multiseriate rays >10 cells wide. Multiseriate rays are extremely high. Stem of a 50 cm-high shrub, sand dune, mountain zone, White Sand Dunes, Colorado, USA. *Rosa arkansana*, tangential section.

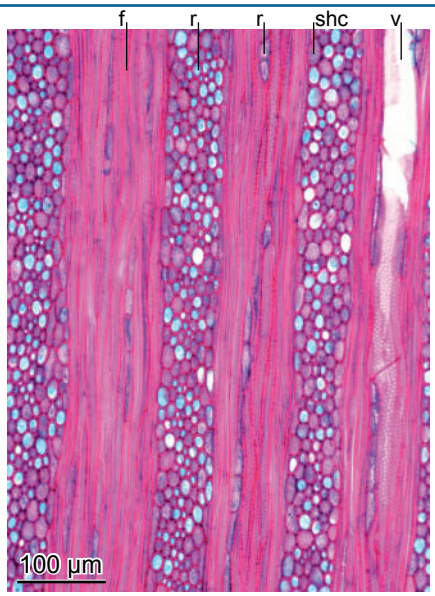
**Right Fig. 31.** Stem with remaining primary vascular bundles located between unlignified, radial parenchyma zones. Fibers in the latewood are thick-walled. Root collar of a 40 cm-high hemicryptophyte, dry meadow, Valpellina, Aosta, Italy. *Potentilla recta*, transverse section.

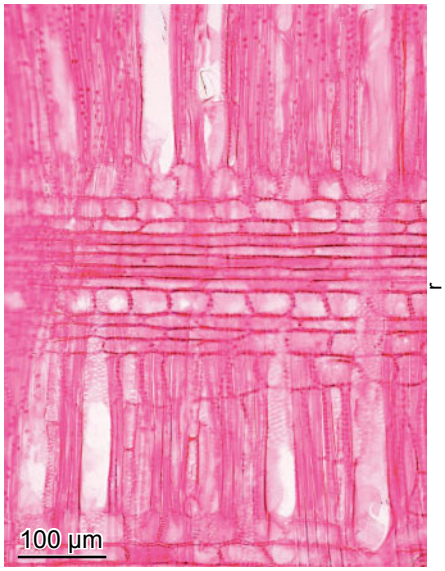



**Left Fig. 32.** Stem with remaining primary vascular bundles. The xylem of the bundles consists of vessels and pervasive parenchyma. Rhizome of a 5 cm-high prostrate hemicryptophyte, limestone gravel, subalpine zone, Grisons, Switzerland. *Geum reptans*, transverse section.

**Right Fig. 33.** Stem with remaining primary vascular bundles. The parenchyma zones between the bundles contain crystals (druses). Rhizome of a 10 cm-high hemicryptophyte, limestone rock, mountain zone, Grisons, Switzerland. *Potentilla caulescens*, transverse section, polarized light.




**Left Fig. 34.** Sheet cells on large rays. Stem of a 1.5 m-high shrub, coastal *Picea sitchensis* forest, Oregon, USA. *Holodiscus discolor*, tangential section.

**Right Fig. 35.** Heterocellular ray with central procumbent and one row of marginal square and upright cells. Stem of a 4 m-high tree, cultivated, mountain, subtropical climate, Tenerife, Canary Islands. *Eriobotrya japonica*, radial section.

**Characteristics of the phloem and the cortex**

Characteristic of the family are the regularly arranged rectangular cells in the phellem (**Figs. 36**, **37** and **42**) The phloem anatomy of the Rosaceae is heterogeneous. A uniform structure is characteristic of most hemicryptophytes; sieve tubes and parenchyma cells cannot be distinguished on transverse sections and sclerenchyma cells are absent (**Fig. 37**). Tangential bands of sclereids characterize the genera *Cowania*, *Crataegus*, *Cydonia*, *Exochorda*, *Pyrus* and *Sorbus* (**Figs. 38-41**). Radially oriented groups of sclerenchyma were found in a few *Prunus* species as well as in *Holodiscus* (**Fig. 42**). Ray dilatations occur in all life forms but are rather indistinct (**Fig. 39**). Prismatic crystals or crystal druses were found in all life forms and in all subfamilies. Particular for all *Prunus* species is the dense band of persistent phellem cells which compresses and deforms the phloem (**Figs. 43** and **44**).

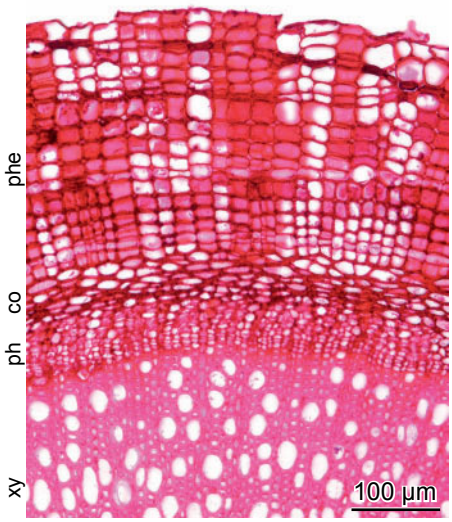



**Fig. 36.** Layers of strictly radially oriented square and rectangular cork cells of the phellem. Rhizome of a 5 cm-high hemicryptophyte, meadow, subalpine, Briançon, France. *Alchemilla alpina*, transverse section.

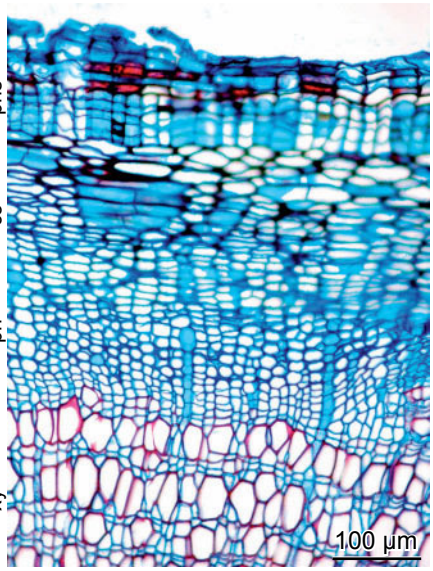



**Fig. 37.** Fairly uniform phloem. Sieve tubes and parenchyma cells cannot be distinguished. Rhizome of a 10 cm-high chamaephyte, bog, Yamal Peninsula, Siberia, Russia. *Rubus chamaemorus*, transverse section.

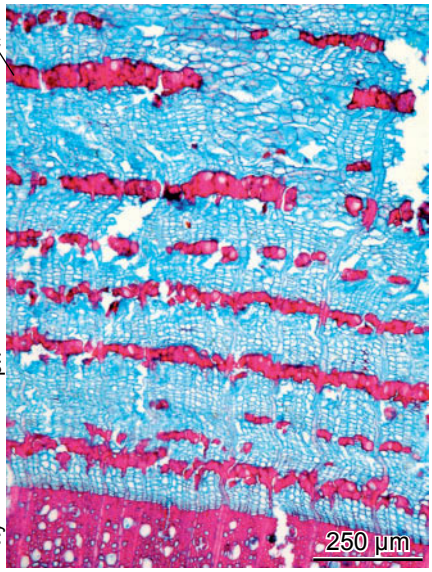
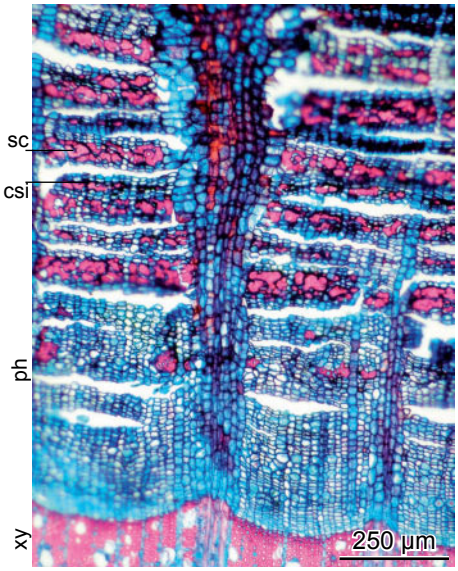
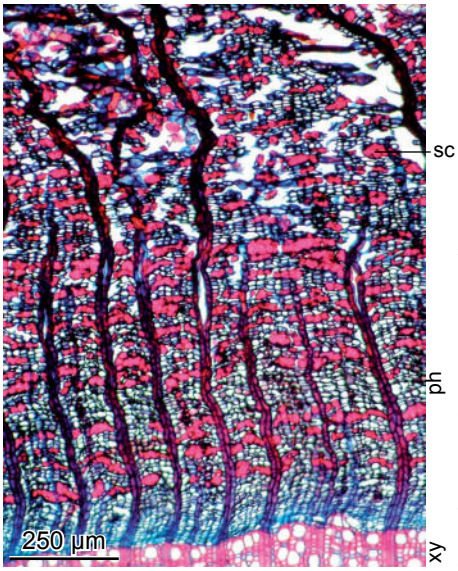


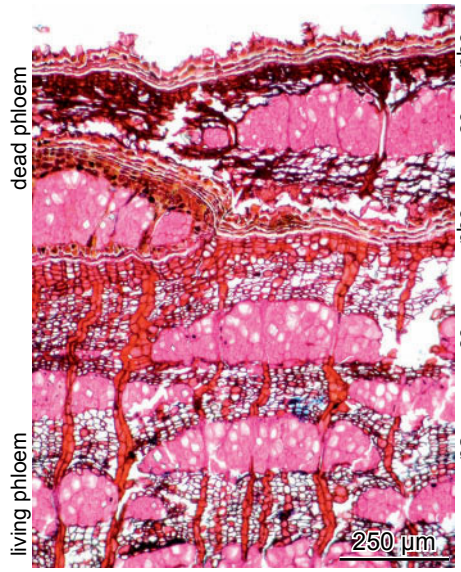

**Fig. 38.** Phloem with almost continuous bands of sclerenchyma. Stem of a 4 m-high tree, cultivated, dry slope, Tbilisi, Georgia. *Pyrus orientalis*, transverse section.

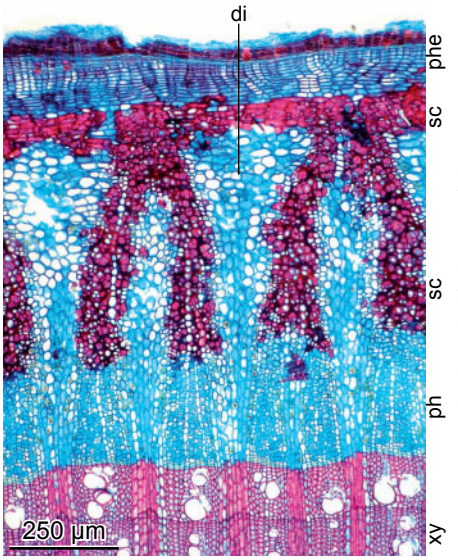



**Left Fig. 39.** Tangential bands of sieve-tubes and parenchyma situated outside of the cambium. Sclerenchymatisation (red) occurs in the forth year after phloem formation. Stem of a 1.5 m-high shrub, dry meadow, mountain zone, Grisons, Switzerland. *Rosa elliptica*, transverse section.

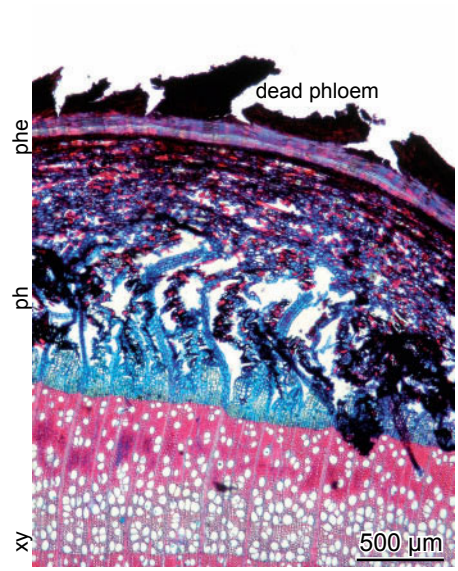
**Right Fig. 40.** Tangential bands of sclerenchyma are interrupted by rays. Stem of a 4 m-high tree, hedge, mountain zone, Rigi, Schwyz, Switzerland. *Sorbus aria*, transverse section.

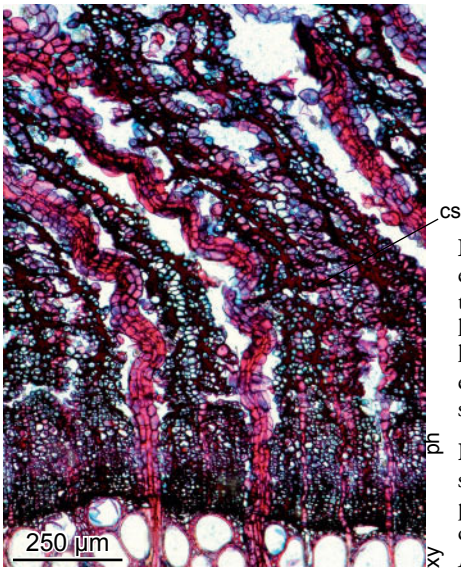



**Left Fig. 41.** Tangentially arranged groups of sclerenchyma cells. Sclerenchymatisation occurs also in rays. Stem of a 2.5 m-high shrub, hedge, mountain zone, Bern, Switzerland. *Crataegus monogyna*, transverse section.

**Right Fig. 42.** An unlignified primary phloem and radially oriented sclerenchymatic strips meet a tangential band of sclerenchyma cells of the cortex. The phellem consists of uniformly oriented rectangular cork cells. Stem of a high shrub, coastal *Picea sitchensis* forest, Oregon, USA. *Holodiscus discolor*, transverse section.




**Left Fig. 43.** A dense band of phellem embraces the soft phloem zone. Only the turgescent phloem cells resist the phellem pressure. Stem of a 2.5 m-high shrub, hedge on a dry slope, hill zone, Schaffhausen, Switzerland. *Prunus spinosa*, transverse section.

**Right Fig. 44.** Curved rays and compressed sieve-tubes (dark red) are a result of the phellem pressure. Stem of a 5 m-high tree, cultivated, hill zone, Zürich, Switzerland. *Prunus amygdalus*, transverse section.

## Ecological trends and relations to life forms

Anatomical trends between hemicryptophytes and all other life forms are obvious. The following features occur only in hemicryptophytes (Rosoideae): remaining primary vascular bundles, pervasive parenchyma, absence of fibers, thick-walled vessels, scalariform intervessel pits, absence of rays, uniform phloem. Helical thickenings are absent.

Plant size is related to vessel size. Vessels with a diameter <20 µm occur only in small plants with a maximum height of 40 cm. In contrast, vessels with a diameter >50 µm exist only in plants >80 cm in height.

## Discussion in relation to previous studies

The xylem of all the genera of the life forms tree, shrub and dwarf shrub that are described here were characterized before (excluding *Coeloglossum*). Gregory (1994) mentioned 112 references. Schweingruber (1990) described 56 European species, Itoh (1997) 46 Japanese, Shu-Yin Zhang (1992) 300 Chinese, and Benkova and Schweingruber (2004) 60 Russian species. Metcalfe and Chalk (1957) also mentioned briefly some hemicryptophytes (*Alchemilla*, *Agrimonia*, *Potentilla*). Liu and Zhang (2007) describe 5 herbaceous *Potentilla* species from Mongolia and Stepanova et al. (2007) 26 *Potentilla* species from Russia. The present study confirms all previous observations of trees, shrubs and dwarf shrubs. Most observations of hemicryptophytes are new (50 species) to this study.

Holdheide (1951) described the bark of *Pyrus communis*, *P. malus*, *Sorbus aucuparia*, *S. aria*, *Prunus padus* and *P. mahaleb*. New to this study are bark descriptions of 107 species.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **158** |
| 1 | growth rings distinct and recognizable | 153 |
| 2 | growth rings absent | 5 |
| 3 | ring-porous | 17 |
| 4 | semi-ring-porous | 105 |
| 5 | diffuse-porous | 48 |
| 7 | vessels in diagonal and/or radial patterns | 4 |
| 9 | vessels predominantly solitary | 141 |
| 9.1 | vessels in radial multiples of 2-4 common | 14 |
| 10 | vessels in radial multiples of 4 or more common | 13 |
| 11 | vessels predominantly in clusters | 26 |
| 13 | vessels with simple perforation plates | 157 |
| 14 | vessels with scalariform perforation plates | 3 |
| 20 | intervessel pits scalariform | 24 |
| 20.1 | intervessel pits pseudoscariform to reticulate | 1 |
| 22 | intervessel pits alternate | 149 |
| 31 | vessel-ray pits with large apertures, *Salix/Laurus* type | 1 |
| 36 | helical thickenings present | 52 |
| 39.1 | vessel cell-wall thickness >2 µm | 47 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 37 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 106 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 25 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 11 |
| 50 | <100 vessels per mm$^2$ in earlywood | 3 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 110 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 44 |
| 58 | Dark-staining substances in vessels and/or fibers (gum, tannins) | 22 |
| 60.1 | fibers absent | 28 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 4 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 133 |
| 65 | septate fibers present | 4 |
| 68 | fibers thin-walled | 6 |
| 69 | fibers thick-walled | 66 |
| 70 | fibers thin- to thick-walled | 76 |
| 70.2 | tension wood present | 4 |
| 75 | parenchyma absent or unrecognizable | 15 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 119 |
| 79 | parenchyma paratracheal | 10 |
| 79.1 | parenchyma pervasive | 30 |
| 89 | parenchyma marginal | 8 |
| 89.2 | ring shake, *Saxifraga* type | 1 |
| 96 | rays uniseriate | 75 |
| 97 | rays width predominantly 1-3 cells | 65 |
| 98 | rays commonly 4-10-seriate | 42 |
| 99 | rays commonly >10-seriate | 48 |
| 99.1 | vascular bundle form remaining | 40 |
| 99.2 | stem lobed | 3 |
| 100.2 | rays not visible in polarized light | 37 |
| 103 | rays of two distinct sizes (tangential section) | 9 |
| 102 | ray height >1 mm | 56 |
| 104 | ray: all cells procumbent (radial section) | 25 |
| 105 | ray: all cells upright or square | 61 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 23 |
| 107 | ray: heterocellular with 2-4 cell upright rows (radial section) | 42 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 6 |
| 110 | rays with sheet cells (tangential section) | 19 |
| 117 | rayless | 30 |
| 136 | prismatic crystals present | 16 |
| 144 | druses present | 30 |
| 153 | crystal sand present | 1 |
| R1 | groups of sieve tubes present | 18 |
| R2 | groups of sieve tubes in tangential rows | 28 |
| R2.1 | groups of sieve tubes in radial rows | 1 |
| R3 | distinct ray dilatations | 33 |
| R4 | sclereids in phloem and cortex | 44 |
| R6 | sclereids in radial rows | 8 |
| R6.1 | sclereids in tangential rows | 28 |
| R7 | with prismatic crystals | 32 |
| R8 | with crystal druses | 35 |
| R9 | with crystal sand | 1 |
| R10 | phloem not well structured | 52 |
| R12 | with laticifers, oil ducts or mucilage ducts | 1 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 101 |

# Rubiaceae

**Number of species, worldwide and in Europe**

The cosmopolitan Rubiaceae family has 550 genera with 9000 species. In Europe, there are 10 genera with ca. 230 species, primarely herbs lianas and dwarf shrubs.

**Analyzed material**

The xylem and phloem of 31 Rubiaceae species are analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | | >80 |
| Nanophanerophytes (0.5-4 m) | 3 | |
| Lianas | 4 | ca. 3 |
| Hemicryptophytes and geophytes | 24 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 1 | |
| Hill and mountain | 19 | |
| Mediterranean | 8 | |
| Subtropical | 3 | |

**Analyzed species:**

*Asperula aristata* L.
*Asperula cynanchica* L.
*Asperula purpurea* (L.) Ehrendorf
*Asperula taurina* Pacz.
*Asperula tinctoria* L.
*Crucianella maritima* L.
*Cruciata laevipes* Opiz
*Galium album* L.
*Galium anisophyllum* Vill.
*Galium boreale* L.
*Galium coloradoense* W.F. Wight
*Galium laevigatum* L.
*Galium lucidum* All.
*Galium megalospermum* All.
*Galium mollugo* L.
*Galium obliqum* Vill.
*Galium pusillum* L.
*Galium rotundifolium* L.
*Galium rubrum* L.
*Galium suberosum* Siebt. et Sm.
*Galium sylvaticum* L.
*Galium timeroi* Jord.
*Galium verum* L.
*Galium x pomeranicum* Retz
*Phyllis nobla* L.
*Plocama pendula* Ait.
*Putoria calabrica* (L.fil.) DC.
*Rubia fruticosa* Ait.
*Rubia peregrina* L.
*Rubia tenuifolia* D'Urv.
*Sherardia arvensis* L.

*Rubia tinctoria* (photo: Zinnert)

*Galium mollugo* (photo: Zinnert)

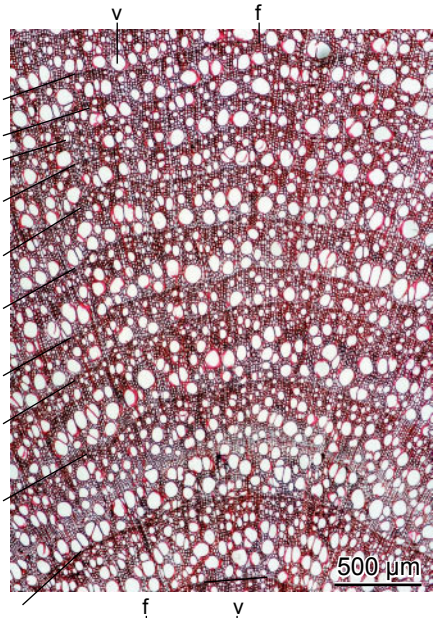
*Galium odoratum*

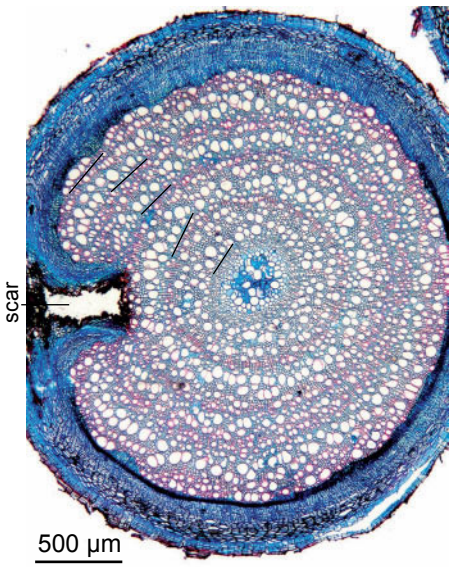
*Galium luteum*

**Characteristics of the xylem**

The xylem within the of Rubiaceae family varies widly (Jansen et al. 2002) but it is relatively homogeneous among the herbaceous to slightly lignified species in the tribe Rubiae. Rings are distinct in the ring-porous lianas, e.g. the *Rubia* species (**Fig. 1**) and the dwarf shrub *Putoria calabrica*. Perennial herbs with semi-ring-porous xylem have distinct rings (**Figs. 2** and **3**). Rings are indistinct in species with a diffuse-porous xylem (**Figs. 4** and **5**). *Sherardia arvensis* is an annual herb and therefore has only one ring (**Fig. 6**). Solitary vessels are characteristic of all the analyzed *Asperula* and *Rubia* species. They can be slightly clustered in specimens with high vessel density (**Figs. 2-4**). Vessels form radial multiples in the shrubs *Plocama pendula* (**Fig. 7**) and *Phyllis nobla*. Earlywood vessel diameters typically vary between 20-40 µm and vessel frequency between <100/mm$^2$ in *Plocama pendula* and *Phyllis nobla* and 200-500/mm$^2$ in all herbaceous species. All vessels contain simple perforations and round to slightly laterally extended pith apertures (**Figs. 8** and **13**). Fibers have minutely bordered pits. Fibers are thin- to thick- and thick-walled. The presence of thin-walled living fibers was observed in several species, e.g *Galium album* (**Fig. 9**). Axial parenchyma is apotracheal (**Fig. 7**), paratracheal and pervasive (**Figs. 10**, **11** and **19**). Fibers are rare or absent in species with pervasive parenchyma.

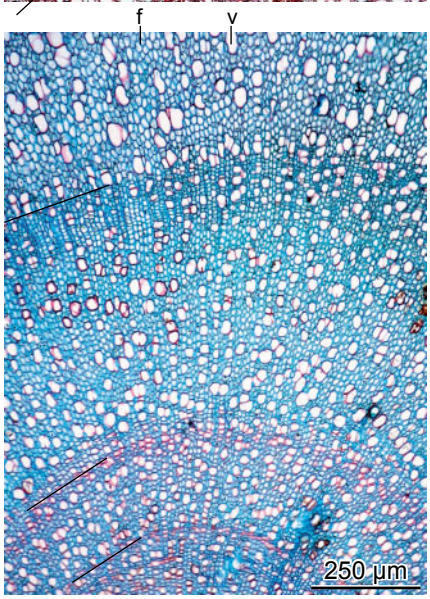
Rays are absent in the majority of analyzed species and in small herbaceous species such as *Asperula taurina* (**Fig. 12**). Transitions occur between short, axial parenchyma cells and elongated, axial ray cells (**Fig. 12**). Most species have uniseriate (**Figs. 13** and **14**) or biseriate rays (**Fig. 15**). In the present material, multiseriate rays exist only in the shrub *Phyllis nobla* (**Fig. 16**). Ray cells in species with uniseriate rays are exclusively square or upright (**Fig. 17**). Rhaphides were observed in the xylem of *Rubia fruticosa*.

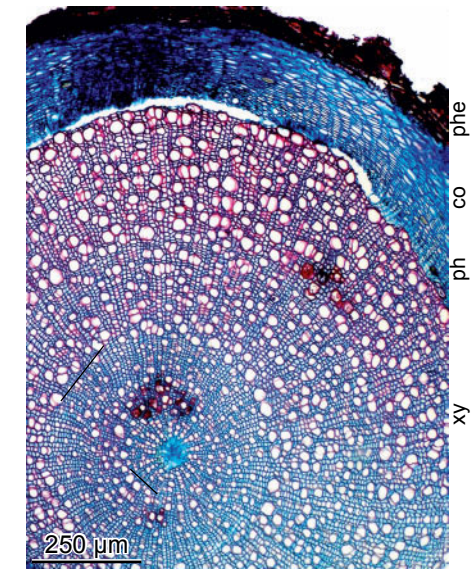



**Left Fig. 1.** Distinct annual rings of a ring-porous xylem. Liana, hedge, Mediterranean climate, Cyprus. *Rubia tenuifolia*, transverse section.

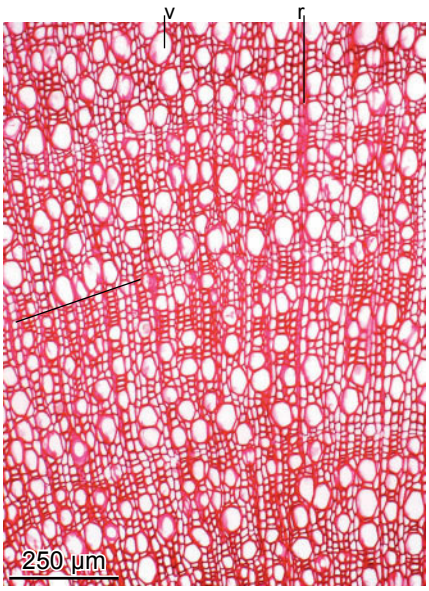
**Right Fig. 2.** Distinct annual rings of a semi-ring-porous xylem of a six-year-old hemicryptophyte. Root collar of a 40 cm-high herb, meadow, mountain zone, Alps, Switzerland. *Galium lucidum*, transverse section.

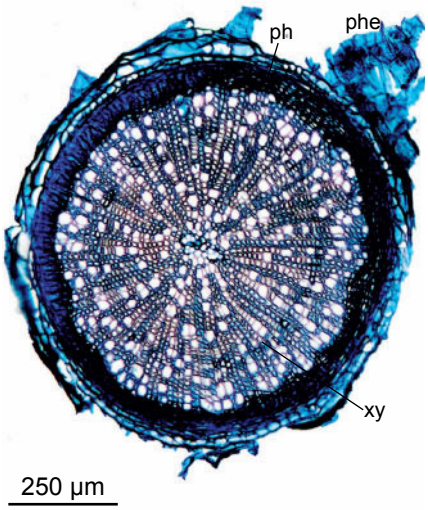



**Left Fig. 3.** Distinct annual rings of a slightly semi-ring-porous xylem. Vessels are solitary or clustered. Rhizome of a 50 cm-high hemicryptophyte, abandoned field, hill zone, Vienna, Austria. *Galium album*, transverse section.

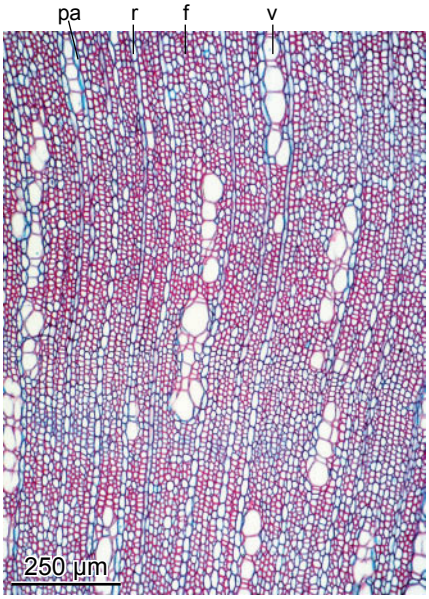
**Right Fig. 4.** Indistinct annual rings. Most vessels are solitary. Rhizome of a 40 cm-high hemicryptophyte, moist meadow, hill zone, Bavaria, Germany. *Galium mollugo*, transverse section.

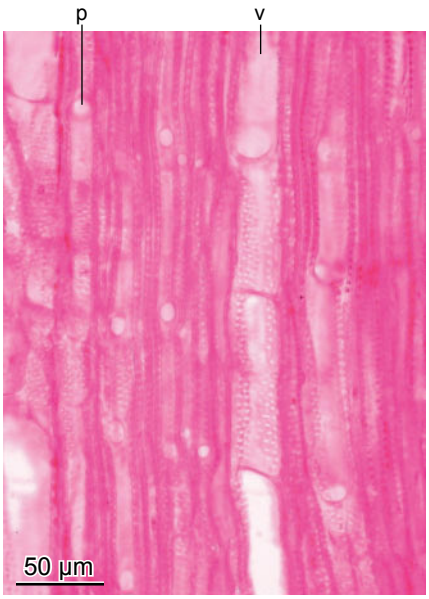



**Left Fig. 5.** Indistinct annual rings with primarely solitary vessels. Stem of a 20 cm-high dwarf shrub, Mediterranean, coast, Spain. *Crucianella maritima*, transverse section.

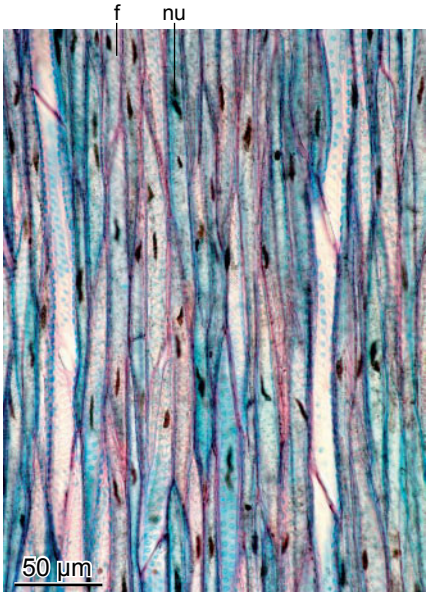
**Right Fig. 6.** One annual ring in a therophyte. Root collar of an 8 cm-high annual plant, dry meadow, hill zone, Burgenland, Austria. *Sherardia arvensis*, transverse section.

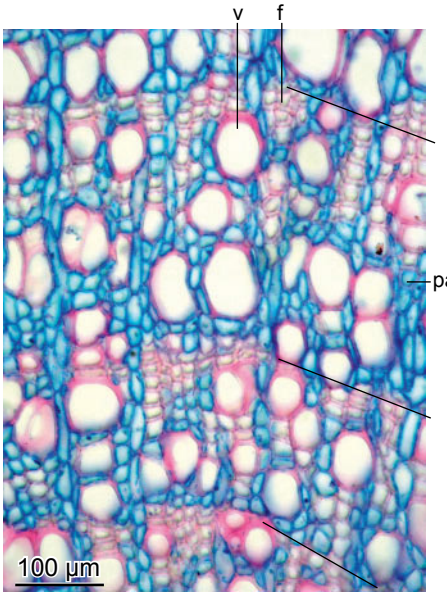



**Left Fig. 7.** Indistinct ring in the xylem with vessels in radial multiples and apotracheal parenchyma. Stem of a 2 m-high shrub, succulent zone, subtropical climate, Tenerife, Canary Islands. *Plocama pendula*, transverse section.

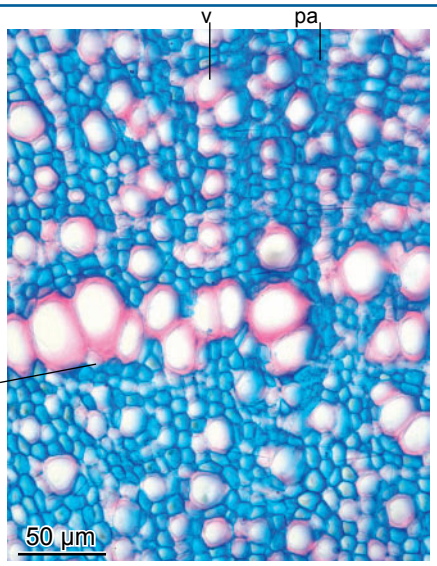
**Right Fig. 8.** Vessels with simple perforations and small round intervessel pits. Rhizome of a hemicryptophyte, on a rock, hill zone of the Italian Alps. *Galium rubrum*, radial section.

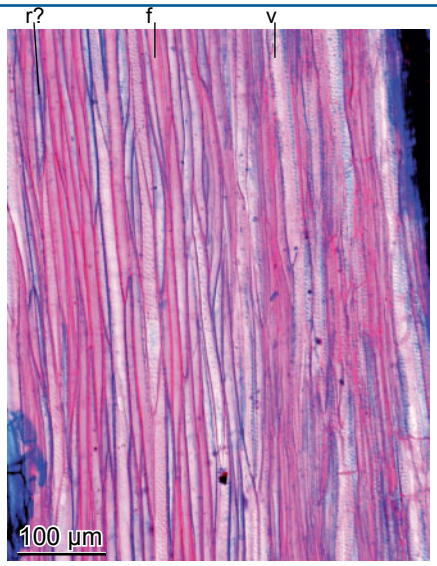



**Left Fig. 9.** Living fibers with cell nuclei. Rhizome of a 50 cm-high hemicryptophyte, abandoned field, hill zone of Vienna, Austria. *Galium album*, tangential section.

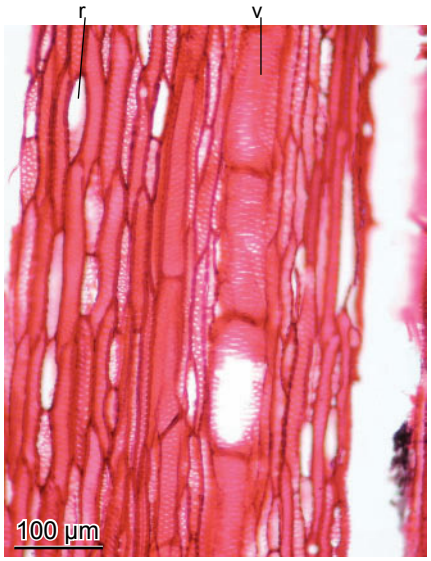
**Right Fig. 10.** Paratracheal parenchyma surrounding solitary vessels. Rhizome of a 30 cm-high hemicryptophyte, dry meadow, mountain zone, Alps, France. *Asperula aristata*, transverse section.

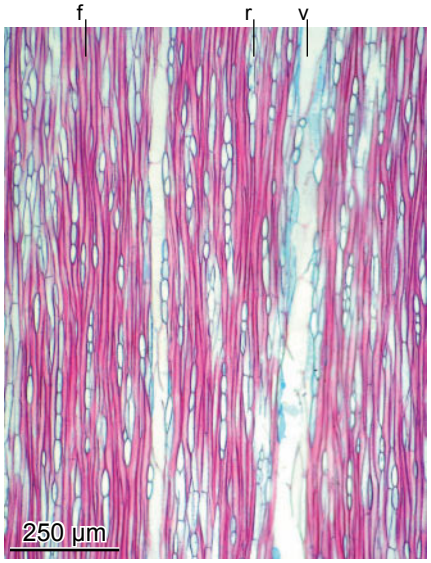



**Left Fig. 11.** Pervasive parenchyma around solitary, thick-walled vessels. Root collar of a 20 cm-high hemicryptophyte, dry river bed, mountain zone, Alps, France. *Galium pusillum*, transverse section.

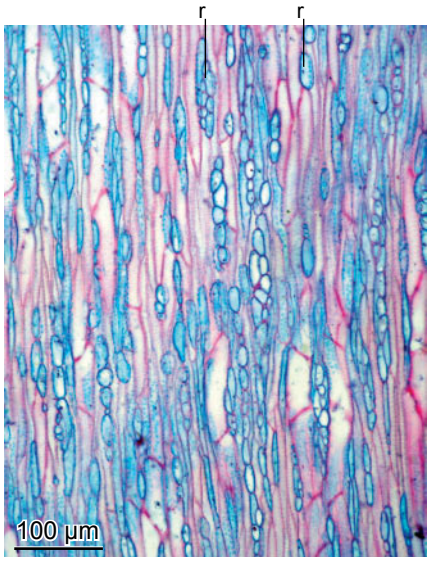
**Right Fig. 12.** Almost rayless xylem. Rhizome of a 30 cm-high hemicryptophyte, canyon, hill zone, southern Alps, Switzerland. *Asperula taurina*, tangential section.




**Left Fig. 13.** Uniseriate rays. Stem of a liana, *Quercus suber* forest, French Mediterranean coast. *Rubia peregrina*, tangential section.

**Right Fig. 14.** Uniseriate rays with unlignified cell walls. Stem of a shrub, succulent zone, subtropical climate, Tenerife, Canary Islands. *Plocama pendula*, transverse section.



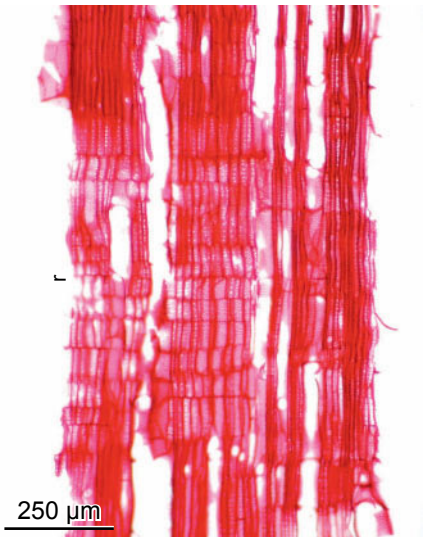


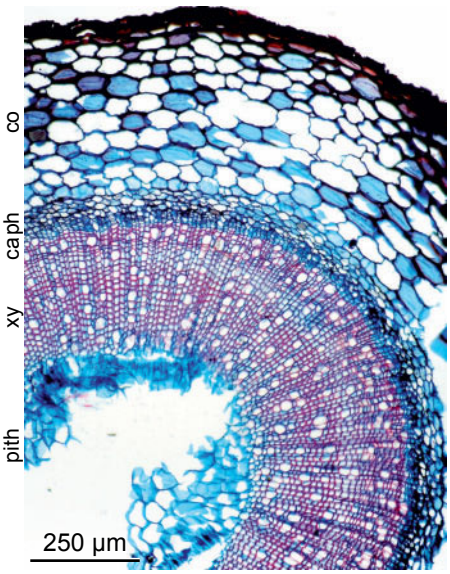

**Fig. 15.** Uni- and biseriate rays with unlignified cell walls. Rhizome of a 30 cm-high hemicryptophyte, dry meadow, mountain zone, Alps, France. *Asperula aristata*, transverse section.

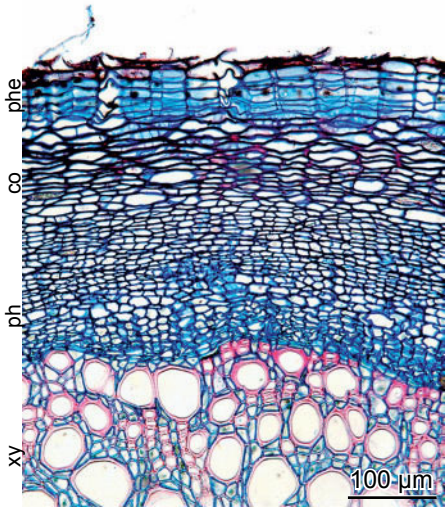
**Fig. 16.** 2-5-seriate rays with sheet cells. Stem of an 80 cm-high shrub, laurel zone, subtropical climate, Tenerife, Canary Islands. *Phyllis nobla*, tangential section.

**Fig. 17.** Upright ray cells. Stem of a 20 cm-high dwarf shrub, Mediterranean zone, southern Spain. *Putoria calabrica*, radial section.

### Characteristics of the phloem and the cortex

Bark of the Rubiaceae family has a simple construction. It is characterized by radially oriented parenchyma and sieve tubes (**Figs. 17-20**) and the absence of sclerenchyma (**Fig. 20**). The presence of rhaphides in idioblasts (**Fig. 21**) is common but not mandatory; e.g. they were found only in one of the 3 specimens of *Galium mollugo* analyzed. Rhaphides seem to be absent in the bark of *Crucianella maritima* and *Putoria calabrica*. Sclereids are only present in the cortex of the shrub *Plocama pendula* (**Fig. 22**).




**Left Fig. 18.** Pith, xylem, phloem and bark. A thick cortex with large parenchyma cells exists outside a small, loosely structured phloem. Rhizome of a 30 cm-high herb, canyon, hill zone, southern Alps, Switzerland. *Asperula taurina*, transverse section.

**Right Fig. 19.** The simply constructed phloem and cortex contain only a few large idioblasts with rhaphides. Cells of the phellem are radially flat. Bark of a root collar of a 40 cm-high herb, meadow, mountain zone, Alps, Switzerland. *Galium lucidum*, transverse section.

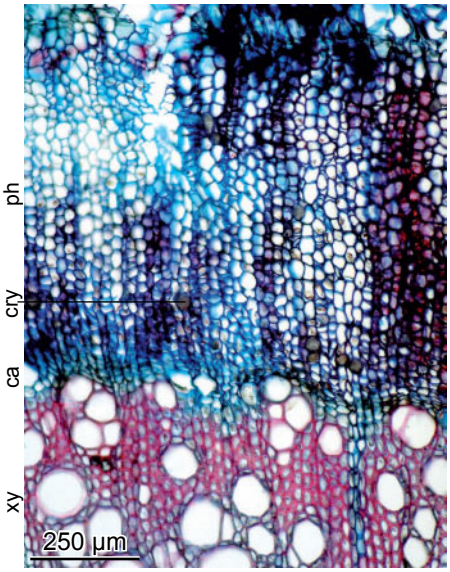



**Fig. 20.** Simply constructed phloem. Parenchyma and sieve tubes cannot be distinguished. Rhaphids (gray) are in some parenchyma cells. Bark of a liana, succulent zone, subtropical climate, Tenerife, Canary Islands. *Rubia fruticosa*, transverse section.

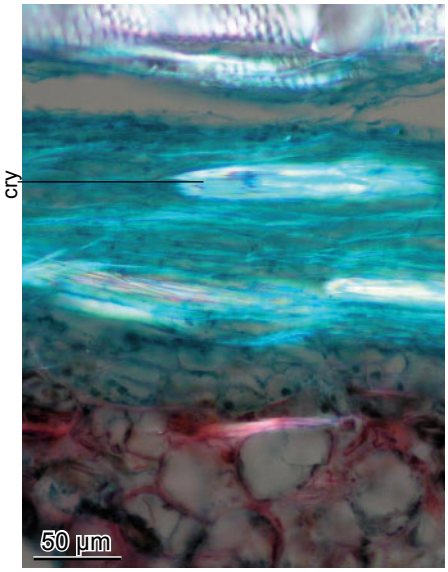



**Fig. 21.** Rhaphides in the phloem. Bark of a rhizome of a 30 cm-high hemicryptophyte, dry meadow, mountain zone, Alps, France. *Asperula aristata*, radial section, polarized light.

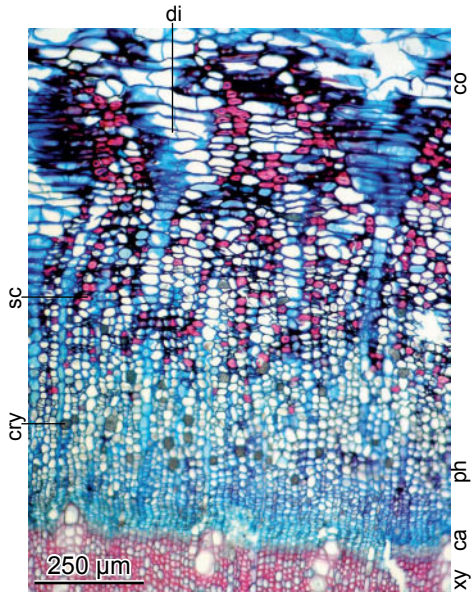



**Fig. 22.** Simply constructed phloem. Parenchyma and sieve tubes cannot be distinguished. Many cells contain rhaphides (gray). In the dilated cortex are some sclerotized cells (red). Bark of a shrub, succulent zone, subtropical climate, Tenerife, Canary Islands. *Plocama pendula*, transverse section.

### Ecological trends in the xylem

Temperate regions (Mediterranean, hill, mountain, subalpine and alpine zone) are dominated by hemicryptophytes while the subtropical climate in Macaronesia is dominated by shrubs. Vessels with a diameter >80 µm are typical for lianas as well as for some *Rubia* species. There is a close correlation between the formation of rays and life form. Therophytes and hemicryptophytes generally lack rays whereas distinct rays are present in shrubs.

### Discussion in relation to previous studies

The xylem of the Rubiaceae was the subject of an extended study by Jansen et al. (2002). The present study includes only a small fraction of the family. Jansen et al. (2002) classify some shrubs included in this study: two shrubs from the Canary Islands (*Plocama*, *Phyllis*) and one from Spain (*Putoria*) and some lianas and hemicryptophytes of the tribe Rubiae (*Asperula*, *Crucianella*, *Galium*, *Rubia*).

All species described here belong to the subfamily Rubioideae, tribe Rubiae. They are described for the first time. The presence of numerous very small vessels and the absence of rays is characteristic for most herbaceous species. In contrast to Jansen et al. (2002), rhaphides tend to be absent in the xylem but are very frequent in the phloem and the cortex.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **31** |
| 1 | growth rings distinct and recognizable | 20 |
| 2 | growth rings absent | 10 |
| 2.1 | only one ring | 1 |
| 4 | semi-ring-porous | 22 |
| 5 | diffuse-porous | 12 |
| 9 | vessels predominantly solitary | 30 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 10 | vessels in radial multiples of 4 or more common | 1 |
| 11 | vessels predominantly in clusters | 5 |
| 13 | vessels with simple perforation plates | 31 |
| 39.1 | vessel cell wall thickness >2 µm | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 26 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 5 |
| 50 | <100 vessels per mm$^2$ in earlywood | 1 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 29 |
| 56 | tylosis with thin walls | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 31 |
| 68 | fibers thin-walled | 14 |
| 69 | fibers thick-walled | 14 |
| 70 | fibers thin- to thick-walled | 3 |
| 75 | parenchyma absent or unrecognizable | 4 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 21 |
| 79 | parenchyma paratracheal | 21 |
| 79.1 | parenchyma pervasive | 10 |
| 89.1 | parenchyma marginal thin walled, dark in polarized light | 1 |
| 96 | rays uniseriate | 9 |
| 97 | ray width predominantly 1-3 cells | 7 |
| 105 | ray: all cells upright or square | 11 |
| 117 | rayless | 19 |
| 120 | storied axial tissue (parenchyma, fibers, vessels, tangential section) | 4 |
| 136 | prismatic crystals present | 4 |
| 149 | rhaphides present | 1 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R10 | phloem not well structured | 27 |
| R11 | with rhaphides | 26 |

# Rutaceae

**Number of species, worldwide and in Europe**

The cosmopolitan Rutaceae family includes 150 genera with 1500 species. In Europe, there are 4 genera with 17 species.

**Analyzed material**

The xylem and phloem of 4 genera with 8 species are analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | 2 | numerous |
| Nanophanerophytes (0.5-4 m) | 1 | a few |
| Woody chamaephytes | 4 | 3 |
| Hemicryptophytes | 1 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 2 | |
| Mediterranean | 6 | |

**Analyzed species:**

*Citrus limon* (L.) Burm fil.
*Citrus sinensis* (L.) Osbeck
*Dictamnus albus* L.
*Poncirus trifoliata* (L.) Raf.
*Ruta angustifolia* Pers.
*Ruta chalepensis* Pers.
*Ruta graveolens* L.
*Ruta montana* (L.) L.

*Poncirus trifoliata* (photo: Zinnert)

*Dictamnus albus* (photo: Zinnert)

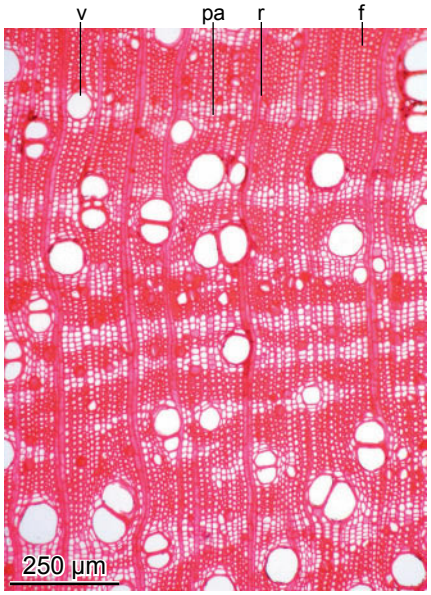
*Citrus sinensis* (photo: Lauerer)

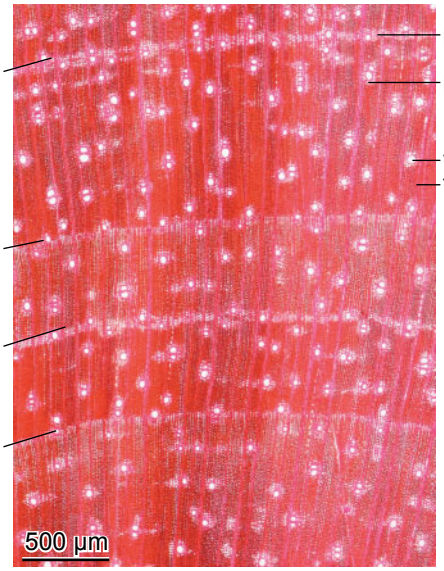
*Ruta graveolens* (photo: Zinnert)

**Characteristics of the xylem**

Irregular, tangential growth zones are present in *Citrus* (**Fig. 1**), and annual rings occur in all other genera (*Dictamnus*, *Poncirus*, *Ruta*; **Figs. 3** and **4**). *Poncirus trifoliata* is diffuse-porous (**Fig. 2**) and *Dictamnus* and *Ruta* species are semi-ring-porous (**Figs. 3** and **4**). Vessels are solitary (**Fig. 2**) or in radial multiples, and are occasionally tangentially or slightly diagonally arranged (**Fig. 3**). Earlywood vessels with a diameter from 50-100 µm and a density of 50-90/mm$^2$ are characteristic of *Citrus* and *Poncirus* (**Figs. 1** and **2**). Vessel diameter is smaller (30 µm) and vessel density is higher (150-300/mm$^2$) in *Dictamnus* and *Ruta* (**Figs. 3** and **4**). Vessels of all species have simple perforations. Intervessel pits are round in alternating position. We found helical thickenings in *Poncirus trifoliata* and *Ruta chalepensis* and vascular tracheids in *Ruta graveolens* and *Ruta montana* (**Fig. 5**). Vessels of old individuals of all species contain dark-staining substances. Fibers containing small pits with slit-like apertures are thin- to thick-walled (**Figs. 3**, **5** and **6**) or thick-walled (**Figs. 1**, **2**, **4** and **6**). Parenchyma is paratracheal (**Figs. 6** and **7**). Apotracheal parenchyma occurs in various forms: diffuse, aliform (**Fig. 6**) and arranged in tangential bands (**Fig. 1**).

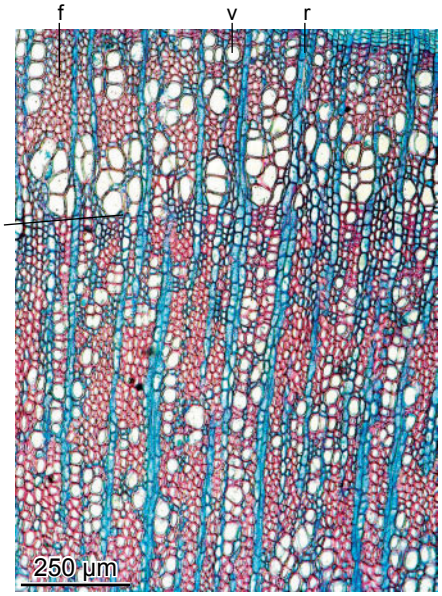
Ray width varies from 2-4-seriate (**Figs. 8**, **9** and **11**). Rays are homocellular with procumbent cells (**Fig. 10**) or heterocellular with one to a few cell rows of square and upright cells (**Fig. 9**). Transitions between different ray types are frequent. Homocellular rays with exclusively upright cells were observed in *Dictamnus albus*. Prismatic crystals in chambers occur in *Citrus* (**Fig. 11**) and *Poncirus*, while crystal druses occur in rays of *Dictamnus albus*.

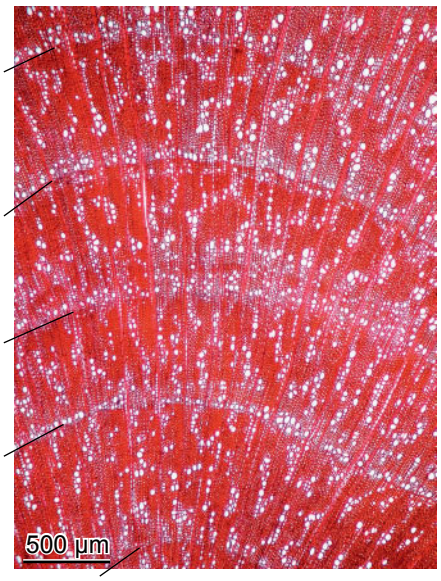



**Left Fig. 1.** Xylem with growth zones and tangential layers of parenchyma cells. Vessels are solitary and in short, radial multiples. Stem of a 5 m-high tree, plantation, Mediterranean, Samos, Greece. *Citrus sinensis*, transverse section.

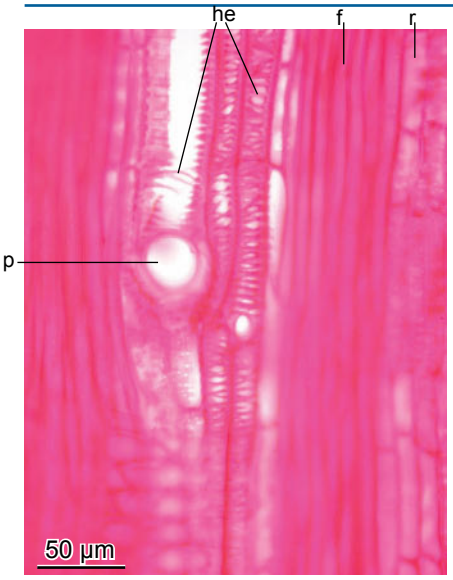
**Right Fig. 2.** Xylem with annual rings and bands of terminal parenchyma. Vessels are mainly solitary. Stem of a 1 m-high shrub, hill zone, Botanical Garden Munich, Bavaria, Germany. *Poncirus trifoliata*, transverse section.

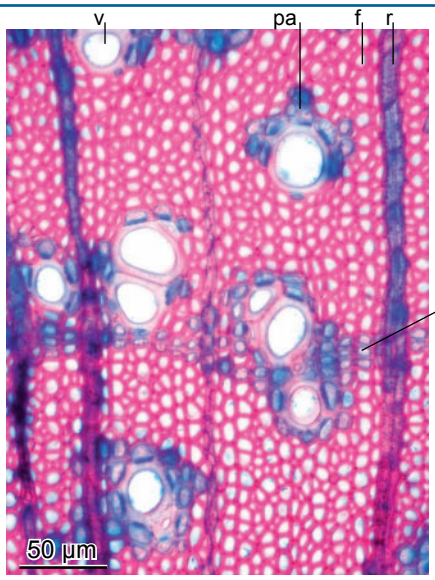



**Left Fig. 3.** Semi-ring-porous xylem. Vessels occur in long, radial multiples. Parenchyma is paratracheal and apotracheal. Root collar of an 80 cm-high hemicryptophyte, garden, hill zone, Blaufelden, Bavaria, Germany. *Dictamnus albus*, transverse section.

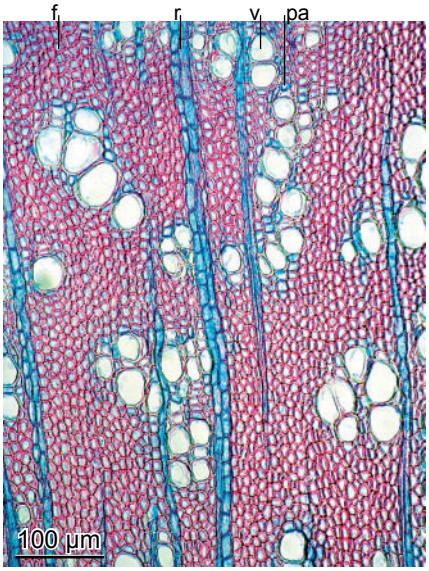
**Right Fig. 4.** Semi-ring-porous xylem. Vessels are solitary in long, radial slightly diagonal arranged multiples. Stem of a 60 cm-high dwarf shrub, on rock, Mediterranean, Mallorca, Spain. *Ruta angustifolia*, transverse section.

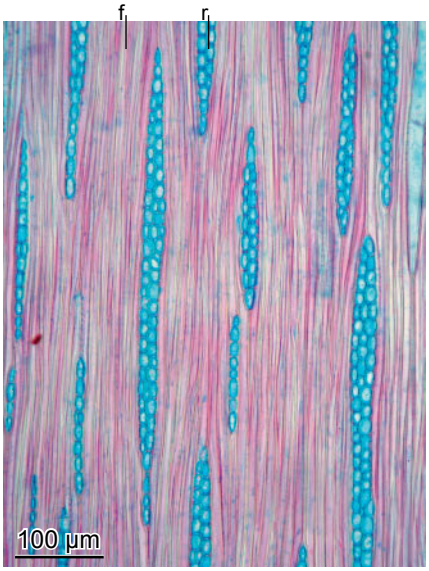



**Left Fig. 5.** Vessels with helical thickenings. Stem of a 1 m-high shrub, hill zone, Botanical Garden Munich, Bavaria, Germany. *Poncirus trifoliata*, radial section.

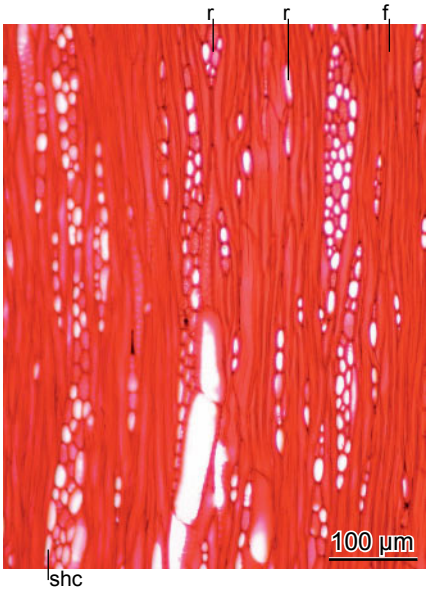
**Right Fig. 6.** Thick-walled vessels are accompagnied by paratracheal parenchyma cells. Stem of a 1 m-high shrub, hill zone, Botanical Garden Munich, Bavaria, Germany. *Poncirus trifoliata*, transverse section.

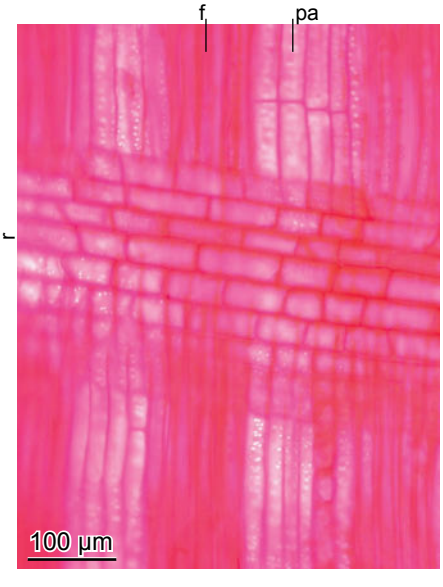



**Left Fig. 7.** Scanty paratracheal parenchyma around vessels groups. Root collar of an 80 cm-high hemicryptophyte, garden, hill zone, Blaufelden, Bavaria, Germany. *Ruta angustifolia*, transverse section.

**Right Fig. 8.** Mainly 2-3-seriate rays. Stem of a 4 m-high tree, plantation, Mediterranean, Hammamet, Tunesia. *Citrus limon*, tangential section.



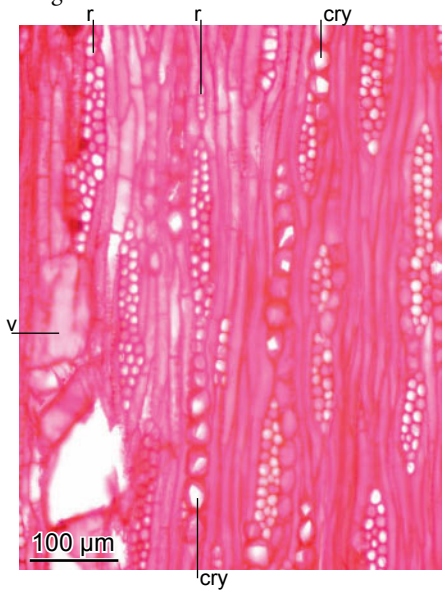



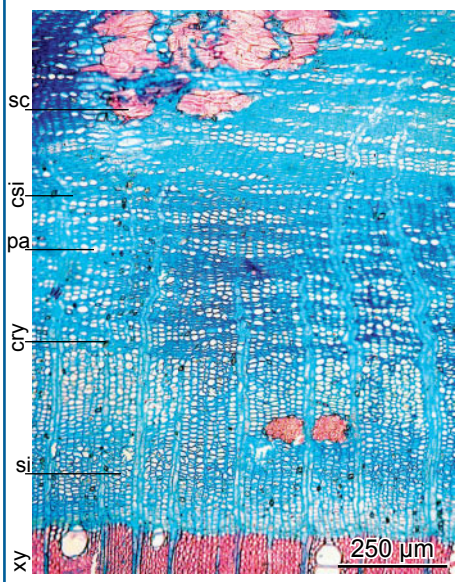

**Fig. 9.** 1-4-seriate rays. Stem of a 60 cm-high dwarf shrub, on rock, Mediterranean, Mallorca, Spain. *Ruta angustifolia*, tangential section.

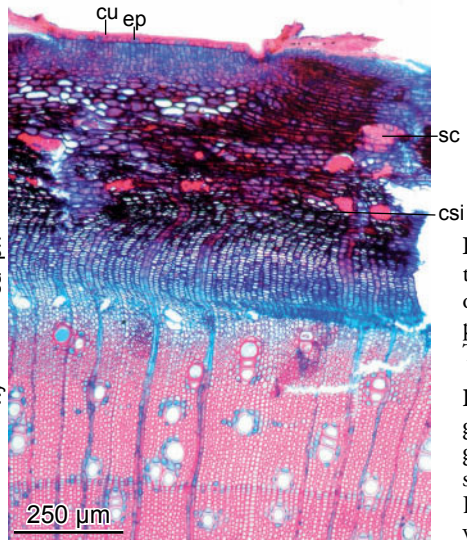
**Fig. 10.** Homocellular ray consisting of procumbent cells. Stem of a 5 m-high tree, plantation, Mediterranean, Samos, Greece. *Citrus sinensis*, radial section.

**Fig. 11.** Prismatic crystal druses in long, radially oriented chambers. Stem of a 5 m-high tree, plantation, Mediterranean, Samos, Greece. *Citrus sinensis*, tangential section.

**Characteristics of the phloem and the cortex**

The phloem structure is heterogeneous within the family. Irregular bands of compressed cells (**Figs. 12** and **13**) and groups of sclerenchyma occur in most species be it in round (**Figs. 12** and **13**) or radial groups (**Fig. 14**). Prismatic crystals occur in *Citrus* and *Poncirus* and crystal druses in *Dictamnus* and *Ruta*. Oil ducts were observed in twigs of *Citrus*, *Ruta* and *Poncirus* (**Figs. 15** and **16**).




**Left Fig. 12.** Phloem with irregular tangential layers of collapsed cells and a few groups of sclerenchyma. Stem of a 4 m-high tree, plantation, Mediterranean, Hammamet, Tunesia. *Citrus limon*, transverse section.

**Right Fig. 13.** Phloem with irregular tangential layers of collapsed cells and a few groups of sclerenchyma. Stem of a 1 m-high shrub, hill zone, Botanical Garden Munich, Bavaria, Germany. *Poncirus trifoliata*, transverse section.

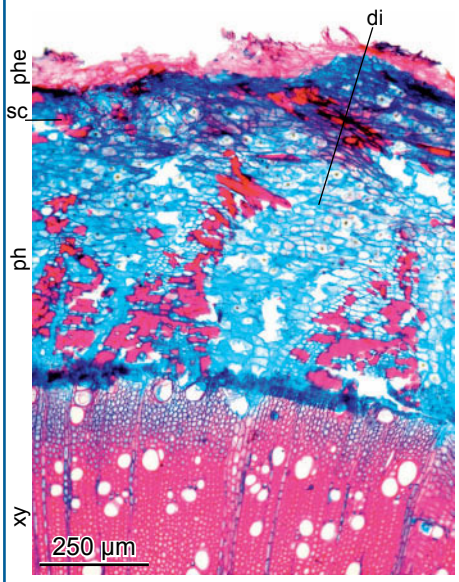



**Fig. 14.** Phloem with irregular, radially oriented sclerenchyma cells. Stem of a 50 cm-high dwarf shrub, ruderal site, Mediterranean, Ohanes, Andalusia. *Ruta montana*, transverse section.

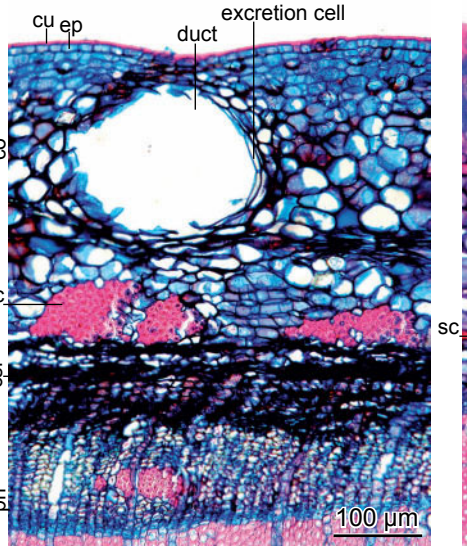



**Fig. 15.** Large oil duct in the cortex of a twig. Stem of a 4 m-high tree, plantation, Mediterranean, Hammamet, Tunesia. *Citrus limon*, transverse section.

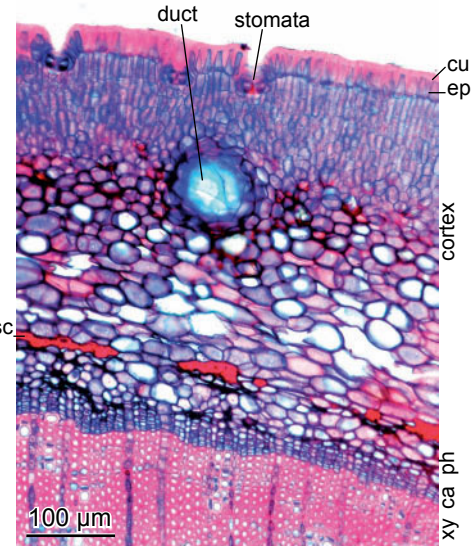



**Fig. 16.** Large oil duct in the cortex of a twig. Stem of a 1 m-high shrub, hill zone, Botanical Garden Munich, Bavaria, Germany. *Poncirus trifoliata*, radial section.

**Discussion in relation to previous studies**

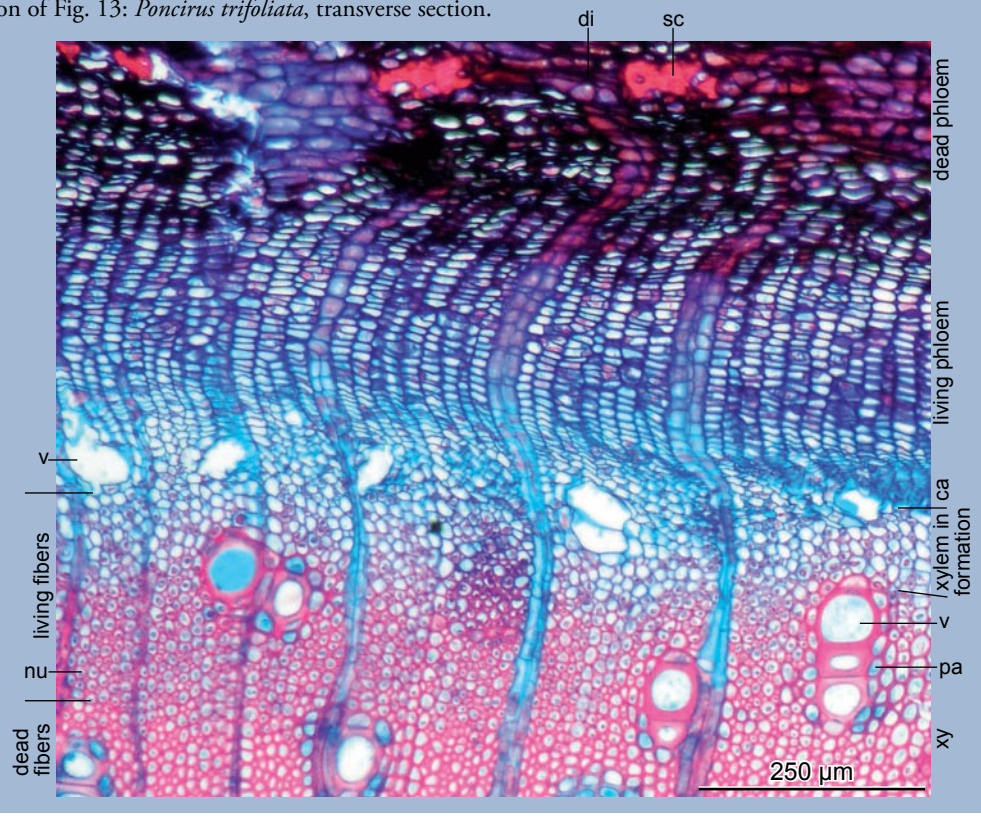
Primarely tropical genera have been described before. Gregory (1994) mentioned 130 references. *Citrus* was studied by Greguss (1945), Huber and Rouschal (1954), Fahn et al. (1986) and Schweingruber (1990). Ruta was subject of studies by Fahn et al. (1986) and Schweingruber (1990). All bark descriptions are new to this study.

The anatomical structure of the xylem within the family is very heterogeneous. The arrangement of vessels and parenchyma of *Citrus* and *Poncirus* are similar but the genera *Dictamnus* and *Ruta* are different. We do not have enough of material for a more precise classification. Particular for the family is the presence of oil ducts in the cortex. Bark structure might be helpful for the differentiation of species.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **8** |
| 1 | growth rings distinct and recognizable | 6 |
| 2 | growth rings absent | 2 |
| 4 | semi-ring-porous | 3 |
| 6 | vessels in intra-annual tangential rows | 2 |
| 7 | vessels in diagonal and/or radial patterns | 1 |
| 9 | vessels predominantly solitary | 5 |
| 9.1 | vessels in radial multiples of 2-4 common | 4 |
| 10 | vessels in radial multiples of 4 or more common | 1 |
| 11 | vessels predominantly in clusters | 3 |
| 13 | vessels with simple perforation plates | 8 |
| 22 | intervessel pits alternate | 8 |
| 29 | vestured pits | 1 |
| 36 | helical thickenings present | 2 |
| 39.1 | vessel cell-wall thickness >2 µm | 6 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 5 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 3 |
| 50 | <100 vessels per mm$^2$ in earlywood | 3 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 1 |
| 58 | Dark-staining substances in vessels and/or fibers (gum, tannins) | 3 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 2 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 6 |
| 69 | fibers thick-walled | 3 |
| 70 | fibers thin- to thick-walled | 6 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 4 |
| 79 | parenchyma paratracheal | 8 |
| 97 | ray width predominantly 1-3 cells | 6 |
| 98 | rays commonly 4-10-seriate | 2 |
| 104 | ray: all cells procumbent (radial section) | 4 |
| 105 | ray: all cells upright or square | 2 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 2 |
| 108 | ray: heterocellular with >4 cell upright rows (radial section) | 2 |
| 142 | prismatic crystals in axial chambered cells | 3 |
| 144 | druses present | 1 |
| R1 | groups of sieve tubes present | 3 |
| R2 | groups of sieve tubes in tangential rows | 7 |
| R3 | distinct ray dilatations | 4 |
| R4 | sclereids in phloem and cortex | 5 |
| R6 | sclereids in radial rows | 1 |
| R8 | with crystal druses | 5 |
| R12 | with laticifers, oil ducts or mucilage ducts | 4 |
| P2 | with laticifers or intercellular canals | 1 |

Detailed illustration of Fig. 13: *Poncirus trifoliata*, transverse section.



# Salicaceae



**Number of species, worldwide and in Europe**

The cosmopolitan Salicaceae family includes 58 genera with 1210 species. In Europe, there are 2 genera (*Salix* and *Populus*) with 79 species.

**Analyzed material**

The xylem and phloem of 3 genera (*Chosenia*, *Populus*, *Salix*) with 39 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | 16 | numerous |
| Nanophanerophytes (0.5-4 m) | 12 | numerous |
| Woody chamaephytes | 11 | a few |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 14 | |
| Arctic and boreal | 10 | |
| Hill and mountain | 14 | |
| Mediterranean | 1 | |

**Analyzed species:**

*Chosenia arbutifolia* Pall.
*Populus canadensis* Moench
*Populus nigra* L.
*Populus suaveolens* Fisch ex Loud.
*Populus tremula* L.
*Populus tremuloides* Michx.
*Salix alba* L.
*Salix appendiculata* Vill.
*Salix arbuscula* L.
*Salix arctica* Pallas
*Salix aurita* L.
*Salix berberidifolia* Pall.
*Salix brachycarpa* Nutt.
*Salix breviserrata* B. Flod
*Salix canariensis* C. Sm ex Link
*Salix caprea* L.
*Salix cinerea* L.
*Salix daphnoides* L.
*Salix foetida* Schleicher
*Salix fragilis* L.
*Salix glabra* Scop.
*Salix glaucosericea* B. Flod
*Salix hastata* L.
*Salix helvetica* L.
*Salix herbacea* L.
*Salix incana* Schrank
*Salix lanata* L.
*Salix myrsinifolia* Salisb.
*Salix myrtilloides* L.
*Salix planifolia* Pursh
*Salix polaris* Wahlenberg
*Salix pulchra* Cham.
*Salix purpurea* L.
*Salix repens* L.
*Salix reticulata* L.
*Salix retusa* L.
*Salix schwerini* E. Wolf
*Salix viminalis* L.
*Salix waldsteiniana* Willd.

*Salix retusa*

*Salix retusa*

*Salix alba*

*Salix alba* (photo: Aas)

*Populus nigra*

*Populus nigra* (photo: Aas)

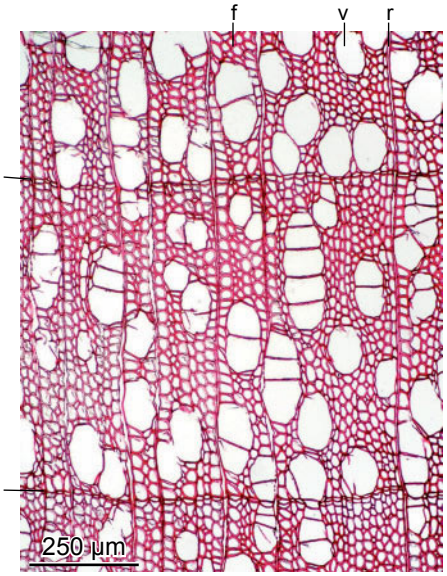
**Characteristics of the xylem**

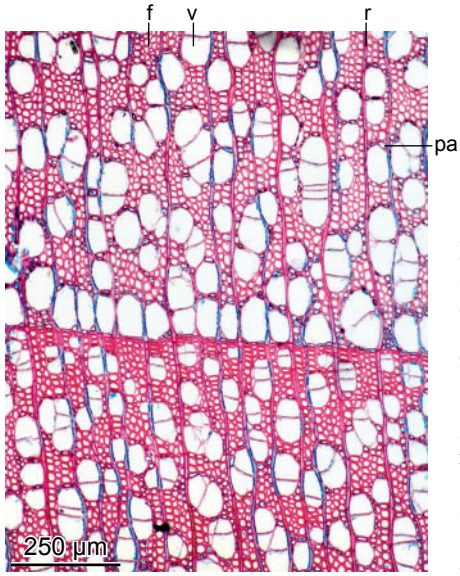
Characteristic of the family is a uniform life-form composition. There are no therophytes and hemicryptophytes. All species have vessels with simple perforations and large ray-vessel pits, fibers with small pits (<2 µm) and uniseriate rays.

Ring boundaries are distinct in all species (**Figs. 1-4**). Diffuse-porosity is the dominant vessel distribution pattern within the family (**Figs. 1**, **3**, **4**). Some species show a tendency to semi-ring-porosity (**Fig. 2**). Vessels are arranged solitary (**Fig. 3**) or in short radial multiples (**Figs. 1**, **2**, **4**). Only *Salix retusa* has distinct vessels groups (**Fig. 4**). Earlywood vessels with a diameter of 30-50 µm or 50-100 µm are characteristic of all species. Vessel density varies between 100-300/mm$^2$ but is extremely low in *Salix reticulata* (**Fig. 3**) and extremely high in *Salix retusa* (**Fig. 4**). Vessels of all species have simple perforations. Intervessel pits are large and round or polyangular and are arranged in alternating position (**Fig. 5**). Vessel-ray pits are extremely large (**Fig. 6**). Vessels of a few species have thin-walled tylosis.

Fibers containing small pits with slit-like apertures (**Fig. 7**) are thin- and thin- to thick-walled in all species. Transitions between the two fiber types occur within individuals. The occurrence of tension wood is a genus-specific feature (*Populus* and *Salix*; **Fig. 8**).

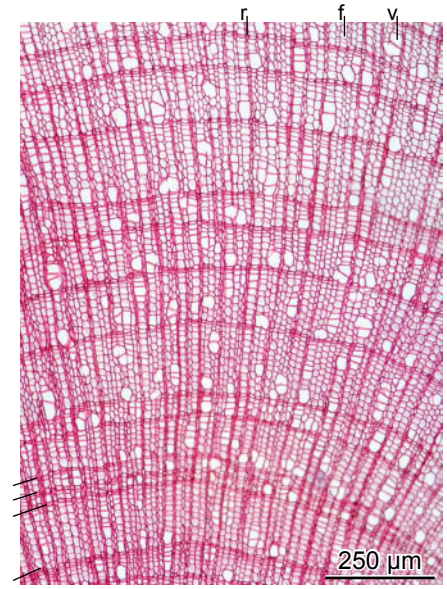
The distribution of axial parenchyma is often difficult to determine, especially on slides stained only with safranin. A unicellular row of marginal (terminal) parenchyma was observed in a few *Populus* and *Salix* species (**Figs. 8** and **9**). Paratracheal parenchyma occurs in *Populus* (**Fig. 10**). Rays are uniseriate and homocellular with procumbent cells in *Chosenia* and *Populus* and heterocellular in *Salix* with central procumbent and a few rows of upright marginal cells (**Figs. 11** and **12**).

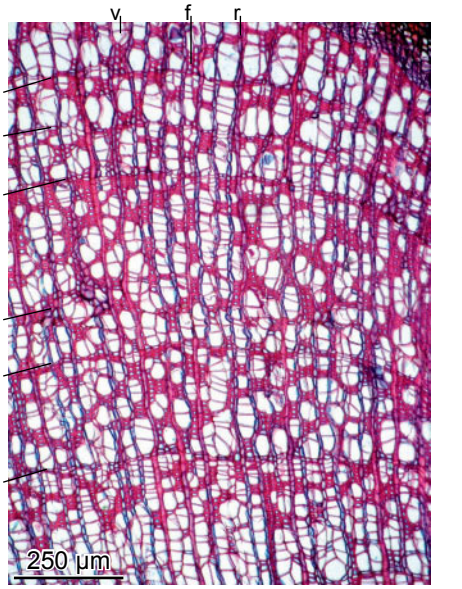



**Left Fig. 1.** Diffuse-porous xylem with a distinct annual ring boundaries. Most vessels are arranged in short, radial multiples. Stem of a 15 m-high tree, riparian, boreal zone, Jakutsk, Siberia, Russia. *Populus suaveolens*, transverse section.

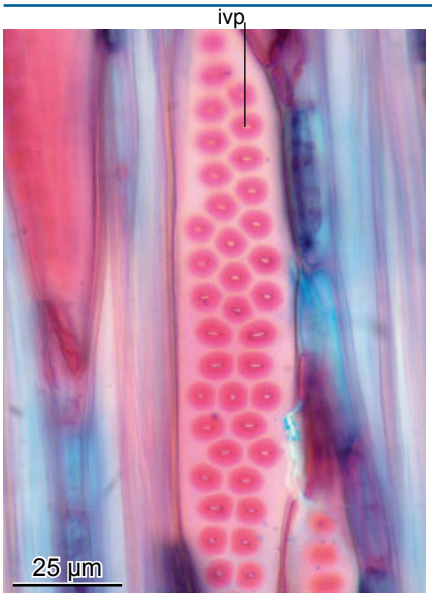
**Right Fig. 2.** Slightly semi-ring-porous xylem. Most vessels are arranged in short, radial multiples. Stem of a 6 m-high tree, dry rock field, hill zone, Hohtenn, Valais, Switzerland. *Populus tremula*, transverse section.

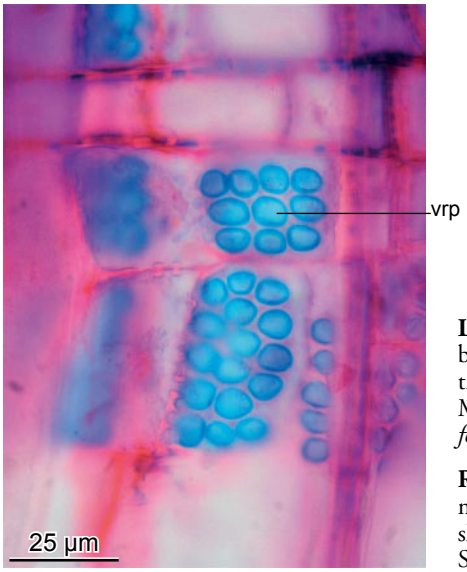



**Left Fig. 3.** Diffuse-porous xylem with few vessels (<100/mm$^2$). Ring boundaries are marked by one or two rows of flat cells (parenchyma). Vessels are arranged solitary or in short radial multiples. Stem of a prostrate dwarf shrub, windy crest, alpine zone, Julier Pass, Grisons, Switzerland. *Salix reticulata*, transverse section.

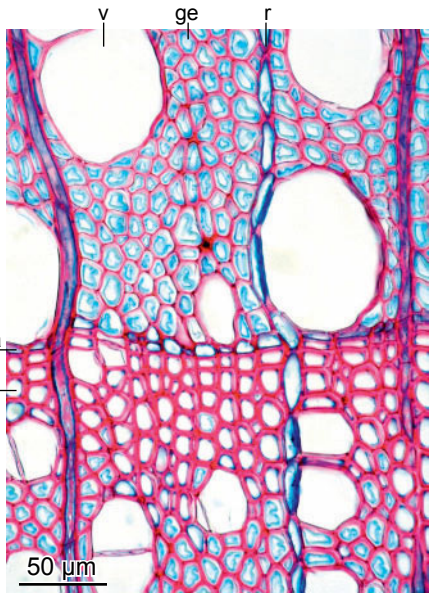
**Right Fig. 4.** Diffuse-porous xylem with few vessels (ca. 350/mm$^2$). Ring boundaries are marked by one or two rows of flat cells (parenchyma). Stem of a prostrate dwarf shrub, snowbed, subalpine zone, Davos, Switzerland. *Salix retusa*, transverse section.



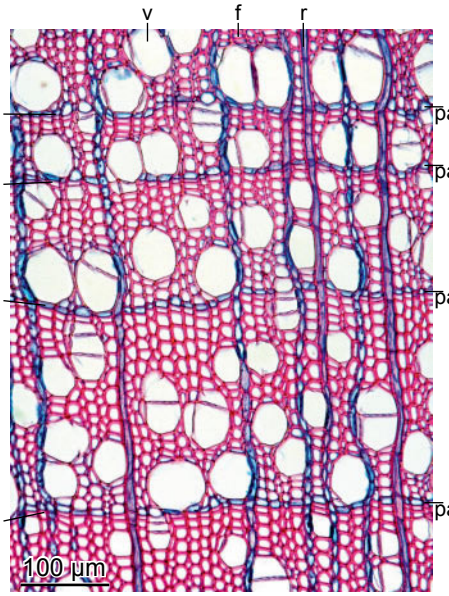

**Left Fig. 5.** Round and polyangular, large, bordered intervessel pits. Stem of a prostrate dwarf shrubs, meadow, alpine zone, Monte Vista, Colorado, USA. *Salix planifolia*, radial section.

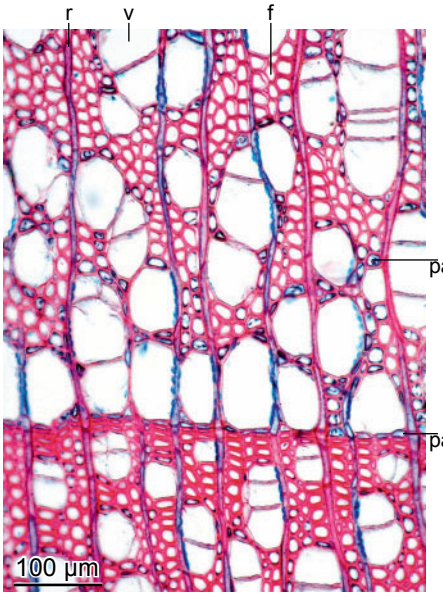
**Right Fig. 6.** Large vessel-ray pits located in marginal ray cells. Stem of a prostrate dwarf shrub, snowbed, subalpine zone, Davos, Switzerland. *Salix retusa*, radial section.




**Left Fig. 7.** Fibers with small pits with slit-like apertures. Stem of a 15 m-high tree, riparian, boreal zone, Jakutsk, Siberia, Russia. *Populus suaveolens*, radial section.

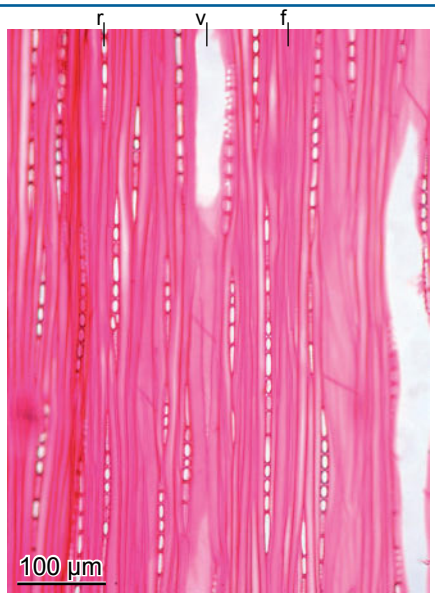
**Right Fig. 8.** Tension wood. Gelatinous fibers (blue) in the earlywood. Stem of a 4 m-high tree, wet meadow, subalpine zone, Engadin, Grisons, Switzerland. *Salix myrsinifolia*, transverse section.

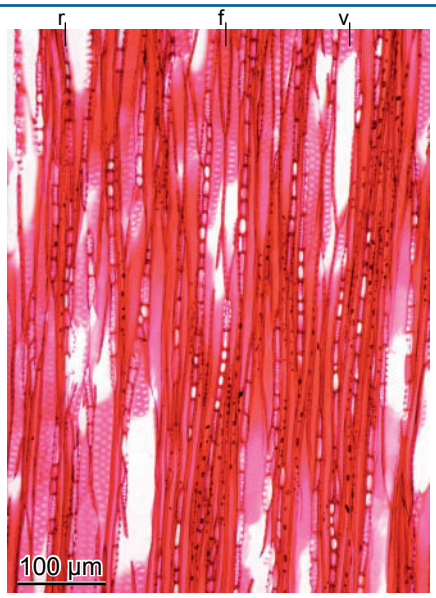



**Left Fig. 9.** One row of parenchyma cells at annual ring boundaries. Stem of a 50 cm-high upright dwarf shrub, glacier forefield, subalpine zone, Lötschental, Valais, Switzerland. *Salix foetida*, transverse section.

**Right Fig. 10.** Paratracheal and terminal parenchyma. tem of a 6 m-high tree, dry rock field, hill zone, Hohtenn, Valais, Switzerland. *Populus tremula*, transverse section.




**Left Fig. 11.** Uniseriate rays with partially axially elongated cells. Stem of a 10 m-high tree, riparian, hill zone, Bern, Switzerland. *Salix viminalis*, tangential section.

**Right Fig. 12.** Uniseriate rays with partially axially elongated cells. Stem below ground of a prostrate dwarf shrub, snowbed, alpine zone, Davos, Switzerland. *Salix herbacea*, tangential section.

### Characteristics of the phloem and the cortex

Characteristic of the family are the intra-annual, often tangentially arranged layers of sieve tubes and parenchyma. Tangential bands and strips of sclerenchyma occur in all observed species (**Figs. 13-15**). Multilayered intra-annual sclerenchyma occur in fast-growing individuals (**Fig. 13**), but is rare in stressed species of the alpine and arctic zone (**Figs. 16** and **17**). Round groups of sclerenchyma occur only in the cortex of *Populus* species (**Fig. 22**). Dilatations are rare (**Fig. 18**). Crystals occur in all species (**Fig. 19**), mostly as prismatic crystals and only rarely as crystal druses. Crystals are primarily grouped around the sclerenchyma groups. A combination of both crystal types occurs only in *Salix planifolia* and *S. purpurea* (**Fig. 18**). One or a few phellem layers occur in most *Salix* species (**Figs. 20** and **21**). The phellem is thick and multilayered in *Populus*. Round groups of sclerenchyma occur only in the cortex (**Fig. 22**).

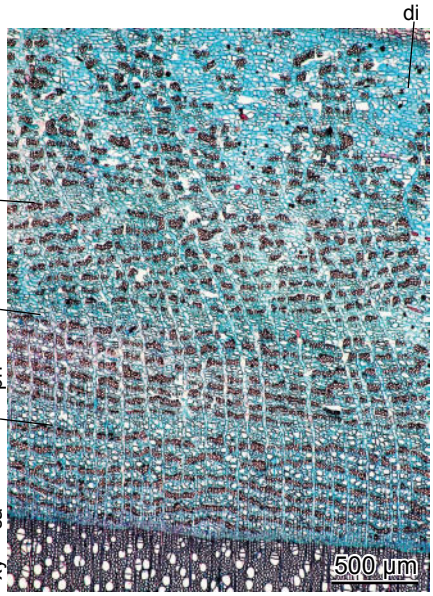



**Fig. 13.** Phloem with tangential layers of sclerenchyma cells. The layer without sclerenchyma probably represents the first intra-annual part (early phloem). Stem of a 10 m-high tree, riparian, hill zone, Bern, Switzerland. *Salix viminalis*, transverse section.

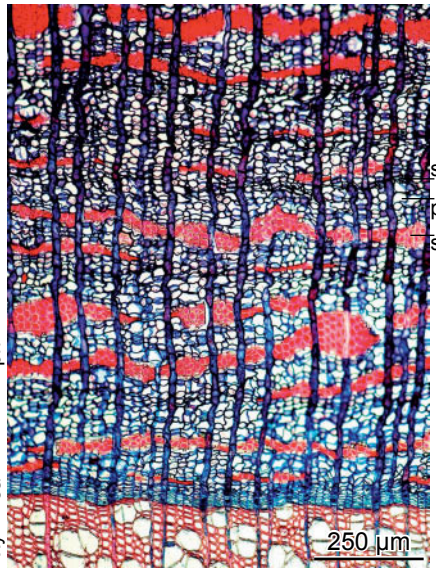



**Fig. 14.** Phloem with tangential layers of large, unlignified parenchyma cells, layers of small sieve tubes (blue) and sclerenchyma cells (red). The width of sclerenchyma bands varies. Stem of a 6 m-high tree, dry rock field, hill zone, Hohtenn, Valais, Switzerland. *Populus tremula*, transverse section.

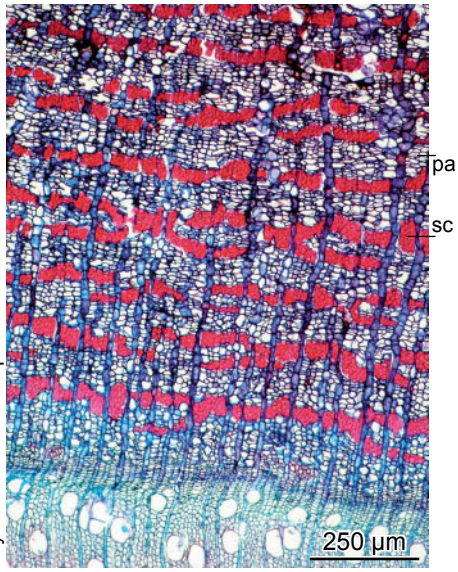
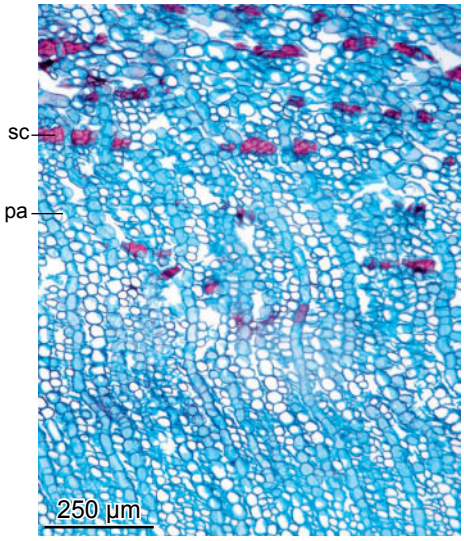
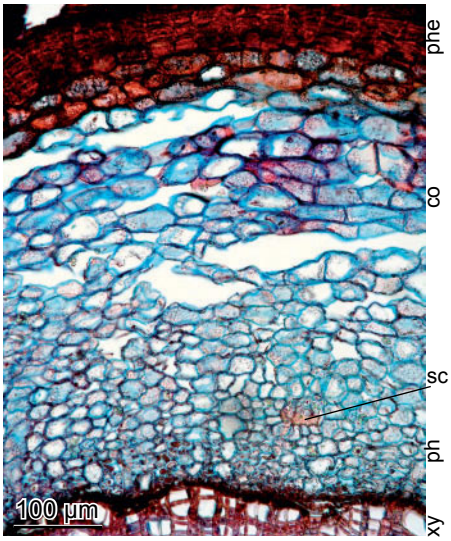


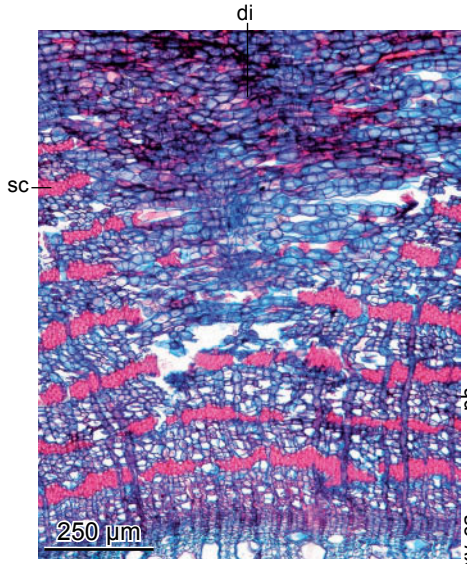

**Fig. 15.** Phloem with tangential layers of large unlignified parenchyma cells, layers of small sieve tubes (blue) and sclerenchyma cells (red). Stem of a 2 m-high shrub, glaciar forefield, subalpine zone, Lötschental, Valais, Switzerland. *Salix appendiculata*, transverse section.

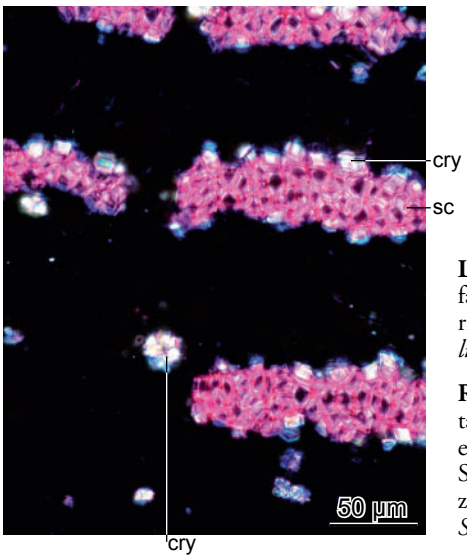



**Left Fig. 16.** Uniform phloem with a few groups of sclerenchyma cells. The structure is typical for individuals on stressed sites. Stem of a 1.5 m-high shrub, riparian, timberline in the boreal zone, Quebec, Canada. *Salix lanata*, transverse section.

**Right Fig. 17.** Uniform phloem with hardly any sclerenchyma cells. The structure is typical for individuals on extremely stressed sites. Below ground stem of a prostrate dwarf shrub, snowbed, arctic zone, Svalbard, Norway. *Salix polaris*, transverse section.




**Left Fig. 18.** Dilatation in the phloem of a fast-growing tree. Stem of a 10 m-high tree, riparian, hill zone, Zürich, Switzerland. *Salix purpurea*, transverse section.

**Right Fig. 19.** Prismatic crystals and crystal druses in the phloem. Crystals are located mainly around the sclerenchyma groups. Stem of a 10 m-high tree, riparian, hill zone, Birmensdorf, Zürich, Switzerland. *Salix purpurea*, transverse section.

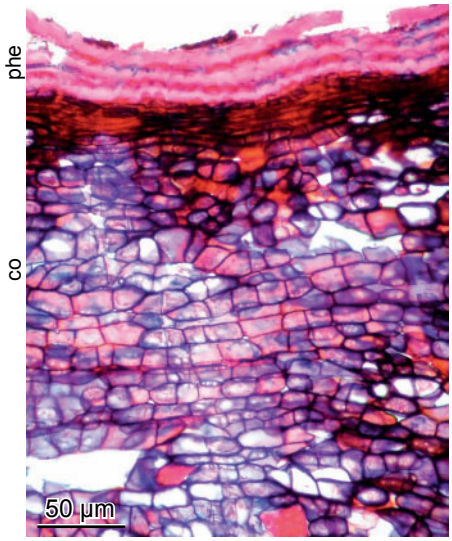



**Fig. 20.** One small layer of phellem outside of the cortex. Stem of a 2 m-high shrub, glacier forefield, subalpine zone, Lötschental, Valais, Switzerland. *Salix appendiculata*, transverse section.

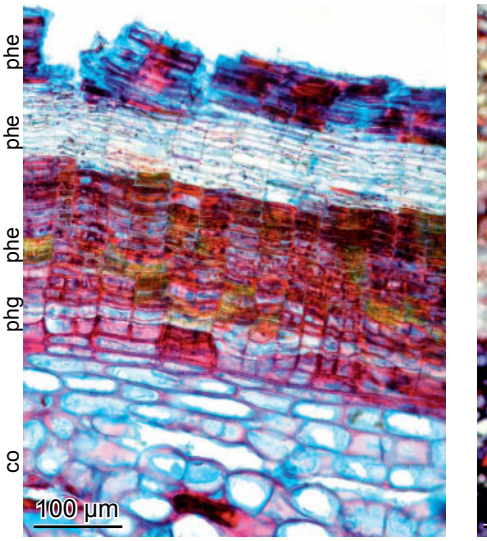



**Fig. 21.** Three layers of phellem located outside of the cortex. Stem of a 1.5 m-high shrub, riparian, boreal zone, Quebec, Canada. *Salix lanata*, transverse section.

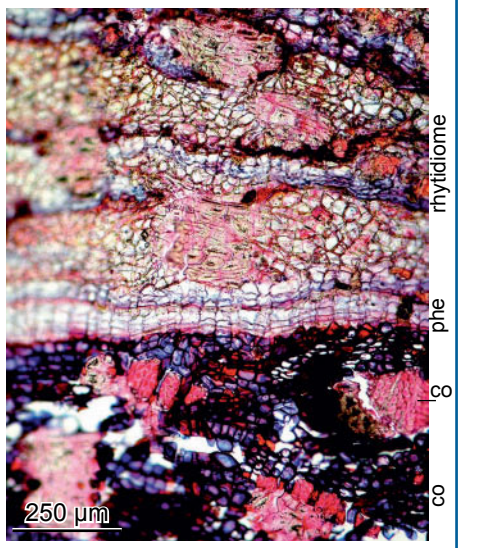



**Fig. 22.** Irregular layers of phellem. Groups of sclerenchyma occur in the cortex and in the phellem. Stem of a 6 m-high tree, dry rock field, hill zone, Hohtenn, Valais, Switzerland. *Populus tremula*, transverse section.

**Discussion in relation to previous studies**

The xylem of all genera (trees, shrubs and dwarf shrubs) was characterized before. Gregory (1994) mentioned 104 references concerning the genera *Chosenia*, *Populus* and *Salix*. The xylem of dwarf shrubs was described by Schweingruber (1990; 8 European species) and Benkova and Schweingruber (2004; 13 Russian species). Holdheide (1951) described the bark of *Populus nigra* and *Salix alba* in detail. New to this study are the descriptions of the bark of 8 species.

The anatomical structure of the xylem and the phloem is homogeneous throughout the family. The differentiation of taxa is limited. *Populus* principally has homocellular rays whereas *Salix* has heterocellular rays. The high number of radially oriented vessel groups seems to differentiate *Salix retusa* from most other *Salix* species. The low number of solitary vessels seems to be characteristic for *Salix reticulata*. Anatomical differences between life forms (trees, shrubs and dwarf shrubs) from different vegetation belts, e.g. hill zone vs. alpine zone seem to be absent.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **39** |
| 1 | growth rings distinct and recognizable | 39 |
| 5 | diffuse-porous | 39 |
| 7 | vessels in diagonal and/or radial patterns | 38 |
| 9 | vessels predominantly solitary | 38 |
| 9.1 | vessels in radial multiples of 2-4 common | 38 |
| 13 | vessels with simple perforation plates | 39 |
| 22 | intervessel pits alternate | 39 |
| 31 | vessel-ray pits with large apertures, *Salix/Laurus* type | 39 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 18 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 22 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 2 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 28 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 11 |
| 56 | tylosis with thin walls | 8 |
| 58 | dark staining substances in vessels and/or fibers (gum, tannins) | 3 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 39 |
| 68 | fibers thin-walled | 11 |
| 70 | fibers thin- to thick-walled | 28 |
| 70.2 | tension wood present | 28 |
| 75 | parenchyma absent or unrecognizable | 28 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 79 | parenchyma paratracheal | 2 |
| 89 | parenchyma marginal | 4 |
| 96 | rays uniseriate | 38 |
| 104 | ray: all cells procumbent (radial section) | 6 |
| 105 | ray: all cells upright or square | 1 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 6 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 26 |
| R2 | groups of sieve tubes in tangential rows | 17 |
| R3 | distinct ray dilatations | 7 |
| R4 | sclereids in phloem and cortex | 17 |
| R6.1 | sclereids in tangential rows | 17 |
| R7 | with prismatic crystals | 12 |
| R8 | with crystal druses | 5 |

# Salvadoraceae

**Number of species, worldwide and in Europe**

The Salvadoraceae family includes 3 genera with 12 species. Representatives occur mainly in SE Asia and Africa. No species of the family are found in Europe.

**Analyzed species:**
*Salvadora persica* L.

**Analyzed material**
Analyzed is the xylem from the shrub *Salvadora persica* L. from the dry subtropical climate at the seashore of Dhofar, Oman.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes (0.5-4 m) | 1 | 3 |
| **Plants analyzed from different vegetation zones:** | | |
| Subtropical | 1 | |

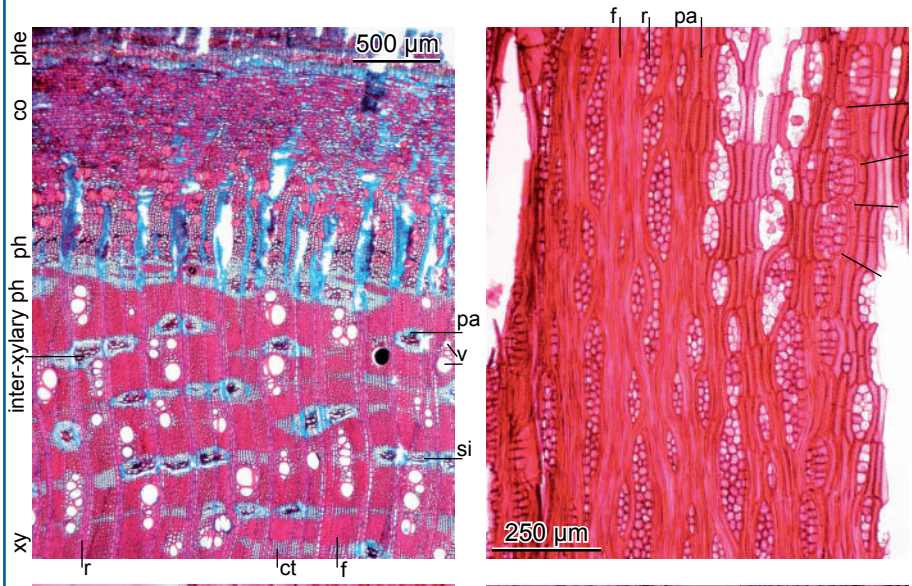
*Salvadora persica*

### Characteristics of the xylem

Annual rings are absent. Characteristic is the presence of a few (<50/mm²), thick-walled, large vessels (>100 µm) with simple perforations. Included phloem is surrounded by parenchyma (paratracheal and vasicentric), thick-walled fiber groups and 1-4-seriate rays. Ray cells contain prismatic crystals. Parenchyma is storied and fibers partially storied (**Figs. 1-4**).

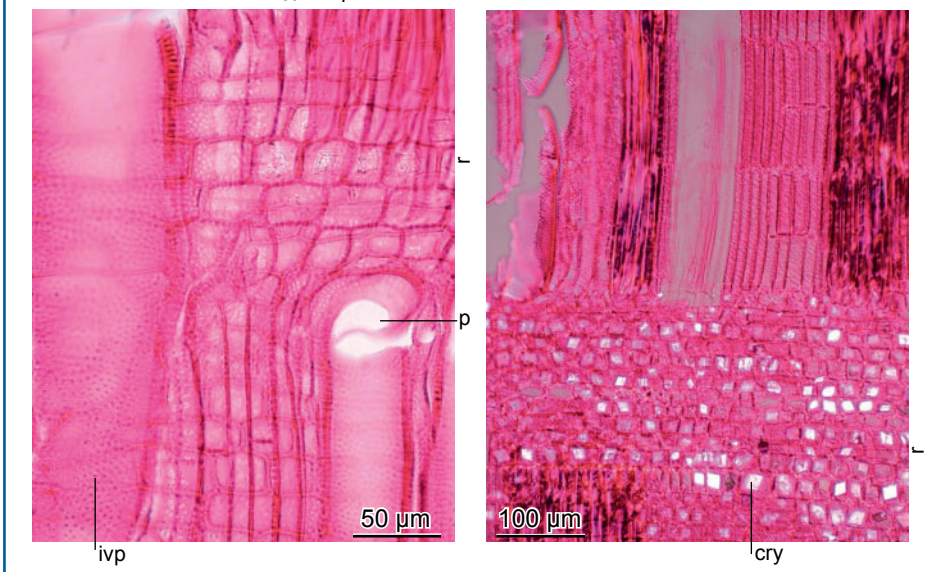
### Discussion in relation to previous studies

Carlquist (2002) studied 3 genera (*Azima*, *Salvadora* and *Dobera*). Descriptions of *Salvadora persica* and *Dobera glabra* are given by Jagiella and Kürschner 1987 and Fahn et al. 1986 described *Salvadora persica*. For further studies, see Gregory (1994). The present study confirms all results from earlier studies.




**Left Fig. 1.** Interxylary groups of phloem are surrounded by thin-walled parenchymatic cells and conjunctive tissue. Shrub, sea coast, tropical climate, Dhofar, Oman. *Salvadora persica*, transverse section.

**Right Fig. 2.** Between the storied parenchymatic cells occur 2-4-seriate rays. Shrub, sea coast, tropical climate, Dhofar, Oman. *Salvadora persica*, tangential section.




**Left Fig. 3.** Vessel with a simple perforation and small, alternating intervessel pits. Shrub, sea coast, tropical climate, Dhofar, Oman. *Salvadora persica*, radial section.

**Right Fig. 4.** Prismatic crystals in ray cells. Shrub, sea coast, tropical climate, Dhofar, Oman. *Salvadora persica*, radial section.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **1** |
| 2 | growth rings absent | 1 |
| 5 | diffuse-porous | 1 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 1 |
| 39.1 | vessel cell-wall thickness >2 µm | 1 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 1 |
| 50 | <100 vessels per mm² in earlywood | 1 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 1 |
| 69 | fibers thick-walled | 1 |
| 70 | fibers thin- to thick-walled | 1 |
| 79 | parenchyma paratracheal | 1 |
| 97 | ray width predominantly 1-3 cells | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 120 | storied axial tissue (parenchyma, fibers, vessels, tangential section) | 1 |
| 135 | interxylary phloem present | 1 |
| 136 | prismatic crystals present | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 1 |

# Santalaceae



**Number of species, worldwide and in Europe**

The Santalaceae family includes 34 genera with 540 species. Species occur in subtropical climate and temperate regions, mainly in the Old World. In Western Europe occur 3 genera with 21 species. The major genus *Thesium* includes 18 species.

**Analyzed material**

Analyzed is the xylem and phloem from 9 species of Santalaceae.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes (0.5-4 m) | 1 | 1 |
| Therophytes | 1 | |
| Hemicryptophytes and geophytes | 7 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 1 | |
| Hill and mountain | 4 | |
| Mediterranean | 3 | |
| Subtropical | 1 | |

**Analyzed species:**

*Comandra umbellata* Nutt.
*Osyris alba* L.
*Thesium alpinum* L.
*Thesium arvense* Horv.
*Thesium bavarum* Schrank
*Thesium divaricatum* Mert et W.D. J. Koch
*Thesium humile* Vahl
*Thesium linophyllon* L.
*Thesium pyrenaicum* Pourr.

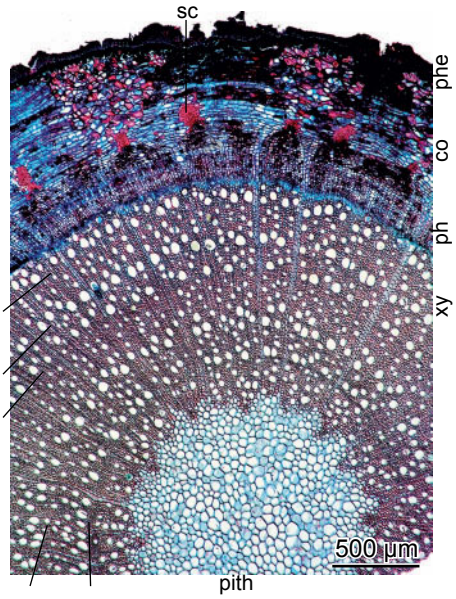
**Right:** *Osyris alba* (photo: Stützel)

*Thesium pyrenaicum* (photo: Zinnert)

**Characteristics of the xylem**

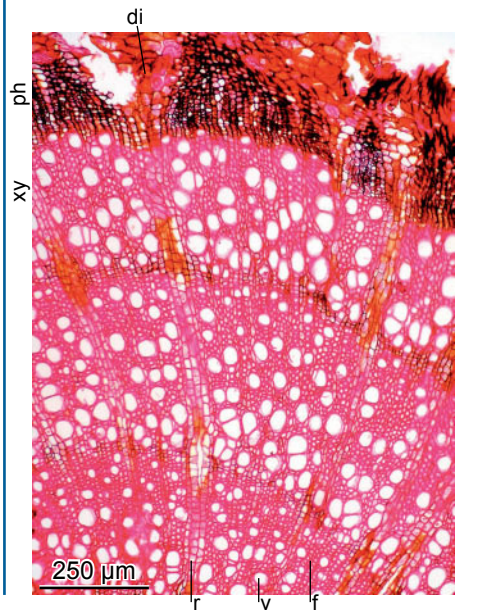
Annual rings are distinct in all species except *Comandra umbellata*. Ring distinctness is indicated by semi-ring porosity (**Figs. 1-3**). Earlywood vessel diameter varies from 30-60 µm and vessel density from 300-500/mm$^2$. Simple perforations (**Figs. 4** and **10**) and fibers with distinctly bordered pits are characteristic of all species (**Fig. 5**). Parenchyma is apotracheal (**Fig. 1**) and often marginal in 5 *Thesium* species (**Fig. 2**).

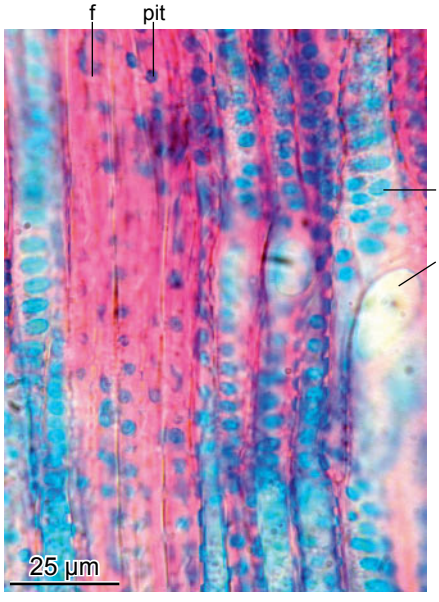
Fibers are fairly thick-walled (**Figs. 1-3**), especially in *Thesium arvense* and *T. bavarum*. Ray width distinguishes species: rays are predominantly uniseriate in *Thesium humile* (**Fig. 6**), large (4-10 cells wide) in *T. divaricatum* and *T. pyrenaicum* (**Fig. 9**) and smaller (1-3 cells wide) in all other species (**Figs. 7** and **8**). All *Thesium* species have square or upright ray cells (**Fig. 10**). Rays are extremely heterocellular in *Osyris alba*. Lignification of ray cells is limited in most species (**Figs. 2** and **6-9**).



**Left Fig. 1.** Six distinct annual rings in a semi-ring-porous xylem. Distinct ray dilatations and groups of sclereids are present in the bark. Stem of a 60 cm-high shrub, hedge, Mediterranean zone, Alps, France. *Osyris alba*, transverse section.

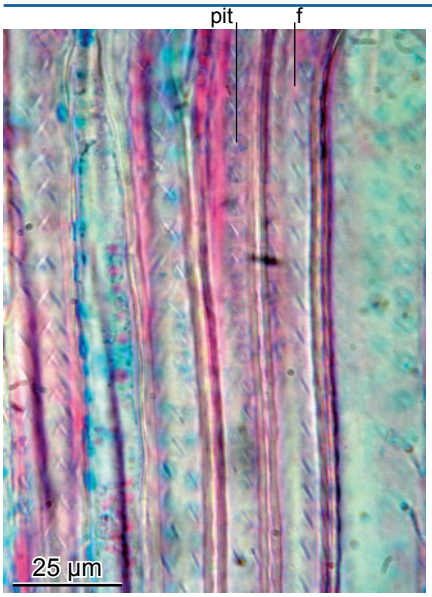
**Right Fig. 2.** Three distinct annual rings in a semi-ring-porous xylem with a large band of marginal, unlignified parenchyma. Ray dilatations and small groups of sclereids in the bark are characteristic. Root collar of a 10 cm-high herb, dry meadow, hill zone, eastern Alps, Austria. *Thesium arvense*, transverse section.

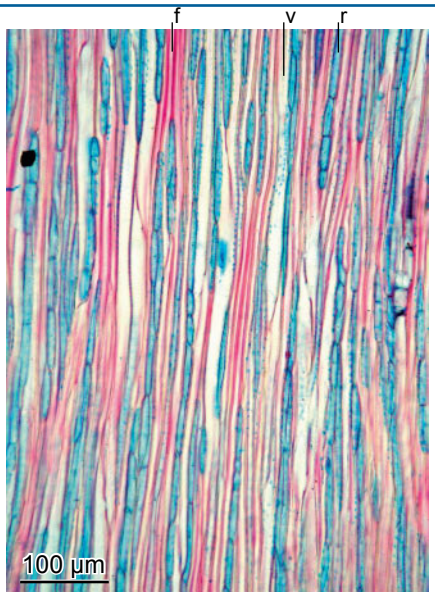



**Left Fig. 3.** Three distinct annual rings in a semi-ring-porous xylem. Ray dilatations occur in the bark. Root collar of a 10 cm-high herb, dry meadow, mountain zone, Alps, France. *Thesium pyrenaicum*, transverse section.

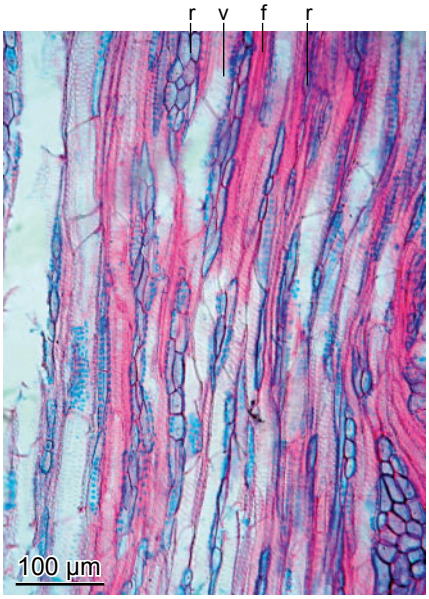
**Right Fig. 4.** Vessels with simple perforations and large pits with round or elliptic apertures (blue). Root collar of a 10 cm-high herb, dry meadow, hill zone, Alps, Austria. *Thesium linophyllon*, radial section.

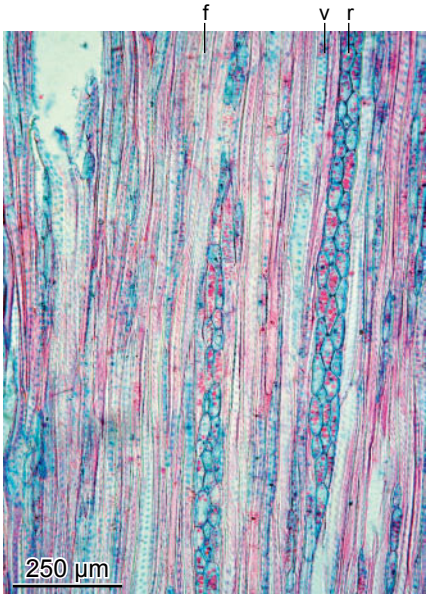



**Left Fig. 5.** Fibers with large pits (>3 µm) and gash-like apertures. Stem of a 60 cm-high shrub, hedge, Mediterranean zone, Alps, France. *Osyris alba*, radial section.

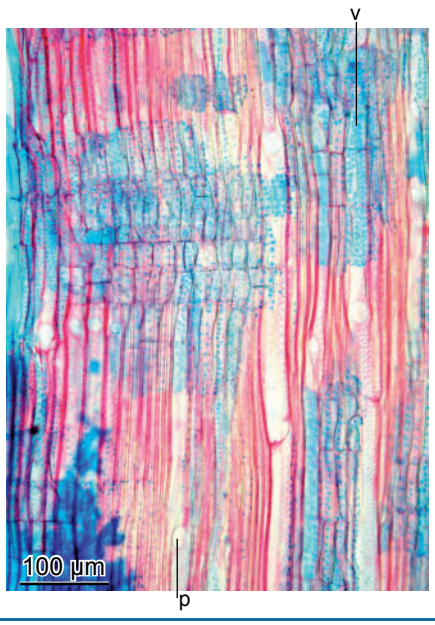
**Right Fig. 6.** Uniseriate rays with extremely elongated cells. Root collar of a 12 cm-high herb, dry meadow, thermophile zone, subtropical climate, Gomera, Canary Islands. *Thesium humile*, tangential section.




**Left Fig. 7.** 1-4-seriate rays. Root collar of a 10 cm-high herb, dry meadow, mountain zone, pinyon, Rocky Mountains, Colorado, USA. *Comandra umbellata*, tangential section.

**Right Fig. 8.** 1-3-seriate rays. Stem of a 60 cm-high shrub, hedge, Mediterranean zone, Alps, France. *Osyris alba*, tangential section.

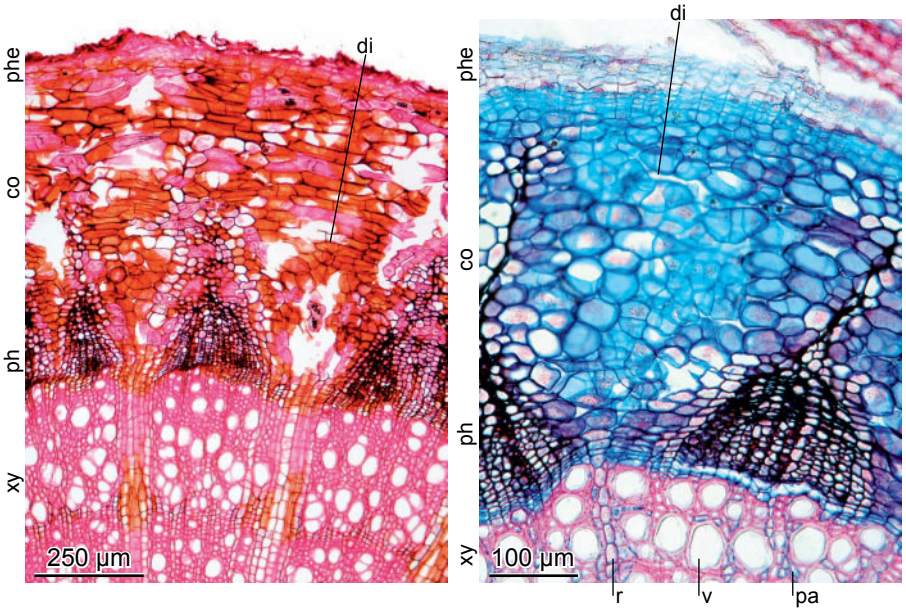



**Left Fig. 9.** Multiseriate, unlignified rays (5-10 cells wide) in semi-ring-porous wood with distinct annual rings. Root collar of a 25 cm-high herb, *Quercus ilex* forest, Mediterranean zone, Alps, France. *Thesium linophyllon*, transverse section.

**Right Fig. 10.** Rays with square and upright cells. And vessels with simple perforations. Root collar of a 12 cm-high herb, dry meadow, thermophile zone subtropical climate, Gomera, Canary Islands. *Thesium humile*, radial section.

### Characteristics of the phloem and the cortex

Bark structures are typical for the family: Distinct ray dilatations that divide the wedge-like parenchyma/sieve-tube parts of the phloem (**Figs. 11** and **12**) and smaller or larger groups of sclereids occur in all species (**Figs. 1** and **11**). Crystal druses were only found in *Osyris alba*.




**Left Fig. 11.** Bark with triangular phloem groups between ray dilatations. Root collar of a 10 cm-high herb, dry meadow, mountain zone, Alps, France. *Thesium pyrenaicum*, transverse section.

**Right Fig. 12.** Bark with triangular phloem groups between dilatations. Root collar of a 10 cm-high herb, dry meadow, mountain zone, pinyon, Rocky Mountains, Colorado, USA. *Comandra umbellata*, transverse section.

### Ecological trends in the xylem and the bark

There is not enough material to to detect any ecological trends.

### Discussion in relation to previous studies

Gregory (1994) mentions 24 articles in which Sanatlaceae species have been described. Most described species occur in the tropics. The xylem of the Mediterranean *Osyris alba* was described by Huber and Rouschal (1954) and by Schweingruber (1990).

Descriptions of *Osiris alba* agree with earlier studies. All *Thesium* species are described here for the first time.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **9** |
| 1 | growth rings distinct and recognizable | 9 |
| 4 | semi-ring-porous | 9 |
| 9 | vessels predominantly solitary | 9 |
| 11 | vessels predominantly in clusters | 3 |
| 13 | vessels with simple perforation plates | 9 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 8 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 1 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fibert racheids) | 9 |
| 69 | fibers thick-walled | 2 |
| 70 | fibers thin- to thick-walled | 6 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 9 |
| 89 | parenchyma marginal | 5 |
| 96 | rays uniseriate | 1 |
| 97 | ray width predominantly 1-3 cells | 7 |
| 98 | rays commonly 4-10-seriate | 2 |
| 105 | ray: all cells upright or square | 9 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 1 |
| R1 | groups of sieve tubes present | 9 |
| R2 | groups of sieve tubes in tangential rows | 1 |
| R2.1 | groups of sieve tubes in radial rows | 0 |
| R3 | distinct ray dilatations | 8 |
| R4 | sclereids in phloem and cortex | 8 |
| R7 | with prismatic crystals | 1 |
| R8 | with crystal druses | 1 |

# Sapindaceae



**Number of species, worldwide and in Europe**

The cosmopolitan Sapindaceae family includes 144 genera with 1630 species. In Europe, there are 2 genera with 16 species (*Acer* 15 species and *Aesculus hippocastaneum*).

**Analyzed material**

The xylem and phloem of 2 genera with 15 species are analyzed here. We include the Aceraceae and Hippocastaneaceae in the family of Sapindaceae. Only these two genera are analyzed.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | 15 | 103 genera |
| **Plants analyzed from different vegetation zones:** | | |
| Subalpine | 1 | |
| Hill and mountain | 6 | |
| Mediterranean | 8 | |

**Analyzed species:**

*Acer campestre* L.
*Acer heldreichii* Orph. ex Boiss.
*Acer hycranum* Fischer et Meyer
*Acer monspessulanum* L.
*Acer negundo* L.
*Acer obtusatum* Waldstett et Kitt
*Acer obtusifolium* Sibth. et Sm.
*Acer opalus* Miller
*Acer opalus* ssp. *granatense* Miller
*Acer platanoides* L.
*Acer pseudoplatanus* L.
*Acer sempervirens* L.
*Acer tataricum* L.
*Acer trautvetteri* Medvedev
*Aesculus hippocastaneum* L.

*Acer platanoides*

*Acer pseudoplatanus* (photo: Zinnert)

*Acer pseudoplatanus*

*Aesculus carnea*

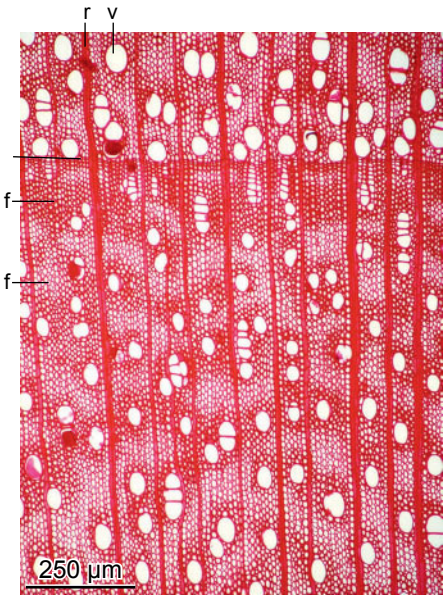
*Aesculus hippocastaneum* (photo: Zinnert)

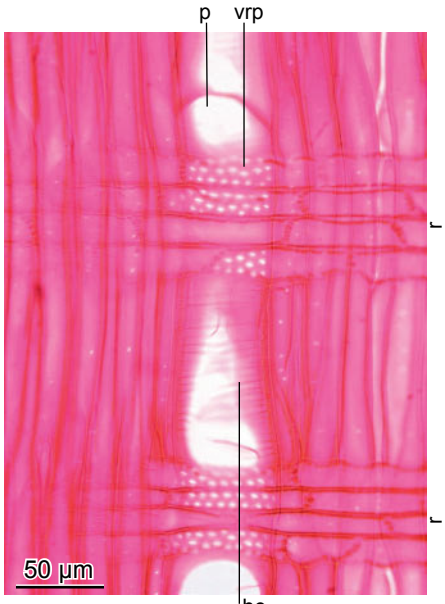
**Characteristics of the xylem and phloem**

*Various species of Acer*

All species are diffuse-porous and have distinct annual rings (**Fig. 1**). Ring boundaries are indicated by tangentially flat fibers in the latewood. Earlywood vessel diameter varies from 40-80 µm and vessel density from 50-80/mm$^2$ (**Fig. 1**). Vessels have simple perforations, large intervessel pits and helical thickenings (**Fig. 2**). In specimens with large rings, patches of relatively thin-walled fibers alternate with patches of thicker walled fibers (**Figs. 1** and **3**). Parenchyma is rare, scanty paratracheal or apotracheal diffuse and often difficult to recognize (**Fig. 3**).

2-5-seriate homocellular rays with procumbent cells are characteristic of the family (**Figs. 3**, **4** and **5**). Crystals are absent, rare or in axially chambered cells (**Fig. 6**). Phloem structures are relatively uniform. Sieve tubes and parenchyma cells and bands of sclerenchyma are arranged in tangential rows (**Fig. 7**). Prismatic crystals are frequent (**Fig. 8**) and occasionally located in axial chambers.




**Left Fig. 1.** Diffuse-porous xylem with distinct ring boundaries. Patches of relatively thin-walled fibers alternate with patches of thicker walled fibers. Low vessel density is characteristic. Stem of an 8 m-high tree, canyon, hill zone, Sofia, Bulgaria. *Acer tataricum*, transverse section.

**Right Fig. 2.** Vessel with helical thickenings and ray cells in the cross field with slightly enlarged pits. Homocellular ray with procumbent cells. Stem of a 6 m-high tree, canyon, Mediterranean zone, Treonik, Macedonia. *Acer obtusatum*, radial section.

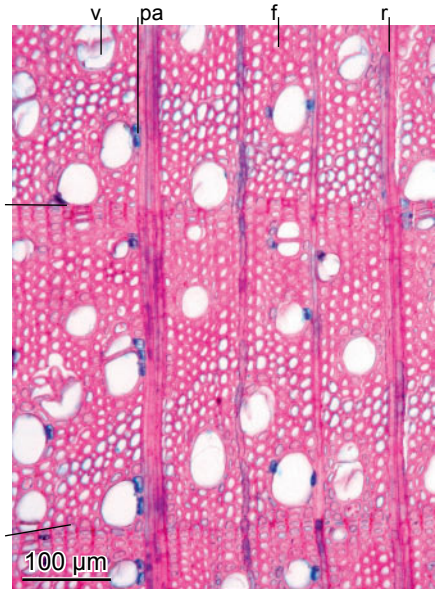



**Fig. 3.** Rare, scanty paratracheal parenchyma (blue cells). Stem of a 10 m-high tree, *Carpinus* forest, hill zone, Burgundy, France. *Acer campestre*, transverse section.

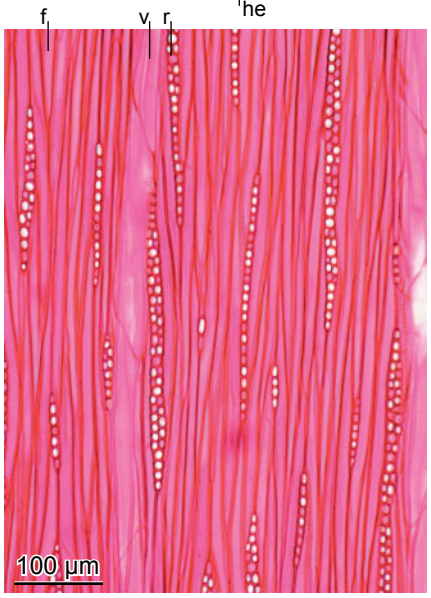



**Fig. 4.** Uni- and bi-seriate rays. Stem of a 6 m-high tree, garden, hill zone, Bern, Switzerland. *Acer negundo*, tangential section.

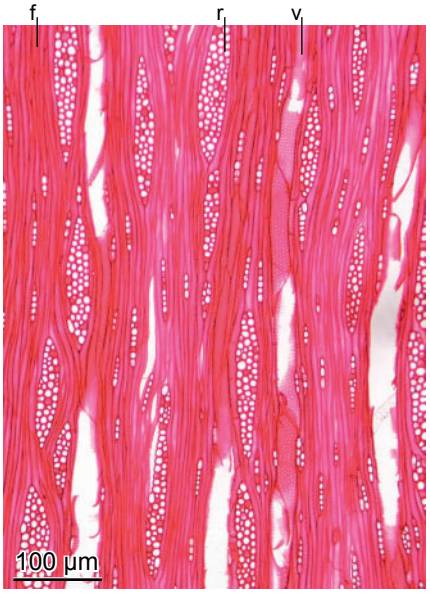



**Fig. 5.** 1-5-seriate rays. Stem of a 5 m-high tree, maccia, Mediterranean zone, Bitola, Macedonia. *Acer heldreichii*, tangential section.

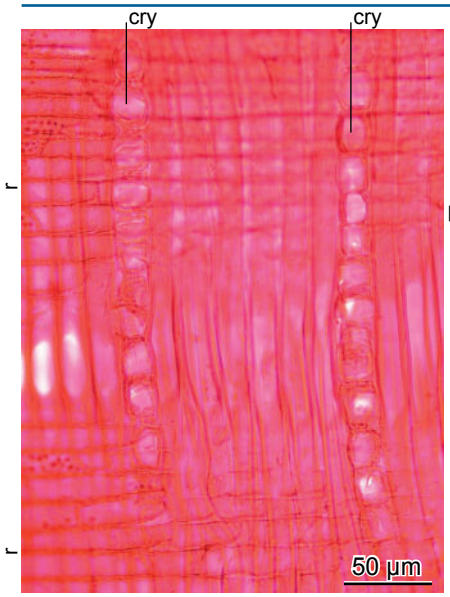



**Fig. 6.** Prismatic crystals in axially chambered cells. Stem of a 5 m-high tree, canyon, Mediterranean zone, Cyprus, Greece. *Acer obtusifolium*, radial section.

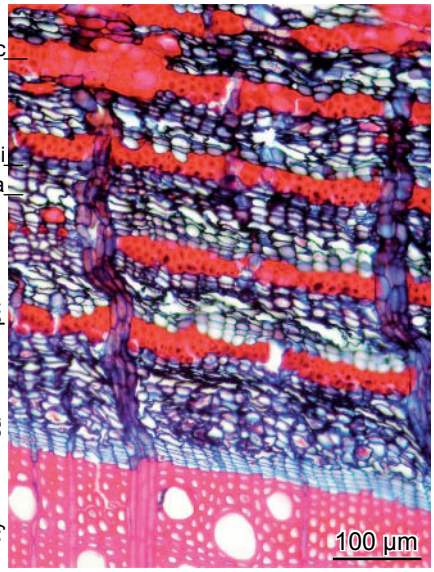



**Fig. 7.** Tangential layers of unlignified parenchyma cells, collapsed sieve tubes and lignified groups of sclerenchyma cells. Stem of a 6 m-high tree, Mediterranean zone, rock field, Pyrenees, France. *Acer monspessulanum*, transverse section.

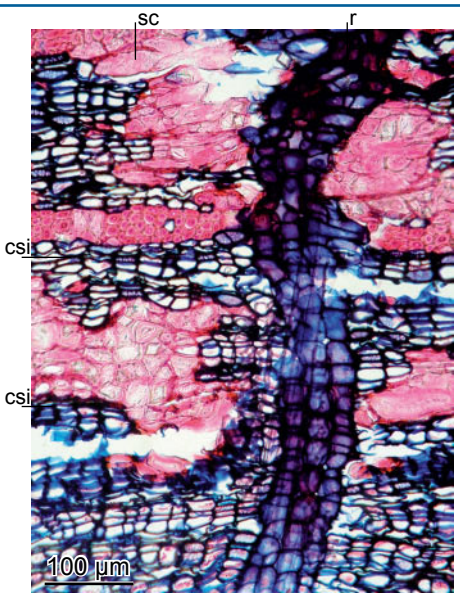



**Fig. 8.** Tangential layers of unlignified parenchyma cells, collapsed sieve tubes and mostly irregular groups of sclerenchyma with prismatic crystals. Stem of a 12 m-high tree, beech forest, hill zone, Ticino, Switzerland. *Acer pseudoplatanus*, transverse section.

*Aesculus hippocastaneum*

The xylem of *Aesculus hippocastaneum* is distinguished from *Acer* sp. by its high vessel density (**Fig. 9**), uniseriate rays (**Fig. 10**) and lack of crystals. Particular features in the radial section were not observed (**Fig. 11**).

The phloem consists of alternating rows of interrupted, tangential, double rows of sclereids and unlignified sieve tubes and parenchyma rows (**Fig. 12**). Characteristic for this species are the extremely large prismatic crystals (**Fig. 13**).

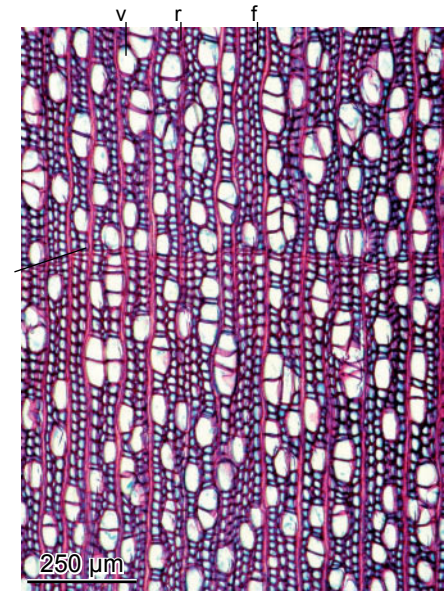



**Fig. 9.** Diffuse-porous xylem with distinct rings. Characteristic is the high vessel density. Stem of a 15 m-high tree, hill zone, Botanical Garden Batumi, Georgia. *Aesculus hippocastaneum*, transverse section.

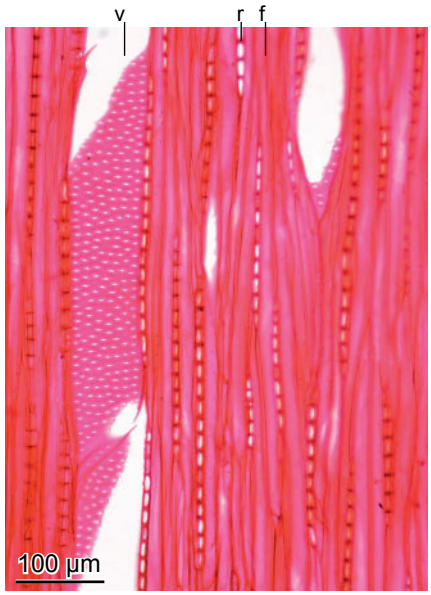



**Fig. 10.** Uni-seriate rays and a vessel with large intervessel pits arranged in alternating and opposite position. Stem of an 8 m-high tree, plantation, hill zone, Vienna, Austria. *Aesculus hippocastaneum*, tangential section.

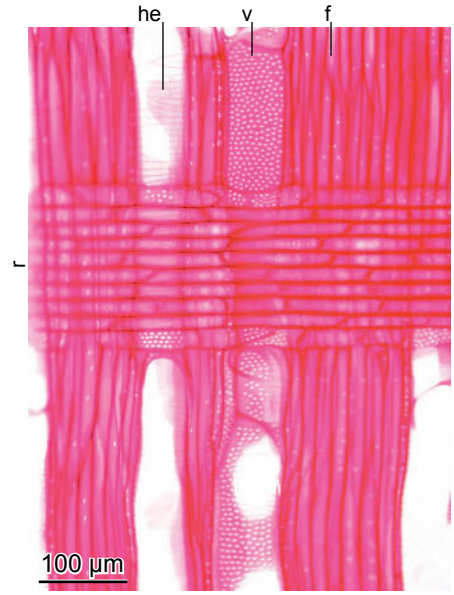
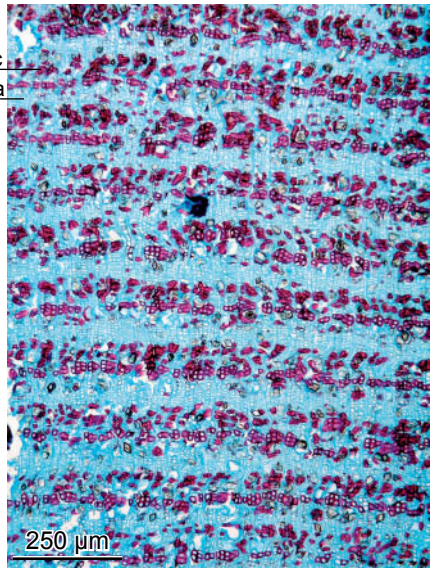



**Fig. 11.** Vessel with helical thickenings and ray cells in the cross field with slightly enlarged pits. Homocellular ray with procumbent cells. Stem of an 8 m-high tree, plantation, hill zone, Vienna, Austria. *Aesculus hippocastaneum*, radial section.



**Left Fig. 12.** Phloem with alternating rows of sclereids, unlignified sieve tube and parenchyma. Stem of a 15 m-high tree, hill zone, Botanical Garden Batumi, Georgia. *Aesculus hippocastaneum*, transverse section.

**Right Fig. 13.** Extremely large prismatic crystals and crystal druses in unlignified parenchyma cells. Stem of a 15 m-high tree, hill zone, Botanical Garden Batumi, Georgia. *Aesculus hippocastaneum*, transverse section.

## Discussion in relation to previous studies

The tropical species were described and anatomically classified mainly by Klaassen (1999). Many *Acer* species as well as *Aesculus hippocastaneum* were described by several authors (Gregory 1994). Ray width of specimens from well-grown stems seems to differentiate *Acer campestre*, *A. platanoides* and *A. pseudoplatanus* (Grosser 1977). The bark of *Acer campestre*, *A. platanoides*, *A. pseudoplatanus* and *Aesculus hippocastaneum* was described by Holdheide (1951).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **15** |
| 1 | growth rings distinct and recognizable | 15 |
| 5 | diffuse-porous | 15 |
| 9 | vessels predominantly solitary | 14 |
| 9.1 | vessels in radial multiples of 2-4 common | 15 |
| 13 | vessels with simple perforation plates | 15 |
| 21 | intervessel pits opposite | 1 |
| 22 | intervessel pits alternate | 15 |
| 36 | helical thickenings present | 15 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 1 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 15 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 1 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 14 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 1 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 5 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 15 |
| 67 | thick- and thin-walled fiber bands, *Acer* type | 14 |
| 70 | fibers thin- to thick-walled | 15 |
| 70.2 | tension wood present | 6 |
| 75 | parenchyma absent or unrecognizable | 1 |
| 79 | parenchyma paratracheal | 14 |
| 96 | rays uniseriate | 1 |
| 97 | ray width predominantly 1-3 cells | 7 |
| 98 | rays commonly 4-10-seriate | 9 |
| 104 | ray: all cells procumbent (radial section) | 15 |
| 105 | ray: all cells upright or square | 0 |
| 136 | prismatic crystals present | 3 |
| 142 | prismatic crystals in axial chambered cells | 5 |
| R2 | groups of sieve tubes in tangential rows | 7 |
| R4 | sclereids in phloem and cortex | 7 |
| R6.1 | sclereids in tangential rows | 7 |
| R7 | with prismatic crystals | 7 |
| R8 | with crystal druses | 1 |

# Saxifragaceae



**Number of species, worldwide and in Europe**

The Saxifragaceae family includes 30 genera with 550 species in the northern hemisphere but also in the South American Andes. In Western Europe there are 2 genera with 127 species. The majority belongs to *Saxifraga* (123 species) and only 4 species to *Chrysosplenium*. Four genera with 75 species are endemic in Western Europe. Macaronesia has no endemic species.

**Analyzed material**

Analyzed is the xylem and phloem from 27 species of Saxifragaceae.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes (0.5-4 m) | | 1? |
| Hemicryptophytes and geophytes | 27 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 20 | |
| Boreal | 1 | |
| Hill and mountain | 6 | |

**Analyzed species:**

*Saxifraga aizoides* L.
*Saxifraga aspera* L.
*Saxifraga bryoides* L.
*Saxifraga bulbifera* L.
*Saxifraga caesia* L.
*Saxifraga caespitosa* L.
*Saxifraga callosa* Sm.
*Saxifraga cotyledon* L.
*Saxifraga cuneifolia* L.
*Saxifraga exarata* ssp. *exarata* Vill.
*Saxifraga moschata* Wulfen
*Saxifraga muscoides* All.
*Saxifraga mutata* L.
*Saxifraga oppositifolia* L.
*Saxifraga oppositifolia* ssp. *putoranica* L.
*Saxifraga paniculata* Mill.
*Saxifraga rotundifolia* L.
*Saxifraga seguieri* Spreng.
*Saxifraga stellaris* L.
*Saxifraga tridactylites* L.

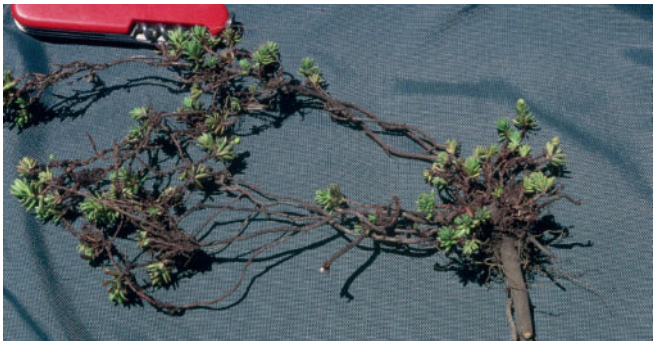
*Bergenia crassifolia* (L.) Fritsch
*Heuchera americana* L.
*Heuchera hallii* Gray.
*Mitella ovalis* Greene
*Tiarella cordifolia* L.
*Tiarella unifoliata* Hook
*Tolmiea menziesii* (Pirsh.) Torrey

*Saxifraga rotundifolia*

*Saxifraga paniculata*

*Heuchera americana*

*Chrysosplenium alternifolium*



*Saxifraga aizoides*

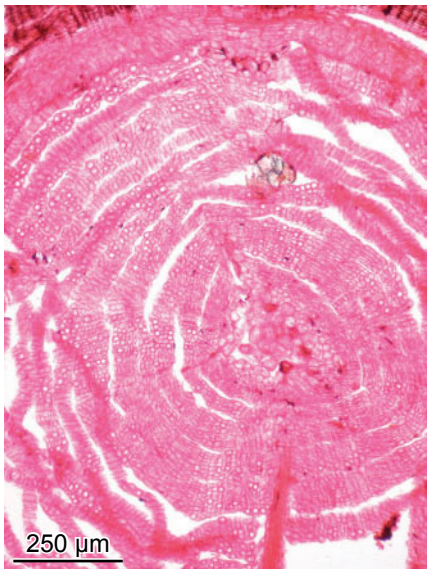
*Saxifraga aizoides*

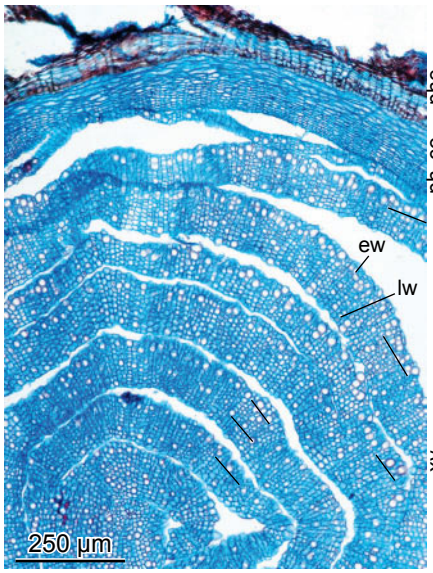
**Characteristics of the xylem**

The family is divided into the clades *Saxifraga s. str.* and *Heuchera* (*Heuchera*, *Mitella*, *Tiarella*, *Tolmeia*). *Bergenia crassifolia* is isolated. Since the anatomical differences are very striking, we present the clades separately.

*Clade Saxifraga*

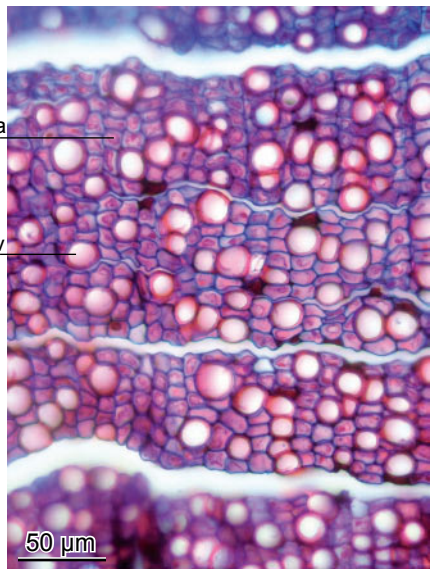
Many perennial *Saxifraga* species have distinct annuals rings (12 out of 19 analyzed species; **Figs. 1** and **2**). Ring boundaries are often indicated by very fragile primary walls between the earlywood and latewood cells. Ring shake is therefore frequent (**Figs. 1-3**). Most species are diffuse-porous and only rarely slightly semi-ring-porous (**Fig. 2**). The diameter of the small, isolated, round and fairly thick-walled vessels (1.5-2 µm) varies from 15-35 µm (**Fig. 3**). Vessel density varies from 200-500/mm$^2$. Vessel-cell walls with pseudoscalariform pitting (reticulate thickening) and simple perforations are characteristic of all *Saxifraga* members (**Fig. 4**). Vessel thickenings are almost annular in the Crassulaceae family and rather pseudoscalariform in *Saxifraga* species. Fibers could not be detected in perennial species. It is impossible to distinguish them from parenchyma cells in the transverse section and difficult to detect them in the radial section. Fibers occur only in the annual above ground shoot of *Saxifraga bulbifera* and *Saxifraga tridactylites* and form a compact ring in the latewood (**Fig. 6**). Parenchyma is pervasive in all perennial species (**Fig. 5**). Rays and crystals are absent.

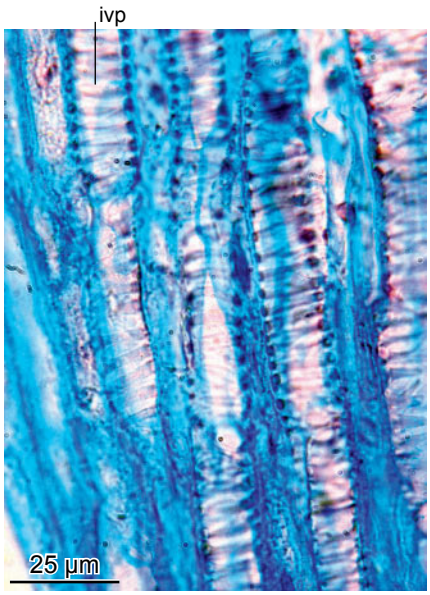



**Left Fig. 1.** More than 10 recognizable rings in a diffuse-porous, rayless xylem. Separated layers (ring shake) consist of the latewood of the previous year and the earlywood of the following year. Rhizome of a 5 cm-high herb, meadow, subalpine zone, Alps, Switzerland. *Saxifraga oppositifolia*, transverse section.

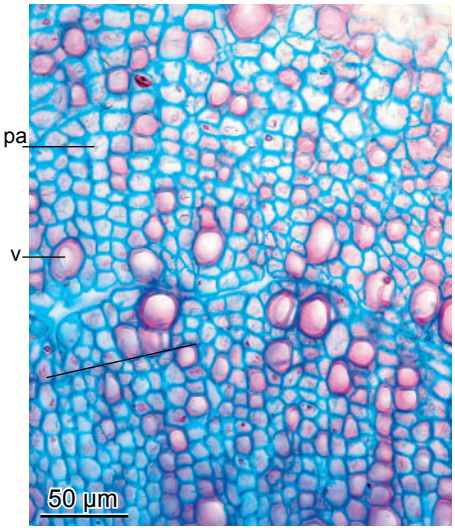
**Right Fig. 2.** Distinct rings in a diffuse-porous, rayless xylem. Latewood-ring boundaries do not correspond with the tangential layers; the weak zone lies just after the earlywood. A layer consists of the latewood of the previous year and the earlywood of the following year. Ring counting has to be based on the occurrence of earlywood vessels. Rhizome of a 5 cm-high herb, dry rock, alpine zone, Alps, Switzerland. *Saxifraga caesia*, transverse section.

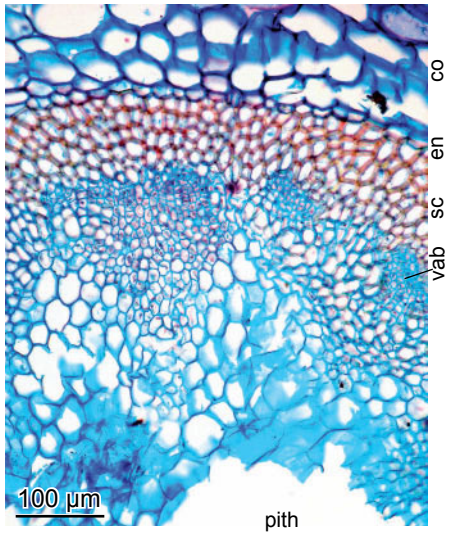



**Left Fig. 3.** Thick-walled vessels are embedded in pervasive parenchyma. Tangential cracks occur in middle lamella between neighboring axial parenchyma cells. Rays are absent. Rhizome of a 5 cm-high herb, dry rock, alpine zone, Alps, Switzerland. *Saxifraga oppositifolia*, transverse section.

**Right Fig. 4.** Unlignified, pseudoscalariform lateral vessel wall pitting. Rhizome of a 5 cm-high herb, dry rock, alpine zone, Alps, Switzerland. *Saxifraga moschata*, radial section.




**Left Fig. 5.** Thick-walled, lignified vessels are embedded in a thin-walled, pervasive, unlignified parenchyma. Rays are absent. Rhizome of a 5 cm-high herb, dry rock, alpine zone, Alps, Switzerland. *Saxifraga oppositifolia*, transverse section.

**Right Fig. 6.** A belt of lignified fibers (red) surrounds the xylem of vascular bundles. Stem basis of a 15 cm-high annual plant, dry meadow, hill zone, Alps, Switzerland. *Saxifraga bulbifera*, transverse section.



*Clade Heuchera*

There is not enough material to make a sound classification, but the analysed 5 species belonging to 4 genera (*Heuchera*, *Mitella*, *Tiarella*, *Tolemia*) are clearly distinct from the clade *Saxifraga*: Annual rings are marked by semi-ring porosity (**Figs. 7** and **8**). Vessels have scalariform perforations (5-15 bars; **Fig. 9**). Intervessel pits are small and round (**Fig. 10**) or scalariform (**Fig. 11**). Vessels are embedded in the fiber tissue (**Fig. 8**). Fiber pits are distinctly bordered. Parenchyma, when recognizable, is paratracheal. Large rays separate fiber/vessel compartments and large rays consist of square and upright cells (sometimes confluent to the fiber tissue). Rays are absent in the fiber/vessel groups (**Fig. 8**). Crystal druses occur in the pith.

*Bergenia crassifolia and B. ciliata*

Large rays occur between large vascular bundles (**Fig. 12**). The xylem is composed of vessels and pervasive parenchyma (**Fig. 13**). Vessels have simple and scalariform perforations and gash-like to scalariform intervessel pits. Scalariform intervessel pits and scalariform perforations can often not be differentiated. Crystal druses are frequent in the pith and the rays.

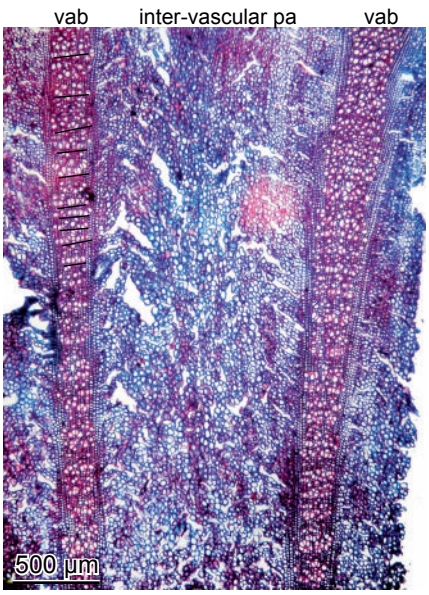



**Fig. 7.** Ring boundaries are indicated by semi-ring porosity in the radial strips of vessel/fiber zones between very large rays. Ring boundaries are absent in the parenchymatic ray zones. Rhizome of a 10 cm-high plant, dry rock, alpine zone, Rocky mountains, Colorado, USA. *Heuchera hallii*, transverse section.

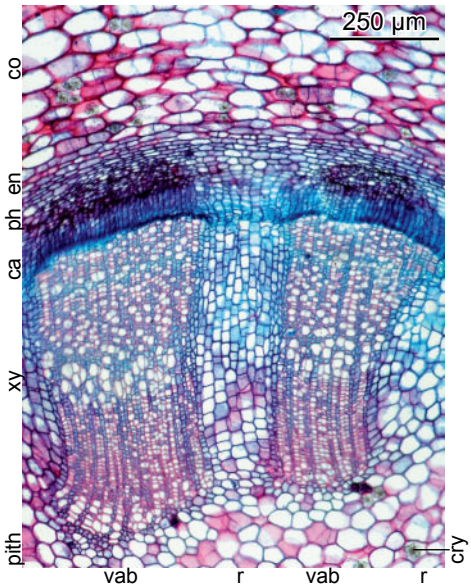



**Fig. 8.** Semi-ring-porous xylem. Large rays separate vessel/fiber zones. Rhizome of a 15 cm-high plant, garden, hill zone, Botanical Garden Zürich, Switzerland. *Tiarella cordifolia*, transverse section.

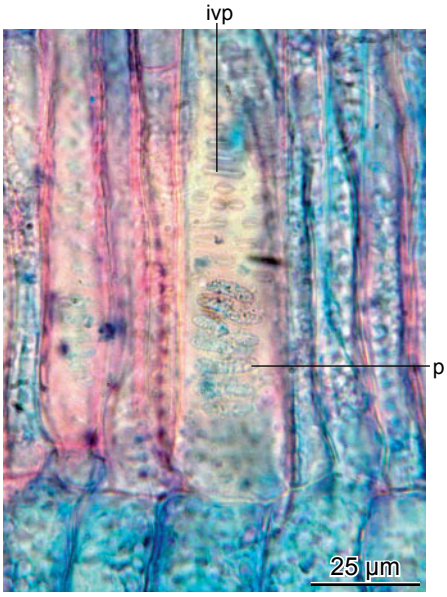
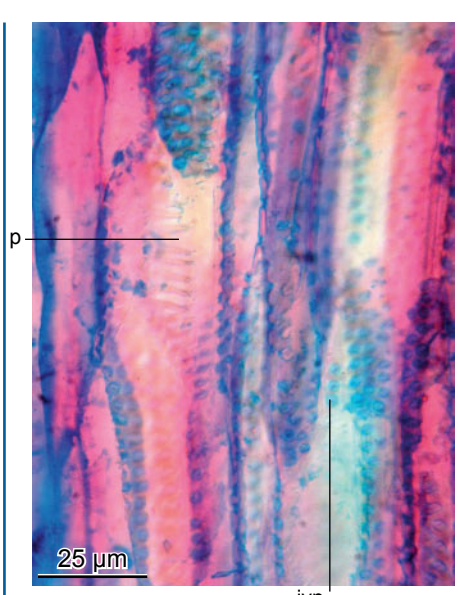
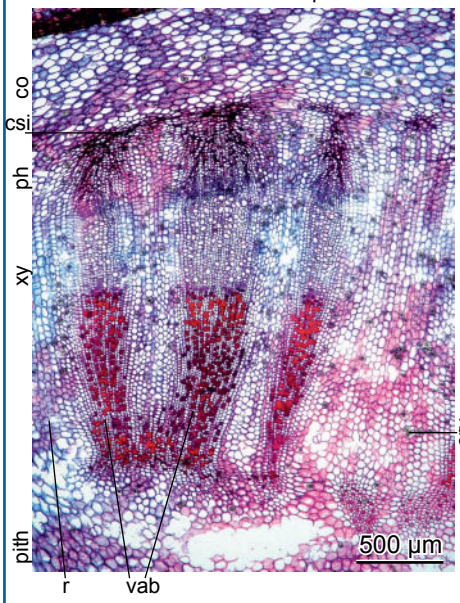


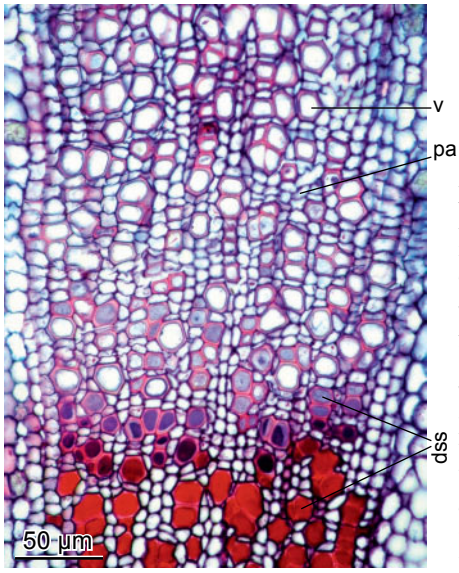

**Fig. 9.** Transition between scalariform intervessel pitting and scalariform perforation. Rhizome of a 15 cm-high plant, garden, hill zone, Botanical Garden Zürich, Switzerland. *Mitella ovalis*, radial section.



**Left Fig. 10.** Vessels with small round intervessel pits and scalariform perforations. Rhizome of a 15 cm-high plant, moist conifer forest, hill zone, Coeur d'Alene, Idaho, USA. *Tiarella unifoliata*, radial section.

**Right Fig. 11.** Scalariform intervessel pitting and scalariform perforation. Rhizome of a 25 cm-high plant, garden, hill zone, Botanical Garden of Zürich, Switzerland. *Heuchera americana*, radial section.




**Left Fig. 12.** Single vascular bundles are laterally separated by large rays in the first ring. Many pith and ray cells contain crystal druses and most cells contain dark substances (tannins?). Rhizome of a 25 cm-high succulent plant, Botanical Garden Halle, Germany. *Bergenia ciliata*, transverse section.

**Right Fig. 13.** Fiber-less xylem of a vascular bundle. Fairly thick-walled vessels are embedded in pervasive parenchyma. Rhizome of a 15 cm-high succulent plant, Botanical Garden Halle, Germany. *Bergenia ciliata*, transverse section.

### Ecological trends in the xylem

The temperate zone of Europe is characterized by the presence of the genera *Saxifraga* and *Chrysosplenium*. The temperate zone of North America is dominated by *Heuchera*, *Tierella* and *Mitella*. The subtropical climate of the Macaronesian zone is primarily differentiated by the absence of the Saxifragaceae family. North American species have fibers and scalariform perforation wheras in Europeans species fibers are in the majority of analyzed species missing and vessel perforations are simpe. In Europe fibers seem to be present only in stems of annual *Saxifraga* species (*S. bulbifera*, *S. tridactylites*). Altitudinal gradients could not be detected. We do not have enough material to detect ecological trends in North American species.

### Ecological trends in the phloem and the cortex

North American species contain crystals in the bark and the pith wheras Europeans species have neither.

**Characteristics of the phloem and the cortex**

*Clade Saxifraga*

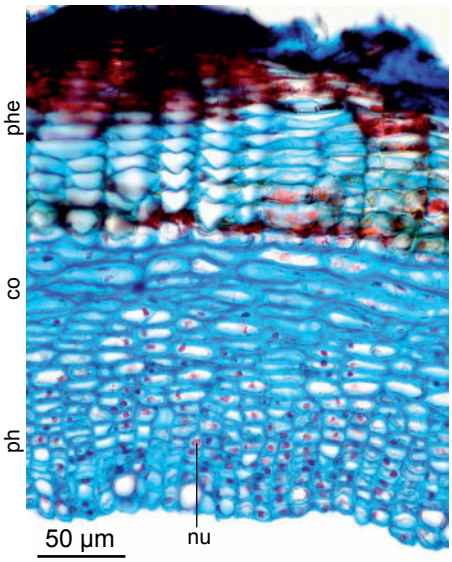
The bark is not well structured. Sieve tubes and parenchyma cells normally cannot be distinguished (**Fig. 14**). Many species have a well-developed phellem with often square to rectangular, thick-walled cork cells. The phellem is extraordinarily thick on individuals with exposed stems, e.g. *Saxifraga oppositifolia* (**Fig. 15**). Crystals and sclerenchyma are absent.

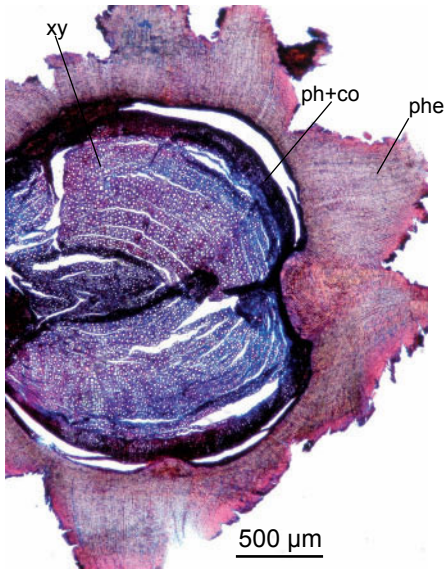
*Clade Heuchera*

The phloem is not well structured (**Fig. 16**). In contrast to the clade *Saxifraga* all species contain crystal druses (**Fig. 17**). The phellem is never extremely thick.

*Clade Bergenia*

In the radial oriented strands of parenchyma cells distinct groups of small sieve tubes occur (**Fig. 18**). Bergenia species contain crystal druses in the large rays.




**Left Fig. 14.** Phloem and cortex with a uniform anatomy. Parenchyma and sieve tubes cannot be distinguished. Most cells contain nuclei and are therefore living. A phellogen produces a thick phellem. Rhizome of a 5 cm-high herb, meadow, alpine zone, Alps, Switzerland. *Saxifraga moschata*, transverse section.

**Right Fig. 15.** Exposed stem with an extremely thick phellem. Rhizome of a 5 cm-high herb, meadow, subalpine zone, Alps, Switzerland. *Saxifraga oppositifolia*, transverse section.

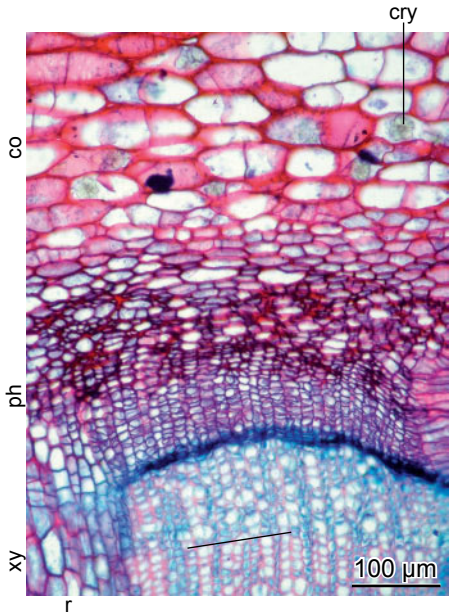



**Fig. 16.** Sightly differentiated phloem. Parenchyma cells are often slightly larger than sieve tubes. The large cortex cells contain crystal druses. Rhizome of a 15 cm-high plant, moist conifer forest, hill zone, Coeur d'Alene, Idaho, USA. *Tiarella unifoliata*, transverse section.

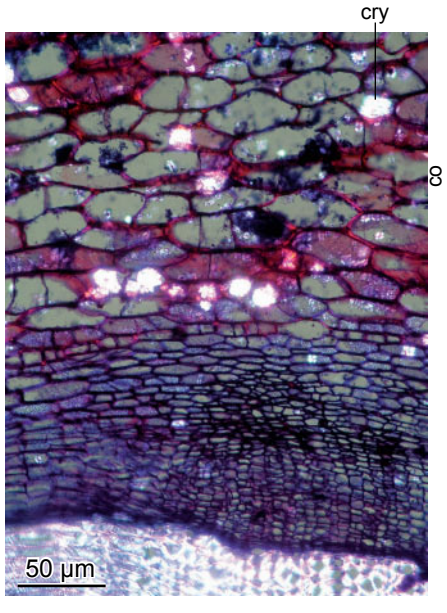



**Fig. 17.** Crystal druses in the cortex. Rhizome of a 15 cm-high plant, garden, hill zone, Botanical Garden Zürich, Switzerland. *Tiarella cordifolia*, transverse section.

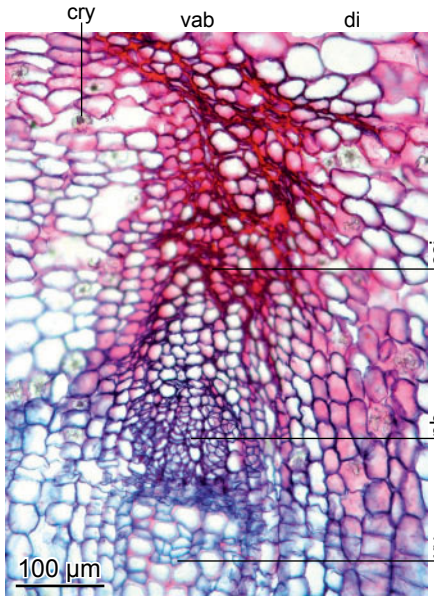



**Fig. 18.** The living phlosem consists on gruops of small sieve tubes and larger parenchyma cells. Sieve cells in the older phloem are collapsed. Rhizome of a 15 cm-high succulent plant, Botanical Garden Halle, Germany. *Bergenia ciliata*, transverse section.

**Discussion in relation to previous studies**

Since most species within the family of Saxifragaceae are herbaceous, their xylem has not been comprehensively analyzed. Metcalfe and Chalk (1957) mention "considerable anatomical variations even within the genus and section of *Saxifraga*". They observed distinct collateral bundles, small vessels and simple perforations and Carlquist (2001) detected scalariform intervessel pits and scalariform perforations within the family. Most results of the present study are new.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **27** |
| 1 | growth rings distinct and recognizable | 17 |
| 2 | growth rings absent | 9 |
| 2.1 | only one ring | 1 |
| 4 | semi-ring-porous | 6 |
| 5 | diffuse-porous | 18 |
| 9 | vessels predominantly solitary | 23 |
| 9.1 | vessels in radial multiples of 2-4 common | 1 |
| 11 | vessels predominantly in clusters | 5 |
| 13 | vessels with simple perforation plates | 21 |
| 14 | vessels with scalariform perforation plates | 6 |
| 20 | intervessel pits scalariform | 6 |
| 20.1 | intervessel pits pseudoscariform to reticulate | 20 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 18 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 8 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 3 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 24 |
| 60.1 | fibers absent | 19 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 7 |
| 65 | septate fibers present | 5 |
| 70 | fibers thin- to thick-walled | 5 |
| 70.1 | intra-annual thick-walled tangential fiber bands | 1 |
| 79 | parenchyma paratracheal | 3 |
| 79.1 | parenchyma pervasive | 21 |
| 89 | parenchyma marginal | 1 |
| 89.2 | ring shake, *Saxifraga* type | 12 |
| 96 | rays uniseriate | 1 |
| 99 | rays commonly >10-seriate | 9 |
| 99.1 | vascular bundle form remaining | 8 |
| 102 | ray height >1 mm | 5 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 22 |
| 117 | rayless | 17 |
| 136 | prismatic crystals present | 3 |
| 144 | druses present | 1 |
| R6 | sclereids in radial rows | 7 |
| R7.1 | with acicular crystals | 26 |
| R9 | with crystal sand | 1 |

# Simmondsiaceae

**Number of species, worldwide and in Europe**

The Simmondsiaceae family includes 1 genera with 1 species. *Simmondsia chinensis* is endemic to SW Northern America.

**Analyzed material**

Described here is the shrub *Simmondsia chinensis* growing in the *Cereus giganteus* steppe (arid climate) of Arizona, USA.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes (0.5-4 m) | 1 | 1 |
| **Plants analyzed from different vegetation zones:** | | |
| Arid | 1 | |

**Analyzed species:**

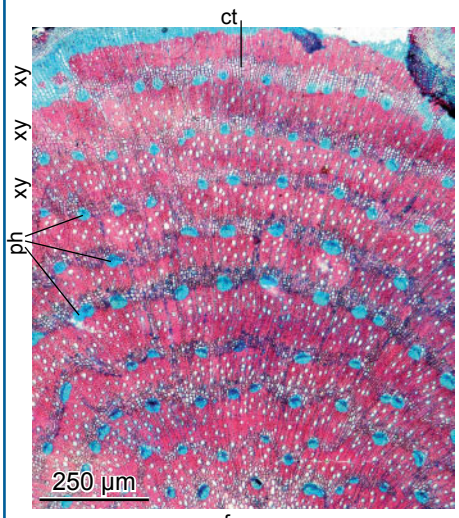
*Simmondsia chinensis* C.K. Schneid.

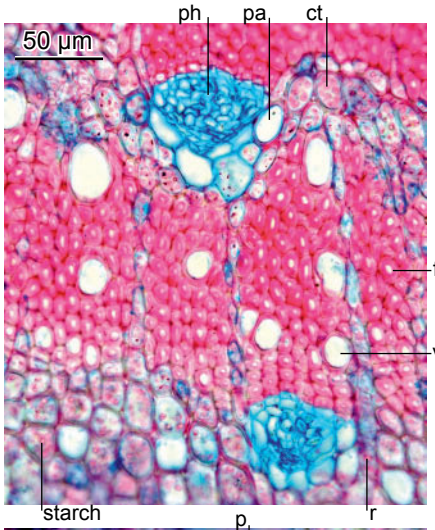
*Simmondsia chinensis*

### Characteristics of the xylem and phloem

Annual rings are absent (**Fig. 1**). Round groups of sieve tubes and parenchyma are present (interxylary phloem; **Fig. 2**). Conjunctive tissue is arranged in irregular tangential bands (**Fig. 1**). Vessels are small in diameter (<20 µm) and they have simple perforations (**Fig. 4**). Some vessels have thin helical thickenings. Fibers are round and thick-walled (**Fig. 4**). Rays are primarely uniseriate, but some are 2-3-seriate (**Fig. 3**). Ray cells are typically square and upright, rarely procumbent.

The phloem has a simple structure. The external part of the phellem contains a band of thick-walled, lignified sclereids (**Fig. 5**).




**Left Fig. 1.** Xylem without growth zones. Groups of interxylary phloem are arranged in tangential rows. Stem of an 80 cm-high shrub, *Cereus giganteus* steppe, Tucson, Arizona, USA. *Simmondsia chinensis*, transverse section.

**Right Fig. 2.** Groups of interxylary phloem cells are surrounded by a few unlignified parenchyma cells, conjunctive parenchymatic tissue with thin-walled lignified cell walls, lignified thick-walled fibers and solitary vessels. The uniseriate rays are radially discontinuous. Origin see **Fig. 1**. transverse section.

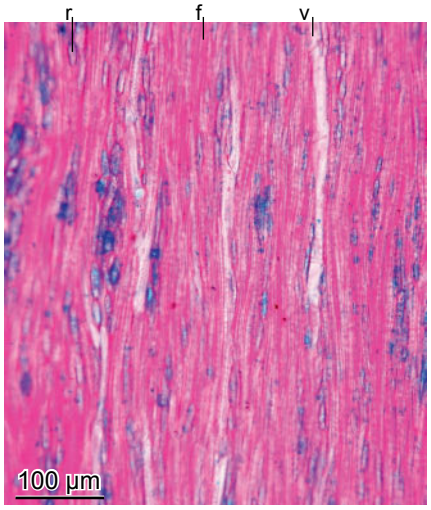



**Fig. 3.** Rays with 1-3 cells in width. Origin see **Fig. 1**, tangential section.

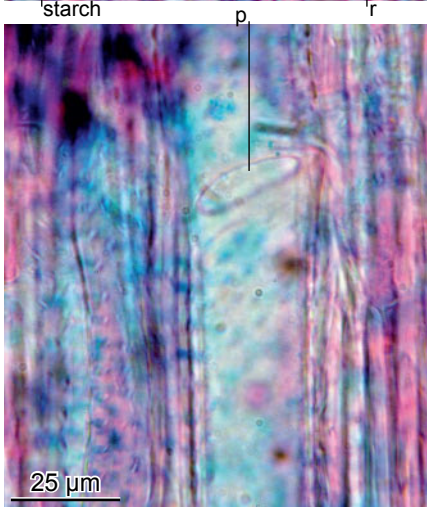



**Fig. 4.** Vessel with a simple perforation. Origin see **Fig. 1**, radial section.

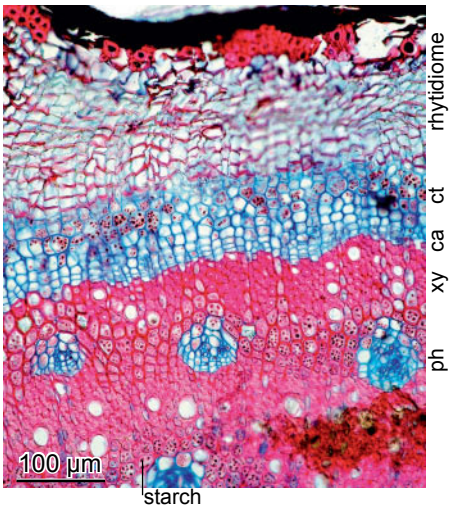



**Fig. 5.** Simple structured phloem. The external part of the periderm (former cortex) contains a band of thick-walled, lignified sclereids. Origin see **Fig. 1**, transverse section.

### Discussion in relation to previous studies

All the described features are also characteristic of the Amaranthaceae. The anatomical stem structure suggests that *Simmondsia chinensis* belongs to the Caryophyllales (Balthazar 2000 and Carlquist 2002). The present results agree with those from Carlquist (2002).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **1** |
| 2 | growth rings absent | 1 |
| 9 | vessels predominantly solitary | 1 |
| 13 | vessels with simple perforation plates | 1 |
| 22 | intervessel pits alternate | 1 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 1 |
| 50.1 | 100-200 vessels per mm² in earlywood | 1 |
| 61 | fiber pits small (<3 µm = libriform fibers) | 1 |
| 69 | fibers thick-walled | 1 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 98 | rays commonly 4-10-seriate | 1 |
| 105 | ray: all cells upright or square | 1 |
| 135 | interxylary phloem present | 1 |
| 136 | prismatic crystals present | 1 |
| R6.1 | sclereids in tangential rows | 1 |
| R7 | with prismatic crystals | 1 |
| R10 | phloem not well structured | 1 |

# Staphyleaceae

**Number of species, worldwide and in Europe**

The northern hemispheric Staphylaceae family includes 5 genera with 50 species. In Europe occur the two desribed species.

**Analyzed species:**

*Staphylea colchica* Stev.
*Staphylea pinnata* L.

**Analyzed material**

The xylem and phloem of 1 genus with 2 species is analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Nanophanerophytes (0.5-4 m) | 2 | 7 genera |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 2 | |

*Staphylea pinnata*

*Staphylea pinnata*

### Characteristics of the xylem

The xylem of both species is diffuse-porous and has distinct rings (**Fig. 1**). Vessels are solitary (**Figs. 1** and **6**). Vessel walls have scalariform perforations with >15 bars (**Fig. 2**), helical thickenings, tylosis (**Fig. 3**) and vessel-ray pits with horizontally enlarged apertures (**Fig. 4**). Fibers have large pits with slit-like apertures (>3 µm; **Fig. 5**) and are mostly thin- to thick-walled (**Fig. 6**). The distribution of axial parenchyma is mostly scanty paratracheal, rarely apotracheal, and diffuse in aggregates (**Fig. 6**). Rays are heterocellular with central procumbent and 2-6 marginal, square and upright cells (**Fig. 7**). Rays are 2-4-seriate with sheet cells (**Fig. 8**). A few crystal druses were observed in *Staphylea colchica*.

### Characteristics of the phloem and the cortex

Sieve tubes and parenchyma rows alternate in indistinct tangential bands. Groups of sclerenchyma cells are rare (**Figs. 9** and **10**). Ray dilatations are distinct (**Fig. 10**). Crystal druses occur mainly in ray cells.

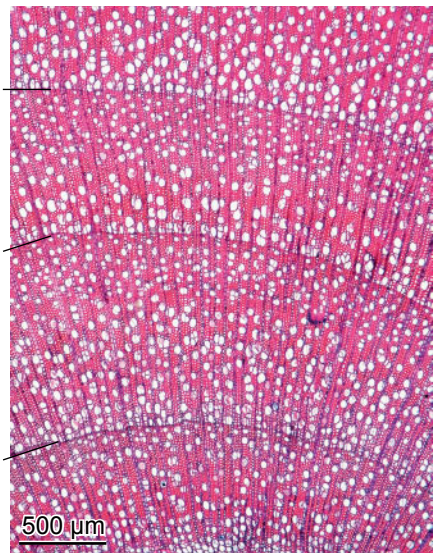



**Fig. 1.** Diffuse- to semi-ring-porous xylem with distinct annual rings. Stem of a 2 m-high shrub, hill zone, Botanical Garden Munich, Bavaria, Germany. *Staphylea colchica*, transverse section.

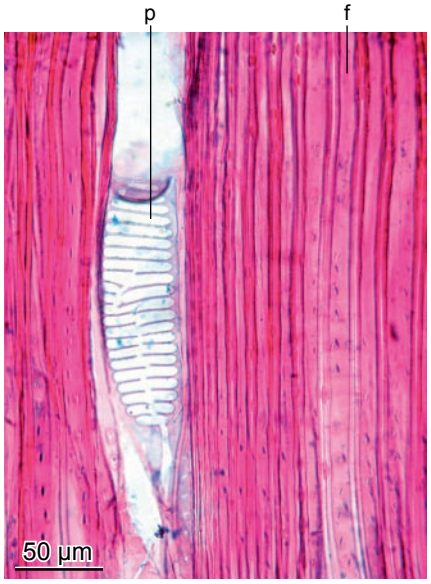



**Fig. 2.** Vessel with a scalariform perforation of 20 bars. Stem of a 2 m-high shrub, hill zone, Botanical Garden Munich, Bavaria, Germany. *Staphylea colchica*, radial section.

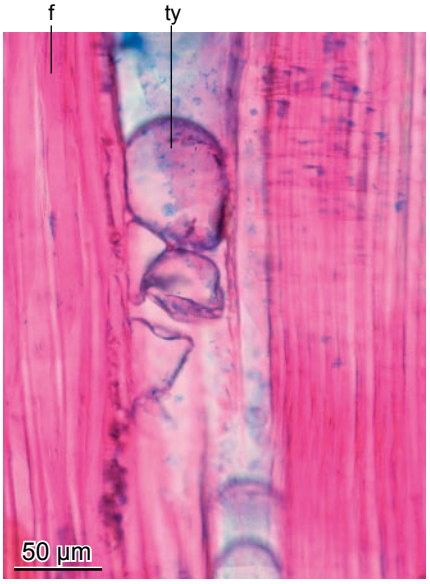



**Fig. 3.** Thin-walled tylosis in a vessel. Stem of a 2 m-high shrub, hill zone, Botanical Garden Munich, Bavaria, Germany. *Staphylea colchica*, radial section.

**Fig. 4.** Horizontally enlarged ray-vessel pits. Stem of a 2 m-high shrub, garden, hill zone, Zürich, Switzerland. *Staphylea pinnata*, radial section.

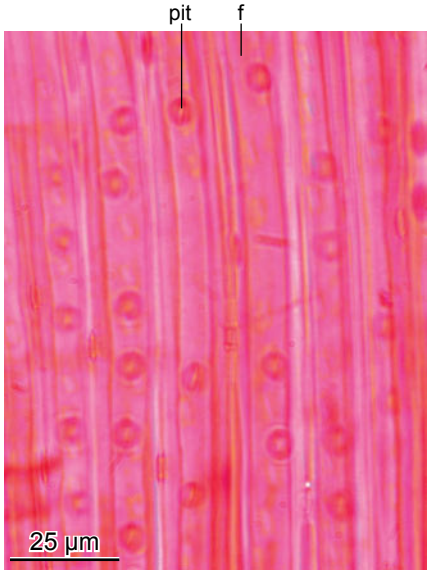



**Fig. 5.** Large fiber pits. Stem of a 2 m-high shrub, garden, hill zone, Zürich, Switzerland. *Staphylea pinnata*, radial section.

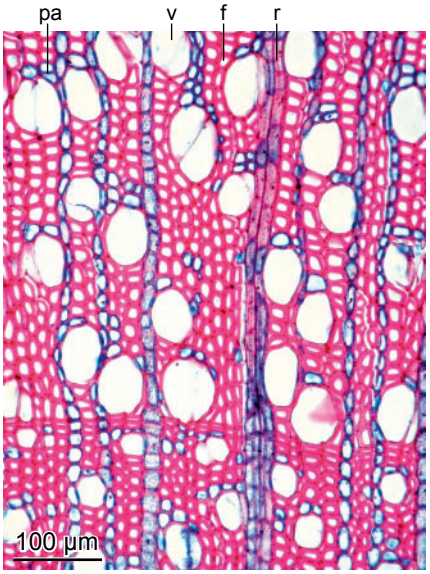
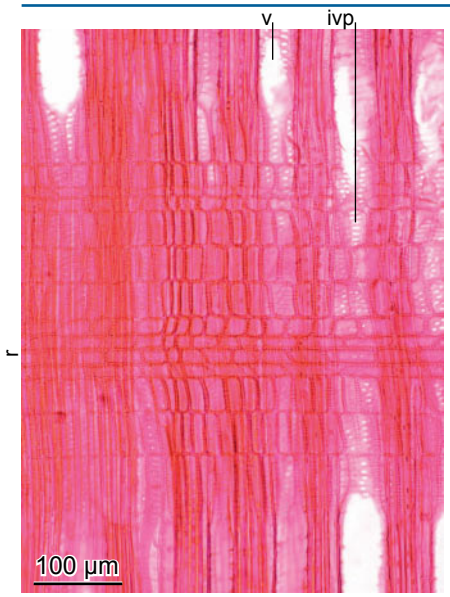
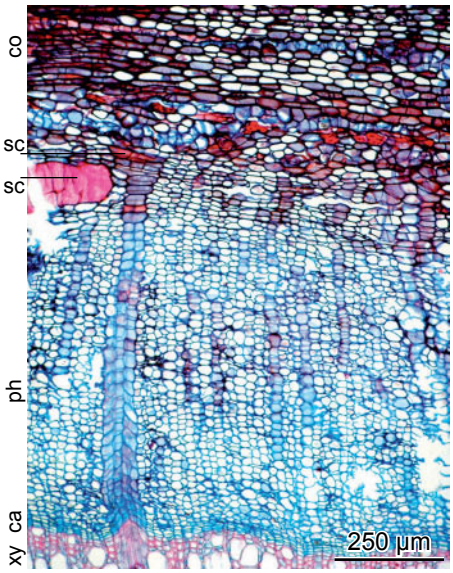


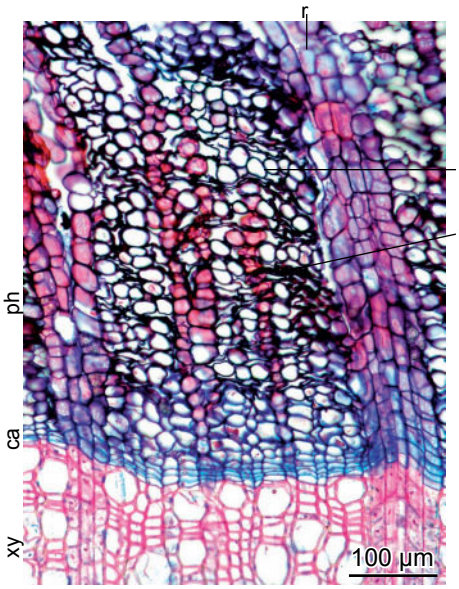

**Fig. 6.** Scanty paratracheal and rarely apotracheal diffuse parenchyma. Stem of a 2 m-high shrub, garden, hill zone, Zürich, Switzerland. *Staphylea pinnata*, transverse section.



**Left Fig. 7.** Heterocellular ray with a few procumbent central, and many square and upright marginal cells. Stem of a 2 m-high shrub, garden, hill zone, Zürich, Switzerland. *Staphylea pinnata*, radial section.

**Right Fig. 8.** 1-5-seriate, heterocellular rays. The large ray has sheet cells. Stem of a 2 m-high shrub, garden, hill zone, Zürich, Switzerland. *Staphylea pinnata*, tangential section.




**Left Fig. 9.** Phloem and cortex with a group of sclerenchyma cells and some lignified fibers within a tissue of unlignified sieve tubes and parenchyma cells. Stem of a 2 m-high shrub, garden, hill zone, Zürich, Switzerland. *Staphylea pinnata*, transverse section.

**Right Fig. 10.** Tangential rows of cells and collapsed sieve-tubes. Stem of a 2 m-high shrub, hill zone, Botanical Garden Munich, Bavaria, Germany. *Staphylea colchica*, transverse section.

## Discussion in relation to previous studies

The anatomy of the xylem of the five genera of Staphyleaceae was described by Carlquist and Hoeckman (1985). *Staphylea pinnata* was described by Greguss (1945), Grosser (1977) and Schweingruber (1990). Gregory (1994) mentioned 34 references concerning the xylem anatomy of Staphyleaceae. Holdheide (1951) described the bark of *Staphylea pinnata*.

The horizontally enlarged ray-vessel pits and the scalariform perforations bring *Staphylea* sp. close to the Hamamelidaceae.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **2** |
| 1 | growth rings distinct and recognizable | 2 |
| 5 | diffuse-porous | 2 |
| 9 | vessels predominantly solitary | 2 |
| 14 | vessels with scalariform perforation plates | 2 |
| 22 | intervessel pits alternate | 2 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 2 |
| 36 | helical thickenings present | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 2 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 2 |
| 56 | tylosis with thin walls | 2 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 2 |
| 70 | fibers thin- to thick-walled | 2 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 2 |
| 79 | parenchyma paratracheal | 1 |
| 98 | rays commonly 4-10-seriate | 2 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 1 |
| 110 | rays with sheet cells tangential section | 1 |
| 136 | prismatic crystals present | 1 |
| R2 | groups of sieve tubes in tangential rows | 2 |
| R3 | distinct ray dilatations | 2 |
| R4 | sclereids in phloem and cortex | 2 |
| R8 | with crystal druses | 2 |

# Tamaricaceae



**Number of species, worldwide and in Europe**

The Tamaricaceae family includes 4 genera with 78 species in Eurasia and Africa. Most of the species belong to *Tamarix* (54). The family is represented by 3 genera (*Myricaria*, *Reaumuria* and *Tamarix*) and 15 species in Europe.

**Analyzed material**

The xylem and phloem of 9 Tamaricaceae species has been analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | 8 | ca. 10 |
| Nanophanerophytes (0.5-4 m) | 1 | 1 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 1 | |
| Mediterranean | 2 | |
| Arid | 5 | |
| Subtropical | 1 | |

**Analyzed species:**

*Myricaria germanica* (L.) Desv.
*Tamarix aphylla* (L.) G. Karsten
*Tamarix articulata* Wahl.
*Tamarix balanse* J.Gray
*Tamarix bovenana* Bunge
*Tamarix canariensis* Willd.
*Tamarix gallica* L.
*Tamarix parviflora* DC
*Tamarix pentandra* Pallas

*Tamarix* sp.

*Myricaria germanica*

**Characteristics of the xylem**

The anatomical structure of the species analyzed is quite uniform (**Figs. 1-3**). Annual rings occur in the present material in most species, but they are indistinct in *Tamarix articulata* (**Fig. 3**). The ring boundaries of most species are defined by ring-porosity or semi-ring-porosity (**Figs. 1** and **2**). Characteristic of all species are large earlywood vessels with diameters >100 µm and a cell wall thickness of 4-6 µm (**Fig. 7**). Vessels are primarely solitary or in small groups. Perforations are always simple (**Fig. 4**) and intervessel pits and vessel-ray pits are very small and numerous (**Fig. 4**). The radial walls of fibers are perforated by round pits with a diameter of 1-2 µm (**Fig. 5**). Fibers are mostly thin- or thin- to thick-walled (**Figs. 6-8**). Tension wood was not observed. Axial parenchyma is vasicentric paratracheal and sometimes also patchy marginal (**Figs. 7** and **8**). Parenchyma is always storied (**Fig. 9**) and fibers and vessels mostly storied. Rays are always homocellular with procumbent cells. Ray width varies between 4-6 cells in *Myricaria germanica* (**Fig. 10**) and >10 cells in all *Tamarix* species (**Figs. 11** and **12**). Lateral ray cells of living material contain dark-staining substances (**Fig. 6**). Distinct sheet cells were observed only in *Myricaria germanica* (**Fig. 10**). Prismatic crystals occur in some species (*Myricaria germanica*, *Tamarix aphylla*, *T. articulata*, *T. balanse*; **Fig. 13**).

**Fig. 1.** Ring-porous to semi-ring-porous wood. Vessels are solitary or in small, often radial groups. Stem of a 1.2 m-high shrub, riverbed, subalpine zone, temperate climate, Morteratsch Glacier forefield, Switzerland. *Myricaria germanica*, transverse section.

**Fig. 2.** Ring-porous to semi-ring-porous wood. Vessels are solitary or in groups. Stem of a 5 m-high tree, dune, hyperarid climate, Germa, Libya. *Tamarix balanse*, transverse section.

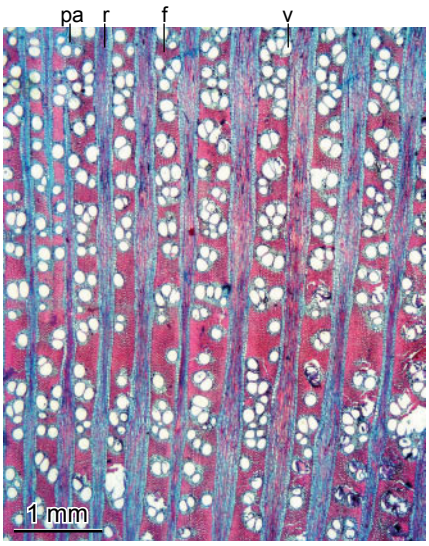



**Fig. 3.** Wood with indistinct rings. Vessels are in groups. Stem of a 10 m-high tree, cultivated, hyperarid climate, Germa, Libya. *Tamarix articulata*, transverse section.

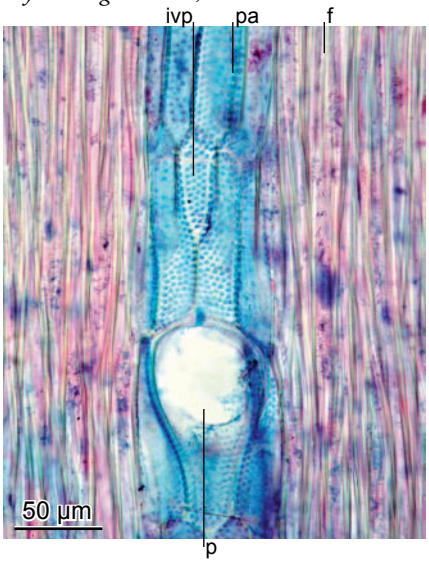



**Fig. 4.** Vessel with simple perforation and minute inter-vessel pits. Stem of a 4 m-high tree, sea shore, subtropical climate, Sur, Oman. *Tamarix aphylla*, radial section.

**Fig. 5.** Fiber with round, minute pits. Stem of a 4 m-high tree, coast, subtropical climate, Gomera, Canary Islands. *Tamarix canariensis*, radial section.

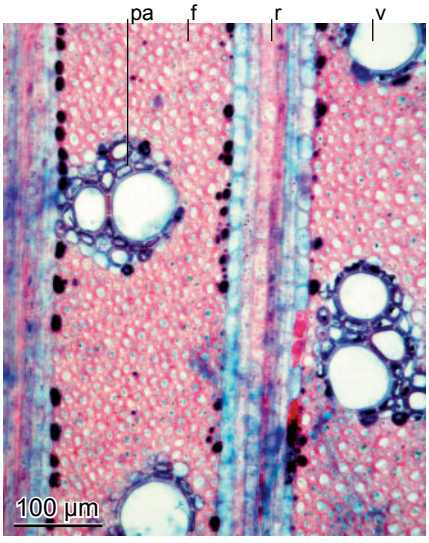
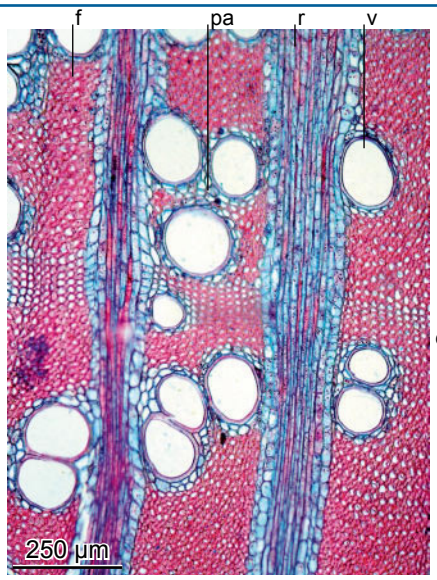
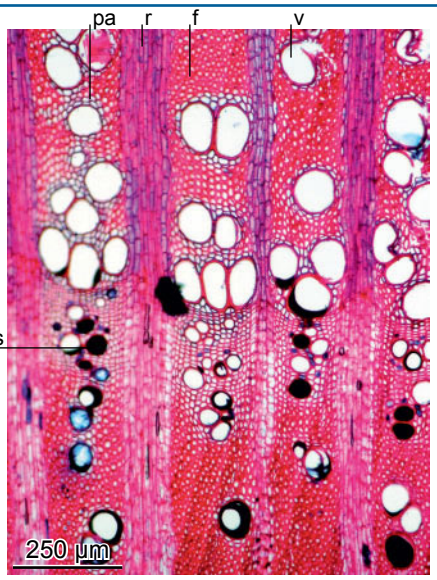


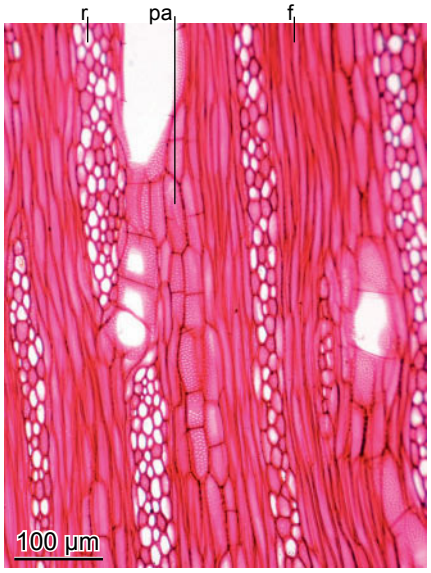

**Fig. 6.** Vessels with vasicentric parenchyma. Adjacent living cells of large rays are filled with dark-staining substances. Stem of a 4 m-high tree, sea shore, subtropical climate, Sur, Oman. *Tamarix aphylla*, transverse section.



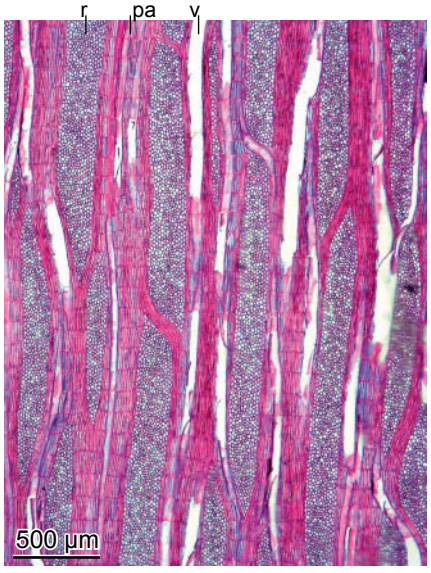

**Left Fig. 7.** Thick-walled vessels (5 µm) with vasicentric parenchyma. Lateral cells of large rays are larger than those in the center. Stem of a 10 m-high tree, cultivated, hyperarid climate, Germa, Libya. *Tamarix articulata*, transverse section.

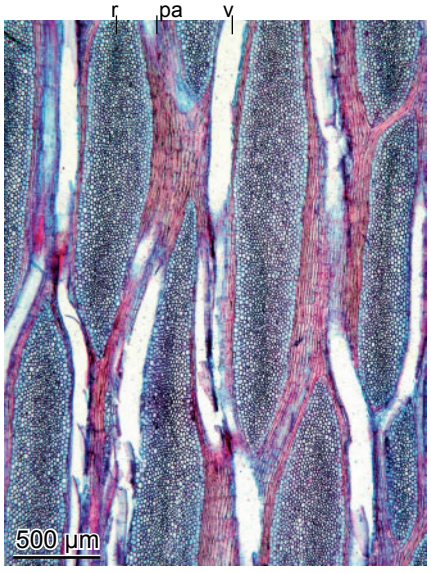
**Right Fig. 8.** Dark-staining substances in vessels in the heartwood. Stem of a 5 m-high tree, dune, hyperarid climate, Germa, Libya. *Tamarix gallica*, transverse section.




**Left Fig. 9.** Storied parenchyma cells and fibers adjacent to large rays. Stem of a 5 m-high tree, dune, hyperarid climate, Germa, Libya. *Tamarix balanse*, tangential section.

**Right Fig. 10.** Rays with 4-6 cells in width, partially with sheet cells. Stem of a 1.2 m-high shrub, riverbed, subalpine zone, temperate climate, Morteratsch Glacier forefield, Switzerland. *Myricaria germanica*, tangential section.



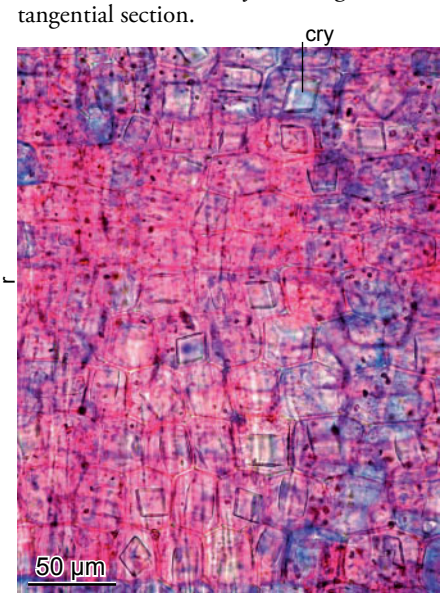




**Fig. 11.** Rays >10 cells in width and distinct storied parenchyma cells. Stem of a 5 m-high tree, dune, hyperarid climate, Germa, Libya. *Tamarix balanse*, tangential section.

**Fig. 12.** Rays >20 cells in width. Stem of a 10 m-high tree, cultivated, hyperarid climate, Germa, Libya. *Tamarix articulata*, tangential section.

**Fig. 13.** Prismatic crystals in ray cells. Stem of a 10 m-high tree, cultivated, hyperarid climate, Germa, Libya. *Tamarix articulata*, radial section.

### Characteristics of the phloem and the cortex

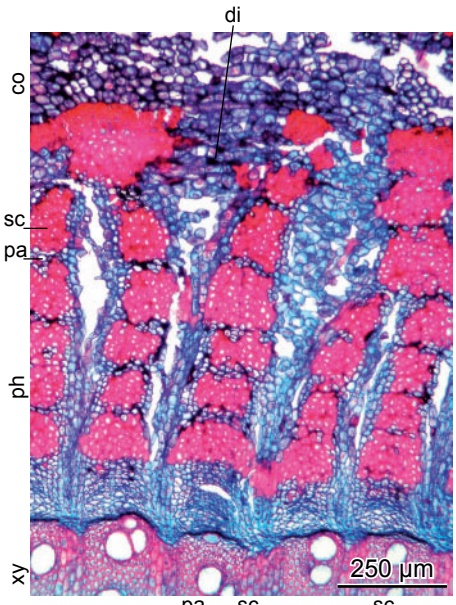
Characteristic of all species are the tangential bands (probably annual) of compartments of sclereids in the late part of the phloem. The compartments are more-or-less square in *Myricaria* (**Fig. 14**) and sickle-shaped in *Tamarix*. Rays of *Myricaria* contain cells with unlignified walls (**Fig. 14**). In contrast, *Tamarix* rays are intensively sclerotized (**Figs. 15-17**). A few cells with unlignified walls separate the annual compartments from each other. Phloem formation starts with thin-walled groups of parenchyma and sieve tubes. Sieve tubes collapse in the second ring and are no longer visible (**Fig. 17**). Dilations occur only in *Myricaria germanica* (**Fig. 1**).

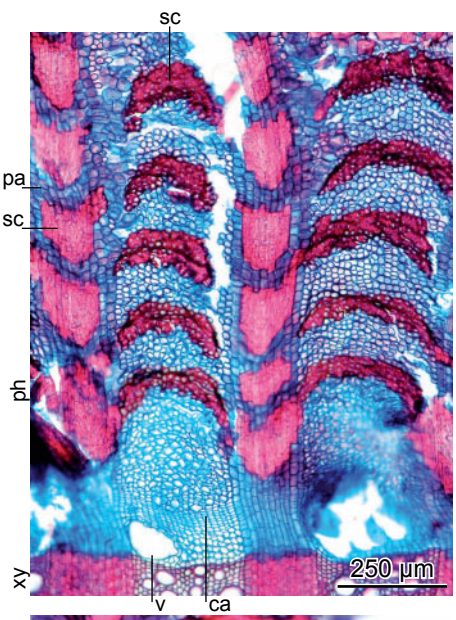
### Characteristic features of taxa

As Fahn et al. 1986 mention, vessel arrangement, vessel density, vessel diameter, vessel wall thickness, ray width and the occurrence of prismatic crystals could be features that differentiate species. Since we have not enough material from different sites it is difficult to classify these observations as taxonomically important species. The relatively small rays of *Myricaria germanica* (**Fig. 10**) distinguish this species from all *Tamarix* species.

### Ecological trends and relations to life forms

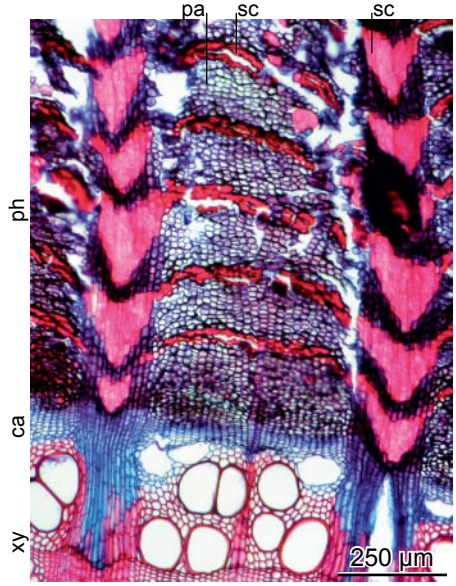
Generally, we did not find any ecologically significant features even though the material comes from an extremely wide ecological spectrum. Ring-porosity occurs in all sites analyzed, e.g. *Myricaria germanica* growing in a river bed in front of a glacier of the Alps, as well as *Tamarix gallica* growing on dunes around a lake in a hyperarid climate. We observed only one exception: *Tamarix articulata* growing in a plain around a village in the Central Sahara does not form an earlywood zone and therefore rings are indistinct (**Fig. 3**).

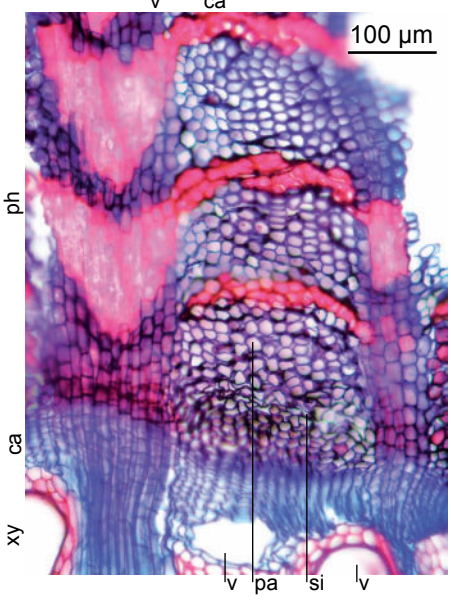



**Left Fig. 14.** Square groups of sclereids are arranged in tangential layers between dilated rays in the phloem. The groups are tangentially separated from unlignified parenchyma cells. Ray cells are primarely unlignified. Stem of a 1.2 m-high shrub, riverbed, subalpine zone, temperate climate, Morteratsch Glacier forefield, Switzerland. *Myricaria germanica*, transverse section.

**Right Fig. 15.** Sickle-shaped groups of sclereids are arranged in tangential layers between rays in the phloem. The groups are tangentially separated of unlignified parenchyma cells. Groups of sclereids in the rays correspond with the tangential layers between them. Stem of a 5 m-high tree, dune, hyperarid climate, Germa, Libya. *Tamarix balanse*, tangential section.




**Left Fig. 16.** Similar anatomical structure to that in **Fig. 15**. Xylem formation is in process (March 07). Stem of a 5 m-high tree, dune, hyperarid climate, Germa, Libya. *Tamarix gallica*, transverse section.

**Right Fig. 17.** Phloem structure of the first three rings. The first ring outside the cambium contains parenchyma and sieve tubes. Sieve tubes collapse afterwards and are no longer visible. Stem of a 5 m-high tree, dune, hyperarid climate, Germa, Libya. *Tamarix gallica*, transverse section.

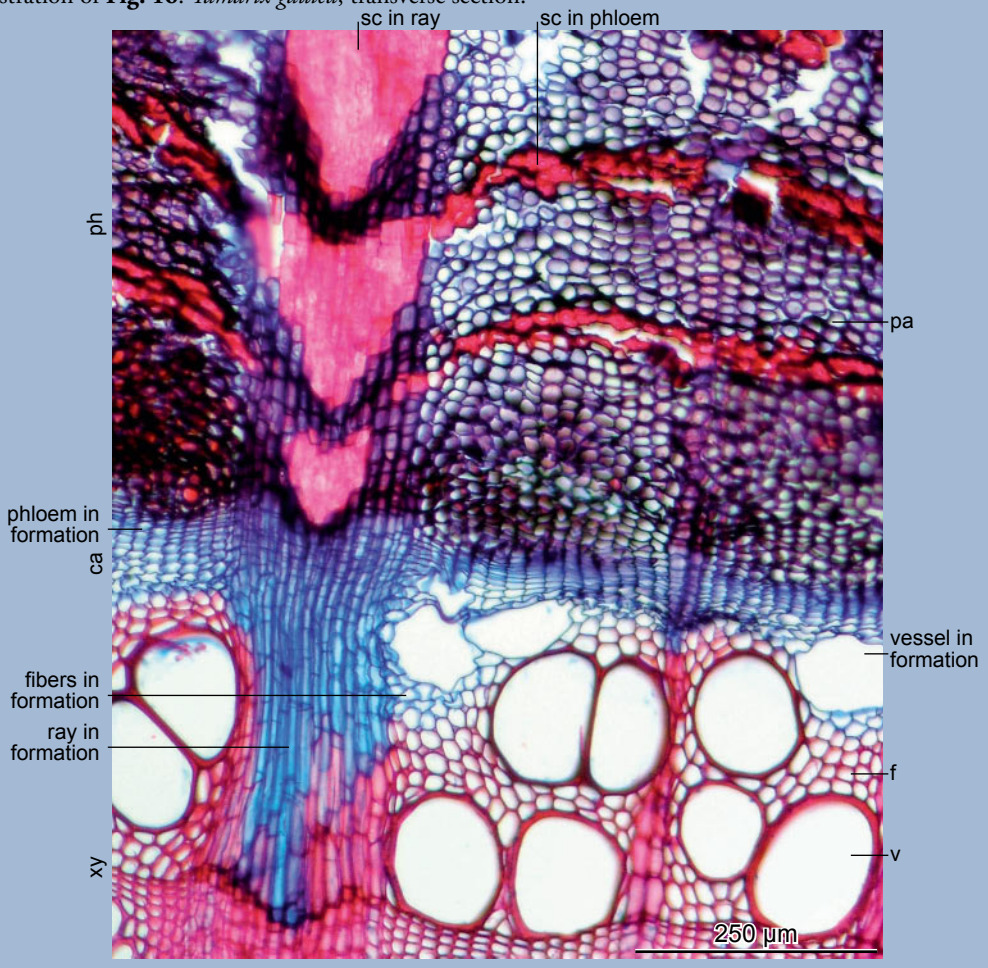
## Discussion in relation to previous studies

Comparative studies of the xylem of 4 genera were made by Brunner (1908) and Fahn et al. (1986). Many other authors, see Gregory (1994), described different species of *Tamarix* and *Myricaria*, e.g. Greguss (1959) and Schweingruber (1990). Metcalfe and Chalk (1957) referred to many additional references. The bark of *Myricaria germanica* was described by Holdheide (1951). The results of the present study are in agree with all previous studies.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **9** |
| 1 | growth rings distinct and recognizable | 8 |
| 2 | growth rings absent | 1 |
| 3 | ring-porous | 7 |
| 4 | semi-ring-porous | 1 |
| 5 | diffuse-porous | 2 |
| 9 | vessels predominantly solitary | 6 |
| 11 | vessels predominantly in clusters | 6 |
| 13 | vessels with simple perforation plates | 9 |
| 39.1 | vessel cell-wall thickness >2 µm | 1 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 5 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 6 |
| 50 | <100 vessels per mm² in earlywood | 1 |
| 50.1 | 100-200 vessels per mm² in earlywood | 8 |
| 58 | dark-staining substances in vessels and/or fibers (gum, tannins) | 5 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 9 |
| 70 | fibers thin- to thick-walled | 9 |
| 79 | parenchyma paratracheal | 9 |
| 89 | parenchyma marginal | 7 |
| 98 | rays commonly 4-10-seriate | 1 |
| 99 | rays commonly >10-seriate | 8 |
| 103 | rays of two distinct sizes (tangential section) | 1 |
| 104 | ray: all cells procumbent (radial section) | 7 |
| 106 | ray: heterocellular with upright 1 cell row (radial section) | 1 |
| 110 | rays with sheet cells (tangential section) | 2 |
| 120 | storied axial tissue (parenchyma, fibers, vessels, tangential section) | 9 |
| 136 | prismatic crystals present | 4 |
| R1 | groups of sieve tubes present | 4 |
| R2 | groups of sieve tubes in tangential rows | 4 |
| R3 | distinct ray dilatations | 2 |
| R4 | sclereids in phloem and cortex | 6 |
| R6 | sclereids in radial rows | 1 |
| R6.1 | sclereids in tangential rows | 6 |
| R7 | with prismatic crystals | 4 |

Detailed illustration of **Fig. 16**: *Tamarix gallica*, transverse section.



# Thymelaeaceae

**Number of species, worldwide and in Europe**

The cosmopolitan Thymelaeaceae family includes 50 genera with 500 species. In Europe, there are 3 genera with 35 species.

**Analyzed material**

The xylem and phloem of 2 genera with 15 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Woody chamaephytes | 15 | 8 |
| **Plants analyzed from different vegetation zones:** | | |
| Boreal and subalpine | 4 | |
| Hill and mountain | 5 | |
| Mediterranean | 4 | |
| Arid | 2 | |

**Analyzed species:**

*Daphne alpina* L.
*Daphne cneorum* L.
*Daphne gnidium* L.
*Daphne laureola* L.
*Daphne laureola* ssp. *philippi* Rouy
*Daphne mezereum* L.
*Daphne oleoides* Schreber
*Daphne petraea* Leybold
*Daphne pontica* L.
*Daphne striata* Tratt
*Thymelaea dioica* (Gouan) All.
*Thymelaea hirsuta* (L.) Endl.
*Thymelaea microphylla* Coss. et DR.
*Thymelaea sanamuda* All.
*Thymelaea tartonraira* (L.) All.

*Daphne striata* (photo: Landolt)

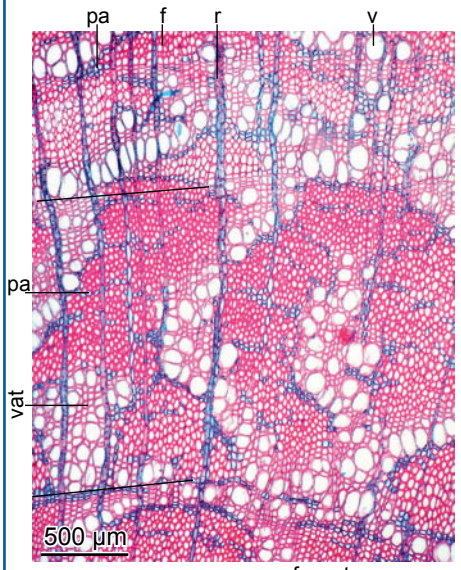
*Daphne mezereum*

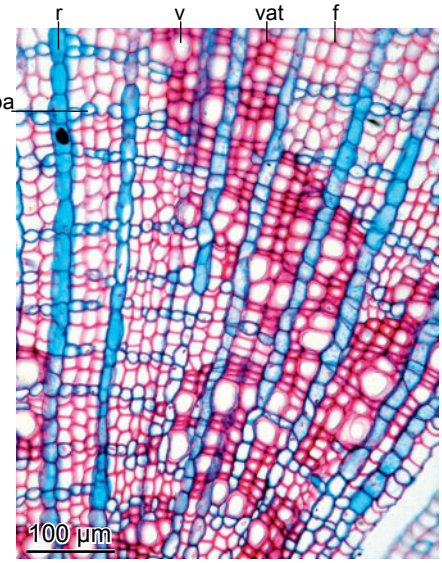
*Thymelaea hirsuta* (photo: Zinnert)

*Daphne alba* (photo: Landolt)

**Characteristics of the xylem**

Ring boundaries of all *Daphne* and most *Thymelaea* species are distinct (**Figs. 1-4**), except those of *Thymelaea sanamuda* and *T. hirsuta* (**Fig. 5**). Ring boundaries are expressed by the different size of vessels between the latewood and earlywood (**Figs. 1** and **4**), by a band of terminal parenchyma cells (**Fig. 2**) or by a row of flat fibers in the latewood (**Fig.** 3). All species with distinct rings are diffuse- to semi-ring-porous. Vessels are mostly arranged in diagonal (**Figs. 1**, **5** and **10**) to radial patterns (**Fig. 3**). Vessels are solitary in *Thymelaea dioica* and *T. tartonraira* (**Fig. 4**). The earlywood vessel diameter varies from 30-50 µm and vessel density varies from 80-300/mm$^2$. Vessel cell walls are mostly thin-walled, only ocasionally thick-walled. Vessel thickness varies among species from different sites. Perforations are simple and intervessel pits are large, round and arranged in opposite position (**Fig. 6**). Helical thickenings occur sporadically in different species in the genera *Daphne* and *Thymelaea* (**Fig. 7**). Their presence or absence varies within species, e.g. in *Daphne pontica*. Ray-vessel pits are bordered and fairly large (3 µm in diameter; **Fig. 8**). Fibers are mostly thin-walled (**Figs. 2** and **9**), but ocasionally thin- to thick-walled (**Figs. 1** and **4**). Fiber pits are small with a diameter of 2 µm and have slit-like apertures. Vessels are almost always surrounded by vasicentric tracheids (**Figs. 2** and **9**). Since we have no macerates it is often difficult to differentiate them from vessels. Parenchyma is mostly apotracheal, diffuse in aggregates (**Figs. 1**, **2**, **9** and **10**) and marginal but parenchyma can also surround vessel groups (**Fig. 11**). Rays are basically uniseriate (**Fig. 12**), but locally 2-3-seriate. Cellular ray composition varies from homocellular, where all cells are procumbent (**Fig. 13**), to heterocellular with one to many square and upright cells (**Fig.14**), to homocellular with exclusively upright cells.




**Left Fig. 1.** Semi-ring-porous xylem. Vessels are arranged in diagonal pattern. Unlignified parenchyma cells are apotracheal and arranged in tangential aggregates. Stem of an 80 cm-high shrub, steppe, Mediterranean zone, Carboneras, Andalusia, Spain. *Daphne gnidium*, transverse section.

**Right Fig. 2.** Diagonal pattern of vessels and vascicular tracheids embedded in a tissue of thin-walled fibers. Tangential bands of parenchyma cells indicate ring boundaries. Stem of a 15 cm-high chamaephyte, meadow, alpine zone, Davos, Grisons, Switzerland. *Daphne striata*, transverse section.

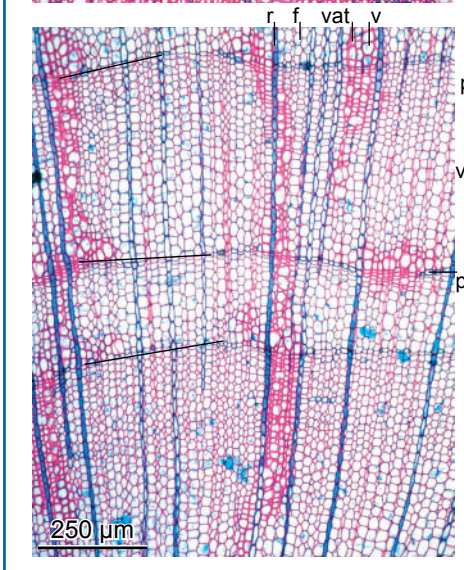



**Fig. 3.** Radial strips of vessels and vascular tracheids are embedded in a thin-walled tissue of fibers. Stem of an 80 cm-high shrub, beech forest, hill zone, Jura, Switzerland. *Daphne laureola*, transverse section.

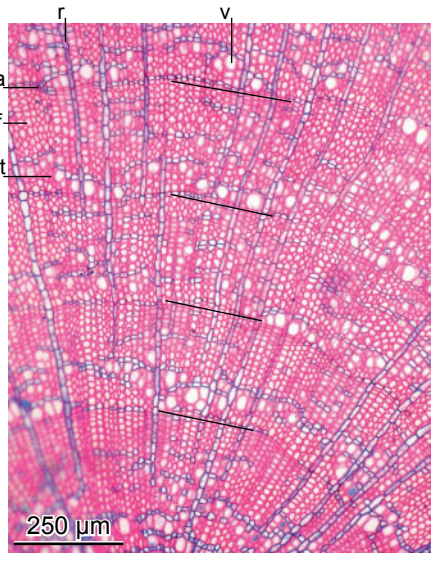



**Fig. 4.** Semi-ring-porous xylem. Parenchyma cells are in uniseriate tangential layers (apotracheal in aggregates). Stem of a 50 cm-high dwarf shrub, meadow, Mediterranean, Catalonia, Spain. *Thymelaea tartonraira*, transverse section.

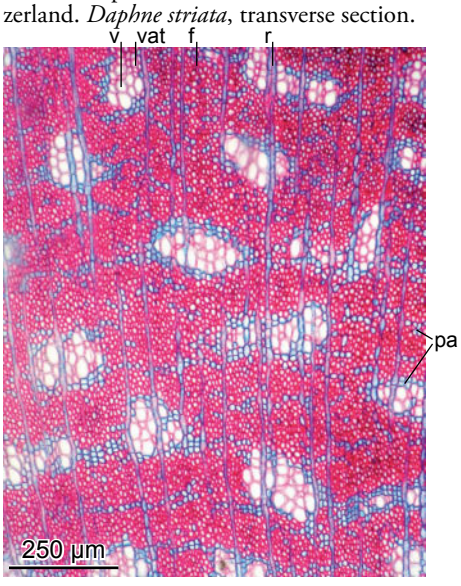
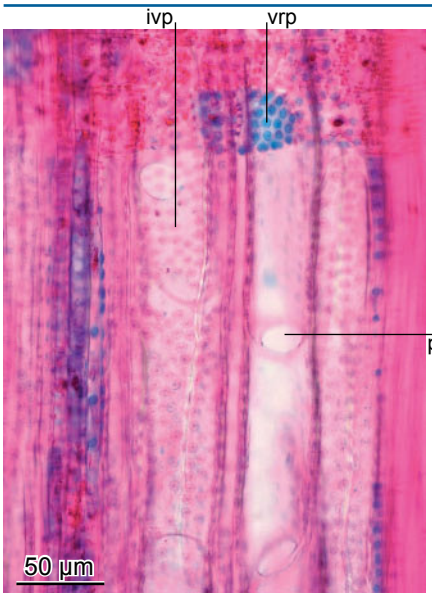
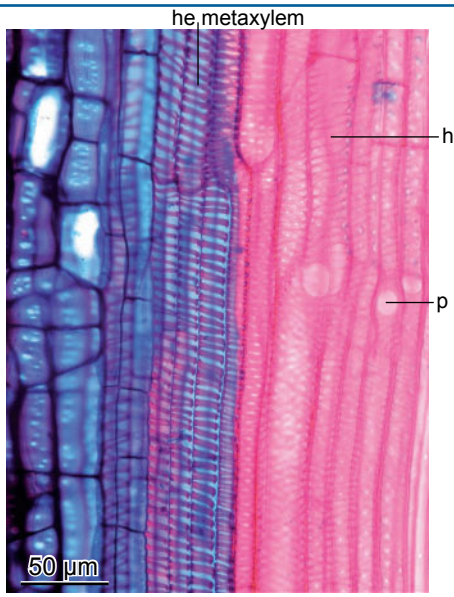


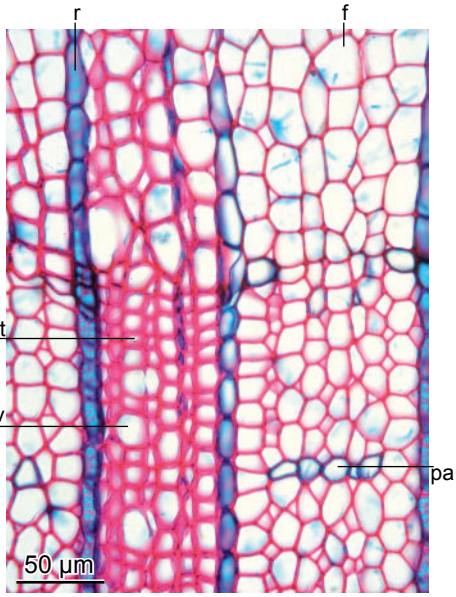

**Fig. 5.** Xylem without growth zones (see also **Fig. 11**). Stem of a 1 m-high shrub, steppe, Mediterranean zone, Carboneras, Andalusia, Spain. *Thymelaea hirsuta*, transverse section.



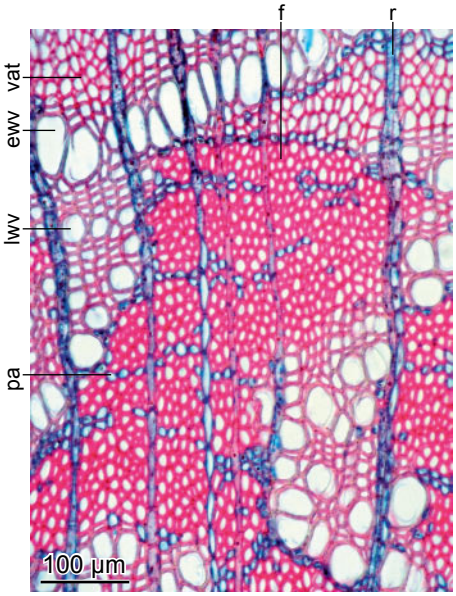

**Left Fig. 6.** Vessels with simple perforations and large, round intervessel pits. Stem of an 80 cm-high shrub, steppe, Mediterranean zone, Carboneras, Andalusia, Spain. *Daphne gnidium*, radial section.

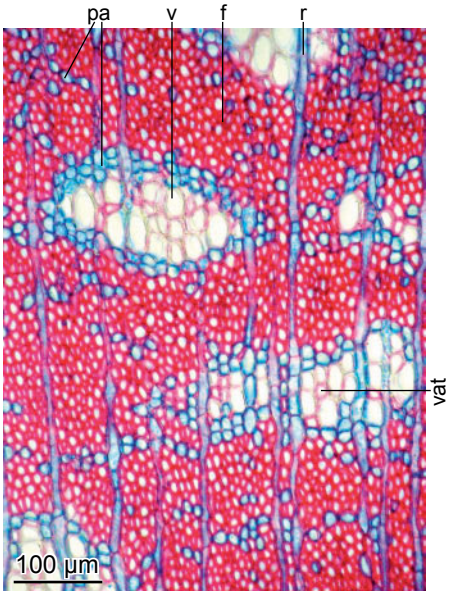
**Right Fig. 7.** Vessel thickenings around the pith: thick-walled helical thickenings and ring-shaped thickenings in unlignified vessels of the metaxyem; thin-walled helical thickenings in lignified vessels and vascular tracheids of the secondary xylem. Stem of an 80 cm-high shrub, beech forest, hill zone, Jura, Switzerland. *Daphne laureola*, radial section.




**Left Fig. 8.** Large, unlignified, bordered ray-vessel pits and large, lignified, bordered intervessel pits. Stem of a 50 cm-high dwarf shrub, *Pinus sylvestris* forest, Mediterranean zone, Pyrenees, Spain. *Thymelaea dioica*, radial section.

**Right Fig. 9.** A radial strip of fairly thick-walled vessels and vascular tracheids is delimted by unlignified uniseriate rays. Fibers on both sides of the strip are thin-walled. Stem of an 80 cm-high shrub, beech forest, hill zone, Jura, Switzerland. *Daphne laureola*, transverse section.




**Left Fig. 10.** Apotraceal parenchyma cells in horizontal, uni- and biseriate layers within a thin- to thick-walled fiber tissue. Stem of an 80 cm-high shrub, steppe, Mediterranean zone, Carboneras, Andalusia, Spain. *Daphne gnidium*, transverse section.

**Right Fig. 11.** Paratracheal and apotracheal parenchyma. Parenchyma cells surround vessel groups and vascular tracheids. They are solitary or in irregular, tangential uniseriate layers. Stem of a 1 m-high shrub, steppe, Mediterranean zone, Carboneras, Andalusia, Spain. *Thymelaea hirsuta*, transverse section.

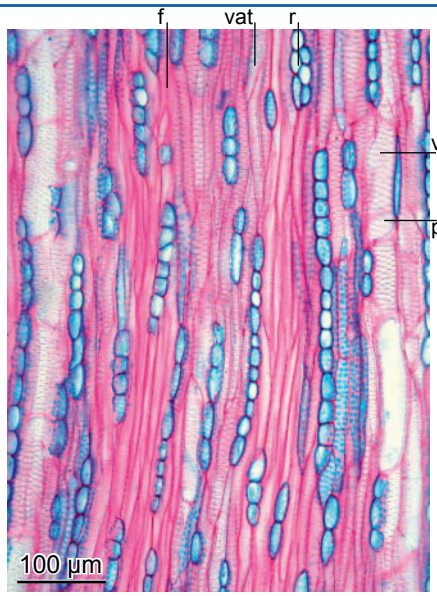



**Fig. 12.** Uniseriate, unlignified rays. Stem of a 50 cm-high dwarf shrub, *Pinus sylvestris* forest, Mediterranean zone, Pyrenees, Spain. *Thymelaea dioica*, tangential section.

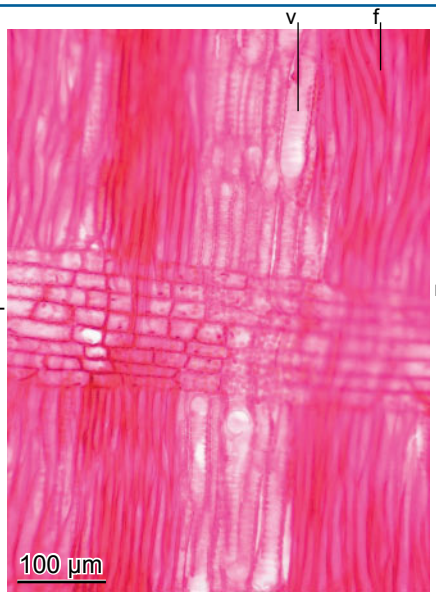



**Fig. 13.** Homocellular ray consisting of procumbent cells. Stem of a 20 cm-high chamaephyte, hill zone, Botanical Garden Zürich, Switzerland. *Daphne petraea*, radial section.

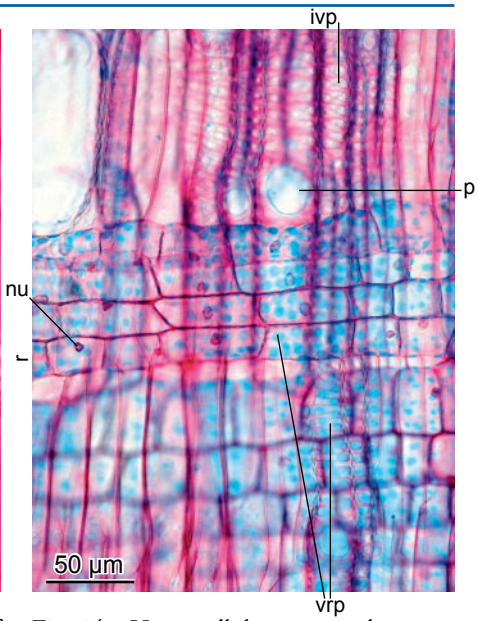



**Fig. 14.** Heterocellular ray with many square and upright marginal cells. Stem of an 80 cm-high dwarf shrub, riparian, subalpine zone, Davos, Grisons, Switzerland. *Daphne mezereum*, radial section.

**Characteristics of the phloem, the cortex and the pith**

Characteristic of all species is the presence of a unique fiber type: they are soft (difficult to cut properly), thick-walled, do not reflect polarized light and stain red in safranin. They look like lignified gelatinous fibers (**Fig. 15**). Such fibers are solitary, to varying degrees located between an unlignified sieve tube/parenchyma tissue (**Figs. 16-19**) or they are absent. Tubes (laticifer-like) occur in most species in various amounts (**Figs. 19** and **20**). They contain mucilage or gum products. The phellem consists of a belt of thin-walled, flat cork cells (**Fig. 17**).

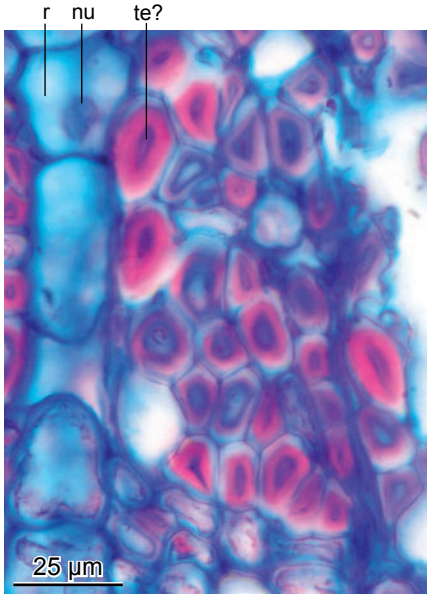



**Fig. 15.** Partially lignified fibers in the phloem. See text for further explanations. Stem of a 10 cm-high chamaephyte, *Pinus nigra* forest, Mödling, Wienerwald, Austria. *Daphne cneorum*, transverse section.

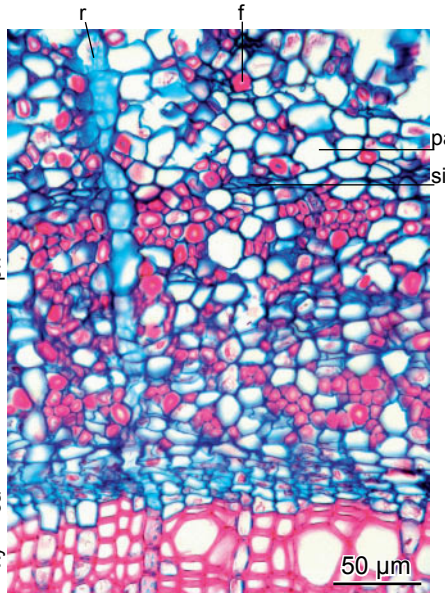



**Fig. 16.** Phloem with many lignified fibers located within an unlignified tissue of parenchyma and sieve tubes. Stem of a 30 cm-high dwarf shrub, meadow, subalpine zone, Carpathians, Georgia. *Daphne pontica*, transverse section.

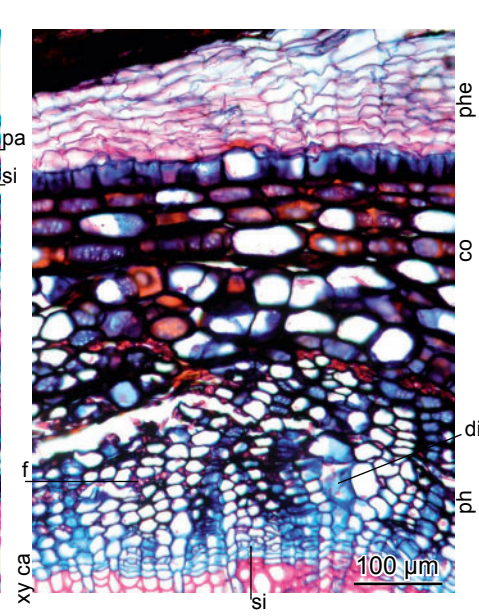



**Fig. 17.** Phloem with very small fibers. Uniformly structured phellem. Stem of a 15 cm-high chamaephyte, meadow, alpine zone, Davos, Grisons, Switzerland. *Daphne striata*, transverse section.

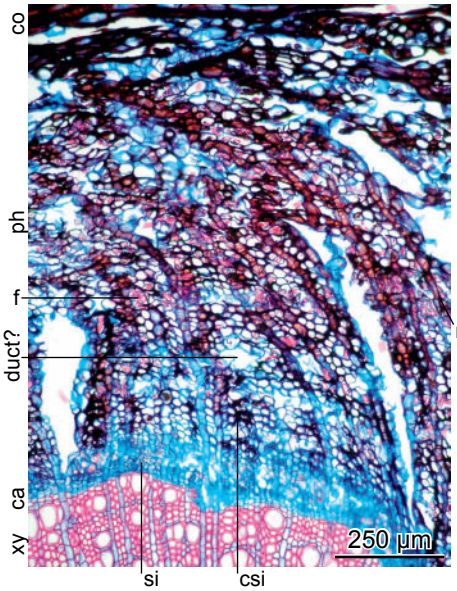



**Fig. 18.** Phloem with many solitary fibers. Stem of a 50 cm-high dwarf shrub, *Pinus sylvestris* forest, Mediterranean zone, Pyrenees, Spain. *Thymelaea dioica*, transverse section.

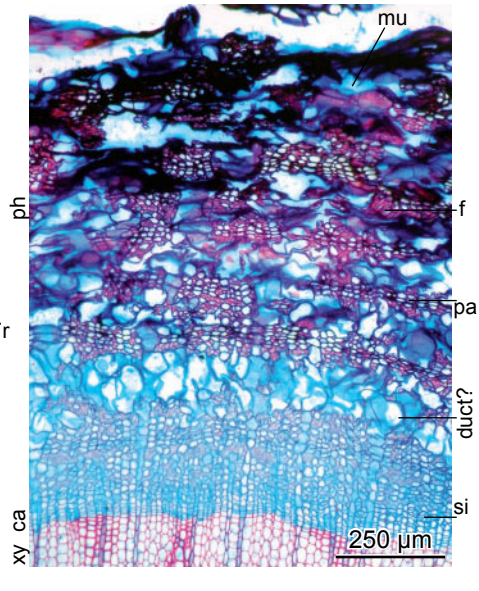



**Fig. 19.** Phloem with fiber groups and ducts in annual (?) tangential layers. Stem of an 80 cm-high shrub, beech forest, hill zone, Jura, Switzerland. *Daphne laureola*, transverse section.

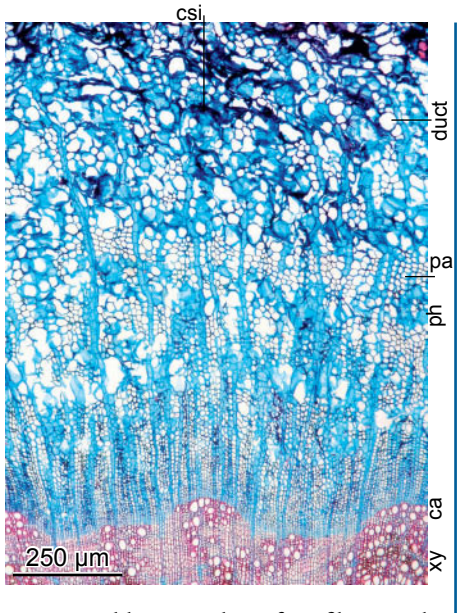



**Fig. 20.** Phloem with a few fibers and ducts. Stem of an 80 cm-high dwarf shrub, riparian, subalpine zone, Davos, Grisons, Switzerland. *Daphne mezereum*, transverse section.



## Ecological trends and relations to life forms

Individuals grown in temperate regions have distinct annual rings. Growth zones of some individuals grown in Mediterranean and arid regions are often indistinct and are probably not annual, e.g. in *Thymelea hirsuta* and *T. microphylla* from arid regions. Other site-relevant anatomical characteristics were not found.

## Discussion in relation to previous studies

Many tropical genera have been described, e.g. *Aquilaria*, *Wikstroemia* and *Edgeworthia* (Gregory 1994). Fahn et al. (1986) described *Thymelaea hirsuta*, Greguss (1945) described 7 European *Daphne* species and Schweingruber (1990) 10 European *Daphne* and 3 *Thymelaea* species. It is likly that species differentiation is possible but we do not have enough of material to differentiate site-dependent and species-specific features (Schweingruber 1990). Particular is the occurrence of the gelatinous fiber type in the phloem (**Fig. 15**), the occurrence of fiber tracheids and the tangential layers of parenchyma cells in the xylem. Here we confirm the anatomical analysis from previous authors. Anatomical features of the bark are described for the first time here.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **15** |
| 1 | growth rings distinct and recognizable | 15 |
| 2 | growth rings absent | 3 |
| 4 | semi-ring-porous | 10 |
| 5 | diffuse-porous | 12 |
| 7 | vessels in diagonal and/or radial patterns | 13 |
| 9 | vessels predominantly solitary | 5 |
| 9.1 | vessels in radial multiples of 2-4 common | 6 |
| 10 | vessels in radial multiples of 4 or more common | 2 |
| 11 | vessels predominantly in clusters | 4 |
| 13 | vessels with simple perforation plates | 15 |
| 22 | intervessel pits alternate | 15 |
| 36 | helical thickenings present | 8 |
| 39.1 | vessel cell-wall thickness >2 µm | 8 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 15 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 1 |
| 50 | <100 vessels per mm$^2$ in earlywood | 3 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 12 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 15 |
| 60.1 | fibers absent | 0 |
| 61 | fiber-pits small and simple to minutely bordered (<3 µm = libriform fibers) | 15 |
| 68 | fibers thin-walled | 9 |
| 70 | fibers thin- to thick-walled | 7 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 15 |
| 79 | parenchyma paratracheal | 1 |
| 89 | parenchyma marginal | 15 |
| 96 | rays uniseriate | 15 |
| 97 | ray width predominantly 1-3 cells | 1 |
| 104 | ray: all cells procumbent (radial section) | 6 |
| 105 | ray: all cells upright or square | 8 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 8 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 1 |
| R3 | distinct ray dilatations | 2 |
| R4 | sclereids in phloem and cortex | 10 |
| R6 | sclereids in radial rows | 0 |
| R12 | with laticifers, oil ducts or mucilage ducts | 7 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 9 |

# Tiliaceae



**Number of species, worldwide and in Europe**

The cosmopolitan Tiliaceae family includes 50 genera with 450 species. Most of the species grow in the tropics. In Europe, there is one genus (*Tilia*) with 6 species.

**Analyzed species:**

*Tilia amurensis* Rupr.
*Tilia cordata* Miller
*Tilia platyphyllos* Scop.
*Tilia rubra* D.C.
*Tilia tomentosa* Moench

**Analyzed material**

The xylem and phloem of 1 genus with 5 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | 5 | more than 100 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 4 | |
| Mediterranean | 1 | |

**Right:** *Tilia cordata*

*Tilia platyphyllos*

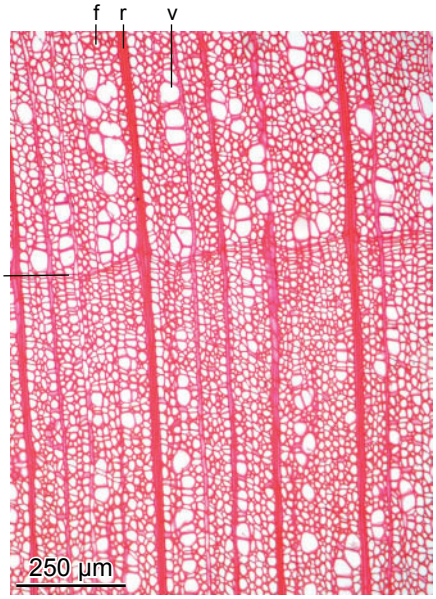
*Tilia cordata*

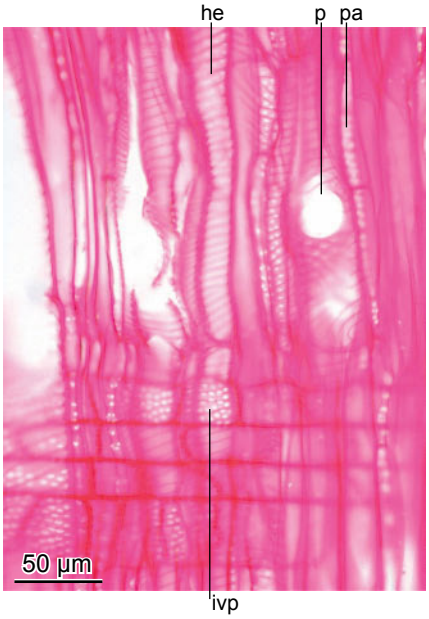
### Characteristics of the xylem

The xylem of the species analyzed cannot be distinguished from each other. Ring boundaries are diffuse- to semi-ring-porous and have distinct rings (**Fig. 1**). Vessels occur in short radial multiples and/or in radial groups (**Fig. 1**). Vessel walls have simple perforations, distinct helical thickenings and intervessel pits are arranged in alternating position (**Fig. 2**). Fibers are mostly thin-walled, but are occasionally thin- to thick-walled (**Fig. 3**). The distribution of axial parenchyma is apotracheal diffuse in aggregates (**Fig. 3**). Rays are normally 2-3-, rarely up to 4-seriate. Rays are larger in slightly bent parts of stems. Rays of all species are either homocellular with procumbent cells or heterocellular with one row of square or upright marginal cells (**Fig. 2**). Crystals are absent.

### Characteristics of the phloem and the cortex

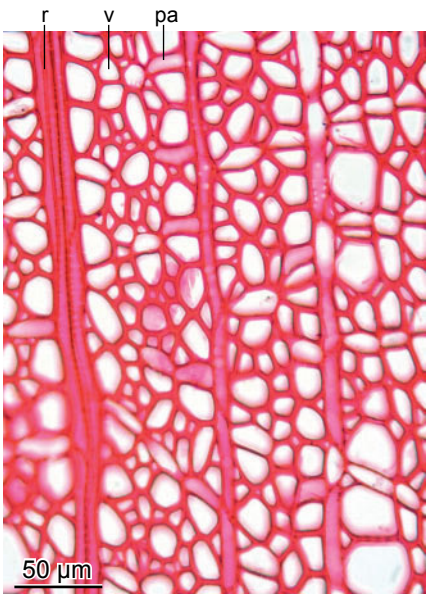
Multi-cellular, tangential, unlignified sieve tube/parenchyma bands alternate with a unicellular band of very thin-walled square parenchyma cells (cork?) and a multicellular band of thick-walled fibers (**Fig. 5**). Ray dilatations are very distinct. Crystal druses occur in the cortex (**Fig. 6**). Some ray cells produce mucilage. Normal and mucilage-producing ray cells are not distinguishable.

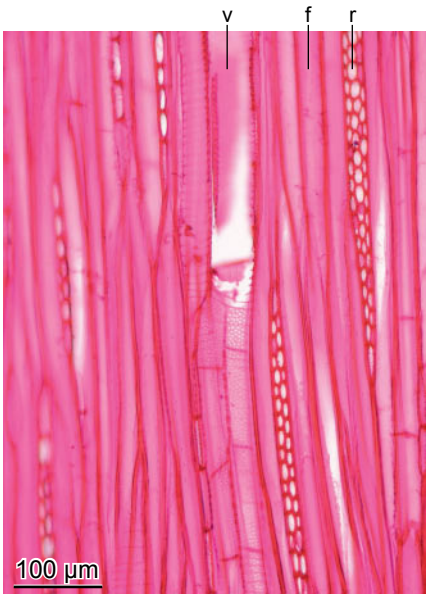



**Left Fig. 1.** Semi-ring-porous xylem with a distinct annual ring boundary. Rays are enlarged at the ring boundary. Stem of a young, 15 m-high tree, oak forest, Mediterranean zone, Pec, Kosovo. *Tilia tomentosa*, transverse section.

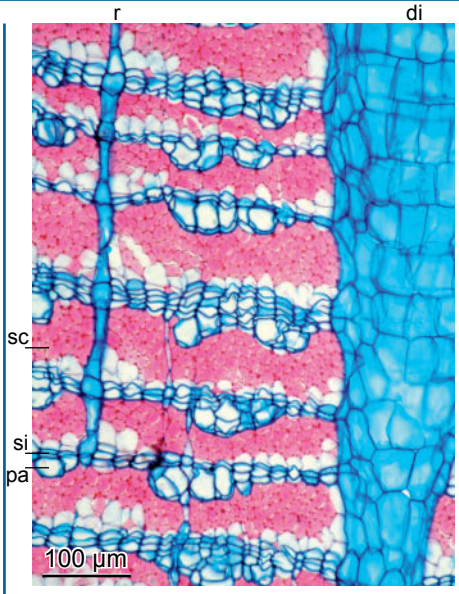
**Right Fig. 2.** Vessels with helical thickenings and simple perforations. The ray is homocellular. Stem of a young, 15 m-high tree, oak forest, Mediterranean zone, Pec, Kosovo. *Tilia tomentosa*, radial section.

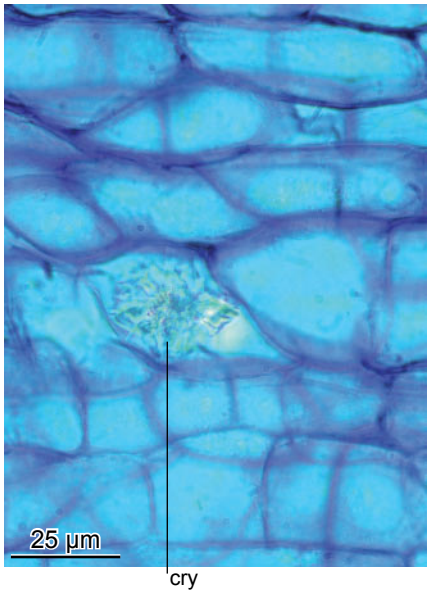



**Left Fig. 3.** Parenchyma is apotracheal in aggregates. Fibers are thin- to thick-walled. Stem of a young, 15 m-high tree, oak forest, Mediterranean zone, Pec, Kosovo. *Tilia tomentosa*, transverse section.

**Right Fig. 4.** 1-3-seriate rays. Stem of an old, 20 m-high tree, maple forest, hill zone, Elburs Mountains, Iran. *Tilia rubra*, tangential section.




**Left Fig. 5.** Phloem with alternating bands of thin-walled, unlignified sieve tube/parenchyma and thick-walled, lignified fiber bands. Stem of a 10 m-high tree, *Tilia cordata* forest, hill zone, Lugano, Ticino, Switzerland. *Tilia cordata*, transverse section.

**Right Fig. 6.** Crystal druse in a parenchyma cell of the cortex. Stem of a 20 m-high tree, beech forest, hill zone, Zürich, Switzerland. *Tilia cordata*, transverse section.

## Discussion in relation to previous studies

Most previous studies have concentrated on tropical Tiliaceae species. The xylem of this genus was subject of many studies (Gregory 1994). Holdheide (1951) described the bark of *Tilia cordata* and *Tilia platyphyllos* in detail. The present study confirms the results of previous authors.

The xylem within the genus *Tilia* is very homogeneous and species cannot be distinguished. The structure of the phloem of *Tilia* is similar to that of many Malvaceae species. This feature brings the Tiliaceae (*Tilia* sp.) close to the Malvaceae family, as grouping has been proposed on the basis of molecular biological studies (Judd et al. 2002).

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **5** |
| 1 | growth rings distinct and recognizable | 5 |
| 4 | semi-ring-porous | 5 |
| 5 | diffuse-porous | 3 |
| 9.1 | vessels in radial multiples of 2-4 common | 4 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 5 |
| 22 | intervessel pits alternate | 5 |
| 36 | helical thickenings present | 5 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 5 |
| 50 | <100 vessels per mm$^2$ in earlywood | 4 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 5 |
| 68 | fibers thin-walled | 5 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 5 |
| 97 | ray width predominantly 1-3 cells | 5 |
| 98 | rays commonly 4-10-seriate | 3 |
| 104 | ray: all cells procumbent (radial section) | 5 |
| 106 | ray: heterocellular with 1 upright cell row (radial section) | 2 |
| R2 | groups of sieve tubes in tangential rows | 1 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R6.1 | sclereids in tangential rows | 1 |
| R8 | with crystal druses | 1 |
| R16 | phellem consists of regular arranged rectangular cells, Rosaceae type | 1 |
| P2 | with laticifers or intercellular canals | 2 |

# Trochodendraceae

**Number of species, worldwide and in Europe**

The Trochodendraceae family includes 1 genus with 1 species in Southeast Asia, Taiwan. No represantives are found in Europe.

**Analyzed material**

The xylem and phloem of the tree *Trochodendron aralioides* is analyzed here. It grows in the hill zone of the temperate climate of Southeast Asia. The material was collected in the Botanical Garden Zürich, Switzerland.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | 1 | 1 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 1 | |

**Analyzed species:**
*Trochodendron aralioides* Sieb et Zucc.

**Right:** *Trochodendron aralioides* (photo: Stützel)

*Trochodendron aralioides*

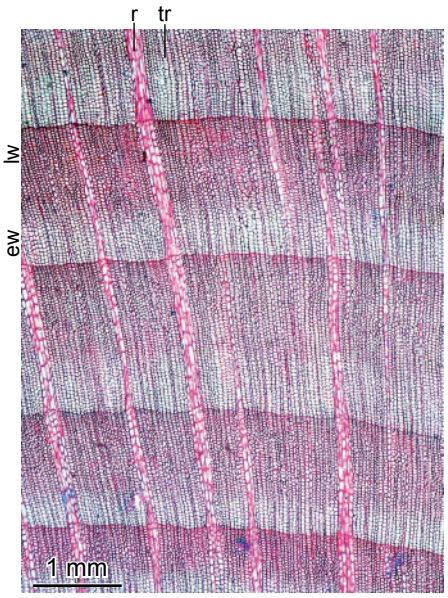
*Trochodendron aralioides* (photo: Stützel)

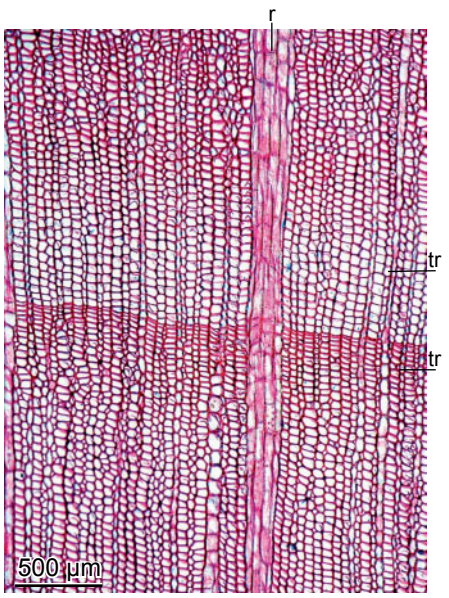
### Characteristics of the xylem

The conifer-like, vesselless wood has distinct rings with distinct earlywood and latewood (**Figs. 1** and **2**). Tracheids are thin- to thick-walled and often contain gelatinous layers (tension wood; **Fig. 3**). Radial cell walls of tracheids have distinctly bordered, round pits in the latewood and scalariform pits in the earlywood (**Fig. 4**). Axial parenchyma is rare or absent. Rays occur in two forms: uniseriate rays with upright cells and larger, heterocellular rays (2-4 square or upright marginal cells) with 3-6 cells width (**Figs. 5** and **6**). Large, simple pits arranged in axial rows occur in cells of uniseriate rays (**Fig. 7**). Crystals are absent.

### Characteristics of the phloem and the cortex

The phloem is simply structured. Parenchyma cells and sieve-tube element cells cannot be distinguished. Large rays are dilated. A belt of thick-walled sclereids is outside the phloem (**Fig. 8**). The cortex and the pith contain isolated, irregularly formed sclereids (**Fig. 9**). Prismatic crystals mainly occur in the belt of sclereids.




**Left Fig. 1.** Conifer-like xylem, consisting of tracheids, with distinct annual rings. Branch with a diameter of 3 cm of a 4 m-high tree, hill zone, cultivated, Botanical Garden Zürich, Switzerland. *Trochodendron aralioides*, transverse section.

**Right Fig. 2.** Vesselless xylem. Rings with distinct earlywood and latewood. For origin see **Fig. 1**. Transverse section.

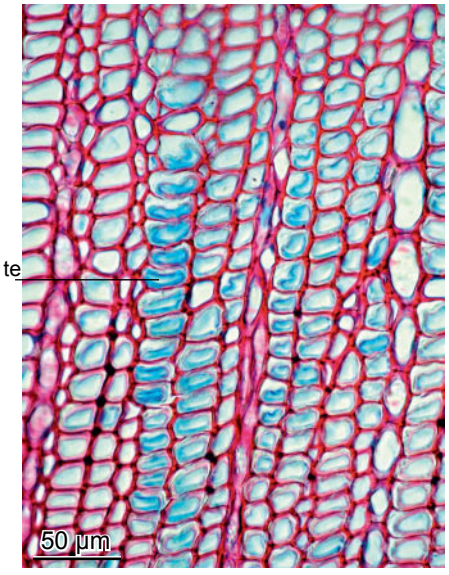



**Fig. 3.** Tension wood. Tracheids with gelatinous layers (blue). For origin see **Fig. 1**. Transverse section.

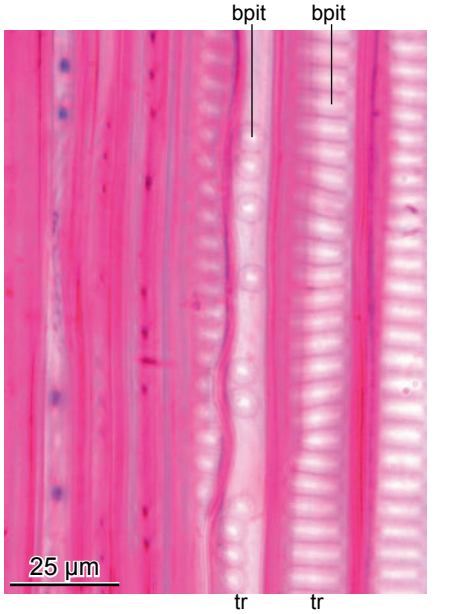
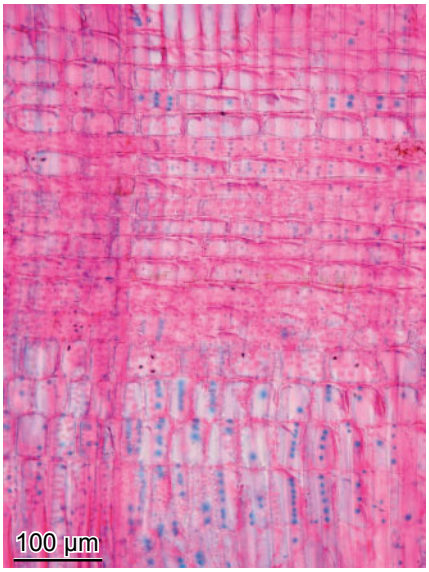
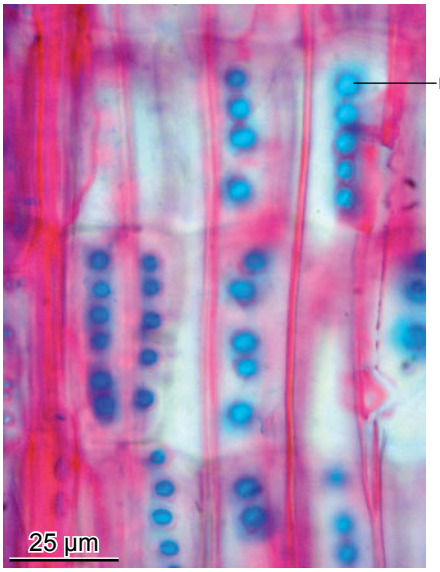



**Fig. 4.** Tracheids with scalariform bordered pits in the earlywood and round pits in the latewood. For origin see **Fig. 1**. Radial section.

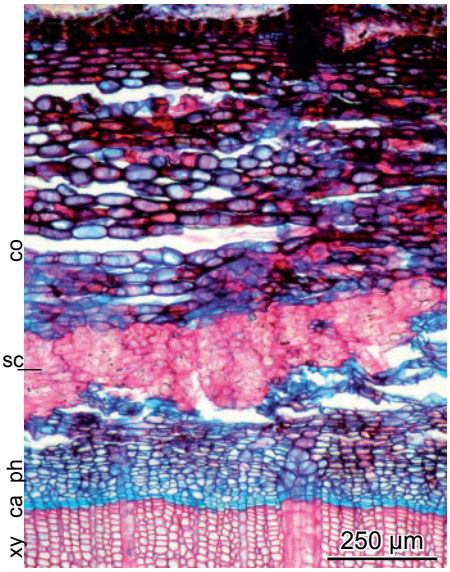
**Fig. 5.** Rays of two types: Uniseriate and multiseriate rays with 3-5 cells in width and partially with sheet cells. For origin see **Fig. 1**. Tangential section.

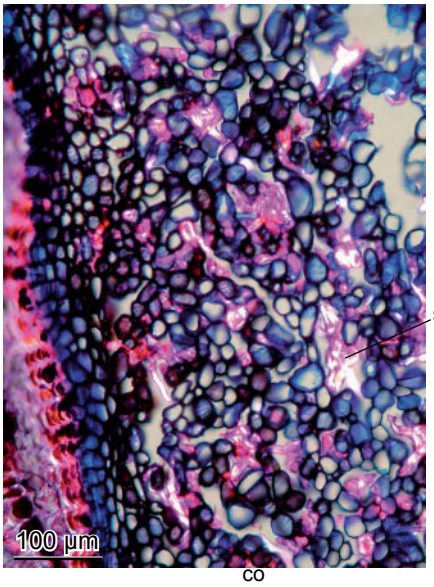



**Left Fig. 6.** Heterocellular rays with 2-4 marginal upright cells. For origin see **Fig. 1**. Radial section.

**Right Fig. 7.** Large, simple pits arranged in axial rows in an uniseriate ray. For origin see **Fig. 1**. Radial section.




**Left Fig. 8.** Simply structured phloem. is A tangential band of thick-walled sclereids is outside the phloem. For origin see **Fig. 1**. Transverse section.

**Right Fig. 9.** Irregular formed, single sclereids arranged in axial rows in the cortex. For origin see **Fig. 1**. Radial section.

## Discussion in relation to previous studies

Gregory (1994) mentions 23 studies in which *Trochodendron* was described. A good description is given by Richter and Dallwitz under *http://www.biologie.uni-hamburg.de/b-online/wood/german/trotrara.htm*. Kuo-Hang et al. (2007) describe tension wood of *Trochodendron*.

The present study confirms all results from earlier studies.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **1** |
| 1 | growth rings distinct and recognizable | 1 |
| 59 | vessels absent or indistinguishable from fibers | 1 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 1 |
| 68 | fibers thin-walled | 1 |
| 69 | fibers thick-walled | 1 |
| 70.2 | tension wood present | 1 |
| 75 | parenchyma absent or unrecognizable | 1 |
| 96 | rays uniseriate | 1 |
| 98 | rays commonly 4-10-seriate | 1 |
| 105 | ray: all cells upright or square | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R7 | with prismatic crystals | 1 |
| R10 | phloem not well structured | 1 |

# Ulmaceae



**Number of species, worldwide and in Europe**

The comopolitan Ulmaceae family includes 6 genera with 40 species. In Europe, there are 3 genera (*Celtis*, *Ulmus*, *Zellkova*) with 10 species.

**Analyzed material**

The xylem and phloem of 3 genera with 6 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | 6 | numerous |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 3 | |
| Mediterranean | 3 | |

**Analyzed species:**

*Celtis australis* L.
*Celtis caucasica* Willd.
*Ulmus glabra* Huds., syn. *scabra*, syn. *montana*
*Ulmus laevis* Pall.
*Ulmus minor* Mill., syn. *campestris*
*Zellkova carpinifolia* Dippl.

*Celtis australis* (photo: Zinnert)

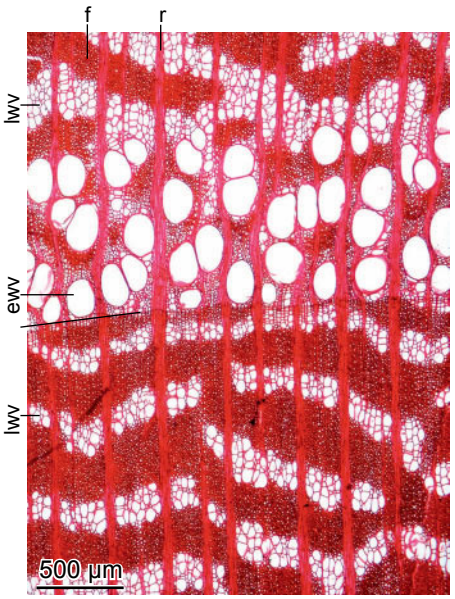
*Ulmus glabra*

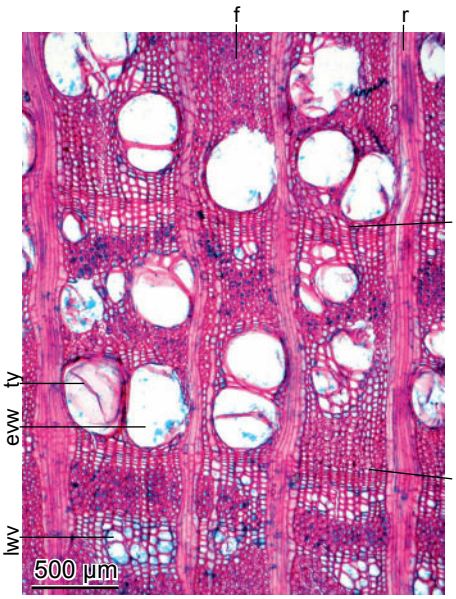
*Ulmus glabra*

### Characteristics of the xylem

Ring boundaries are distinct (**Figs. 1** and **2**). All species analyzed are ring-porous (**Figs. 1** and **2**). Characteristic of all species are the tangential, diagonal or dendritic vessel distribution patterns (**Figs. 1** and **2**). Latewood vessels are arranged in groups. Earlywood vessels with a diameter between 150-250 µm and a vessel density of 100-200/mm$^2$ are characteristic of all species. Vessels of all species have simple perforations. Intervessel pits are round and arranged in alternating position. Helical thickenings occur in all genera (**Fig. 3**). Vessels of most species contain tylosis (**Fig. 4**).

Fibers are thick and thin- to thick-walled (**Figs. 1** and **2**) and have small pits with slit-like apertures. Transitions between both features occur within individuals. The occurrence of tension wood is a specific feature for all species analyzed (**Fig. 5**). Parenchyma is paratracheal and marginal (**Fig. 5**). Rays are 3-7 cells wide in all species (**Fig. 6**) and consist of procumbent cells or are heterocellular, with one to a few rows of square and upright cells. Prismatic crystals are frequent in *Celtis* (**Fig. 7**) and *Zellkova* but are rare or absent in *Ulmus*.




**Left Fig. 1.** Ring-porous xylem with a distinct annual ring boundary. Latewood vessel groups are arranged in tangential patterns. Stem of a 10 m-high tree, riparian, hill zone, Birmensdorf, Zürich, Switzerland. *Ulmus glabra*, transverse section.

**Right Fig. 2.** Ring-porous xylem with a distinct annual ring boundary. Latewood vessels are arranged in tangential patterns (lowest ring). Large vessels contain tylosis. Fibers are arranged in groups and are thick-walled. Stem of a 6 m-high tree, dry hill zone, Botanical Garden Tbilisi, Georgia. *Celtis caucasica*, transverse section.

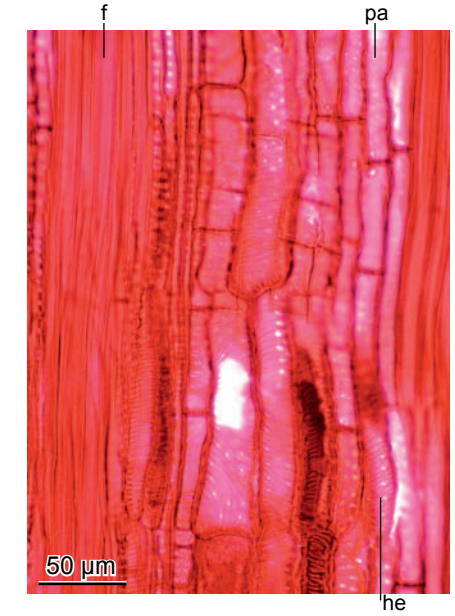



**Fig. 3.** Helical thickenings in small latewood vessels. Stem of a 8 m-high tree, *Quercus pubescens* forest, submediterranean zone, Anduze, Cevennes, France. *Celtis australis*, radial section.

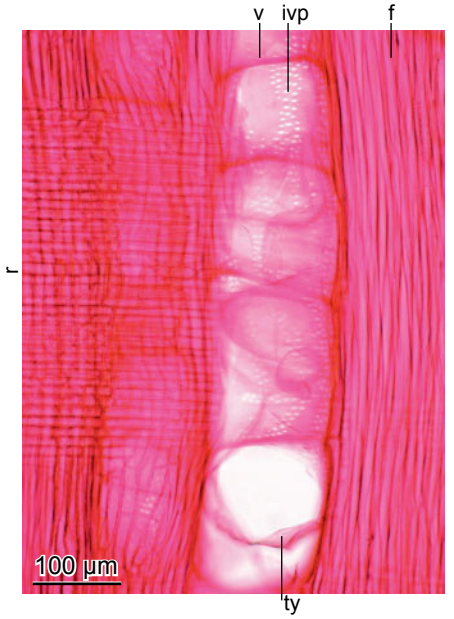



**Fig. 4.** Tylosis in a large earlywood vessel. Stem of a 6 m-high tree, *Quercus pubescens* forest, hill zone, Valtellina, Italy. *Ulmus minor*, radial section.

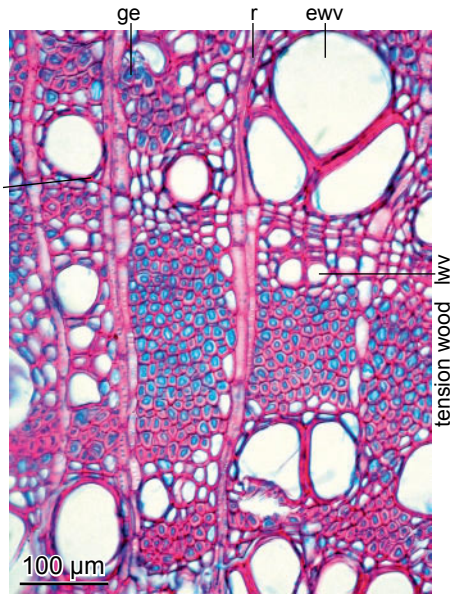
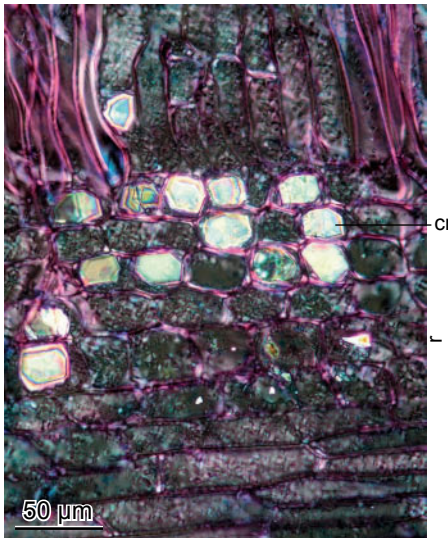



**Fig. 5.** Gelatinous fibers in the latewood (blue; tension wood). Parenchyma is paratracheal and marginal. Twig of a 5 m-high tree, dry hill zone, Botanical Garden Tbilisi, Georgia. *Zellkova carpinifolia*, transverse section.

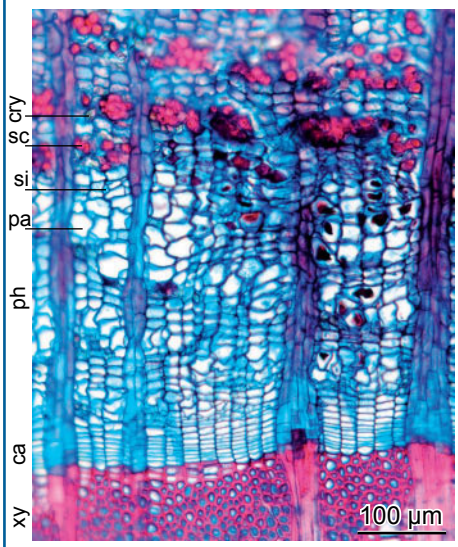


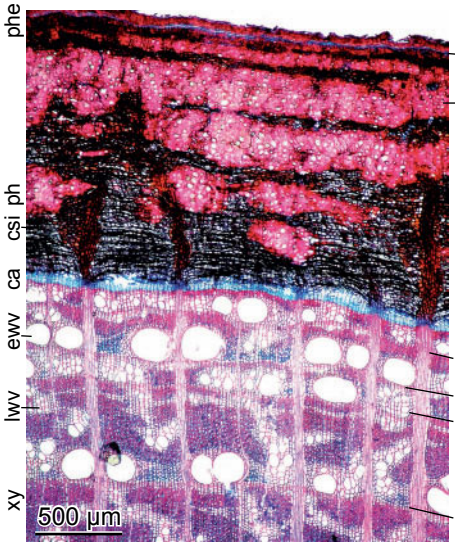

**Left Fig. 6.** Rays, 2-6 cells wide. Stem of a 5 m-high tree, dry hill zone, Botanical Garden Tbilisi, Georgia. *Zellkova carpinifolia*, tangential section.

**Right Fig. 7.** Large prismatic crystals in ray cells. Stem of a 6 m-high tree, dry hill zone, Botanical Garden Tbilisi, Georgia. *Celtis caucasica*, radial section, polarized light.

**Characteristics of the phloem and the cortex**

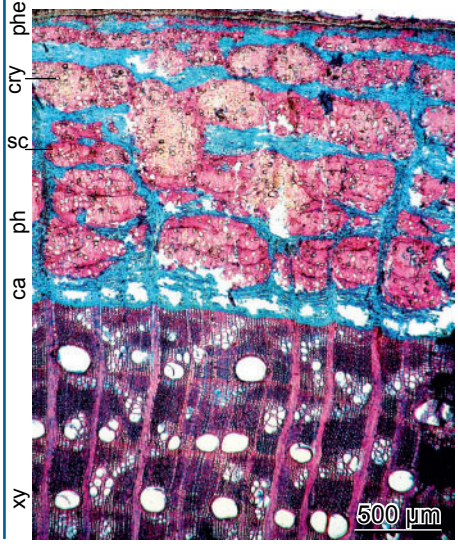
Characteristic of well-grown individuals are the tangentially arranged layers of parenchyma and sieve tubes (**Fig. 8**). Sieve tubes are collapsed in the older phloem (**Fig. 9**). Sclerenchyma occurs in large bands (**Fig. 9**) and in large groups (**Fig. 10**). Large mucilage ducts are specific for *Ulmus* (**Fig. 11**). Large prismatic crystals occur in the axial parenchyma and the sclerenchyma (**Fig. 10**).

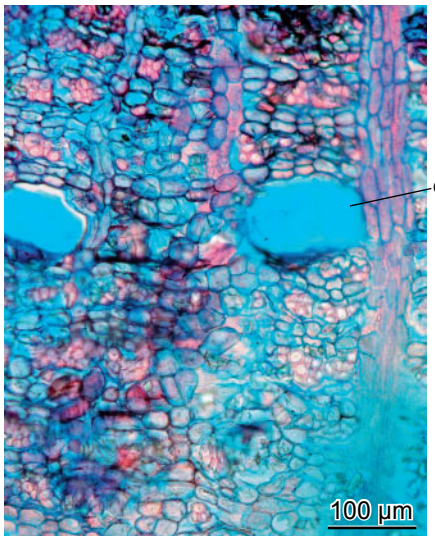



**Left Fig. 8.** Young phloem in the cambial zone. Groups of small sieve tubes and large parenchyma cells alternate tangentially. Sclerotization of parenchyma cells occurs after a few years (red). Stem of a 6 m-high tree, *Quercus pubescens* forest, hill zone, Valtellina, Italy. *Ulmus minor*, transverse section.

**Right Fig. 9.** Large, tangential, dense bands of sclerotized cells are located outside of the unlignified phloem. Sieve tubes are collapsed. Stem of an 8 m-high tree, *Quercus pubescens* forest, hill zone, Trento, Trentino, Italy. *Celtis australis*, transverse section.




**Left Fig. 10.** Large, tangentially arranged groups of sclerenchyma cells with many prismatic crystals. Stem of a 6 m-high tree, dry hill zone, Botanical Garden Tbilisi, Georgia. *Celtis caucasica*, transverse section.

**Right Fig. 11.** Phloem with large mucilage ducts. Stem of a 6 m-high tree, *Quercus pubescens* forest, hill zone, Valtellina, Italy. *Ulmus minor*, transverse section.

**Discussion in relation to previous studies**

The xylem of all genera analyzed here have been characterized before. Gregory (1994) mentions 142 references concerning 12 genera. Holdheide (1951) described the bark of *Celtis australis* and *Ulmus glabra* in detail. Newly described here is the bark of 3 species.

The few specimens analyzed here do not allow differentiation of species within genera. The presence of mucilage ducts in the phloem differentiates *Ulmus* from *Celtis* and *Zellkova*.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **6** |
| 1 | growth rings distinct and recognizable | 6 |
| 3 | ring-porous | 6 |
| 6 | vessels in intra-annual tangential rows | 6 |
| 7 | vessels in diagonal and/or radial patterns | 4 |
| 8 | vessels in dendritic patterns | 1 |
| 13 | vessels with simple perforation plates | 6 |
| 22 | intervessel pits alternate | 6 |
| 36 | helical thickenings present | 6 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 6 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 5 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 2 |
| 56 | tylosis with thin walls | 6 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 6 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 6 |
| 69 | fibers thick-walled | 5 |
| 70 | fibers thin- to thick-walled | 5 |
| 70.2 | tension wood present | 6 |
| 79 | parenchyma paratracheal | 6 |
| 86 | axial parenchyma in narrow bands or lines, *Quercus* type | 1 |
| 89 | parenchyma marginal | 4 |
| 98 | rays commonly 4-10-seriate | 6 |
| 104 | ray: all cells procumbent (radial section) | 4 |
| 105 | ray: all cells upright or square | 1 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 136 | prismatic crystals present | 3 |
| R2 | groups of sieve tubes in tangential rows | 5 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 5 |
| R6.1 | sclereids in tangential rows | 3 |
| R6.2 | sclereids in tangentially arranged groups, *Rhamnus* type | 2 |
| R7 | with prismatic crystals | 5 |
| R12 | with laticifers, oil ducts or mucilage ducts | 2 |
| R16 | phellem consists of regularly arranged rectangular cells, Rosaceae type | 4 |

# Urticaceae



**Number of species, worldwide and in Europe**

The cosmopolitean Urticaceae family includes 40 genera with 900 species. In Europe, there are 2 endemic genera (*Parietaria*, *Urtica*) with 15 species. *Gesnouinia arborea* is endemic to Macaronesia.

**Analyzed material**

The xylem and phloem of 4 genera with 10 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | | numerous |
| Nanophanerophytes (0.5-4 m) | 1 | |
| Hemicryptophytes | 8 | |
| Therophytes | 1 | |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 3 | |
| Mediterranean | 3 | |
| Subtropical | 4 | |

**Analyzed species:**

*Forsskaolea angustifolia* Rtz.
*Forsskaolea tenacissima* L.
*Gesnouinia arborea* L'Hér.
*Parietaria debilis* Forster f.
*Parietaria judaica* L.
*Parietaria officinalis* L.
*Urtica dioica* L.
*Urtica membranacea* Poir.
*Urtica morifolia* Poir.
*Urtica urens* L.

**Right:** *Urtica dioica*

*Gesnouiana arborea*

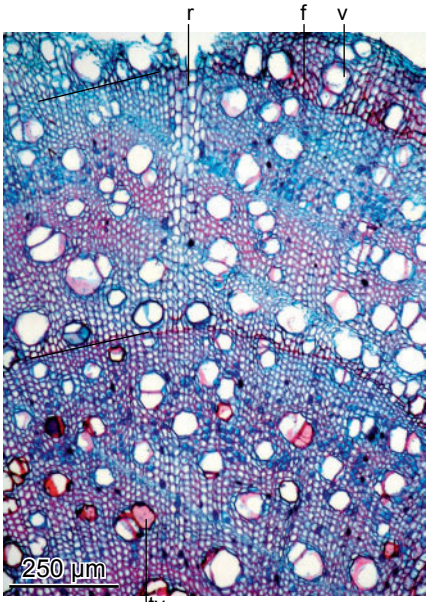
*Urtica dioica*

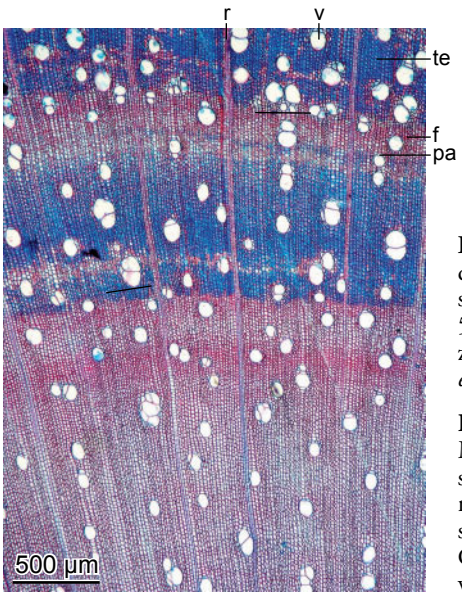
### Characteristics of the xylem

Rings can be distinct (**Figs. 1** and **3**) or indistinct in *Gesnouinia* (**Fig. 2**) and *Urtica*. Rings represent growth zones in *Gesnouinia* (**Fig. 2**). Common to all species are vessels with tylosis (**Figs. 3** and **5**). Vessels have a diameter of >50 µm and are arranged solitary (**Fig. 1**) or in radial multiples or small groups (**Figs. 2** and **3**). Perforations are simple and intervessel pits are round in alternating position and at least partially lateral elongated with rounded edges (scalariform; **Fig. 4**). Fibers are thin- to thick-walled (**Figs. 1**, **3** and **5**) and have small and slit-like pits. Tension wood occurs in all genera (**Figs. 2** and **5**). Parenchyma is paratracheal (**Fig. 5**) and marginal in *Forsskaolea* (**Fig. 3**). Unique for the family is the distribution of parenchyma in *Urtica*. All species have large groups (**Fig. 6**) or tangential layers (**Fig. 7**) of thin-walled, unlignified parenchyma cells. Rays are absent in *Parietaria debilis* and in the vascular bundles of *Urtica* (**Fig. 8**). Large, 4-12-seriate rays exist in *Forsskaolea*, *Gesnouinia*, *Parietaria judaica* and *P. officinalis* (**Fig. 9**). Rays have always sheet cells (**Fig. 9**). The occurrence of permanent vascular bundles is characteristic of *Urtica* (**Fig. 10**). They are laterally separated by large parenchyma zones. Rays are homocellular consisting of square and upright cells (**Fig. 11**) in all species. Crystal druses occur in *Parietaria officinalis* and in all *Urtica* species. Vessel groups in the pith were observed in *Parietaria debilis* and in *Urtica urens* (**Fig. 12**).

### Characteristics of the phloem and the cortex

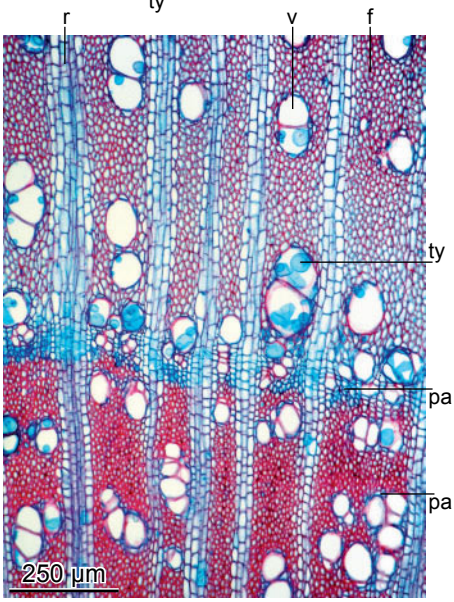
All species have small, often indistinct groups of sieve tubes in the phloem (**Figs. 13-15**) and crystal druses in rays and axial parenchyma cells of the phloem. Dilatations occur occasionally (**Fig. 14**). Isolated sclerenchyma cells are arranged in radial strips (**Fig. 13**), in tangential layers (**Fig. 15**) or irregularly. Mucilage plugs were observed only in the cortex of *Parietaria debilis* (**Fig. 16**).

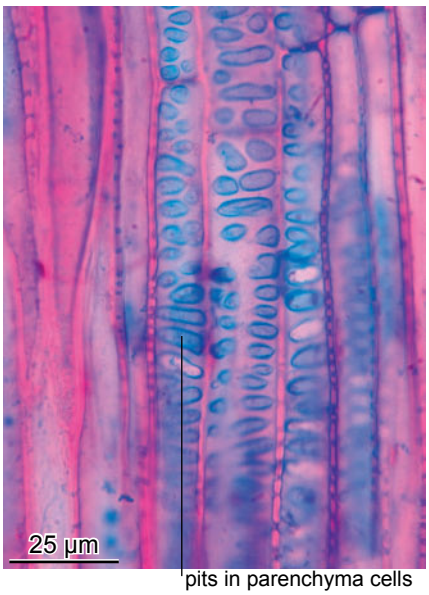



**Left Fig. 1.** Diffuse-porous xylem with distinct annual rings. Vessels are arranged solitary or in small groups. Root collar of a 50 cm-high hemicryptophyte, riparian, hill zone, Güssing, Burgenland, Austria. *Parietaria officinalis*, transverse section.

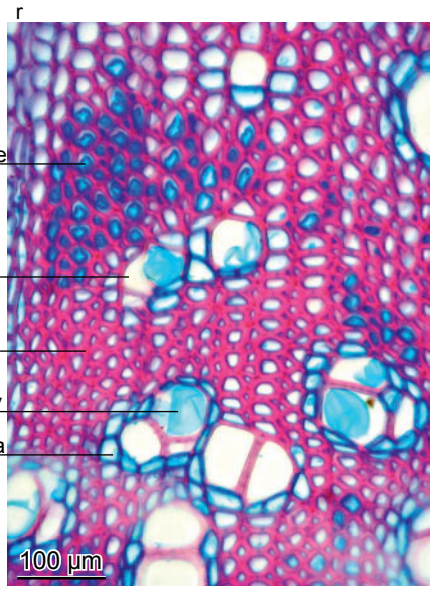
**Right Fig. 2.** Xylem with growth zones. Most vessels are arranged solitary or in short radial multiples. The blue zone represents tension wood. Stem of a 1 m-high shrub, *Laurus* forest, subtropical, Tenerife, Canary Islands. *Gesnouinia arborea*, transverse section.

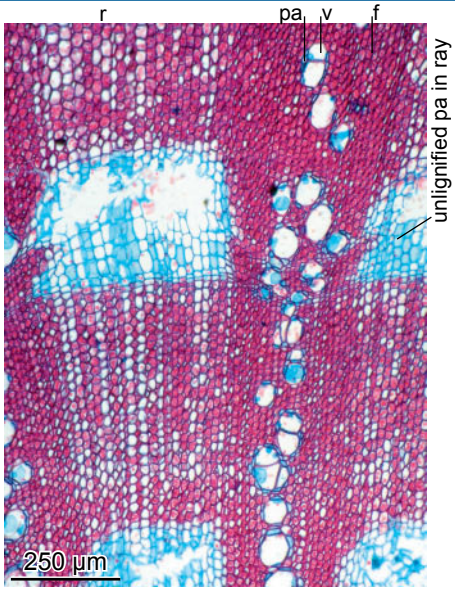



**Left Fig. 3.** Semi-ring-porous xylem. Vessels contain thin-walled, unlignified tylosis. The ring boundary is marked by unlignified fibers and marginal parenchyma cells. Root collar of a 40 cm-high hemicryptophyte, ruderal site, thermophile zone, subtropical, Tenerife, Canary Islands. *Forsskaolea angustifolia*, transverse section.

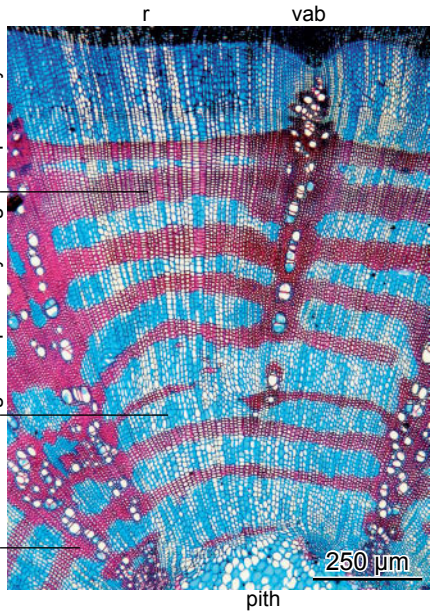
**Right Fig. 4.** Large, laterally elongated pits located in axial parenchyma cells. Root collar of a 50 cm-high hemicryptophyte, riparian, hill zone, Güssing, Burgenland, Austria. *Parietaria officinalis*, radial section.

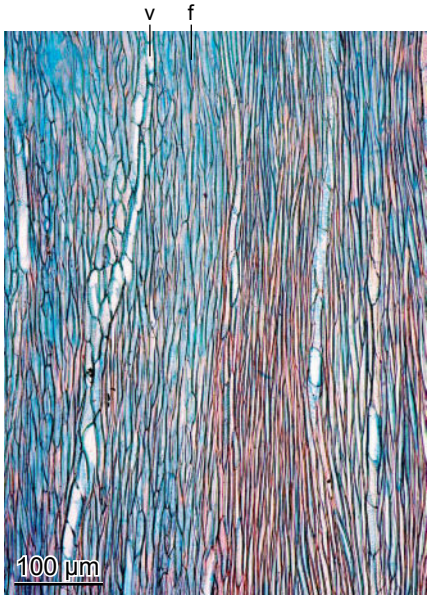



**Left Fig. 5.** Vessels with tylosis are surrounded by paratracheal parenchyma. A group of fibers contains gelatinous fibers (tension wood). Rhizome of a 70 cm-high hemicryptophyte, ruderal site, Mediterranean, Santa Pau, Catalonia, Spain. *Urtica dioica*, transverse section.

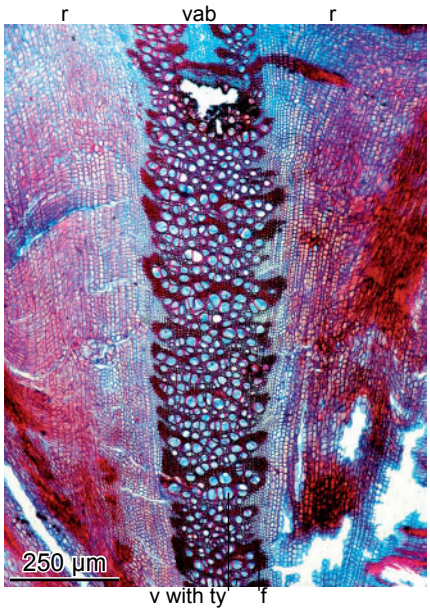
**Right Fig. 6.** Groups of thin-walled, unlignified parenchyma cells located between vascular bundles. Rhizome of a 70 cm-high hemicryptophyte, ruderal site, thermophile zone, Tenerife, Canary Islands. *Urtica membranacea*, transverse section.



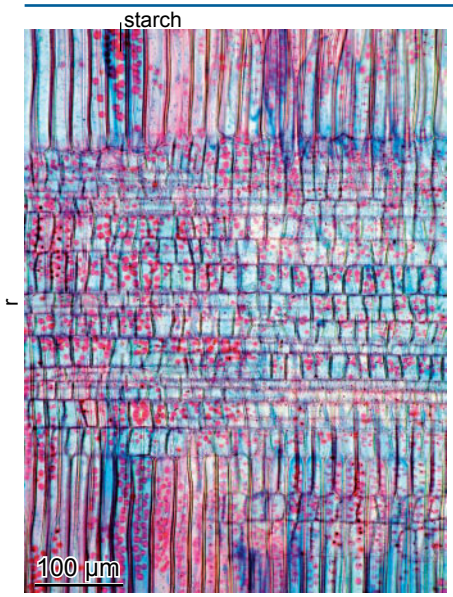

**Left Fig. 7.** Layers of thin-walled, unlignified parenchyma cells between vascular bundles. Rhizome of a 70 cm-high hemicryptophyte, ruderal site, subalpine zone, Akanthiske, Georgia. *Urtica dioica*, transverse section.

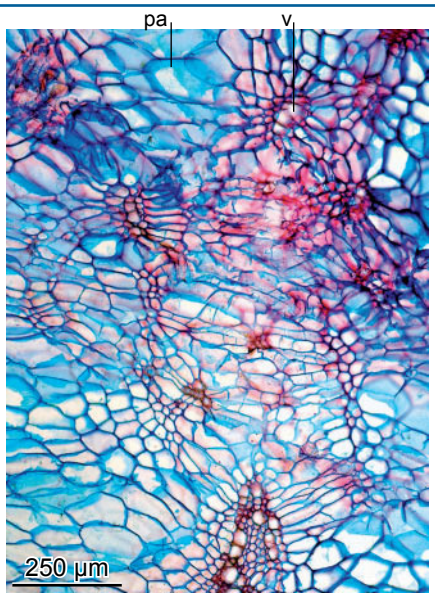
**Right Fig. 8.** Rayless xylem. Root collar of a 40 cm-high therophyte, ruderal site, thermophile zone, Tenerife, Canary Islands. *Parietaria debilis*, tangential section.




**Left Fig. 9.** Large rays (10- to >10-seriate) with sheet cells. Root collar of a 50 cm-high hemicryptophyte, riparian, hill zone, Güssing, Burgenland, Austria. *Parietaria officinalis*, tangential section.

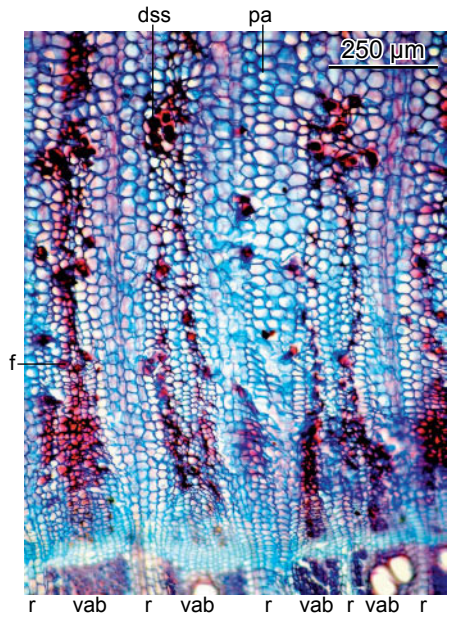
**Right Fig. 10.** Indistinct annual rings in the xylem of a perennial, multi-annual vascular bundle located between parenchymatic tissues. Rhizome of a 50 cm-high hemicryptophyte, ruderal site, subalpine zone, Gasterntal, Switzerland. *Urtica dioica*, transverse section.

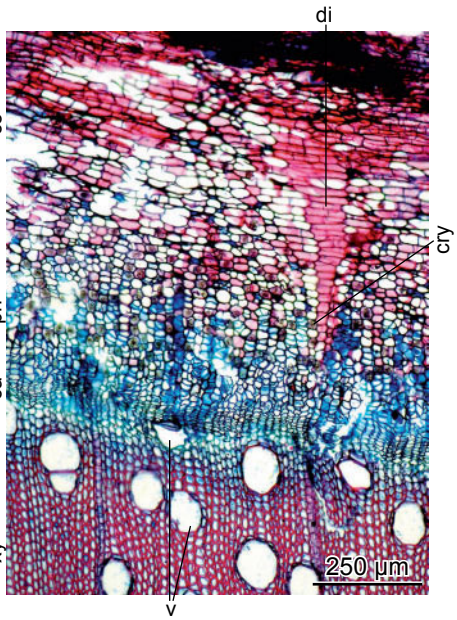



**Left Fig. 11.** Almost homocellular ray consisting of square and upright cells. Only one to two rows of cells are procumbent. Stem of a 1 m-high shrub, *Laurus* forest, subtropical, Tenerife, Canary Islands. *Gesnouinia arborea*, radial section.

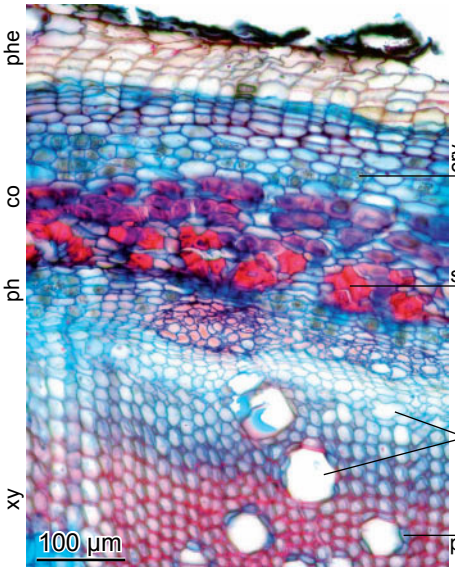
**Right Fig. 12.** Irregular groups of vessels between thin-walled large parenchyma cells in the pith. Rhizome of a 70 cm-high hemicryptophyte, ruderal site, coastal zone, Motril, Andalusia, Spain. *Urtica urens*, transverse section.

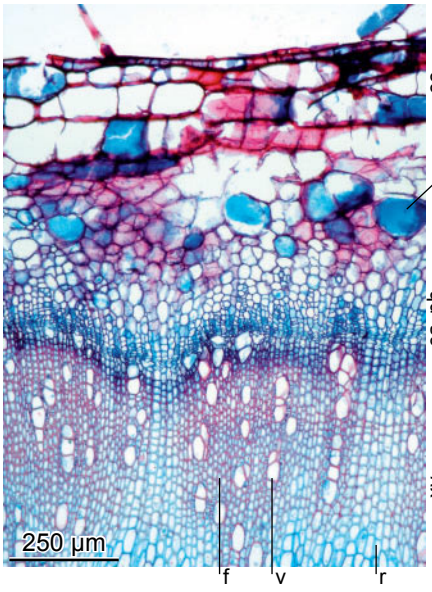



**Left Fig. 13.** Phloem with radial strips of sclerenchymatic cells located between thin-walled, unlignified parenchyma cells. Root collar of a 40 cm-high hemicryptiphyte, ruderal site, arid zone, Sabah, Libya. *Forsskaolea tenacissima*, transverse section.

**Right Fig. 14.** Uniform phloem containing a dilatation. Stem of a 1 m-high shrub, *Laurus* forest, subtropical, Tenerife, Canary Islands. *Gesnouinia arborea*, transverse section.




**Left Fig. 15.** Phloem with discontinuous layers of sclerenchyma cells. The phellem consists of rectangular, uniform, radially oriented cork cells. Rhizome of a 50 cm-high hemicryptophyte, ruderal site, thermophile zone, subtropical, Gomera, Canary Islands. *Urtica morifolia*, transverse section.

**Right Fig. 16.** Large mucilage plugs in the cortex. The phloem contains groups of small sieve tubes. Root collar of a 40 cm-high therophyte, ruderal site, thermophile zone, Tenerife, Canary Islands. *Parietaria debilis*, transverse section.

**Discussion in relation to previous studies**

Metcalfe and Chalk (1957) briefly characterized *Urtica dioica*.

The family is divided into two major groups:

The *Forsskaolea/Parietaria/Gesnouinia* group represents typical stems with a continuous vessel-fiber-ray xylem.

The *Urtica* group has permanent vascular bundles and tangential bands of thin-walled parenchyma. This type of xylem is unique for Angiospermae.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **10** |
| 1 | growth rings distinct and recognizable | 5 |
| 2 | growth rings absent | 4 |
| 2.1 | only one ring | 1 |
| 4 | semi-ring-porous | 1 |
| 5 | diffuse-porous | 5 |
| 6 | vessels in intra-annual tangential rows | 3 |
| 9 | vessels predominantly solitary | 3 |
| 9.1 | vessels in radial multiples of 2-4 common | 8 |
| 10 | vessels in radial multiples of 4 or more common | 2 |
| 11 | vessels predominantly in clusters | 1 |
| 13 | vessels with simple perforation plates | 10 |
| 20 | intervessel pits scalariform | 10 |
| 22 | intervessel pits alternate | 10 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 10 |
| 50 | <100 vessels per $mm^2$ in earlywood | 7 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 2 |
| 56 | tylosis with thin walls | 10 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 10 |
| 68 | fibers thin-walled | 2 |
| 70 | fibers thin- to thick-walled | 9 |
| 70.2 | tension wood present | 6 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 1 |
| 79 | parenchyma paratracheal | 10 |
| 85 | axial parenchyma bands more than three cells wide, *Ficus/Urtica* type | 4 |
| 89 | parenchyma marginal | 2 |
| 97 | ray width predominantly 1-3 cells | 3 |
| 98 | rays commonly 4-10-seriate | 5 |
| 99 | rays commonly >10-seriate | 5 |
| 99.1 | vascular bundle form remaining | 4 |
| 100.1 | rays confluent with ground tissue | 1 |
| 105 | ray: all cells upright or square | 10 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 1 |
| 110 | rays with sheet cells (tangential section) | 4 |
| 117 | rayless | 5 |
| 144 | druses present | 5 |
| R1 | groups of sieve tubes present | 10 |
| R3 | distinct ray dilatations | 3 |
| R4 | sclereids in phloem and cortex | 5 |
| R8 | with crystal druses | 10 |
| P1 | with medullary phloem or vascular bundles | 2 |

# Violaceae



**Number of species, worldwide and in Europe**

The comopolitan Violacea family includes 22 genera with 950 species. Most of them are herbaceous. In Europe, there is one genus (*Viola*) with 92 species. 4 species are endemic on the Canary Islands.

**Analyzed material**

The xylem and phloem of 2 genera with 17 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | | 11 genera |
| Nanophanerophytes (0.5-4 m) | | 1 species |
| Woody chamaephytes | 2 | |
| Hemicryptophytes and geophytes | 15 | |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 4 | |
| Hill and mountain | 10 | |
| Mediterranean | 1 | |
| Subtropical | 2 | |

**Analyzed species:**

*Hybanthus communis* Taub
*Viola arborescens* L.
*Viola biflora* L.
*Viola calcarata* L.
*Viola canadensis* L.
*Viola canina* L.
*Viola chamissoniana* Ging.
*Viola elatior* Fries
*Viola hirta* L.
*Viola labradorica* Schrank
*Viola mirabilis* L.
*Viola odorata* L.
*Viola palustris* L.
*Viola reichenbachiana* Jordan ex Boreau
*Viola rupestris* F.W. Schmidt
*Viola suavis* Bieb.
*Viola tricolor* L.

*Viola tricolor*

*Viola biflora*

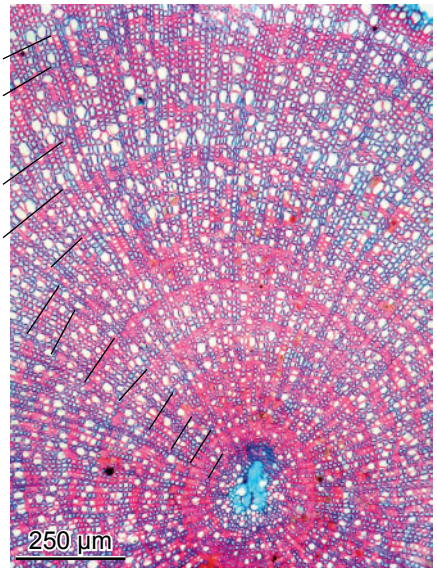
*Viola reichenbachiana* (photo: Zinnert)

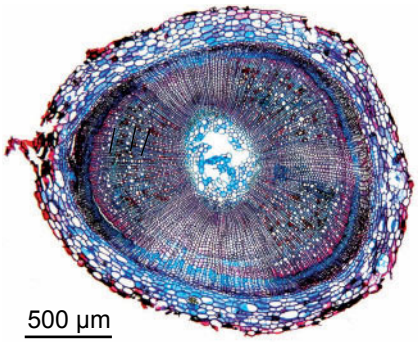
**Characteristics of the xylem**

Annual rings are present in most species (**Figs. 1-3** and **17**). They are indistinct in the subtropical species *Hybanthus communis* (**Fig. 5**) and in the small plants *V. palustris* (**Fig. 4**) and *Viola biflora* of the temperate zone. Rings are indistinct in the rhizome of *Viola calcarata* (**Fig. 6**), which grows 10-20 cm below the soil surface. Ring boundaries are marked by semi-ring-porosity (**Figs. 3** and **7**) and by flat, thick-walled fibers in the latewood (**Figs. 1** and **17**). Vessels are arranged mostly solitary (**Figs. 6** and **8**) or in short radial rows (**Fig. 5**). The earlywood vessel diameter of the majority of species is less than 20 µm. Vessel density varies mostly from 150-300/mm$^2$. Vessels contain exclusively simple perforations (**Fig. 9**). Intervessel pits are usually fairly large (2.5-3.5 µm), in alternating position (**Fig. 9**). They are distinctly scalariform in the rhizome of *Viola calcarata* (**Fig. 10**). 5 out of 19 species have thick-walled vessels (3-4 µm; **Figs. 8** and **13**).

Fibers vary from thin-walled to thin- to thick-walled. It is usually difficult to distinguish fibers from parenchyma cells in the transverse section (**Figs. 7** and **8**) because fiber cell walls are often unlignified. Septate fibers were observed in 2 of 19 species (**Fig. 11**). *Hybanthus communis* contains distinct tension wood (**Fig. 12**).

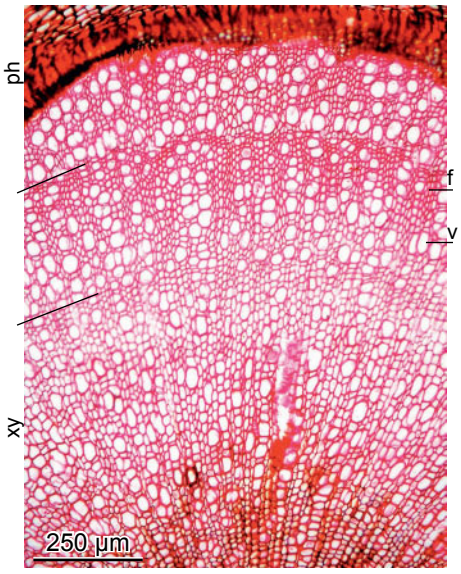
Parenchyma is pervasive in *Viola calcarata* (**Fig. 13**) but is absent or rare in most species. Rays within the vessel/fiber zones are absent in all *Viola* species (**Fig. 14**). Very large rays occur between vascular bundles in a few species (**Figs. 2** and **15**). Rays are uniseriate homocellular with upright cells in *Hybanthus communis* (**Fig. 16**). Crystals are absent in the xylem of all species.

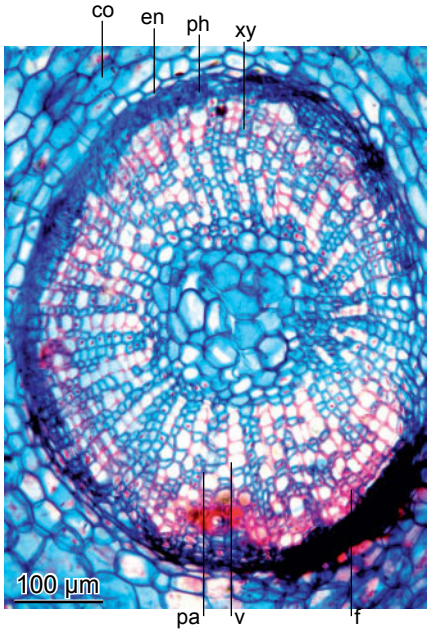



**Left Fig. 1.** Distinct rings of a semi-ring-porous xylem. Stem of a 40 cm-long prostrate chamaephyte, north-facing slope, Mediterranean climate, Andalusia, Spain. *Viola arborescens*, transverse section.

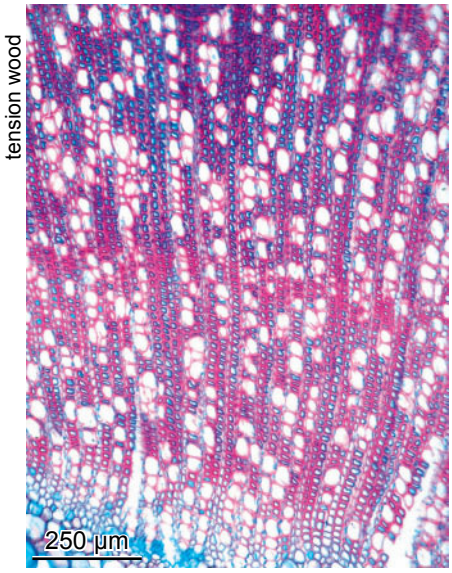
**Right Fig. 2.** Distinct rings of a semi-ring-porous xylem. Between large vascular bundles there are large vessel-free zones. Rhizome of a 5 cm-high hemicryptophyte, beech forest, hill zone, Birmensdorf, Zürich, Switzerland. *Viola reichenbachiana*, transverse section.

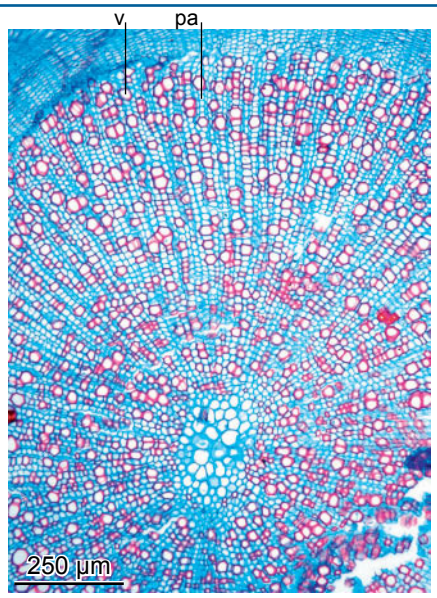



**Left Fig. 3.** Distinct rings of a semi-ring-porous xylem. The first ring is very large. Polar root of a 10 cm-high biannual herb, field, hill zone, Val Stura, Lombardy, Italy. *Viola tricolor*, transverse section.

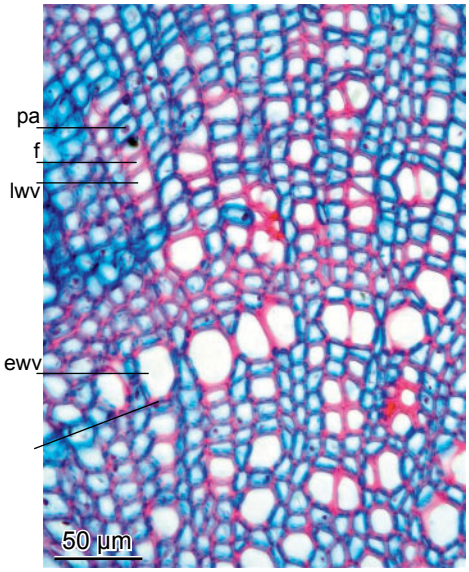
**Right Fig. 4.** Rings are absent. Vessels have almost the same diameter as fibers. Rhizome of a 5 cm-high hemicryptophyte, wet meadow, hill zone, Arcegno, Ticino, Switzerland. *Viola palustris*, transverse section.

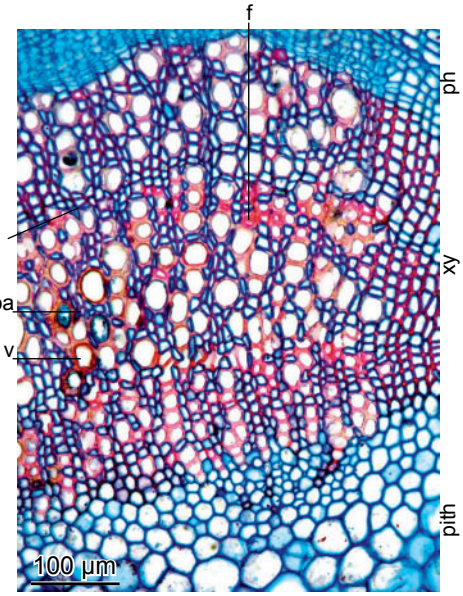



**Left Fig. 5.** Absent rings. Thick-walled vessels are arranged in radial multiples. Stem of a 50 cm-high upright dwarf shrub, greenhouse, Botanical Garden Zürich, Switzerland. *Hybanthus communis*, transverse section.

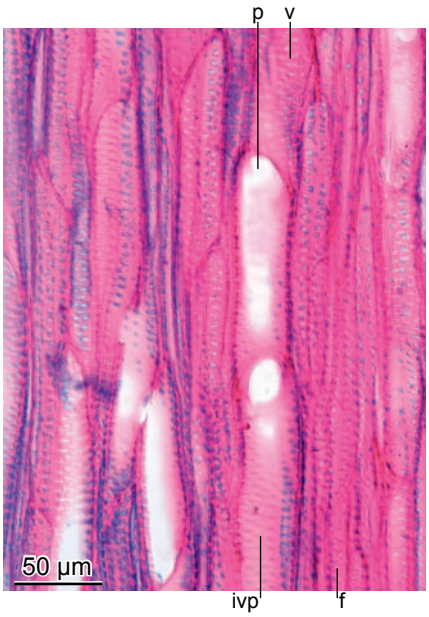
**Right Fig. 6.** Indistinct rings. Xylem with solitary, vessels which are embedded in pervasive parenchyma. Rhizome of a 5 cm-high hemicryptophyte, 20 cm below the surface, meadow, alpine zone, Grand St. Bernhard, France. *Viola calcarata*, transverse section.



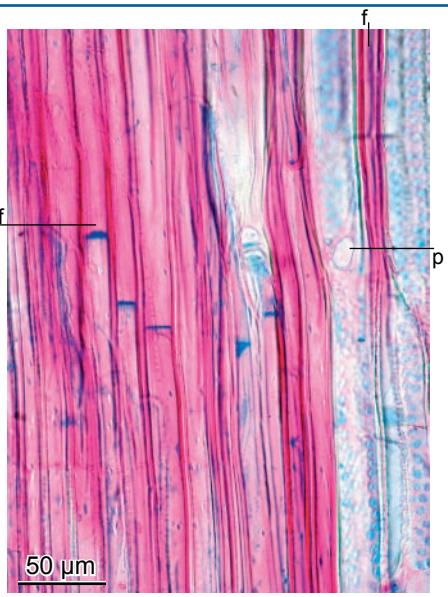

**Left Fig. 7.** Semi-ring-porous xylem. Vessels in the latewood have almost the same diameter as fibers. Rhizome of a 5 cm-high hemicryptophyte, meadow, hill zone, Losone, Ticino, Switzerland. *Viola elatior*, transverse section.

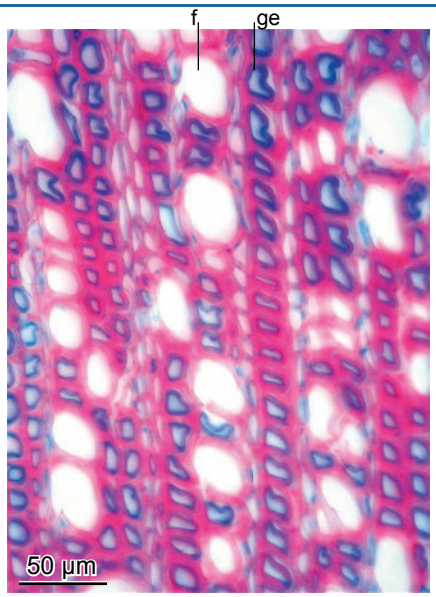
**Right Fig. 8.** Thick-walled solitary vessels are surrounded by unlignified fibers or parenchyma cells. They cannot be distinguished in the transverse section. Rhizome of a 15 cm-high hemicryptophyte, hedge, hill zone, Lucenec, Slovakia. *Viola mirabilis*, transverse section.



**Left Fig. 9.** A vessel with a simple perforation is surrounded by fibers with large pits. Rhizome of a 15 cm-high hemicryptophyte, hedge, hill zone, Lucenec, Slovakia. *Viola mirabilis*, radial section.

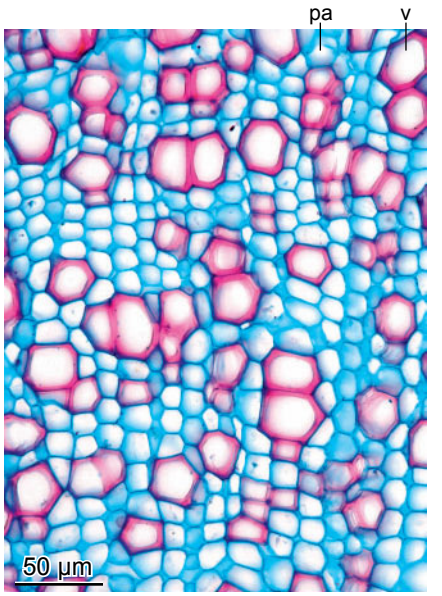
**Right Fig. 10.** Vessels with simple perforations and scalariform intervessel pits. Rhizome of a 5 cm-high hemicryptophyte, 10 cm below the surface, meadow, alpine zone, Grand St. Bernhard, France. *Viola calcarata*, radial section.

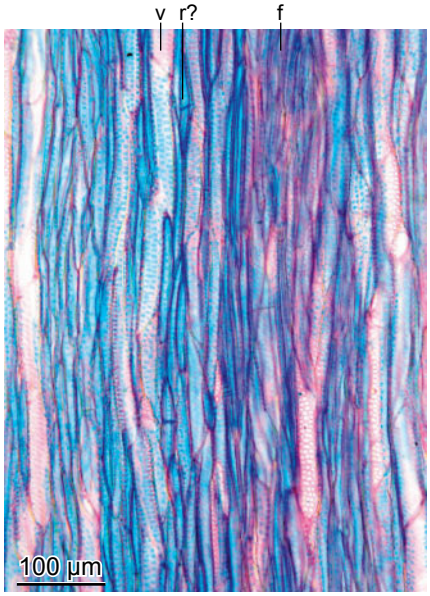



**Left Fig. 11.** Septate fibers with unlignified transverse walls. Stem of a 50 cm-high upright dwarf shrub, greenhouse, Botanical Garden Zürich, Switzerland. *Hybanthus communis*, radial section.

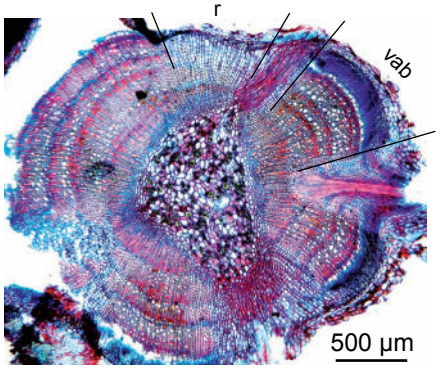
**Right Fig. 12.** Tension wood with gelatinous fibers. Stem of a 50 cm-high upright dwarf shrub, greenhouse, Botanical Garden Zürich, Switzerland. *Hybanthus communis*, transverse section.

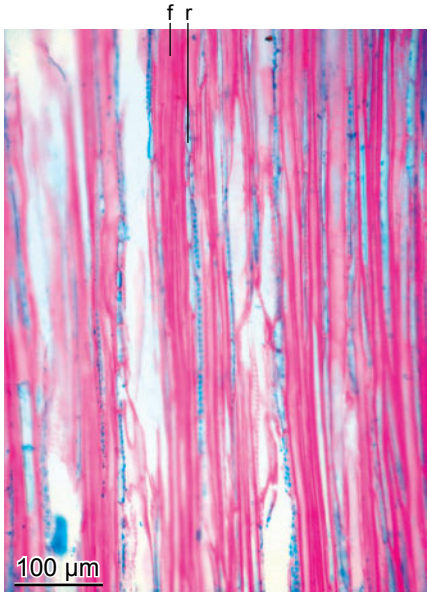



**Left Fig. 13.** Thick-walled vessels surrounded by pervasive parenchyma. Rhizome of a 5 cm-high hemicryptophyte, 10 cm below the surface, meadow, alpine zone, Grand St. Bernhard, France. *Viola calcarata*, transverse section.

**Right Fig. 14.** Rayless xylem. Some cells can be interpreted as ray cells with extremely upright forms. Polar root of a 10 cm-high biannual herb, field, hill zone, Val Stura, Lombardy, Italy. *Viola tricolor*, tangential section.




**Left Fig. 15.** Large vessel-free zones located between large vascular bundles. Distinct rings of a semi-ring-porous xylem. Rhizome of a 5 cm-high hemicryptophyte, dry meadow, Dorenaz, Valais, Switzerland. *Viola odorata*, transverse section.

**Right Fig. 16.** Xylem with very narrow, uniseriate rays. Stem of a 50 cm-high upright dwarf shrub, greenhouse, Botanical Garden Zürich, Switzerland. *Hybanthus communis*, tangential section.

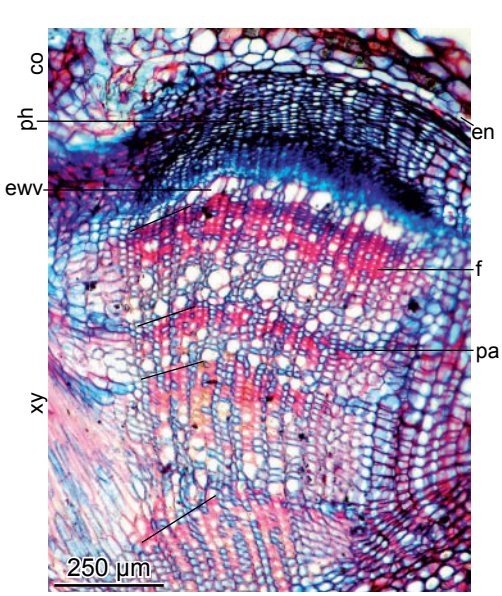
### Characteristics of the phloem and the cortex

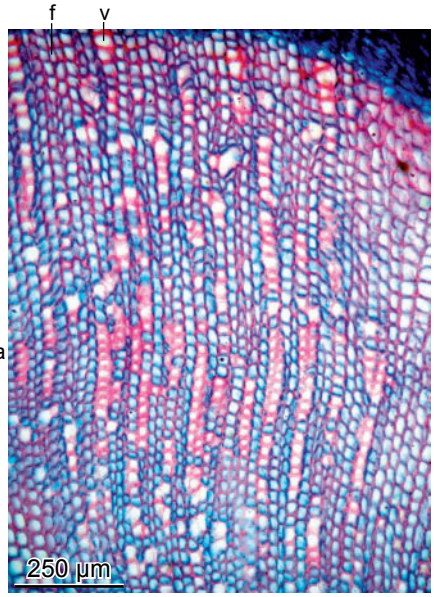
The phloem is uniform in all species (**Figs. 19** and **20**). Parenchyma cells and sieve tubes cannot to be distinguished. Sclerechyma cells and dilatations are absent. *Viola arborescens* has an extremely well developed phellem, *V. biflora* and *V. palustris* both have a very large cortex (**Figs. 20** and **21**). In the material analyzed crystal druses are present in 10 of the 19 species. Prismatic crystals occur in *Hybanthus communis*.

### Ecological trends and relations to life forms

Ring distinctness differentiates the subtropical and tropical species from those found in the temperate and Mediterranean zone. Climate modifies ring distinctness within one species. Rings are distinct and semi-ring-porous in temperate species (**Figs. 17**) and indistinct in subtropical species (**Fig. 18**).

The anatomical structure of rhizomes and stems near the soil surface is homogeneous in most species. A very large cortex and the presence of extremely small vessels separate *Viola biflora* and *V. palustris* from most other species. Uniserate rays separate *Hybanthus communis* from all *Viola species*.




**Left Fig. 17.** Plant growing in a distinctly seasonal climate. The xylem is semi-ring-porous and has distinct rings. Rhizome of a 5 cm-high hemicryptophyte, dry meadow, Dorenaz, Valais, Switzerland. *Viola odorata*, transverse section.

**Right Fig. 18.** Plant growing in a subtropical climate. Rings are absent. Rhizome of a 5 cm-high hemicryptophyte, 10 cm below the surface, ruderal, succulent zone, Canary Islands. *Viola odorata*, transverse section.

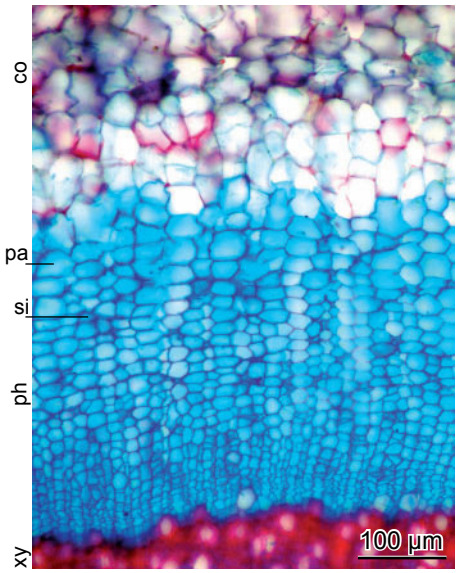



**Fig. 19.** Uniform phloem. Sieve tubes stain darker than parenchyma cells. The phellem is extremely thick. Stem of a 40 cm-long prostrate chamaephyte, north-facing slope, Mediterranean climate, Andalusia, Spain. *Viola arborescens*, transverse section.

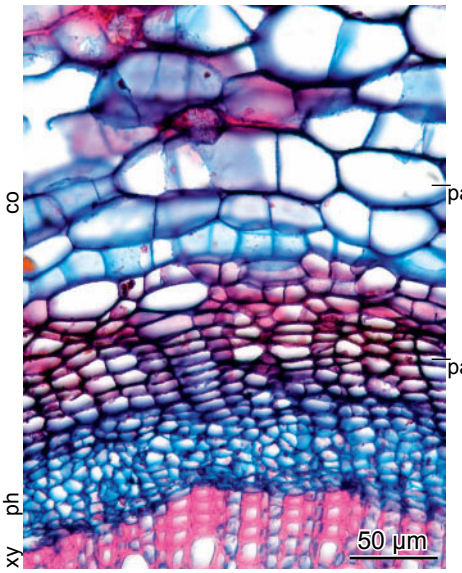



**Fig. 20.** Uniform phloem. Sieve tubes and parenchyma cells cannot be distinguished. The large external cortex cells function as water-storing cells. Rhizome of a 5 cm-high hemicryptophyte, beech forest, hill zone, Birmensdorf, Zürich, Switzerland. *Viola reichenbachiana*, transverse section.

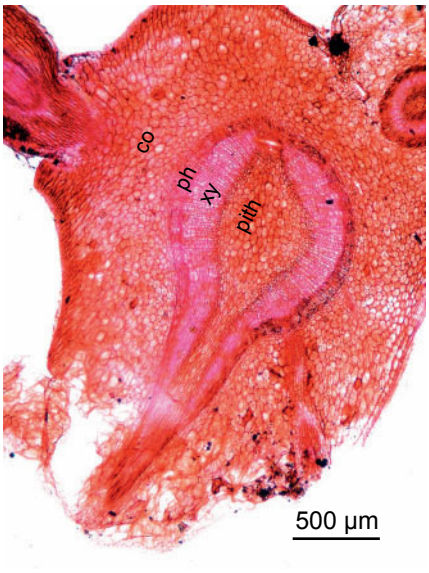



**Fig. 21.** Plant with a small xylem and a large cortex. There is no phellem. Rhizome of a 5 cm-high herb, wet meadow, subalpine zone, Davos, Switzerland. *Viola biflora*, transverse section.

**Discussion in relation to previous studies**

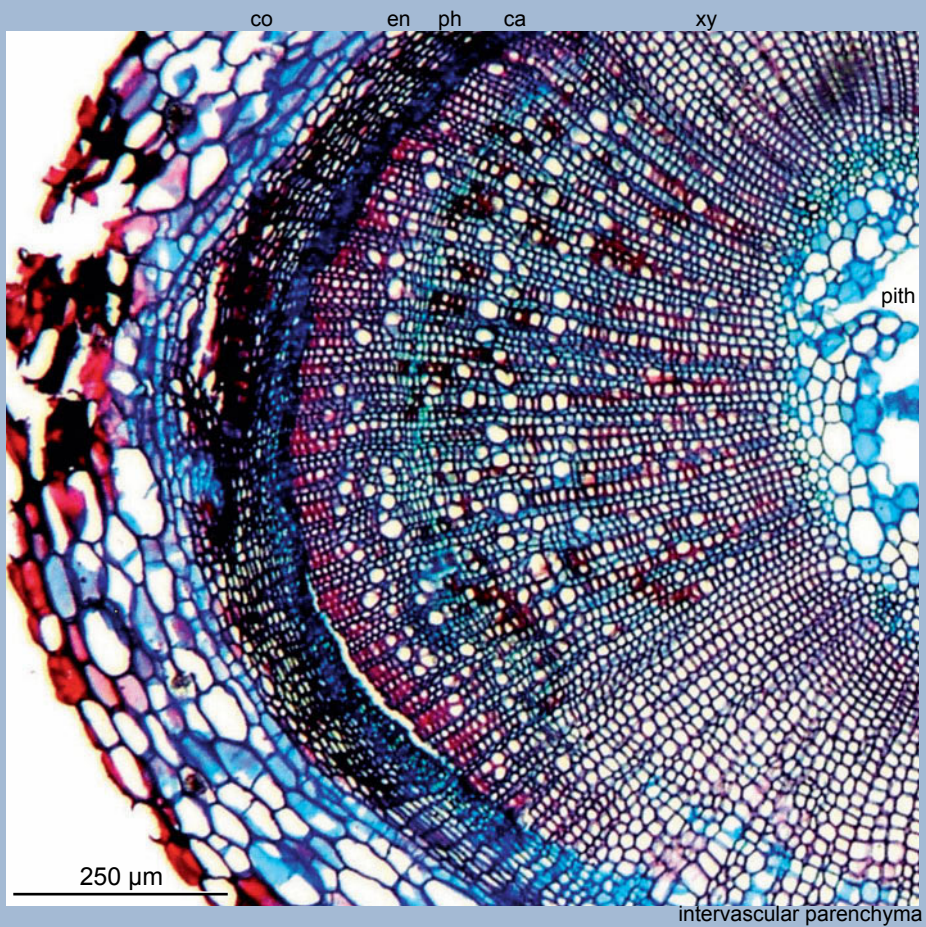
Gregory (1994) mentioned 27 articles about 12 Violaceae genera. Most of them characterized the xylem of tropical tree species. Carlquist (2001 and 1977) described little *Viola* shrub species from Hawaii (*V. chamissoniana* and *Hybanthus communis*). There is a large amount of homogeneity within the genus *Viola* (Hawaii, Canary Islands, Western Europe).

The genus *Viola* is differentiated from all other genera by the absence of rays. In contrast to most genera the genus *Viola* has exclusively simple perforations. Rare parenchyma and fairly small vessels seem to be characteristic of most genera.

**Present features in relation to the number of analyzed specimens**

| IAWA code | | frequency |
|---|---|---|
| | **Total number of specimens (17 species, *Viola odorata* from temperate and subtropical region)** | **18** |
| 1 | growth rings distinct and recognizable | 14 |
| 2 | growth rings absent | 4 |
| 4 | semi-ring-porous | 10 |
| 5 | diffuse-porous | 11 |
| 9 | vessels predominantly solitary | 15 |
| 9.1 | vessels in radial multiples of 2-4 common | 3 |
| 10 | vessels in radial multiples of 4 or more common | 1 |
| 13 | vessels with simple perforation plates | 18 |
| 20 | intervessel pits scalariform | 1 |
| 22 | intervessel pits alternate | 17 |
| 39.1 | vessel cell-wall thickness >2 µm | 5 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 14 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 7 |
| 41 | earlywood vessels: tangential diameter 50-100 µm | 1 |
| 50.1 | 100-200 vessels per mm² in earlywood | 17 |
| 60.1 | fibers absent | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 2 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 16 |
| 65 | septate fibers present | 2 |
| 68 | fibers thin-walled | 4 |
| 69 | fibers thick-walled | 1 |
| 70 | fibers thin- to thick-walled | 14 |
| 70.2 | tension wood present | 1 |
| 75 | parenchyma absent or unrecognizable | 14 |
| 79 | parenchyma paratracheal | 1 |
| 79.1 | parenchyma pervasive | 3 |
| 96 | rays uniseriate | 1 |
| 99.1 | vascular-bundle form remaining | 2 |
| 99.2 | stem lobed | 7 |
| 105 | ray: all cells upright or square | 1 |
| 117 | rayless | 17 |
| R4 | sclereids in phloem and cortex | 1 |
| R7 | with prismatic crystals | 1 |
| R8 | with crystal druses | 10 |
| R10 | phloem not well structured | 17 |

Detailed illustration of **Fig. 2**: *Viola reichenbachiana*, transverse section.



# Vitaceae

**Number of species, worldwide and in Europe**

The Vitaceae family includes 12 genera with 700 species. They are widely distributed, especially common in northern temperate regions. Major genera are *Cissus* (300 species), *Vitis* (60 species), *Ampelopsis* (20 species) and *Parthenocissus* (15 species). Endemic in Europe is one species (*Vitis vinifera*).

**Analyzed material**

The xylem and phloem of 5 Vitaceae species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Liana | 5 | ca. 5 |
| **Plants analyzed from different vegetation zones:** | | |
| Hill and mountain | 4 | |
| Arid | 1 | |

**Analyzed species:**

*Ampelopsis brevipedunculata* (Maxim.) Trautv.
*Cissus quadrangularis* L.
*Parthenocissus inserta* Fritsch.
*Parthenocissus tricuspidata* Planch.
*Vitis vinifera* L.

*Vitis vinifera* (photo: Massad)

*Cissus quadrangularis* (photo: Zinnert)

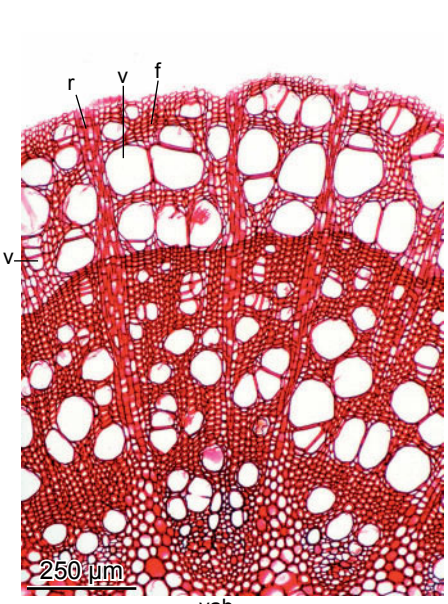
*Vitis vinifera* (photo: Zinnert)

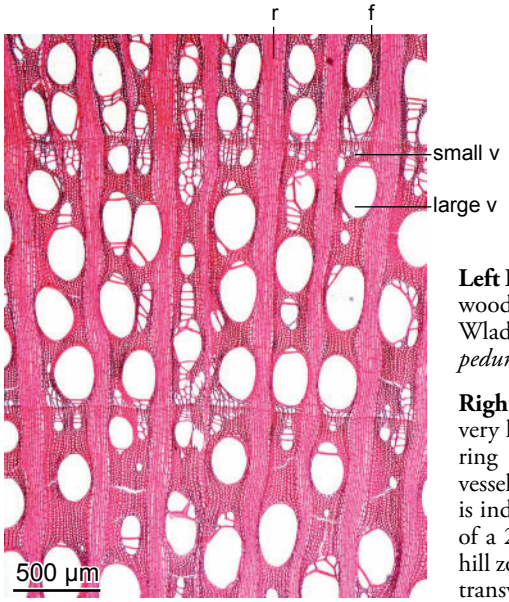
*Parthenocissus tricuspidata*

**Characteristics of the xylem**

Rings are distinct in the majority of analyzed species because most species are principally ring-porous (**Figs. 1-3**). The earlywood with large vessels is often not separated from the next ring by a latewood which causes ring-distinctness to disappear (**Fig. 4**). Therefore, some specimens look diffuse-porous with extremely large vessels. Annual rings are absent in *Cissus quadrangularis* (**Fig. 5**). Vessels are solitary (**Fig. 1**) or form dense clusters (**Fig. 4**). Characteristic of the liana-like Vitaceae is vessel dimorphism. The large earlywood vessels have a diameter up to 250 µm (**Figs. 1-5**). Radially arranged latewood vessels are much smaller (40-50 µm; **Figs. 2** and **3**). Earlywood vessel density is high in fast growing *Parthenocissus* specimes (100-200/mm$^2$; **Fig. 4**) and is low in *Vitis vinifera* specimens (<50/mm$^2$; **Figs. 2** and **3**). Vessels contain exclusively simple perforations (**Fig. 6**). Intervessel pits are predominantly scalariform (**Fig. 6**) or round in opposite position. All species produce small, thin-walled, unlignified tylosis in earlywood vessels (**Figs. 4** and **8**).

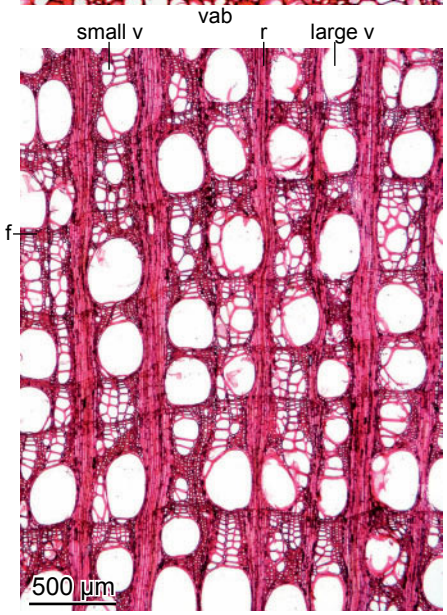
The radial walls of fibers of all species are perforated by very small slit-like or round pits (<2 µm). Septate fibers (**Fig. 7**) were found only in *Ampelopsis brevipedunculata*, *Parthenocissus tricuspidata* and *Vitis vinifera*. Fibers are mostly thin- to thick-walled. Normally fairly thick-walled, lignified parenchyma surrounds the large earlywood vessels (scanty paratracheal; **Fig. 9**). *Cissus quadrangularis* has an additional confluent parenchyma consisting of thin-walled, unlignified cells (**Fig. 5**). All species have large rays (4-10 cells in width; **Fig. 10**). Most ray cells are procumbent and square and occur in variying numbers at the axial ends. In *Cissus quadrangularis* rays can be interpreted as parenchyma between vascular bundles (**Figs. 5** and **9**). Ray height exceeds 5 mm in *Ampelopsis* and *Vitis*. The presence of horizontally oriented scalariform ray-intervessel pits is rather special. Crystals occur in all species in prismatic form (*Ampelopsis*, *Parthenocissus*; **Fig. 11**), as druses (*Cissus quadrangularis*) or as rhaphides (*Cissus quadrangularis* and *Vitis vinifera*; **Fig. 12**).

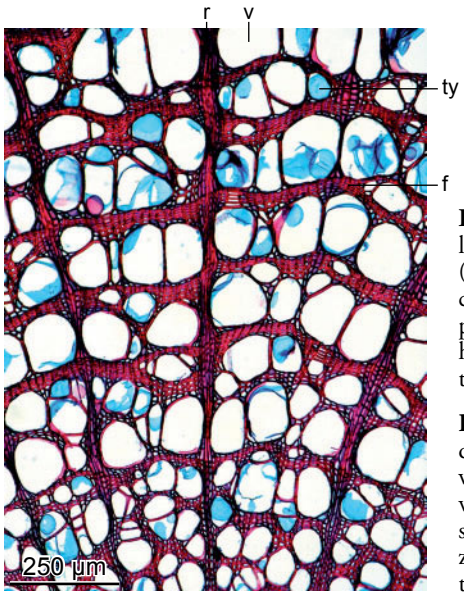



**Left Fig. 1.** Distinct ring of the ring-porous wood. Stem of a liana, Botanical Garden Wladivostok, Russia. *Ampelopsis brevipedunculata*, transverse section.

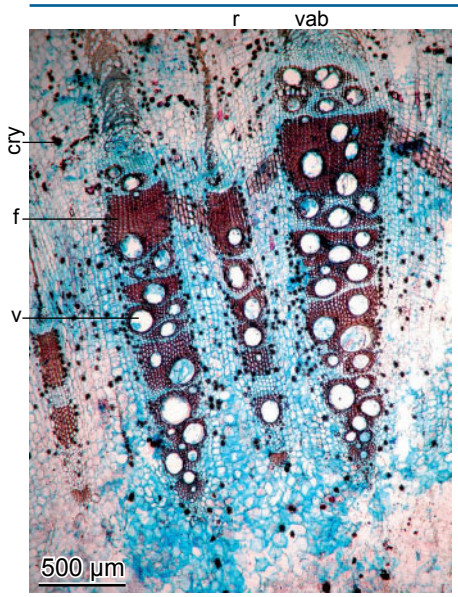
**Right Fig. 2.** Ring-porous wood with a very large earlywood zone in a wide annual ring (1.7 mm). The diameter of the large vessels exceeds 200 µm. The ring boundary is indicated by some radial flat fibers. Stem of a 25 m-long liana, abandoned vineyard, hill zone, Ticino, Switzerland. *Vitis vinifera*, transverse section.

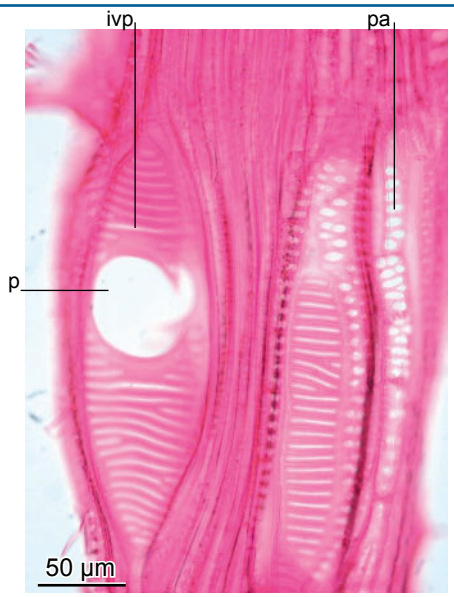



**Left Fig. 3.** Ring-porous wood with a very large earlywood zone in small annual rings (0.25 mm). The ring boundaries are indicated by some radial flat fibers. Stem of a pollarded, 200-year-old plant in an espalier, hill zone, Valais, Switzerland. *Vitis vinifera*, transverse section.

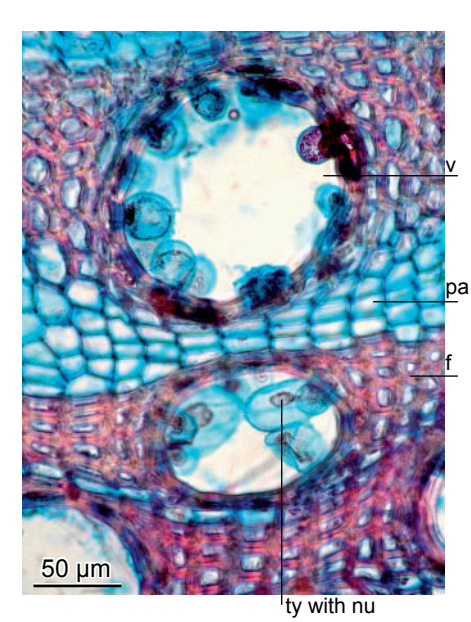
**Right Fig. 4.** Ring-porous wood with indistinct rings. The latewood zone is thick-walled, irregular and partially wedged. The vessels contain thin-walled unlignified tylosis. Stem of a liana, cultivated on a wall, hill zone, Switzerland. *Parthenocissus inserta*, transverse section.



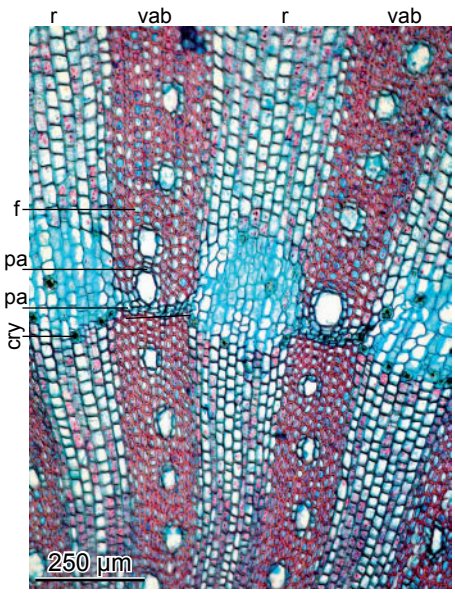

**Left Fig. 5.** Single vascular bundles are separated from large rays by thin-walled, unlignified cells. The tangential zones do not represent annual rings. Many crystal druses (black dots) are in the parenchymatic tissues. Stem of a succulent liana, on a rock, subtropical climate, Dhofar, Oman. *Cissus quadrangularis*, transverse section.

**Right Fig. 6.** Vessel with a simple perforation and scalariform intervessel pits. Stem of a 25 m-long liana, abandoned vineyard, hill zone, Ticino, Switzerland. *Parthenocissus inserta*, radial section.



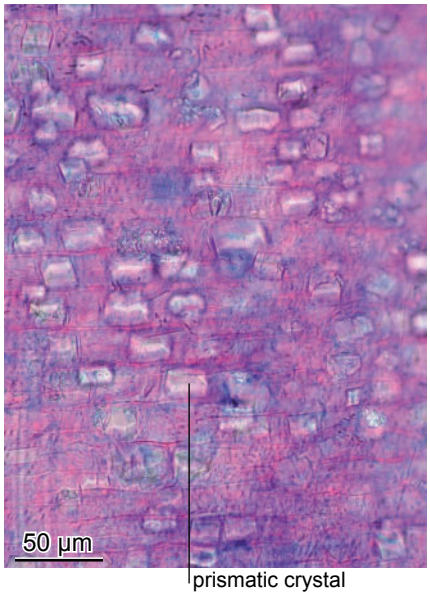

**Left Fig. 7.** Septate fibers. Stem of a pollarded 200-year-old plant in an espalier, hill zone, Valais, Switzerland. *Vitis vinifera*, radial section.

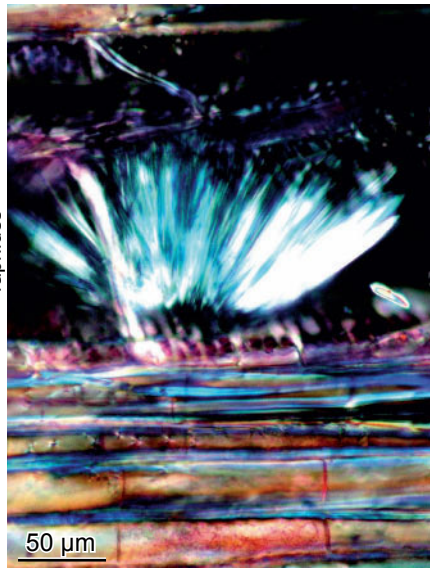
**Right Fig. 8.** Thick-walled parenchyma cells produced tylosis (inside vessels with nuclei). Between the vessels is a parenchyma tissue consisting of thin-walled, unlignified cells. Stem of a succulent liana, on a rock, subtropical climate, Dhofar, Oman. *Cissus quadrangularis*, transverse section.



**Left Fig. 9.** Very large rays between radial vessel/fiber strips. The vessels are surrounded by thin-walled, paratracheal parenchyma. Root, succulent liana, on a rock, subtropical climate, Dhofar, Oman. *Cissus quadrangularis*, transverse section.

**Right Fig. 10.** Very high and large homogeneous rays. The lateral cells are slightly larger than the central cells. Stem of a 25 m-long liana, abandoned vineyard, hill zone, Ticino, Switzerland. *Vitis vinifera*, tangential section.




**Left Fig. 11.** Ray cells with prismatic crystals. Stem of a liana, cultivated, hill zone, Switzerland. *Parthenocissus tricuspidata*, radial section.

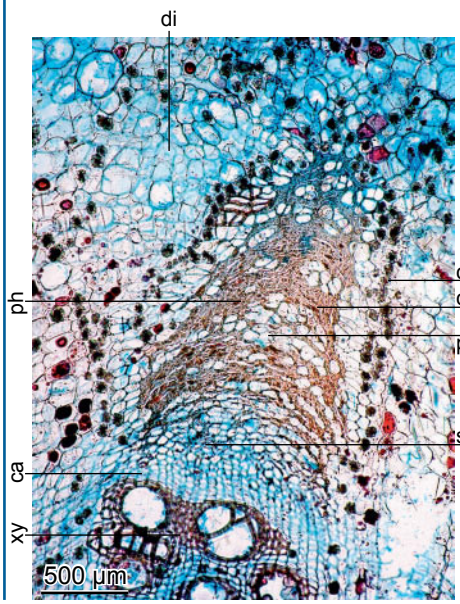
**Right Fig. 12.** Bundle of rhaphides in an earlywood vessel. Stem of a pollarded 200-year-old plant in an espalier, hill zone, Valais, Switzerland. *Vitis vinifera*, radial section, polarized light.

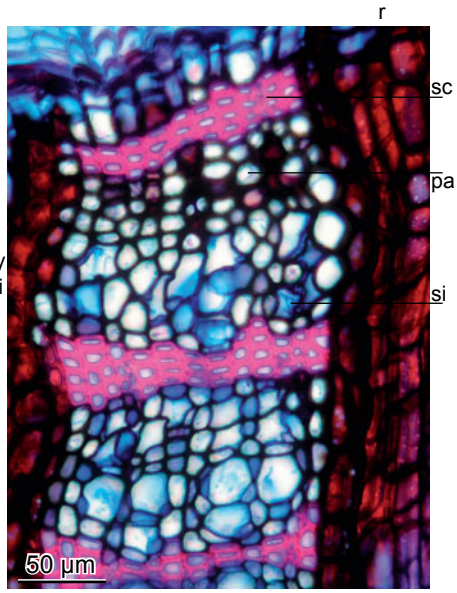
### Characteristics of the phloem and the cortex

Characteristic of all species is the tangential arrangement of sieve tubes and parenchyma (**Figs. 13** and **14**), the presence of ray dilatations (**Figs. 13** and **15**) and the occurrence of rhaphides. Rhaphides occur in enlarged ray-parenchyma cells. Prismatic crystals occupy lateral ray cells in *Parthenocissus* (**Fig. 16**). Rectangular groups of tangentially oriented sclereids occur in *Parthenocissus tripartituts* and *Vitis vinifera* (**Fig. 14**). Crystal druses and laticifers occur in the cortex of *Cissus* and *Parthenocissus* (**Fig. 16**).

### Ecological trends and relations to life forms

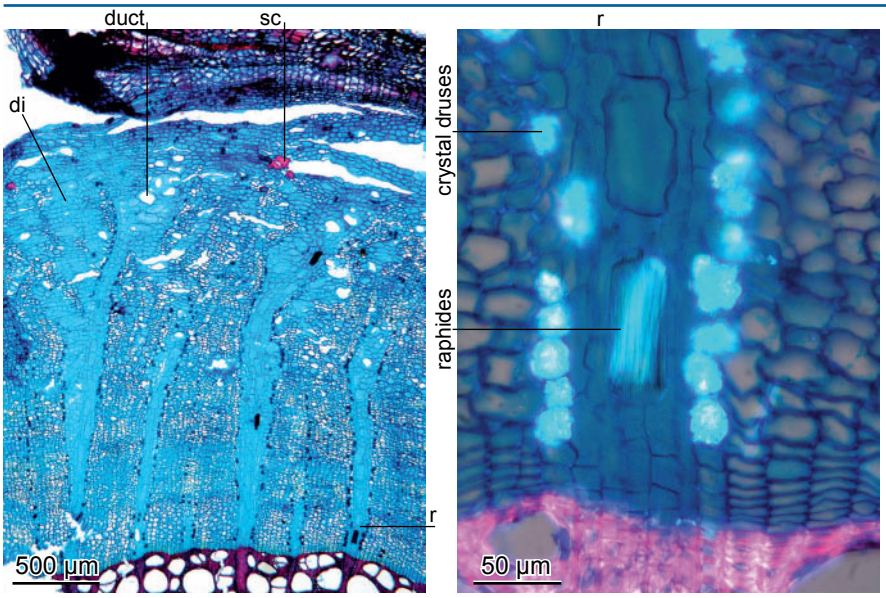
Anatomical variations are related to taxa and/or growth forms. Large vessels are characteristic of the lianas. The abundant thin-walled parenchyma is related to the succulent growth form (*Cissus quadrangularis*).




**Left Fig. 13.** Phloem between dilated rays. Characteristic of the phloem is the tangential arrangement of sieve tubes and parenchyma cells. External sieve tubes are collapsed. Stem of a succulent liana, on a rock, subtropical climate, Dhofar, Oman. *Cissus quadrangularis*, transverse section.

**Right Fig. 14.** Thick-walled tangential groups of lignified sclerenchyma alternate with unlignified sieve tubes and parenchyma cells. Stem of a liana, volcanic rock, abandoned vineyard, La Palma, Canary Islands. *Vitis vinifera*, transverse section.




**Left Fig. 15.** Phloem almost without sclerenchyma. Lateral cells of dilated rays contain crystals (dark spots). Laticifers occur in the outer part of the phloem and the cortex (round openings). Stem of a liana, cultivated on a wall, hill zone, Switzerland. *Parthenocissus inserta*, transverse section.

**Right Fig. 16.** Large ray in the phloem. Crystal druses occupy lateral ray cells. Rhaphides occur in bundles in enlarged cells in the center of the ray. Stem of a liana, cultivated on a wall, hill zone, Switzerland. *Parthenocissus inserta*, transverse section, polarized light.



## Discussion in relation to previous studies

Metcalfe and Chalk (1957) summarized the wood anatomical variability on the basis of some species of the genera *Cissus*, *Leea*, *Parthenocissus*, *Psedera*, *Tetrastigma* and *Vitis*. An IAWA–code classification without description is given for 7 genera in: *http://insidewood.lib.ncsu.edu*. *Vitis vinifera* was described by many autors, e.g. Fahn (1986), Grosser (1977), Schweingruber (1978). Greggus (1958) described *Parthenocissus quinquefolius*, Benkova and Schweingruber (2004) *Ampelopsis brevipedunculata*, *Parthenocissus tricuspidata* and *Vitis amurensis*. For further references see Metcalfe and Chalk (1957) and Gregory (1994).

Each genus has its own specialty (Metcalfe and Chalk 1957) and the present study suggests that the anatomical variability in the family of Vitaceae is much larger than can be shown here.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **5** |
| 1 | growth rings distinct and recognizable | 3 |
| 2 | growth rings absent | 4 |
| 3 | ring-porous | 4 |
| 5 | diffuse-porous | 3 |
| 9 | vessels predominantly solitary | 2 |
| 11 | vessels predominantly in clusters | 3 |
| 13 | vessels with simple perforation plates | 5 |
| 20 | intervessel pits scalariform | 4 |
| 20.1 | intervessel pits pseudoscariform to reticulate | 1 |
| 32 | vessel-ray pits with large horizontal apertures, Hamamelidaceae type | 4 |
| 42 | earlywood vessels: tangential diameter 100-200 µm | 5 |
| 50.1 | 100-200 vessels per $mm^2$ in earlywood | 1 |
| 50.2 | 200-1000 vessels per $mm^2$ in earlywood | 4 |
| 56 | tylosis with thin walls | 5 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 5 |
| 65 | septate fibers present | 3 |
| 69 | fibers thick-walled | 2 |
| 70 | fibers thin- to thick-walled | 3 |
| 79 | parenchyma paratracheal | 5 |
| 98 | rays commonly 4-10-seriate | 4 |
| 99 | rays commonly >10-seriate | 2 |
| 99.1 | vascular-bundle form remaining | 1 |
| 103 | rays of two distinct sizes (tangential section) | 2 |
| 104 | ray: all cells procumbent (radial section) | 1 |
| 105 | ray: all cells upright or square | 1 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 3 |
| 136 | prismatic crystals present | 3 |
| 144 | druses present | 1 |
| 149 | rhaphides present | 2 |
| R1 | groups of sieve tubes present | 4 |
| R2 | groups of sieve tubes in tangential rows | 4 |
| R3 | distinct ray dilatations | 3 |
| R4 | sclereids in phloem and cortex | 2 |
| R7 | with prismatic crystals | 1 |
| R8 | with crystal druses | 3 |
| R11 | with rhaphides | 4 |
| R12 | with laticifers, oil ducts or mucilage ducts | 3 |

# Winteraceae



**Number of species, worldwide and in Europe**

The Winteraceae family includes 5 genera with 90 species in the southwestern Pacific, Madagascar, South-America and Mexico (*Drimys*). The majority belong to *Tasmannia* (40 species) and *Bubbia* (30 species). There are no endemic representatives of the family of Winteraceae in Europe.

**Analyzed species:**

*Belliolum gracile* Sm.
*Bubbia* sp.
*Drimys piperita* Hook f.
*Drimys winteri* Forst
*Tasmannia xerophila* M. Gray
*Zygogynum polyneurum* (Diels) Vink

**Analyzed material**

The xylem and phloem of 6 Winteraceae species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | 5 | ca. 8 |
| **Plants analyzed from different vegetation zones:** | | |
| Alpine and subalpine | 1 | |
| Hill and mountain | 1 | |
| Tropical | 4 | |

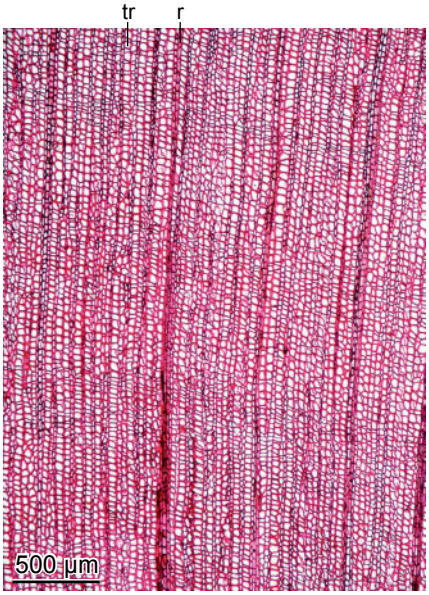
*Drimys winteri* (photo right: Stützel)

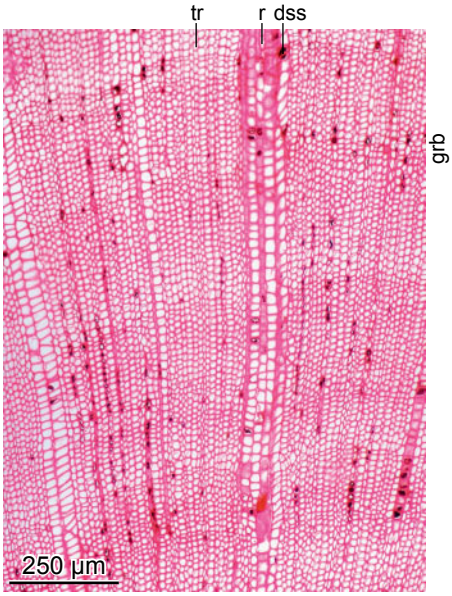
## Characteristics of the xylem

Growth rings are absent from the tropical species (*Bubbia* sp., *Belliolum gracile* and *Drimys piperita*; **Fig. 1**), but recognizable in the species growing in seasonal climates (*Drimys winteri*, *Tasmannia xerophila*; **Fig. 2**). The conifer-like, vesselless wood has thin- to thick-walled tracheids (**Figs. 2** and **5**). Radial cell walls of most tracheids are characterized by large, distinctly bordered pits (**Fig. 3**) with oval to slit-like apertures. Round pits are arranged in 1-3 rows on radial walls (**Fig. 4**). Scalariform pits were observed in the large tracheids of all species (**Fig. 5**) except *Zygogynum polyneurum*. Helical thickenings are absent. Apotracheal diffuse parenchyma rarely occurs (**Fig. 6**). Rays occur in two forms: uniseriate rays with upright cells and larger heterocellular rays (2-4 square or upright marginal cells) with 3-6 cells in width (**Figs. 7** and **8**). Bordered pits (piceoid) with slit-like apertures occur on uniseriate rays and on marginal cells of large rays. They are arranged either in axial uniseriate rows (**Fig. 9**) or in groups (**Fig. 10**).

## Characteristic features of taxa

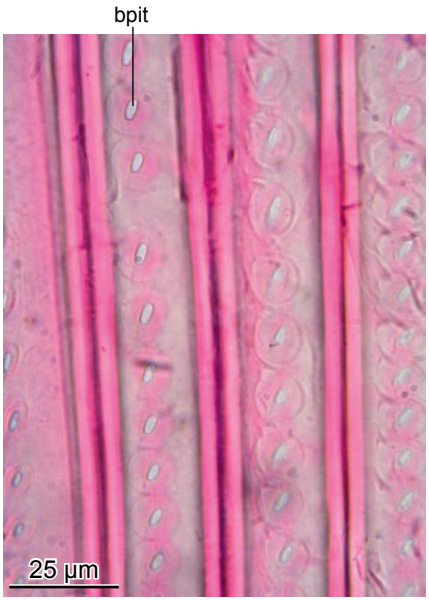
Pit arrangement on rays can sometimes be used to distingish species (**Figs. 9** and **10**).



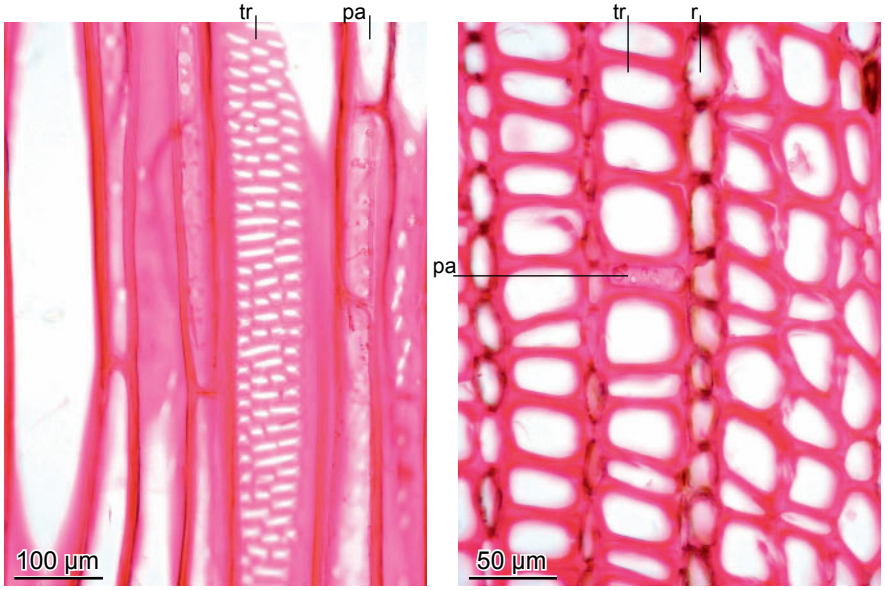

**Left Fig. 1.** Vesselless xylem consisting of tracheids without growth zones. Xylem of a tree, tropics, wood collection Herbarium Leiden. *Bubbia* sp., transverse section.

**Right Fig. 2.** Vesselless xylem with indistinct but recognizable annual rings or growth zones. Xylem of a shrub, subalpine zone, Blue Mountains, Australia. *Tasmannia xerophila*, transverse section.



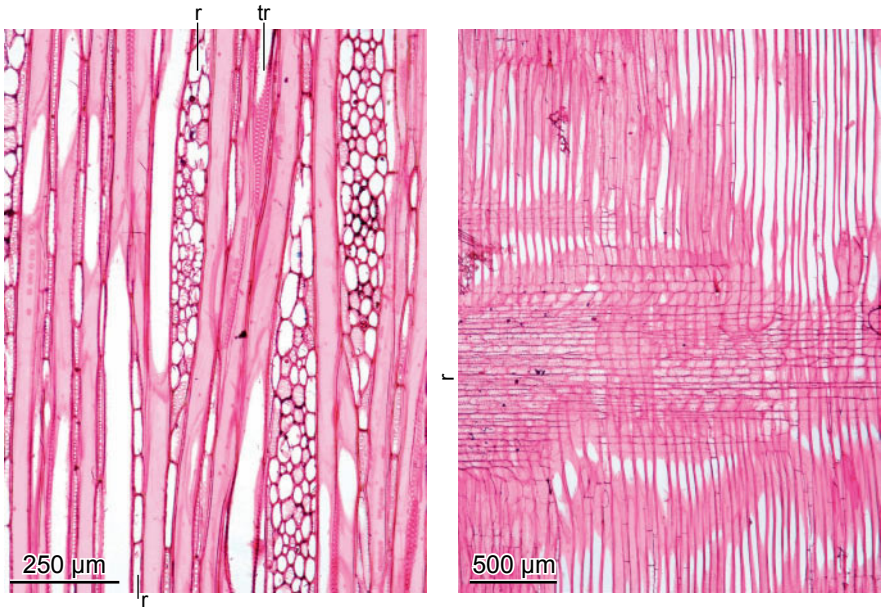
**Left Fig. 3.** Radial walls of tracheids with large bordered pits with oval apterures. Xylem of a tree, tropics, wood collection Herbarium Leiden. *Zygogynum polyneurum*, radial section.

**Right Fig. 4.** Radial walls of tracheids with bordered pits arranged in 1-3 rows. Xylem of a tree, tropics, wood collection Herbarium Leiden. *Belliolum gracile*, radial section.



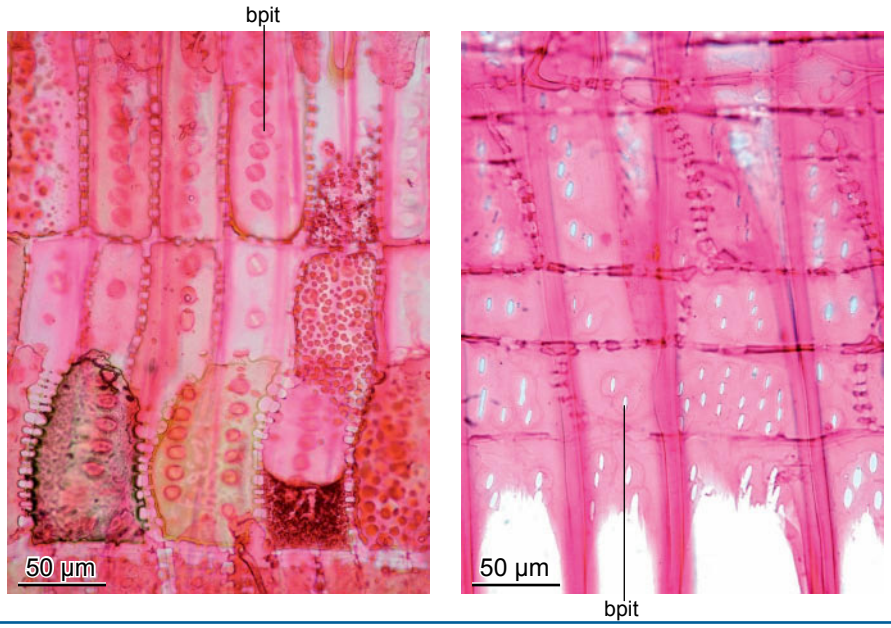

**Left Fig. 5.** Radial walls of tracheids with bordered scalariform pits. Xylem of a tree, tropics, wood collection Herbarium Leiden. *Drimys piperita*, radial section.

**Right Fig. 6.** One parenchyma cell (with simple pits) in a row of tracheids. Xylem of a tree, tropics, wood collection Herbarium Leiden. *Bubbia* sp., transverse section.




**Left Fig. 7.** Ray dimorphism: uniseriate and multiseriate rays (4-6 cells wide) with sheet cells. Xylem of a tree, tropics, wood collection Herbarium Leiden. *Belliolum gracile*, tangential section.

**Right Fig. 8.** Heterocellular ray with procumbent central cells and some square and upright marginal cells. Xylem of a tree, tropics, wood collection Herbarium Leiden. *Belliolum gracile*, radial section.

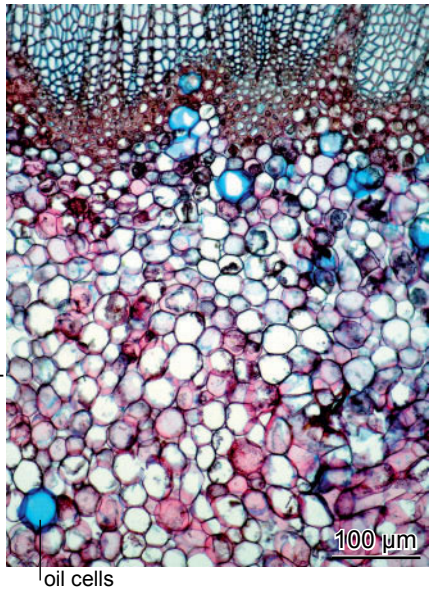


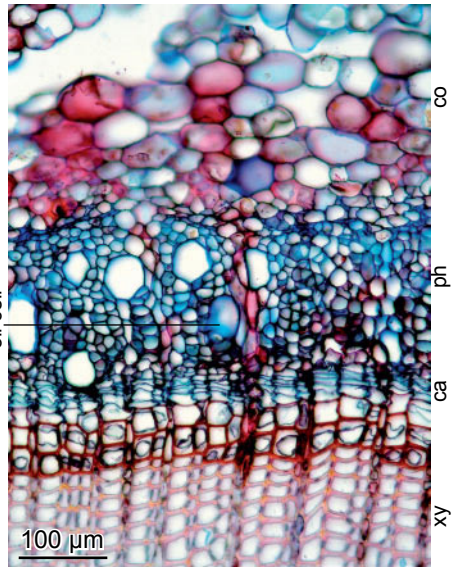

**Left Fig. 9.** Thick-walled marginal ray cells with bordered pits (piceoid) arranged in axial rows. Xylem of a tree, tropics, wood collection Herbarium Leiden. *Bubbia* sp., transverse section.

**Right Fig. 10.** Marginal ray cells with groups of bordered pits (piceoid). Xylem of a tree, tropics, wood collection Herbarium Leiden. *Belliolum gracile*, radial section.

### Characteristics of the phloem, the cortex and the pith

Slides of bark and pith are only available for *Drimys winteri*. The phloem is simply structured. Parenchyma cells and sieve tubes cannot be distinguished. Oil cells occur in the pith (**Fig. 11**), the phloem and the cortex (**Fig. 12**). Oil cells were observed in *Takhtajania perrieri* (Carlquist 2000). A few groups of sclereids occur on the inner side of the cortex. The cortex and the pith contain isolated, irregularly formed sclereids (**Fig. 12**).




**Left Fig. 11.** Pit with a few oil cells. Twig of a 4 m-high tree, Botanical Garden Brissago Island, Switzerland. *Drimys winteri*, transverse section.

**Right Fig. 12.** Phloem with oil cells. Twig of a 4 m-high tree, Botanical Garden Brissago Island, Switzerland. *Drimys winteri*, transverse section.

### Discussion in relation to previous studies

Patel (1974) described the Winteraceae (*Pseudowintera*) of New Zealand. Carlquist (2001) discussed the origin of vesselless wood on the basis of *Exosperumum*, *Belliolum*, *Bubbia*, *Drimys*, *Tasmannia*, *Takhtajania* and *Zygogynum*. These genera were also described in six other studies (see Gregory 1994). Gregory (1994) mentions a total of 30 references for the stem anatomy of Winteraceae. Feild et al. (2000) discuss results of phylogenetic analysis and conclude that vesselless xylem may be secondarily derived. The present study confirms all findings from previous autors.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| **Total number of species** | | **6** |
| 1 | growth rings distinct and recognizable | 3 |
| 2 | growth rings absent | 4 |
| 20 | intervessel pits scalariform | 5 |
| 59 | vessels absent or indistinguishable from fibers | 6 |
| 60 | vascular/vasicentric tracheids, *Daphne* type | 0 |
| 60.1 | fibers absent | 0 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 0 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 6 |
| 70 | fibers thin- to thick-walled | 6 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 6 |
| 98 | rays commonly 4-10-seriate | 6 |
| 108 | ray: heterocellular with >4 upright cell rows (radial section) | 6 |
| 110 | rays with sheet cells (tangential section) | 6 |
| R1 | groups of sieve tubes present | 1 |
| R3 | distinct ray dilatations | 1 |
| R4 | sclereids in phloem and cortex | 1 |
| R12 | with laticifers, oil ducts or mucilage ducts | 1 |
| P2 | with laticifers or intercellular canals | 1 |

# Zygophyllaceae



**Number of species, worldwide and in Europe**

The pantropical Zygophyllaceae family includes 25 genera with 200 species. In Europe, there are 6 genera with 9 species. 27 species occur in the Sahara.

**Analyzed material**

The xylem and phloem of 4 genera with 7 species are analyzed here.

| **Life forms analyzed:** | | Studies from other authors: |
|---|---|---|
| Phanerophytes (>4 m) | | 3 |
| Nanophanerophytes (0.5-4 m) | 2 | approx. 6 |
| Woody chamaephytes | 5 | approx. 11 |
| **Plants analyzed from different vegetation zones:** | | |
| Arid | 7 | |

**Analyzed species:**

*Fagonia arabica* L.
*Fagonia cretica* L.
*Fagonia olivieri* Boiss.
*Larrea cuneifolia* Cav.
*Porlieria hygrometrica* Ruiz
*Zygophyllum fontanesii* Webb
*Zygophyllum gaetulum* Emb. et Maire

*Fagonia cretica* (photo: Zinnert)

*Zygophyllum waterlotii*

*Peganum harmala* (photo: Zinnert)

**Characteristics of the xylem**

Annual rings are not very distinct in the present material. Rings are absent in most species (**Fig. 1**). Ring boundaries, if present, are semi-ring-porous (**Fig. 2**). Vessels are arranged solitary (**Fig. 3**) and often in tangential rows (**Fig. 4**). The earlywood vessel diameter of the majority of species varies between 30-60 µm. Vessel density varies mostly from 200-300/mm$^2$. Vessels contain exclusively simple perforations. Intervessel pits are predominantly small and round and arranged in alternating position. Radial walls of fibers are perforated by small, slit-like or round pits (2-3 µm). Fibers are mostly thin- to thick-walled (**Fig. 3**) or thick-walled (**Fig. 1**). Parenchyma is apotracheal, often in small aggregates (**Fig. 3**). Storied fibers and parenchyma occur in *Larrea cuneifolia*.

Rays are uniseriate or 1-3 cells wide (**Figs. 5-7**). They are homocellular with upright (**Fig. 8**) or procumbent cells or are heterocellular with a few marginal upright cells. Crystals occur in idioblasts (**Figs. 9** and **10**).

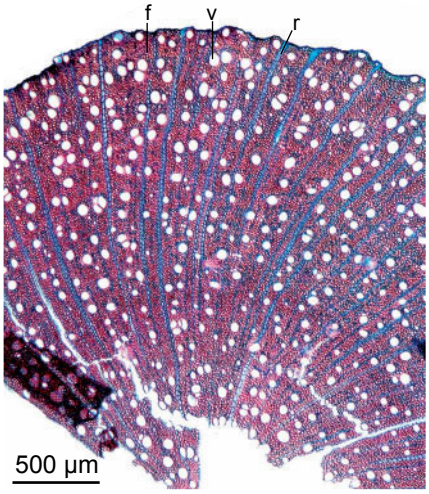



**Fig. 1.** Xylem without growth zones. Root collar, chamaephytes, arid zone, subtropical climate, Tenerife, Canary Islands. *Fagonia cretica*, transverse section.

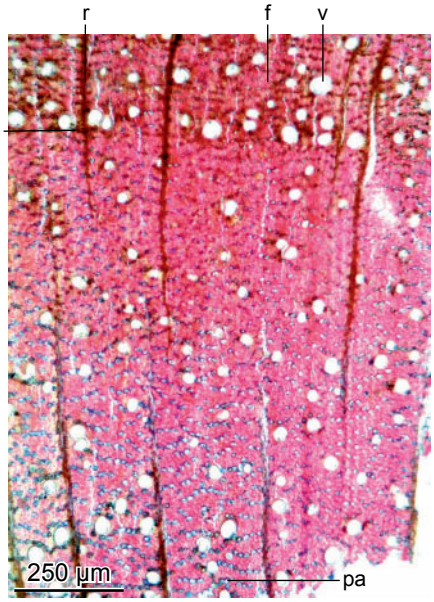



**Fig. 2.** Semi-ring-porous wood with thick-walled fibers and apotracheal parenchyma. Root collar, chamaephytes, shrub steppe, Chile. *Larrea cuneifolia*, transverse section.

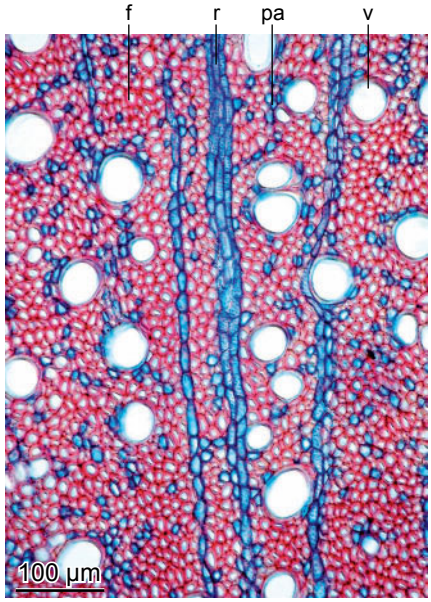



**Fig. 3.** Xylem with solitary vessels, rather thick-walled fibers and apotracheal parenchyma. Root collar, chamaephytes, dry subtropical climate, Tenerife, Canary Islands. *Fagonia cretica*, transverse section.

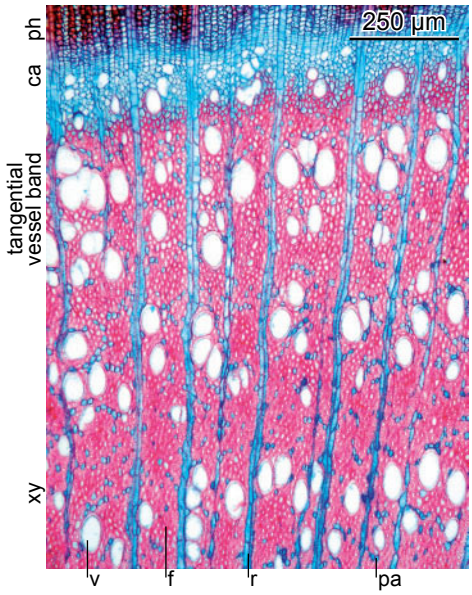



**Fig. 4.** Grouped vessels in intra-annual tangential rows. Root collar, chamaephytes, ruderal site, hyperarid climate, Libya. *Zygophyllum gaetulum*, transverse section.

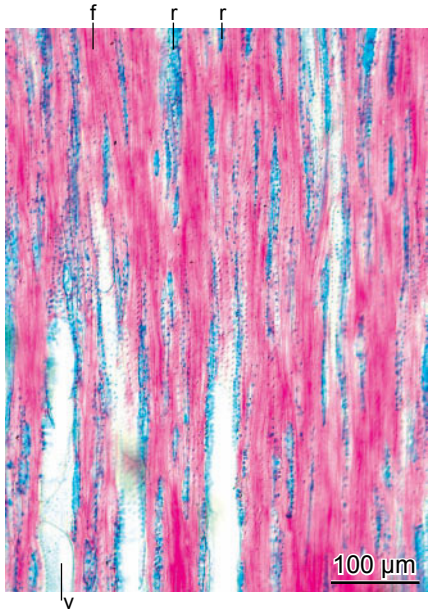



**Fig. 5.** Uniseriate rays with axially elongated, unlignified (blue) cells. Root collar, chamaephytes, desert, hyperarid climate, Libya. *Fagonia olivieri*, tangential section.

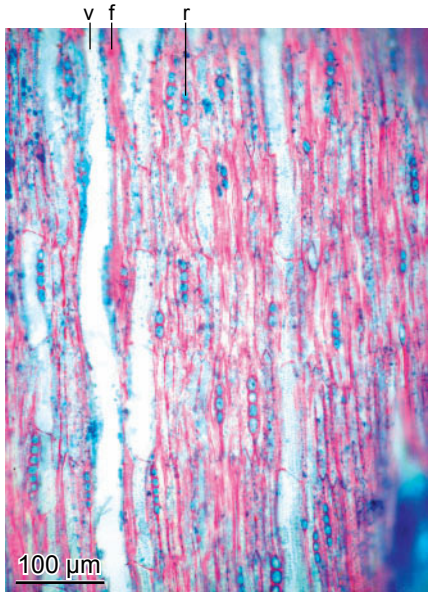



**Fig. 6.** Uniseriate rays with round cells. Stem, small shrub, dry, cold greenhouse, Botanical Garden Basel, Switzerland. *Porlieria hygrometrica*, tangential section.

**Fig. 7.** Rays 2 and 3 cells wide, with large, round cells. Root collar, succulent chamaephyte, hyperarid climate, Libya. *Zygophyllum fontanesii*, tangential section.

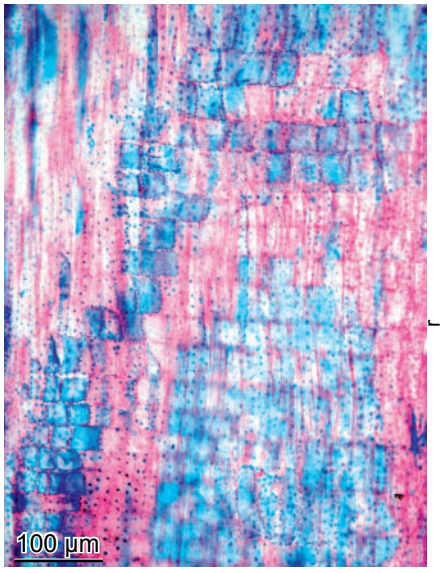



**Fig. 8.** Rays with exclusively upright cells. Root collar, succulent chamaephyte, hyperarid climate, Libya. *Zygophyllum gaetulum*, radial section.

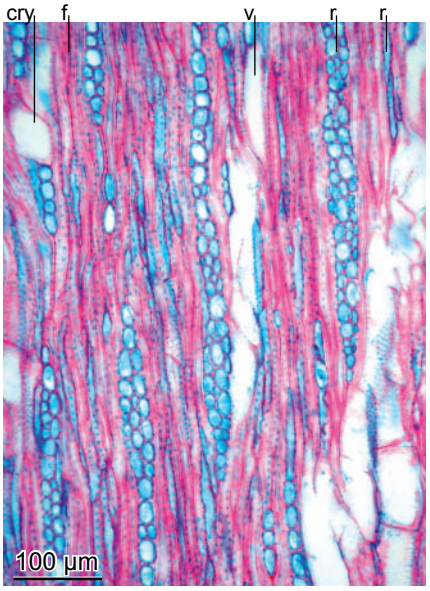


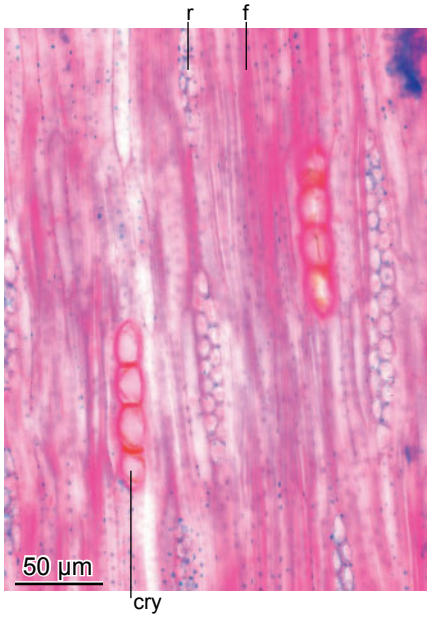

**Fig. 9.** Rays 2 and 3 cell wide, with large, round cells and long, marginal cells. Uniseriated rays are also axially elongated. Root collar, succulent chamaephyte, hyperarid climate, Libya. *Zygophyllum gaetulum*, tangential section.

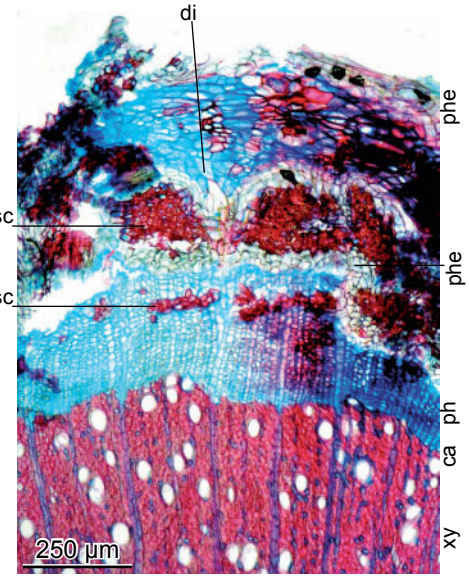
### Characteristics of the phloem and the cortex

Three types of bark structures were observed. Sclereids are arranged in a tangential belt in *Fagonia* (**Fig. 11**) and in radial groups in *Zygophyllum* (**Fig. 12**). Sclereids are absent in *Porlieria hygrometrica*. Tangential rows of collapsed sieve tubes characterize this species (**Fig. 13**). Crystal druses occur in *Zygophyllum*.

### Characteristic features of taxa

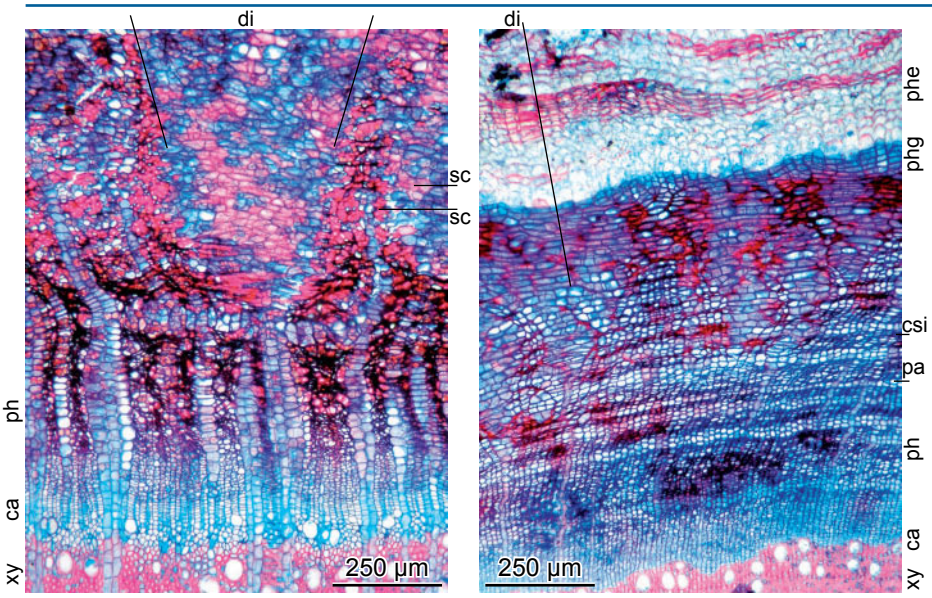
Ray features characterize single species or genera of the present material. Ray cells are oval in *Fagonia* (**Fig. 5**) and round in *Porlieria* (**Fig. 6**) and *Zygophyllum* (**Fig. 7**).




**Left Fig. 10.** Prismatic crystals in idioblasts. Stem, shrub, shrub steppe, Chile. *Larrea cuneifolia*, tangential section.

**Right Fig. 11.** Thick-walled sclereids in a discontinuous tangential belt. Root collar, chamaephytes desert, hyperarid climate, Libya. *Fagonia arabica*, transverse section.




**Left Fig. 12.** Thick-walled sclereids in radial groups between ray dilatations. Root collar, succulent chamaephyte, desert, hyperarid climate, Libya. *Zygophyllum fontanesii*, transverse section.

**Right Fig. 13.** Tangentially layered phloem. Sieve tubes are collapsed in older parts. Stem, small shrub, dry, cold greenhouse, Botanical Garden Basel, Switzerland. *Porlieria hygrometrica*, transverse section.



### Ecological trends and relations to life forms

The material is too limited to detect ecological trends.

### Discussion in relation to previous studies

Gregory (1994) mentioned 38 papers that describe the wood of 2 trees and many shrub-like genera. Carlquist (2005) described 6 genera with 6 species in detail. The wood of the trees *Balanites aegyptica* and *Guiacum officinale* and of the shrubs *Bulnesia* sp. and *Porlieria* sp. are the most frequently described. Fahn et al. (1986) and Neumann et al. (2001) mainly described a few species of *Fagonia*, *Zygophyllum* and *Nitraria* of Israel and the Sahara. Cozzo (1948) and Roig and Videla (2006) characterized 4 genera from arid areas in Argentina. Carlquist (2005) found vestured vessel pits.

The present study confirms all former observations. The anatomical variability presented here is limited. Species with large vessels, e.g. *Balanites* and *Nitraria* are excluded here.

**Present features in relation to the number of analyzed species**

| IAWA code | | frequency |
|---|---|---|
| | **Total number of species** | 7 |
| 1 | growth rings distinct and recognizable | 1 |
| 2 | growth rings absent | 4 |
| 2.1 | only one ring | 2 |
| 4 | semi-ring-porous | 1 |
| 5 | diffuse-porous | 2 |
| 6 | vessels in intra-annual tangential rows | 3 |
| 7 | vessels in diagonal and/or radial patterns | 1 |
| 8 | vessels in dendritic patterns | 1 |
| 9 | vessels predominantly solitary | 7 |
| 13 | vessels with simple perforation plates | 7 |
| 22 | intervessel pits alternate | 7 |
| 39.1 | vessel cell-wall thickness >2 µm | 2 |
| 40.1 | earlywood vessels: tangential diameter <20 µm | 1 |
| 40.2 | earlywood vessels: tangential diameter 20-50 µm | 5 |
| 50.1 | 100-200 vessels per mm$^2$ in earlywood | 6 |
| 50.2 | 200-1000 vessels per mm$^2$ in earlywood | 1 |
| 61 | fiber pits small and simple to minutely bordered (<3 µm = libriform fibers) | 2 |
| 62 | fiber pits large and distinctly bordered (>3 µm = fiber tracheids) | 5 |
| 69 | fibers thick-walled | 4 |
| 70 | fibers thin- to thick-walled | 3 |
| 76 | parenchyma apotracheal, diffuse and in aggregates | 7 |
| 96 | rays uniseriate | 3 |
| 97 | ray width predominantly 1-3 cells | 4 |
| 104 | ray: all cells procumbent (radial section) | 2 |
| 105 | ray: all cells upright or square | 4 |
| 107 | ray: heterocellular with 2-4 upright cell rows (radial section) | 1 |
| 120 | storied axial tissue (parenchyma, fibers, vessels, tangential section) | 1 |
| 136 | prismatic crystals present | 1 |
| R1 | groups of sieve tubes present | 4 |
| R2 | groups of sieve tubes in tangential rows | 1 |
| R3 | distinct ray dilatations | 3 |
| R4 | sclereids in phloem and cortex | 5 |
| R6 | sclereids in radial rows | 3 |
| R6.1 | sclereids in tangential rows | 2 |
| R8 | with crystal druses | 2 |

# References


Aeschimann D, Lauber K, Moser DM, Theurillat J-P (2004) Flora alpina. Ein Atlas sämtlicher 4500 Gefässpflanzen der Alpen. Verlag Paul Haupt. Bern, Stuttgart, Wien.

Akkemik U, Asuma E, Kaya Z, Demir D (2007) Wood anatomy of endemic *Rhamnus* species in the Mediterranean region of Turkey. IAWA J. 28: 301–310.

Anderson LC (1974) A study of systematic wood anatomy of *Cannabis*. Bot Mus Leafl Harvard Univ. 24: 29–36.

Artschwager EF (1920) On the anatomy of *Chenopodium album*. Am J Bot 7: 252–269.

Ashworth VETM, Dos Santos G (1997) Wood anatomy of four Californian mistletoe species (*Phoradendron*, Viscaceae). IAWA J 18: 229–245.

Baas P, Schweingruber FH (1987) Ecologcical trends in the wood anatomy of trees, shrubs and climbers in Europe. IAWA J 8: 245–274.

Bailey IW (1957) Additional notes on the vesselless dicotyledon, *Amborella trichopoda* Baill. J Arnold Arboretum 38: 374–378.

Balthazar M, Endress PK, Yin-Long Q (2000) Phylogenetic relationships in Buxaceae based on nuclear internal transcribed spacers and plastid *ndhF* sequences. Int J Plant Sci 161: 785–795.

Benkova VE, Schweingruber FH (2004) Anatomy of Russian woods. Verlag Paul Haupt. Bern, Stuttgart, Wien.

Bergmann M (1944) Vergleichende Untersuchungen über die Anatomie schweizerischer *Ranunculus*-Arten und deren Gehalt an Anemonol und Saponin. Ber Schweiz Bot Ges 54: 399–522.

Betts MW (1918) Notes on the autecology of certain plants of the Peridotite belt, Nelson. Part I: Structure of some of the plants (No. 1). Trans New Zealand Inst 50: 230–243.

Bittrich V (1993) Caryophyllaceae. In: Kubitzki K, Rohwer JG, Bittrich V (ed) The families and genera of vascular plants. Vol. 2 Flowering plants, Dicotyleodons. Springer-Verlag. Heidelberg.

Blesa Rodriguez AC, Caballero-Ruano A, Jimenez Parrondo MS (1979) Estudio anatomico-fisiologico del leno de las Crasulaceas. An Edafol Agrobiol 38: 2169–2179.

Bramwell D, Bramwell Z (2001) Wild flowers of the Canary Islands. Editorial Rueda SL Alcoron. Madrid.

Brunner (1908) Beiträge zur vergleichenden Anatomie der Tamaricaceen. Jb Hamburg Wiss Anst 26, Beiheft 3: 89–162.

Bruyne de C (1922) Idioplastes and diaphragms in Nymphéacées. CR Acad Sci Paris 175: 452–455.

Busse JS, Evert RF (1999) Vascular differentiation and transition in the seedling of *Arabidopsis thaliana* (Brassicaceae). Int J Plant Sci 160: 241–251.

Butnik AA (1983) A characteristic of anomalous (polycambial) types of secondary thickening in axial organs of the Chenopodiaceae species. Bot Zh SSSR 68: 572–580.

Carlquist S (1970) Wood anatomy of Hawaiian, Macaronesian and other species of *Euphorbia*. Bot J Linnean Soc 63: 181–193.

Carlquist S (1971) Wood anatomy of Macronesian and other Brassicaceae. Aliso 7: 365–384.

Carlquist S (1975) Ecological strategies of xylem evolution. University of California Press. Berkley.

Carlquist S (1975) Wood anatomy of Onagraceae, with notes on alternative modes of photosynthate movement in dicotyledon woods. Ann Missouri Bot Garden 62: 386–424.

Carlquist S (1977) Ecological factors in wood evolution: A floristic approach. Am J Bot 64: 887–896.

Carlquist S (1977) Wood anatomy of Onagraceae: Additional species and concepts. Ann Missouri Bot Garden 64: 627–637.

Carlquist S (1981) Wood Anatomy of Nepenthaceae. Bull Torrey Bot Club 108: 324–330.

Carlquist S (1982) *Exospermum stipitatum* (Winteraceae): Observations in wood, leaves, flowers, pollen and fruit. Aliso 10: 277–289.

Carlquist S (1982) Wood anatomy of Onagraceae: Further species; root anatomy; significance of vestured pits and allied structures in dicotyledons. Ann Missouri Bot Garden 69: 755–769.

Carlquist S (1984) Wood and stem anatomy of Lardizabalaceae with comments on the vining habitat, ecology and systematics. Bot J Linn Soc 88: 257–277.

Carlquist S (1985) Observations on functional wood histology of vines and lianas: Vessel dimorphism, tracheids, vasicentric tracheids, narrow vessels, and parenchyma. Aliso 11: 139–157.

Carlquist S (1985) Wood anatomy and familial status of *Vivianía*. Aliso 11: 159–165.

Carlquist S (1988) Wood anatomy of Cneoraceae: Ecology, relationships, and generic definition. Aliso 12: 7–16.

Carlquist S (1988) Wood anatomy of *Drymis* s.s. (Winteraceae). Aliso 12: 81–95.

Carlquist S (1992) Wood anatomy of selected Cucurbitaceae and its relationship to habit and systematics. Nordic Journal of Botany 12: 347–355.

Carlquist S (1993) Wood and bark anatomy of Aristolochiaceae; Systematic and habitual correlations. IAWA J 14: 341–357.

Carlquist S (1995) Wood anatomy of Berberidaceae: Ecological and phylogenetic considerations. Aliso 14: 85–103.

References


Carlquist S (1995) Wood anatomy of the Caryophyllaceae: Ecological, habital, systematic, and phylogenetic implications. Aliso 14: 1–17.

Carlquist S (1995) Wood and bark anatomy of Ranunculaceae (including *Hydrastis*) and Glaucidiaceae. Aliso 14: 65–84.

Carlquist S (1998) Wood anatomy of Portulacaceae and Hectorellaceae: Ecological, habital, and systematic implications. Aliso 16: 137–153.

Carlquist S (1998) Wood anatomy of Resedaceae. Aliso 16: 127–135.

Carlquist S (2000) Wood and bark anatomy of *Takhtajana* (Winterceae). Phylogenentic and ecological implications. Ann Mo Bot Gard 87: 317–322.

Carlquist S (2000) Wood and stem anatomy of phytolaccoid and rivinoid Phytolacaceae (Caryophyllales): Ecology, systematics, nature of successive cambia. Aliso 19: 13–29.

Carlquist S (2001) Comparative wood anatomy. Springer Series in Wood Science. Springer Verlag. Berlin, Heidelberg, New York.

Carlquist S (2001) Vegetative anatomy of the New Caledonian endemic *Amborella trichopoda*: Relationships with the Illiciales and implications for vessel origin. Pacific Science 55: 305–312.

Carlquist S (2002) Wood anatomy and successive cambia in *Simmondsia* (Simmondsiaceae): Evidence for inclusion in Caryophyllales s.l. Madroño 49: 158–164.

Carlquist S (2002) Wood and bark anatomy of Salvadoraceae: Ecology, relationships, histology of interxylary phloem. J Torrey Bot Soc 129: 10–20.

Carlquist S (2003) Wood anatomy of Polygonaceae: Analysis of a family with exceptional wood diversity. Bot J Linn Soc 141: 25–51.

Carlquist S (2003) Wood and stem anatomy of woody Amaranthaceae s.s.: Ecology, systematics and the problems of defining rays in dicotyledons. Bot J Linn Soc 143: 1–19.

Carlquist S (2004) Lateral meristems, successive cambia and their products: A reinterpretation based on roots and stems of Nyctaginaceae. Bot J Linn Soc 146: 129–143.

Carlquist S (2005) Wood anatomy of Krameriaceae with comparisons with Zygophyllaceae: phylesis, ecology and systematics. Bot J Linn Soc 149: 257–270.

Carlquist S (2007) Successive cambia in Aizoaceae: Products and processes. Bot J Linn Soc 153: 141–155.

Carlquist S, Boggs C.J. (1996) Wood anatomy of Plumbaginaceae. Bull Torrey Bot Club 123: 135–147.

Carlquist S, Grant J R (2005) Wood anatomy of Gentianaceae, tribe Helieae in relation to ecology, habit, systematic and sample diameter. Brittonia 57: 276–291.

Carlquist S, Hoekman DA (1985) Ecological wood anatomy of the woody southern Californian flora. IAWA Bull n.s. 6: 319–347.

Carlquist S, Miller RB (1999) Vegetative anatomy and relationships of *Setchellanthus caeruleus* (Setchellanthaceae). Taxon 48: 289–302.

Carlquist S, Wilson EJ (1995) Wood anatomy of *Drosophyllum* (Droseraceae): Ecological and phylogenetic considerations. Bull Torrey Bot Club 122: 185–189.

Chaffey NB (2002) Wood formation of trees. Cell and molecular biology techniques. Taylor and Francis. London, New York.

Chalk L, Chattaway MM (1937) Identification of woods with included phloem. Trop woods 50: 1–31.

Cheng J-Q, Yang J-J, Liu P (1992) Anatomy and properties of Chinese woods. China Forestry Publ House. Beijing.

Chengsong Z, Johnson BJ, Kositsup B, Beers EP (2000) Exploiting secondary growth in *Arabidopsis*. Construction of xylem and bark cDNA libraries and cloning of three xylem endopeptidases. Plant Physiol 123: 1185–1196.

Cole TCH, Hilger HH (2010) Poster "Angiosperm Phylogeny - APG III". *www2.biologie.fu-berlin.de/sysbot/poster/poster1.pdf*

Costermans L (1989) Native trees and shrubs of South-Eastern Australia. Sidney, Hong- Kong, Chicago, London.

Cozzo D (1948) Anatomia del leno de las especias Argentinas de la tribu Zygophyllaceae. Rev Inst nat Sci Cienc Bot 1: 223–361.

Datta PC, Deb A (1968) Secondary xylem, floral traces and phylogeny of common Indian species of *Rumex*. Beitr Biol Pflanzen 45: 69–90.

Dolan L, Roberts K (1995) Secondary thickening in roots of *Arabidopsis thaliana*. Anatomy and cell surfaces. New Phytol 131: 121–128.

Douglas GE (1936) Studies in the vascular anatomy of the Primulaceae. Amer J Bot 23: 199–212.

Edlmann MLA, de Luca L, Lazzeri S (1994) Atlante anatomico degli alberi ed arbusti della macchia Mediterranea. Relazione e monografie agrarie subtropicali e tropicali. Nuove serie. Florence.

Eggenberg S, Möhl A (2007) Flora Vegetativa. Ein Bestimmungsbuch für Pflanzen der Schweiz im blütenlosen Zustand. Verlag Paul Haupt. Bern, Stuttgart, Wien.

Ellenberg H, Weber HE, Düll R, Wirt V, Werner W, Paulissen D (1991) Zeigerwerte von Pflanzen in Mitteleuropa. Scr Geobot 18: 1–258.

Epple (1995) A Field guide to the plants of Arizona. Falcon, The Globe Pequet Press. Guilford, Ct.

Esau K (1969) The phloem. Gebrüder Bornträger Verlag. Berlin, Stuttgart.

Esau K (1977) Anatomy of seed plants. John Wiley & sons. New York, Chichester, Brisbane, Toronto, Singapore.

Evert RF (2006) Esaus's Plant Anatomy. Meristems, Cells and tissues of the plant body. Their structure, function and development. Wiley and Sons. Hoboken, NJ, USA.

Fahn A, Werker E, Baas P (1986) Wood anatomy and identification of trees and shrubs from Israel and adjacent regions. The Israel Academy of Sciences and Humanities. Jerusalem.

Feild T S, Brodribb T, Holbrook N M (2002): Hardly a relict: freezing of the evolution of vesselless wood in Winteraceae. Evolution 56: 464–478.

Franceschi V R, Nakata P A (2007) Calcium oxalate in plants: Formation and function. Ann Rev Plant Biol 56: 41–71.

Gibson AC (1979) Anatomy of *Koeberlinia* and *Canotia* revisited. Madroño 26: 1–12.

Gregory M (1994) Bibliography of systematic wood anatomy of dicotyledons. IAWA J Suppl 1.

Greguss P (1945) Bestimmung der mitteleuropäischen Laubhölzer und Sträucher auf xylotomischer Basis. Verlag Ungar. Naturwiss. Museums. Budapest.

Grosser D (1977) Die Hölzer Mitteleuropas. Ein mikrophotographischer Lehratlas. Springer Verlag. Berlin, Heidelberg, New York.

Hall JC, Sytsma KJ, Iltis HH (2002) Phylogeny of Capparaceae and Brassicaceae based on chloroplast sequence data. Am J Bot 89: 1826–1842.

Hamet R (1925) Sur les formations cribro-vascularies médullaires de deux Crassulacées. C.R. Ann Sci Paris 180: 1424–1425.

't Hart H, Koek-Noorman J (1989) The origin of the woody Sedoideae (Crassulaceae). Taxon 38: 535–544.

Hayden WJ, Hayden SM (2000) Wood anatomy of the Acalyphoideae (Euphorbiaceae). IAWA J 21: 213–235.

Hayden WJ, Simmons MP, Swanson LJ (1993) Wood Anatomy of *Amanoa* (Euphorbiaceae). IAWA J 14: 205–213.

Heimisch C (1942) Comparative anatomy of the secondary xylem in the Gruniales and Terebintales of S. Wettstein with reference to taxonomic grouping. Lilloa 8: 83–98.

Heklau H (1992) Beiträge zum anomalen sekundären Dickenwachstum im Spross einiger annueller *Atriplex*- und *Chenopodium*-Arten. Flora 186: 23–36.

Hohenester A, Welss W (1993) Exkursionsflora für die Kanarischen Inseln. Eugen Ulmer Verlag. Stuttgart.

Holdheide W (1951) Anatomie mitteleuropäischer Gehölzrinden. In: Freund H, Handbuch der Mikroskopie. Umschau Verlag. Frankfurt/M.

Hollendonner F (1909) Über die Anatomie des Stengels von *Alyssum arduini*. Bot Kötzl 8: 26–40.

Huan G (1986) Comparative studies on the woods of Hamamelidaceae in China. Acta sci nat Univ Sunyatseni 1: 22–28.

Huber B, Rouschal C (1954) Mikrofotographischer Atlas Mediterraner Hölzer. Verlag Haller. Berlin-Gruenewald.

Inside Wood (2004-onwards) Published on the Internet. *http://insidewood.lib.ncsu.edu/*

Itoh T (1995) Anatomical description of Japanese hardwoods. Wood Res and Tech Notes 34: 30–166.

Jacques FMB, De Franceschi D (2007) Menispermaceae wood anatomy and cambial variants. IAWA J 28: 139–172.

Jagiella C, Kürschner H (1987) Atlas der Hölzer Saudi Arabiens. Dr. Ludwig Richert Verlag. Wiesbaden.

Jansen S, Robbrecht H, Beeckman H, Smets E (2002) A survey of the systematic wood anatomy of the Rubiaceae. IAWA J 23: 231–67.

Jaquiot C, Trenard Y, Dirtol D (1973) Atlas d'anatomie des bois des Angiosperms. Centre Technique du Bois, Paris.

Judd WS, Campbell CS, Kellog EA, Stevens PF, Donoghue MJ (2002) Plant systematics. A phylogenetic approach. Sinauer Ass. Inc. Sunderland, MA USA.

Junikka L (1994) Macroscopic bark terminology. IAWA J 15: 3–45.

Kanehira R (1921) Anatomical characters and identifications of Formosan woods. Govt of Formosa. Taihoku.

Keefe JM, Moseley ME jr (1978) Wood anatomy and phylogeny of *Paeonia* section Moutan. J Arnold Arboretum 59: 274–297.

Klaassen R (1999) Wood anatomy of the Sapindaceae. IAWA J Suppl 2.

Kontratieva-Melville EA, Vodolazsky LE (1982) Morphological and anatomical structure of *Arabidopsis thaliana* (Brassicaceae) in ontogenesis. Bot J 67: 1060–1069.

Krumbiegel A, Kästner A (1993) Sekundäres Dickenwachstum von Spross und Wurzel bei annuellen Dikotyledonen. Österreichische Akademie der Wiss. Wien. Biosystematic and Ecology Series 4: 1–49.

Kumazawa M (1935) The structure and affinities of *Paeonia*. Bot Mag Tokyo 49: 306–315.

Kuo-Hang L-L, Chen S-J (1999) Subcellular localization of calcium in the crystal forming sclereids of *Nymphaea tetragona* Geogri. Taiwania 44: 520–528.

Kuo-Hang L-L, Chen S-S, Huang Y-S, Chen S-J, Hsieh Y-I (2007) Growth strains and related wood structures in the leaning trunk and branches of *Trochodendron aralioides* – a vessel-less dicotyledon. IAWA J 28: 211–223.

Lauber K, Wagner G (2007) Flora Helvetica. Flora der Schweiz. Verlag Paul Haupt. Bern, Stuttgart, Wien.

Lemesle R (1956) Revue histologie végétale. Les élements du xylème. Bull Soc Fr 103: 629–677.

Lev Yadun S (1994) Introduction of sclereid differentiation in the pith of *Arabidopsis thaliana* (L.) Heynh. J Exp Bot 45: 1845–1949.

Lindsey AA (1938) Anatomical evidence for the Menyanthaceae. Am J Bot 25: 480–485.

Liu Y-B, Zhang Q-B (2007) Growth rings of roots in perennial forbs in Duolun grassland, Inner Mongolia, China. J Int Plant Biol 49: 144–149.

Ma R, Wu S, Wang F (1994) Studies on anatomy and desert adaptibility of stem secondary xylem in 6 species of *Calligonum*. Acta Bot Sinica 36: 55–60.

## References


Mabberley DJ (1997) The plant-book. A portable dictionary of the vascular plants. Cambridge Univ. Press. Cambridge.

Mennega AMW (2005) Wood anatomy of the subfamily Euphorbioideae. IAWA J 26: 1–68.

Messeri A (1938) Studio anatomico-ecologico del legno secondario di alcune piante del Fezzan. Nuovo g bot ital 45: 267–356.

Metcalfe CR, Chalk L (1957) Anatomy of the dicotyledons. Leaves, stem and wood in relation to taxonomy with notes on economic uses. Clarendon Press. Oxford.

Mikesell JE (1979) Anomalous secondary thickening in *Phytolaca amaericana* L. (Phytolacaceae). Am J Bot 66: 997–1005.

Miller AG, Morris M (1988) Plants of Dhofar. The southern region of Oman. Traditional, economic and medicinal uses. The office of the adviser for conservation of the environment, Diwan of Royal Court. Sultanate of Oman.

Millner ME (1934) Anatomy of *Silene vulgaris* and *Silene maritima* as related to ecological and genetical problems. New Phytol 33: 77–95.

Moss E H (1936) Ecology of *Epilobium angustifolium* with particular reference to rings of periderm in the wood. Am J Bot 23: 114–120.

Neumann K, Schoch W, Détienne P, Schweingruber FH (2001) Woods of the Sahara and the Sahel. An anatomical atlas. Verlag Paul Haupt. Bern, Stuttgart, Wien.

Ogundipe O T (1993) Studies of *Calotropis procera* (Ait.) Ait. f. The anatomy of stems. Phytomorphology 43: 147–152.

Ozenda P (1983) Flore du Sahara. Centre National de la Recherche Scientifique. Paris.

Panshin AJ, Zeeuw De C (1970) Textbook of wood technology. I. Structure, identification, uses, and properties of commercial wood of the United States and Canada. New York.

Patel RN (1974) Wood anatomy of the dicotyledons indigenous to New Zealand. 4 Winteraceae. New Zealand J Bot 12: 19–32.

Patil VS, Kishore SR (2008) Structure and development of inter and intraxylary phloem in *Leptadenia reticulata* (Asclpiadaceae). Polish Bot J 53: 5–13.

Pfeiffer H (1926) Das abnorme Dickenwachstum. In: Linsbauer K (ed) Handbuch der Pflanzenanatomie. Gebrüder Borntträger Verlag. Berlin, Stuttgart.

Prabhakar M, Ramayya N (1979) Anatomical studies of the Indian Portulacaceae: I. Stem wood. Indian J Bot 96–106.

Richter HG (1981) Anatomie des sekundären Xylems und der Rinde der Lauraceae. Sonderbände des Naturwiss. Vereins Hamburg 5. Verlag Parey, Hamburg, Berlin.

Richter HG, Dallwitz MJ (2000 onwards). Commercial timbers: descriptions, illustrations, identification, and information retrieval. In English, French, German, and Spanish. Version: 4th May 2000. *http://biodiversity.uno.edu/delta/*

Roig FA, Videla JE (2006-2010) Anatomia de la madera de arbustos de montana des NW des Mendoza, Argentina. Xama 19-23: 157-238.

Rollins RC (1939) The cruciferous genus *Stanleya*. Lloydia 2: 109–127.

Roth I (1981) Structural pattern of tropical barks. Gebrüder Borntträger Verlag. Berlin, Stuttgart.

Rothmaler W (2005) Exkursionsflora von Deutschland. Gefässpflanzen, Bd. 4. Elsevier, Spektrum Akademischer Verlag. München.

Schneider E, Carlquist S (1995) Vessel origins in Nymphaeaceae: *Euryale* and *Victoria*. Bot J Linn Soc 119: 185–193.

Schneider E, Carlquist S (1995) Vessels in the roots of *Barclaya rotundifolia* (Nypmphaeaceae). Am J Bot 82: 1343–1349.

Schneider E, Carlquist S (1996) Conductive tissue in *Ceratophyllum demersum* (Ceratophyllaceae). Sida 17: 437–443.

Schönfelder P, Schönfelder I (1997) Die Kosmos-Kanarenflora. Franckh-Kosmos Verlag. Stuttgart.

Schweingruber FH (2006) Anatomical characteristics and ecological trends in the xylem and phloem of Brassicaceae and Resedaceae. IAWA J 27: 419–442.

Schweingruber FH (1990) Anatomy of European woods. Verlag Paul Haupt. Bern, Stuttgart, Wien.

Schweingruber FH (2007) Stem anatomy of Caryophyllaceae. Flora 202: 281–292.

Schweingruber FH, Börner A, Schulze E-D (2006) Atlas of woody plant stems. Evolution, structure and environmental modifications. Spinger Verlag. Berlin, Heidelberg, New York.

Schweingruber FH, Poschlod P (2005) Growth rings in herbs and shrubs: life span, age determination and stem anatomy. For Snow Landsc Res 79 (3): 195–415.

Shen Y-F (1954) Phylogeny and wood anatomy of *Nandina*. Taiwania 5: 85–92.

Shu-Yin Zhang (1992) Wood anatomy of the Rosaceae. Rijksherbarium/Hortus Botanicus Leiden.

Sieber M, Kucera LJ (1980) On the stem anatomy of *Clematis vitalba* L. IAWA J n.s. 1: 49–54.

Smith P (1979) A comparative study of the stem structure of the genus *Clematis* with special reference to anatomical changes induced by vegetative propagation. Trans R Soc Edinb Earth Sci 70: 643–664.

Solereder H (1908) Systematic anatomy of the dicotylodons. Oxford.

Stepanova A, Chavchadaze E S, Jansen S (2007) Comparative wood anatomy of perennial shoots of *Potentilla* (Rosaceae) IAWA J 28: 405–421.

Strasburger E (2008) Lehrbuch der Botanik für Hochschulen. Neubearbeitung von Sitte P, Weiler EW, Bresinsky A, Kadereit JW, Körner C. Spektrum Akad Verl. Heidelberg, Berlin.

Takahashi A (1985) Wood anatomical studies of Polycarpicae. II Ranunculales. Sci Rep Osaka Univ 34: 121–144.

Tellini G (1939) Ricerche anatomiche su "*Dianthus arboreus* L. *verus*" (= *D. aciphyllus* Sieb.) Nuovo G Bot Ital 46: 615–642.

Trockenbrodt M (1990) Survey and discussion of the terminology used in bark anatomy. IAWA J 11: 141–166.

Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA (1964–1980) Flora Europaea. 5 vols. University Press. Cambridge.

van der Walt JJA, Werker E, Fahn A (1987) Wood anatomy of *Pelargonium* (Geraniaceae). IAWA J 8: 95–108.

Walter H, Lieth H (1967) Klimadiagramm Weltatlas. Gustav Fischer Verlag. Jena.

Walther H, Breckle W (1991) Ökologie der Erde. UTB Grosse Reihe. Gustav Fischer Verlag. Stuttgart.

Waly M (1999) Wood anatomical characters of the Egyptian *Tamarix* L. species and its taxonomic significance. Taeckholmia 19: 115–125.

Wayne H, England R, Tolbert J (1964) A seasonal study of the vegetative shoot apex of *Myriophyllum heterophyllum*. Am J Bot 51: 349–353.

Weber W (1976) Rocky Mountain Flora. Colorado Ass. Press. Boulder.

Westra L Y T, Koek-Norman J (2004) Wood altas of Euhorbiaceae s.l. IAWA J Suppl 4.

Wheeler EA, Baas P, Gasson PE (eds.) (1989) IAWA-list of microscopic features for hardwood identification. IAWA J 10: 219–332.

Wilson CA, Clyde LC (2000) Agricultural Handbook 709. United States Department of Agriculture, Forest Service *http://www.rmrs.nau.edu/publications/ah_709/index.html*

Zhang X, Chen Y, Chai F, Wu S (2000) Anatomical characteristics and phylogenetic relationships of secondary xylem of Magnoliaceae in China. Bull Bot Res 20: 318–323.

Zimmermann A (1922) Die Cucurbitaceaeen. Beiträge zur Anatomie, Physiologie, Morphologie, Biologie, Pathologie und Systematik. Gustav Fischer Verlag. Jena.

# Alphabetic List of Species


*Abelmoschus esculentus*.....Malvaceae .....254
*Abronia fragrans*.....Nyctaginaceae .....32, 282, 283, 284
*Abronia latifolia*.....Nyctaginaceae .....282, 283
*Abutilon palmeri*.....Malvaceae .....254, 257
*Acacia dealbata*.....Fabaceae.....175
*Acacia greggii*.....Fabaceae.....175, 191
*Acacia mearnsi*.....Fabaceae.....175
*Acacia raddiana*.....Fabaceae.....175, 177, 191
*Acacia senegal*.....Fabaceae.....175
*Acacia tortilis*.....Fabaceae.....175
*Acacia tortuosa*.....Fabaceae.....177
*Acaena splendens*.....Rosaceae.....383
*Acanthophyllum microcephalum*.....Caryophyllaceae.....103, 109, 111
*Acer campestre*.....Sapindaceae.....419, 420
*Acer heldreichii*.....Sapindaceae.....419, 420
*Acer hycranum*.....Sapindaceae.....419
*Acer monspessulanum*.....Sapindaceae.....419, 421
*Acer negundo*.....Sapindaceae.....419, 420
*Acer obtusatum*.....Sapindaceae.....419, 420
*Acer obtusifolium*.....Sapindaceae.....28, 419, 421
*Acer opalus*.....Sapindaceae.....419
*Acer opalus* ssp. *granatense*.....Sapindaceae.....419
*Acer platanoides*.....Sapindaceae.....419
*Acer pseudoplatanus*.....Sapindaceae.....419, 421
*Acer sempervirens*.....Sapindaceae.....419
*Acer tataricum*.....Sapindaceae.....21, 419, 420
*Acer trautvetteri*.....Sapindaceae.....419
*Achyranthes aspera*.....Amaranthaceae.....38, 40, 41, 42
*Achyranthes sicula*.....Amaranthaceae.....38, 40
*Acinos arvensis*.....Lamiaceae .....32
*Acokanthera oblongifolia*.....Apocyanaceae & Asclepiadaceae....54, 56, 58
*Aconitum lycoctonum* ssp. *vulparia*.....Ranunculaceae .....352, 354, 355
*Aconitum napellus* ssp. *lusitanicum*.....Ranunculaceae ....352, 354, 355, 358
*Aconitum variegatum* ssp. *paniculatum*.....Ranunculaceae .....352, 354
*Actaea spicata*.....Ranunculaceae .....352, 359, 361
*Adenium obesum*.....Apocyanaceae & Asclepiadaceae ....54, 55, 56, 57
*Adenocarpus decorticans*.....Fabaceae.....175, 180
*Adenocarpus telonensis*.....Fabaceae.....175
*Adenocarpus viscosus*.....Fabaceae.....175, 178
*Adenolinum lewisii*.....Linaceae.....15, 237, 238, 239
*Adonis aestivalis*.....Ranunculaceae .....353
*Adonis flammea*.....Ranunculaceae ..14, 352, 355, 362, 363, 364
*Adonis vernalis*.....Ranunculaceae .....352, 353, 359
*Aeonium arboreum*.....Crassulaceae.....134, 136
*Aeonium decorum*.....Crassulaceae.....134
*Aeonium simsii*.....Crassulaceae.....134, 137
*Aeonium smithii*.....Crassulaceae.....134, 138
*Aeonium spathulatum*.....Crassulaceae.....134
*Aeonium undulatum*.....Crassulaceae.....134, 136
*Aeonium urbicum*.....Crassulaceae.....17, 134, 136
*Aeonium viscatum*.....Crassulaceae.....23, 134, 137
*Aerva javanica*.....Amaranthaceae.....38, 43
*Aerva persica*.....Amaranthaceae.....38
*Aesculus carnea*.....Sapindaceae.....419
*Aesculus hippocastaneum*.....Sapindaceae.....16, 419, 421, 422
*Aethionema saxatile*.....Brassicaceae.....79
*Aethionema thomasiana*.....Brassicaceae.....15, 79
*Agathophora alopecuroides*.....Amaranthaceae.....38
*Agrimonia eupatoria*.....Rosaceae.....383
*Agrostemma ghitago*.....Caryophyllaceae.....103, 107, 111
*Aichryson parlatorei*.....Crassulaceae.....134, 137
*Aizoon canariense*.....Aizoaceae .....27, 36
*Akebia quinata*.....Lardizabalaceae .....228, 230
*Akebia trifoliata*.....Lardizabalaceae .....228, 229, 231
*Alcea rosea*.....Malvaceae .....254
*Alcea rugosa*.....Malvaceae .....254, 256, 258
*Alchemilla alpina*.....Rosaceae.....32, 383, 385, 392
*Alchemilla decumbens*.....Rosaceae.....383
*Alchemilla fissa*.....Rosaceae.....383
*Alchemilla hoppeana*.....Rosaceae.....383
*Alchemilla hybrida*.....Rosaceae.....383
*Alchemilla pentaphyllea*.....Rosaceae.....383
*Alchemilla sericea*.....Rosaceae.....383
*Alchemilla vulgaris*.....Rosaceae.....383
*Alliaria officinalis*.....Brassicaceae.....79
*Alnus crispa*.....Betulaceae .....73, 75
*Alnus glutinosa*.....Betulaceae .....73, 74
*Alnus hirsuta*.....Betulaceae .....73
*Alnus incana*.....Betulaceae .....73, 74, 77
*Alnus orientalis*.....Betulaceae .....73
*Alnus tenuifolia*.....Betulaceae .....73
*Alnus viridis*.....Betulaceae .....73, 75, 76
*Althaea hirsuta*.....Malvaceae .....254
*Althaea officinalis*.....Malvaceae .....254, 256, 258
*Alyssoides utricularia*.....Brassicaceae.....79
*Alyssum alpestre*.....Brassicaceae.....79
*Alyssum alyssoides*.....Brassicaceae.....79
*Alyssum argenteum*.....Brassicaceae.....23, 79
*Alyssum ligusticum*.....Brassicaceae.....79
*Alyssum lusitanicum*.....Brassicaceae.....29
*Alyssum montanum*.....Brassicaceae.....79
*Alyssum parviflorum*.....Brassicaceae.....79
*Alyssum simplex*.....Brassicaceae.....79
*Amaranthus blithum*.....Amaranthaceae.....38, 40, 42, 43
*Amaranthus caudatus*.....Amaranthaceae.....39
*Amaranthus cruentus*.....Amaranthaceae.....38
*Amaranthus deflexus*.....Amaranthaceae.....38
*Amaranthus hybridus*.....Amaranthaceae.....38, 40, 42
*Amaranthus lividus*.....Amaranthaceae.....38, 39
*Amaranthus retroflexus*.....Amaranthaceae.....38, 40, 42
*Amaranthus standleyanus*.....Amaranthaceae.....38, 40
*Amaranthus viridis*.....Amaranthaceae.....38, 42
*Amborella trichopoda*.....Amborellaceae.....13, 47, 48
*Amelanchier florida*.....Rosaceae.....383
*Amelanchier laevis*.....Rosaceae.....383
*Amelanchier ovalis*.....Rosaceae.....383
*Amelanchier sanguinea*.....Rosaceae.....383
*Amelanchier utahensis*.....Rosaceae.....383, 389, 390
*Amerosedum lanceolatum*.....Crassulaceae.....134
*Amorpha fruticosa*.....Fabaceae.....175, 178, 179
*Ampelopsis brevipedunculata*.....Vitaceae .....465, 466
*Anabasis brevifolia*.....Amaranthaceae.....27, 38
*Anagallis arvensis*.....Primulaceae.....344, 345, 350
*Anagallis foemina*.....Primulaceae.....344
*Anagallis monelli*.....Primulaceae.....344, 350
*Anagyris foetida*.....Fabaceae.....175, 178
*Anastatica hierochuntica*.....Brassicaceae.....79, 80
*Andrachne colchica*.....Euphorbiaceae.....164, 168, 169, 171
*Andromeda polifolia*.....Ericaceae .....19, 156, 162
*Androsace alpina*.....Primulaceae.....344, 348
*Androsace chamaejasme*.....Primulaceae.....345
*Androsace helvetica*.....Primulaceae.....344, 345, 348
*Androsace lactea*.....Primulaceae.....344
*Androsace obtusifolia*.....Primulaceae.....344
*Androsace septentrionalis*.....Primulaceae.....344, 349
*Androsace villosa*.....Primulaceae.....344, 348
*Androsace vitaliana*.....Primulaceae.....344, 345
*Anemone coronaria*.....Ranunculaceae .....352, 354
*Anemone narcissiflora*.....Ranunculaceae .....352
*Anemone nemorosa*.....Ranunculaceae .....352, 354, 355
*Anemone ranunculoides*.....Ranunculaceae .....15, 352, 357
*Antennaria canescens*.....Asteraceae .....32
*Anthyllis cytisoides*.....Fabaceae.....175, 178, 180, 190
*Anthyllis terniflora*.....Fabaceae.....175, 178, 179
*Anthyllis tetraphylla*.....Fabaceae.....175
*Anthyllis vulneraria*.....Fabaceae.....175, 177, 186
*Apocynum androsaemifolium*.....Apocyanaceae & Asclepiadaceae.....54
*Apocynum cannabinum*.....Apocyanaceae & Asclepiadaceae.....54, 58
*Apollonias barbujana*.....Lauraceae .....8, 22, 232, 233, 234, 235
*Aptenia cordifolia*.....Aizoaceae .....35, 36, 37
*Aptenia fruticosa*.....Aizoaceae .....36, 37
*Aquilegia coerulea*.....Ranunculaceae .....352
*Aquilegia vulgaris*.....Ranunculaceae .....29, 352, 353, 359, 361
*Arabidopsis thaliana*.....Brassicaceae.....79
*Arabis alpina, alpina*.....Brassicaceae.....79
*Arabis ciliata*.....Brassicaceae.....79

*Arabis coerulea* ..... Brassicaceae ..... 79
*Arabis hirsuta* ..... Brassicaceae ..... 30, 79, 86
*Arabis nova* ..... Brassicaceae ..... 79
*Arabis procurrens* ..... Brassicaceae ..... 79
*Arabis rosea* ..... Brassicaceae ..... 79
*Arabis subcoriaria* ..... Brassicaceae ..... 79
*Arabis sudetica* ..... Brassicaceae ..... 79
*Arabis turrita* ..... Brassicaceae ..... 79
*Arbutus andrachne* ..... Ericaceae ..... 156, 159, 162
*Arbutus canariensis* ..... Ericaceae ..... 20, 156, 160
*Arbutus unedo* ..... Ericaceae ..... 156, 159, 162
*Arctostaphylos alpina* ..... Ericaceae ..... 156, 158, 162
*Arctostaphylos patula* ..... Ericaceae ..... 156
*Arctostaphylos rubra* ..... Ericaceae ..... 156, 162
*Arctostaphylos uva-ursi* ..... Ericaceae ..... 156, 162
*Arenaria aggregata* ..... Caryophyllaceae ..... 103
*Arenaria biflora* ..... Caryophyllaceae ..... 103, 106, 111
*Arenaria ciliata* ..... Caryophyllaceae ..... 19, 103
*Arenaria serpyllifolia* ..... Caryophyllaceae ..... 30, 103
*Argemone chisosensis* ..... Papaveraceae ..... 304, 307, 308, 309
*Argemone ochroleuca* ..... Papaveraceae ..... 304, 306, 308, 309
*Argemone pleiacantha* ..... Papaveraceae ..... 304
*Aristolochia clematitis* ..... Aristolochiaceae ..... 20, 61, 62, 63, 64, 65
*Aristolochia gigantea* ..... Aristolochiaceae ..... 13, 61, 62, 63, 64, 65
*Aristolochia macrophylla* ..... Aristolochiaceae ..... 15, 19, 61, 62, 63, 64, 65
*Aristolochia manshuriensis* ..... Aristolochiaceae ..... 61, 62, 63, 64, 65
*Aristolochia pallida* ..... Aristolochiaceae ..... 61, 62, 63, 65
*Armeria alpina* ..... Plumbaginaceae ..... 323, 324, 327
*Armeria arctica* ..... Plumbaginaceae ..... 323, 326
*Armeria arenaria* ..... Plumbaginaceae ..... 18, 29, 323, 324, 326, 327
*Armeria maritima* ..... Plumbaginaceae ..... 323, 324, 326
*Artemisia dracunculus* ..... Asteraceae ..... 31
*Artemisia tridentata* ..... Asteraceae ..... 27
*Arthrocneumum fruticosum* ..... Amaranthaceae ..... 38, 40
*Arthrocneumum glaucum* ..... Amaranthaceae ..... 38, 40
*Arthrocneumum macrostachya* ..... Amaranthaceae ..... 38
*Arthrocneumum perenne* ..... Amaranthaceae ..... 38
*Aruncus dioicus* ..... Rosaceae ..... 383
*Asarum europaeum* ..... Aristolochiaceae ..... 61, 62, 63, 64, 65
*Asclepias subverticillata* ..... Apocyanaceae & Asclepiadaceae ..... 54, 58
*Asclepias syriaca* ..... Apocyanaceae & Asclepiadaceae ..... 54
*Asclepias tuberosa* ..... Apocyanaceae & Asclepiadaceae ..... 54
*Asperugo procumbens* ..... Boraginaceae ..... 17
*Asperula aristata* ..... Rubiaceae ..... 28, 395, 397, 398, 399
*Asperula cynanchica* ..... Rubiaceae ..... 395
*Asperula purpurea* ..... Rubiaceae ..... 395
*Asperula taurina* ..... Rubiaceae ..... 395, 396, 398, 399
*Asperula tinctoria* ..... Rubiaceae ..... 395
*Astragalus alpinus* ..... Fabaceae ..... 175
*Astragalus armatus* ..... Fabaceae ..... 175, 181
*Astragalus campestre* ..... Fabaceae ..... 175, 181
*Astragalus cruckshansii* ..... Fabaceae ..... 175, 182
*Astragalus depressus* ..... Fabaceae ..... 175, 181
*Astragalus exscapus* ..... Fabaceae ..... 175, 177, 181
*Astragalus frigidus* ..... Fabaceae ..... 175, 181, 182
*Astragalus fruticosus* ..... Fabaceae ..... 175, 181
*Astragalus glyciphyllos* ..... Fabaceae ..... 175
*Astragalus lentiginosus* ..... Fabaceae ..... 175, 181, 182, 183
*Astragalus leontinus* ..... Fabaceae ..... 175, 181
*Astragalus massiliensis* ..... Fabaceae ..... 175, 181
*Astragalus microcephalus* ..... Fabaceae ..... 175, 183
*Astragalus monspessulanus* ..... Fabaceae ..... 175
*Astragalus penduliflorus* ..... Fabaceae ..... 175
*Astragalus praelongus* ..... Fabaceae ..... 175, 181, 182, 183
*Astragalus sempervirens* ..... Fabaceae ..... 175
*Astragalus stella* ..... Fabaceae ..... 175, 181, 183
*Astragalus subulatus* ..... Fabaceae ..... 175, 183
*Astrantia major* ..... Apiaceae ..... 28
*Atriplex canescens* ..... Amaranthaceae ..... 38
*Atriplex dimorphostegia* ..... Amaranthaceae ..... 38, 44
*Atriplex glauca* ..... Amaranthaceae ..... 38, 42
*Atriplex halimus* ..... Amaranthaceae ..... 38
*Atriplex patula* ..... Amaranthaceae ..... 16, 32, 38, 41, 45
*Atriplex portulacoides* ..... Amaranthaceae ..... 38
*Atriplex prostrata* ..... Amaranthaceae ..... 38
*Atriplex saggitata* ..... Amaranthaceae ..... 38
*Atriplex semibaccata* ..... Amaranthaceae ..... 27, 38, 41, 43
*Aubrieta deltoides* ..... Brassicaceae ..... 79
*Aurinia saxatilis* ..... Brassicaceae ..... 79, 82
*Barbarea intermedia* ..... Brassicaceae ..... 79
*Barbarea vulgaris* ..... Brassicaceae ..... 79, 86
*Belliolum gracile* ..... Winteraceae ..... 470, 471, 472
*Bencomnia sphaerocarpa* ..... Rosaceae ..... 383, 387
*Berberis aetnensis* ..... Berberidaceae ..... 13, 67, 68
*Berberis buxifolia* ..... Berberidaceae ..... 67, 69
*Berberis cretica* ..... Berberidaceae ..... 67, 69, 70
*Berberis empetrifolium* ..... Berberidaceae ..... 67, 68, 69, 70, 71, 72
*Berberis hispanica* ..... Berberidaceae ..... 67
*Berberis julianae* ..... Berberidaceae ..... 16, 21, 27, 67, 68, 69, 70, 71
*Berberis verruculosa* ..... Berberidaceae ..... 67, 70
*Berberis vulgaris* ..... Berberidaceae ..... 29, 67, 70, 72
*Bergenia ciliata* ..... Saxifragaceae ..... 426, 427
*Bergenia crassifolia* ..... Saxifragaceae ..... 423, 425
*Berteroa incana* ..... Brassicaceae ..... 79, 86
*Betula aetnensis* ..... Betulaceae ..... 73
*Betula davurica* ..... Betulaceae ..... 73
*Betula exilis* ..... Betulaceae ..... 73, 74
*Betula glandulosa* ..... Betulaceae ..... 20, 73, 75, 76
*Betula humilis* ..... Betulaceae ..... 73, 74
*Betula nana* ..... Betulaceae ..... 73
*Betula pendula* ..... Betulaceae ..... 73, 75, 77
*Betula pubescens* ..... Betulaceae ..... 73
*Betula tortuosa* ..... Betulaceae ..... 73
*Bidens cernua* ..... Asteraceae ..... 31
*Biscutella brevicaulis* ..... Brassicaceae ..... 79
*Biscutella cichoriifolia* ..... Brassicaceae ..... 79
*Biscutella laevigata* ..... Brassicaceae ..... 79
*Blackstonia perfoliata* ..... Gentianaceae ..... 199, 200, 201, 202
*Boscia arabica* ..... Capparaceae ..... 98, 100
*Bosea cypria* ..... Amaranthaceae ..... 26, 38, 40, 42
*Bosea yervamora* ..... Amaranthaceae ..... 38, 40
*Bougainvillea spectabilis* ..... Nyctaginaceae ..... 28, 282, 283, 284
*Bougainvillea spinosa* ..... Nyctaginaceae ..... 282
*Brassica nigra* ..... Brassicaceae ..... 24, 79
*Brassica oleracea* ..... Brassicaceae ..... 79, 80
*Brassica rapa* ..... Brassicaceae ..... 79
*Brassica repanda* ..... Brassicaceae ..... 79
*Braya alpina* ..... Brassicaceae ..... 79
*Braya humilis* ..... Brassicaceae ..... 79
*Broussonetia papyrifera* ..... Moraceae ..... 268, 269, 270
*Bryonia dioeca* ..... Cucurbitaceae ..... 141, 142, 143, 145, 147, 148
*Bryonia verrucosa* ..... Cucurbitaceae ..... 141, 147
*Bubbia sp.* ..... Winteraceae ..... 470, 471, 472
*Bufonia paniculata* ..... Caryophyllaceae ..... 103
*Bunias erucago* ..... Brassicaceae ..... 79, 86
*Bunias orientalis* ..... Brassicaceae ..... 79
*Buxus sempervirens* ..... Buxaceae ..... 30, 88, 89, 90, 91
*Cadaba longifolia* ..... Capparaceae ..... 98, 99
*Cadaba rotundifolia* ..... Capparaceae ..... 98, 99, 100
*Cakile edentula* ..... Brassicaceae ..... 79
*Cakile maritima* ..... Brassicaceae ..... 19, 79
*Calepina irregularis* ..... Brassicaceae ..... 79
*Calicotome spinosa* ..... Fabaceae ..... 175
*Calicotome villosa* ..... Fabaceae ..... 175
*Calliandra eriophyllum* ..... Fabaceae ..... 175
*Calligonum azel* ..... Polygonaceae ..... 333
*Calligonum comosum* ..... Polygonaceae ..... 21, 332, 333, 334, 336, 337, 340
*Calligonum crinitum* ..... Polygonaceae ..... 332, 336
*Calluna vulgaris* ..... Ericaceae ..... 156, 162
*Calotropis procera* ..... Apocyanaceae & Asclepiadaceae ..... 54, 55, 56, 57, 59
*Caltha palustris* ..... Ranunculaceae ..... 352, 358
*Calystegia sepium* ..... Convolvulaceae ..... 14
*Camelina microcarpa* ..... Brassicaceae ..... 79
*Camelina pilosa* ..... Brassicaceae ..... 79
*Campanula beckiana* ..... Campanulaceae ..... 20
*Cannabis sativa* ..... Cannabaceae ..... 93, 94, 95
*Canotia holocantha* ..... Celastraceae ..... 113, 114, 115, 116, 117
*Capparis spinosa* ..... Capparaceae ..... 98, 99, 100, 101
*Capsella bursa-pastoris* ..... Brassicaceae ..... 14, 79, 82
*Capsella rubella* ..... Brassicaceae ..... 79
*Caragana arborescens* ..... Fabaceae ..... 175
*Caragana jubata* ..... Fabaceae ..... 175, 179
*Caragana pygmaea* ..... Fabaceae ..... 175
*Caragana ussuriensis* ..... Fabaceae ..... 175
*Caralluma quadrangula* ..... Apocyanaceae & Asclepiadaceae ..... 54, 55, 56, 57
*Cardamine alpina* ..... Brassicaceae ..... 79, 85
*Cardamine amara* ..... Brassicaceae ..... 79
*Cardamine bulbifera* ..... Brassicaceae ..... 79, 84
*Cardamine enneaphyllos* ..... Brassicaceae ..... 79, 85
*Cardamine flexuosa* ..... Brassicaceae ..... 79

*Cardamine halleri* ..... Brassicaceae ..... 79
*Cardamine heptaphylla* ..... Brassicaceae ..... 79
*Cardamine hirsuta* ..... Brassicaceae ..... 79
*Cardamine pentaphyllos* ..... Brassicaceae ..... 79
*Cardamine pratensis* ..... Brassicaceae ..... 79
*Cardamine resedifolia* ..... Brassicaceae ..... 79
*Cardaminopsis arenosa* ..... Brassicaceae ..... 79
*Cardaminopsis halleri* ..... Brassicaceae ..... 79
*Cardaria draba* ..... Brassicaceae ..... 79, 81
*Cardopatium corymbosum* ..... Asteraceae ..... 26
*Carpinus betulus* ..... Betulaceae ..... 73, 75, 76, 77
*Carpinus orientalis* ..... Betulaceae ..... 73, 76
*Carpobrotus acinaciformis* ..... Aizoaceae ..... 35
*Carrichtera annua* ..... Brassicaceae ..... 29, 79
*Cassia holosericea* ..... Fabaceae ..... 175
*Cassia obovata* ..... Fabaceae ..... 175
*Cassiope tetragona* ..... Ericaceae ..... 156, 158, 162
*Castanea sativa* ..... Fagaceae ..... 193, 194, 196, 197
*Castilleja arctica* ..... Orobanchaceae ..... 19
*Caylusea hexagyna* ..... Resedaceae ..... 372, 373
*Ceanothus arborescens* ..... Rhamnaceae ..... 376, 381
*Ceanothus fendleris* ..... Rhamnaceae ..... 376
*Ceanothus hearstiorum* ..... Rhamnaceae ..... 376, 380
*Ceanothus integerrimus* ..... Rhamnaceae ..... 376
*Ceanothus velutinus* ..... Rhamnaceae ..... 376, 379, 380, 381
*Celastrus flagellaris* ..... Celastraceae ..... 113, 114, 115, 116
*Celastrus orbiculatus* ..... Celastraceae ..... 113
*Celtis australis* ..... Ulmaceae ..... 450, 452
*Celtis caucasica* ..... Ulmaceae ..... 450, 451, 452
*Centaurea solstitialis* ..... Asteraceae ..... 31
*Centaurium erythraea* ..... Gentianaceae ..... 199, 200, 201
*Cerastium alpinum* ..... Caryophyllaceae ..... 103
*Cerastium arvense* ..... Caryophyllaceae ..... 20, 103
*Cerastium fontanum* ..... Caryophyllaceae ..... 103
*Cerastium glomeratum* ..... Caryophyllaceae ..... 103
*Cerastium latifolium* ..... Caryophyllaceae ..... 103
*Cerastium semidecandrum* ..... Caryophyllaceae ..... 8, 103, 105
*Cerastium sp.* ..... Caryophyllaceae ..... 103
*Ceratonia siliqua* ..... Fabaceae ..... 175
*Ceratophyllum demersum* ..... Ceratophyllaceae ..... 15, 118, 119
*Cercidiphyllum japonicum* ..... Cercidiphyllaceae ..... 120, 121
*Cercis siliquastrum* ..... Fabaceae ..... 175
*Ceropegia fusca* ..... Apocyanaceae & Asclepiadaceae ..... 54, 55, 56, 57, 58
*Chamaecytisus hirsutus* ..... Fabaceae ..... 175
*Chamaecytisus proliferus* ..... Fabaceae ..... 175, 178, 179
*Chamaecytisus purpureus* ..... Fabaceae ..... 175
*Chamaecytisus ratisbonensis* ..... Fabaceae ..... 175
*Chamaecytisus supinus* ..... Fabaceae ..... 175
*Chamaedaphne calyculata* ..... Ericaceae ..... 156
*Chamaerhodos altaica* ..... Rosaceae ..... 383, 388
*Chelidonium majus* ..... Papaveraceae ..... 304, 305, 307, 309
*Cheneloides tomentosa* ..... Amaranthaceae ..... 38, 40, 44, 45
*Chenopodium album* ..... Amaranthaceae ..... 38, 39
*Chenopodium bonus-henricus* ..... Amaranthaceae ..... 38, 39, 40, 41
*Chenopodium frutescens* ..... Amaranthaceae ..... 27, 38, 41
*Chenopodium glaucum* ..... Amaranthaceae ..... 26, 38, 40
*Chenopodium hybridum* ..... Amaranthaceae ..... 38
*Chenopodium murale* ..... Amaranthaceae ..... 38, 45
*Chenopodium polyspermum* ..... Amaranthaceae ..... 38
*Chenopodium strictum* ..... Amaranthaceae ..... 38, 44
*Chenopodium urbicum* ..... Amaranthaceae ..... 38, 40
*Chimaphila umbellata* ..... Ericaceae ..... 156, 158, 160
*Chosenia arbutifolia* ..... Salicaceae ..... 406
*Chrysosplenium alternifolium* ..... Saxifragaceae ..... 423
*Chrysothamnus nauseosus* ..... Rhamnaceae ..... 376, 378
*Chrysothamnus parryi* ..... Rhamnaceae ..... 376, 381
*Chrysothamnus viscidiflorus* ..... Rhamnaceae ..... 376, 378, 380
*Cichorium intybus* ..... Asteraceae ..... 32
*Circaea lutetiana* ..... Onagraceae ..... 290, 291, 293
*Cissus quadrangularis* ..... Vitaceae ..... 20, 465, 466, 467, 468
*Cistanche tinctoria* ..... Orobanchaceae ..... 15
*Cistanthe salsoloides* ..... Portulaccaceae ..... 341, 342, 343
*Cistus albidus* ..... Cistaceae ..... 122
*Cistus clusii* ..... Cistaceae ..... 122
*Cistus creticus* ..... Cistaceae ..... 122, 125
*Cistus crispus* ..... Cistaceae ..... 122, 123
*Cistus ladanifer* ..... Cistaceae ..... 122, 123
*Cistus laurifolius* ..... Cistaceae ..... 122, 123
*Cistus monspeliensis* ..... Cistaceae ..... 122, 123
*Cistus palhinae* ..... Cistaceae ..... 122
*Cistus salvifolius* ..... Cistaceae ..... 122, 123
*Cistus symphytifolius* ..... Cistaceae ..... 122
*Citrullus colocynthis* ..... Cucurbitaceae ..... 141, 142, 143, 147
*Citrus limon* ..... Rutaceae ..... 401, 403, 404
*Citrus sinensis* ..... Rutaceae ..... 401, 402, 403
*Clarkia purpurea* ..... Onagraceae ..... 290, 293, 294, 295
*Claytonia megarhiza* ..... Portulaccaceae ..... 341, 342
*Clematis alpina* ssp. *alpina* ..... Ranunculaceae ..... 352, 353, 367, 369, 370
*Clematis alpina* ssp. *sibirica* ..... Ranunculaceae ..... 352, 367
*Clematis campaniflora* ..... Ranunculaceae ..... 352, 367
*Clematis cirrhosa* ..... Ranunculaceae ..... 352, 367
*Clematis columbiana* ..... Ranunculaceae ..... 352, 367, 368
*Clematis drumondi* ..... Ranunculaceae ..... 352
*Clematis flammula* ..... Ranunculaceae ..... 22, 352, 367, 368, 369, 370
*Clematis hirsutissima* ..... Ranunculaceae ..... 352, 367, 368, 369, 370
*Clematis montevidensis* ..... Ranunculaceae ..... 352, 367, 369
*Clematis recta* ..... Ranunculaceae ..... 24, 352, 368
*Clematis vitalba* ..... Ranunculaceae ..... 352, 367, 368, 370
*Clematis viticella* ..... Ranunculaceae ..... 352, 367
*Cleome arabica* ..... Capparaceae ..... 98, 99, 100, 101
*Cleome brachyphylla* ..... Capparaceae ..... 98, 99, 100, 101
*Cleome diandra* ..... Capparaceae ..... 98
*Cleome isomeris* ..... Capparaceae ..... 98, 99, 100, 101
*Clypeola jonthlaspi* ..... Brassicaceae ..... 79
*Cneorum tricoccum* ..... Ceoraceae ..... 130, 131, 132
*Cocculus pendulus* ..... Menispermaceae ..... 261, 262, 263
*Coincya cheiranthoides* ..... Brassicaceae ..... 79, 81
*Coincya richeri* ..... Brassicaceae ..... 79
*Coleogyne ramosissima* ..... Rosaceae ..... 383, 390
*Colubrina californica* ..... Rhamnaceae ..... 376
*Colutea arborescens* ..... Fabaceae ..... 175
*Colutea atlanica* ..... Fabaceae ..... 175
*Comandra umbellata* ..... Santalaceae ..... 415, 416, 417, 418
*Commicarpus boissieri* ..... Nyctaginaceae ..... 282, 283, 284
*Consolida regalis* ..... Ranunculaceae ..... 352, 353, 362, 363, 364
*Corema album* ..... Ericaceae ..... 156, 162, 163
*Cornulaca monacantha* ..... Amaranthaceae ..... 38
*Coronilla coronata* ..... Fabaceae ..... 175
*Coronilla juncea* ..... Fabaceae ..... 175, 178
*Coronilla minima* ..... Fabaceae ..... 175, 178, 179
*Coronilla vaginalis* ..... Fabaceae ..... 175, 184, 185
*Coronilla valentina* ..... Fabaceae ..... 175, 178, 179
*Coronopus didymus* ..... Brassicaceae ..... 79, 86
*Coronopus squamatus* ..... Brassicaceae ..... 79
*Corydalis aurea* ..... Papaveraceae ..... 304, 307
*Corydalis cava* ..... Papaveraceae ..... 304, 305
*Corydalis solida* ..... Papaveraceae ..... 304, 306
*Corylopsis pauciflora* ..... Hamamelidaceae & Altingiaceae ..... 217, 218, 220
*Corylus avellana* ..... Betulaceae ..... 18, 73, 75, 77
*Corylus colchica* ..... Betulaceae ..... 73
*Corylus colurna* ..... Betulaceae ..... 73
*Corylus heterophylla* ..... Betulaceae ..... 73, 74
*Corylus mandshurica* ..... Betulaceae ..... 25, 73
*Corylus maxima* ..... Betulaceae ..... 73
*Cotinus coggygria* ..... Anacardiaceae ..... 49, 50, 52
*Cotoneaster granatensis* ..... Rosaceae ..... 383
*Cotoneaster horizontalis* ..... Rosaceae ..... 383
*Cotoneaster integerrimus* ..... Rosaceae ..... 383
*Cotoneaster nebrodensis* ..... Rosaceae ..... 383
*Cotoneaster niger* ..... Rosaceae ..... 383
*Cotoneaster nummularius* ..... Rosaceae ..... 383
*Cotoneaster tomentosus* ..... Rosaceae ..... 383
*Cowania mexicana* ..... Rosaceae ..... 383
*Crataegus calycina* ..... Rosaceae ..... 383
*Crataegus curvisepala* ..... Rosaceae ..... 383
*Crataegus laciniata* ..... Rosaceae ..... 383
*Crataegus monogyna* ..... Rosaceae ..... 383, 393
*Crataegus oxyacantha* ..... Rosaceae ..... 383, 385
*Crataegus pinnatifida* ..... Rosaceae ..... 383
*Crataegus pycnoloba* ..... Rosaceae ..... 383
*Crataegus sanguinea* ..... Rosaceae ..... 383
*Cristaria dissecta* ..... Malvaceae ..... 254, 256, 257, 259
*Crotalaria saharae* ..... Fabaceae ..... 175, 178, 184, 190
*Crucianella maritima* ..... Rubiaceae ..... 395, 397, 399
*Cruciata laevipes* ..... Rubiaceae ..... 395
*Cucubalus baccifer* ..... Caryophyllaceae ..... 103, 104, 106, 108, 110, 111
*Cucumis sativus* ..... Cucurbitaceae ..... 14, 141, 142, 143, 144, 147
*Cucurbita maxima* ..... Cucurbitaceae ..... 141
*Cucurbita pepo* ..... Cucurbitaceae ..... 141
*Cucurbita sativa* ..... Cucurbitaceae ..... 141

*Cyclamen purpurascens* ..... Primulaceae ..... 344, 348
*Cydonia oblonga* ..... Rosaceae ..... 383
*Cytisophyllum sessilifolium* ..... Fabaceae ..... 175, 178, 180
*Cytisus austriacus* ..... Fabaceae ..... 175
*Cytisus maderensis* ..... Fabaceae ..... 175
*Cytisus nigricans* ..... Fabaceae ..... 175
*Cytisus patens* ..... Fabaceae ..... 175
*Cytisus pseudodecumbens* ..... Fabaceae ..... 175, 178
*Cytisus scoparius* ..... Fabaceae ..... 175, 177
*Cytisus striatus* ..... Fabaceae ..... 176
*Cytisus tener* ..... Fabaceae ..... 176, 180
*Daboecia cantabrica* ..... Ericaceae ..... 156
*Dalea lanata* ..... Fabaceae ..... 176
*Daphne alba* ..... Thymelaeaceae ..... 439
*Daphne alpina* ..... Thymelaeaceae ..... 439
*Daphne cneorum* ..... Thymelaeaceae ..... 439, 442
*Daphne gnidium* ..... Thymelaeaceae ..... 439, 440, 441
*Daphne laureola* ..... Thymelaeaceae ..... 439, 440, 441, 443
*Daphne mezereum* ..... Thymelaeaceae ..... 439, 442, 443
*Daphne oleoides* ..... Thymelaeaceae ..... 439
*Daphne petraea* ..... Thymelaeaceae ..... 439, 442
*Daphne pontica* ..... Thymelaeaceae ..... 439, 440, 442
*Daphne striata* ..... Thymelaeaceae ..... 20, 439, 440, 442
*Decaisnea fargesii* ..... Lardizabalaceae ..... 228, 229, 230, 231
*Dendromecon rigidum* ..... Papaveraceae ..... 304
*Descurainia bourgeana* ..... Brassicaceae ..... 79, 85
*Descurainia millefolia* ..... Brassicaceae ..... 79, 82, 83
*Descurainia preauxina* ..... Brassicaceae ..... 79, 82
*Descurainia sophia* ..... Brassicaceae ..... 79
*Desmodium glutinosum* ..... Fabaceae ..... 176
*Desmodium illinoense* ..... Fabaceae ..... 176, 185, 189
*Dianthus armeria* ..... Caryophyllaceae ..... 103, 105
*Dianthus balbisii* ..... Caryophyllaceae ..... 103
*Dianthus carthusianorum* ..... Caryophyllaceae ..... 103
*Dianthus caryophyllus* ..... Caryophyllaceae ..... 103
*Dianthus deltoids* ..... Caryophyllaceae ..... 103
*Dianthus furcatus* ..... Caryophyllaceae ..... 103, 107
*Dianthus gratianopolitanus* ..... Caryophyllaceae ..... 104
*Dianthus hispanicus* ..... Caryophyllaceae ..... 103, 105, 106
*Dianthus lumnitzeri* ..... Caryophyllaceae ..... 103
*Dianthus pavonius* ..... Caryophyllaceae ..... 103
*Dianthus repens* ..... Caryophyllaceae ..... 103
*Dianthus seguieri* ..... Caryophyllaceae ..... 22, 103, 106, 108
*Dianthus silvestris* ..... Caryophyllaceae ..... 103
*Dianthus superbus* ssp. *alpestris* ..... Caryophyllaceae ..... 103
*Dicentra formosa* ..... Papaveraceae ..... 304, 307, 308, 309
*Dicentra spectabilis* ..... Papaveraceae ..... 305
*Dicheranthus plocamoides* ..... Caryophyllaceae ..... 103, 106, 109
*Dichroanthus virescens* ..... Brassicaceae ..... 79
*Dictamnus albus* ..... Rutaceae ..... 401, 402
*Dionysia aretioides* ..... Primulaceae ..... 344
*Diplotaxis harra* ..... Brassicaceae ..... 79
*Diplotaxis muralis* ..... Brassicaceae ..... 79
*Diplotaxis tenuifolia* ..... Brassicaceae ..... 23, 29, 79, 86
*Distylium racemosum* ..... Hamamelidaceae & Altingiaceae ... 217, 218, 219, 220
*Dorycnium germanicum* ..... Fabaceae ..... 176
*Dorycnium graecum* ..... Fabaceae ..... 176, 180
*Dorycnium herbaceum* ..... Fabaceae ..... 176
*Dorycnium hirsutum* ..... Fabaceae ..... 176
*Dorycnium intermedium* ..... Fabaceae ..... 176
*Dorycnium pentaphyllum* ..... Fabaceae ..... 176, 178, 180
*Dorycnium suffruticosum* ..... Fabaceae ..... 176
*Draba aizoides* ..... Brassicaceae ..... 79, 80, 81, 85
*Draba aurea* ..... Brassicaceae ..... 79
*Draba dubia* ..... Brassicaceae ..... 79
*Draba nemorosa* ..... Brassicaceae ..... 79
*Draba siliquosa* ..... Brassicaceae ..... 79
*Draba streptocarpa* ..... Brassicaceae ..... 79
*Drimys piperita* ..... Winteraceae ..... 470, 471, 472
*Drimys winteri* ..... Winteraceae ..... 31, 470, 471, 473
*Drosera adelae* ..... Droseraceae ..... 149, 150, 151
*Drosera anglica* ..... Droseraceae ..... 149
*Drosera capensis* ..... Droseraceae ..... 15, 149, 150, 151
*Drosera rotundifolia* ..... Droseraceae ..... 149, 150
*Drosophyllum lusitanicum* ..... Droseraceae ..... 149, 151
*Dryas grandis* ..... Rosaceae ..... 383
*Dryas integrifolia* ..... Rosaceae ..... 383, 387
*Dryas octopetala* ..... Rosaceae ..... 383, 385, 387
*Dryas sumneviczii* ..... Rosaceae ..... 383
*Dyerophytum indicum* ..... Plumbaginaceae ..... 323, 324, 325, 326
*Ecballium elaterinum* ..... Cucurbitaceae ... 24, 141, 142, 143, 146, 148
*Echinospartium boissieri* ..... Fabaceae ..... 176
*Echium bonnettii* ..... Boraginaceae ..... 14
*Einadia nutans* ..... Amaranthaceae ..... 27, 38
*Elaeagnus angustifolia* ..... Eleagnaceae ..... 152, 153
*Elaeagnus pungens* ..... Eleagnaceae ..... 152, 153, 154
*Empetrum nigrum* ..... Ericaceae ..... 156, 161
*Enkianthus campanulatus* ..... Ericaceae ..... 16, 156, 159, 162
*Epilobium alpestre* ..... Onagraceae ..... 290, 294
*Epilobium angustifolium* ..... Onagraceae ..... 27, 290, 291, 293, 294
*Epilobium collinum* ..... Onagraceae ..... 290, 292
*Epilobium dodonaei* ..... Onagraceae ..... 290, 291, 292, 293, 295
*Epilobium fleischeri* ..... Onagraceae ..... 290, 291
*Epilobium hirsutum* ..... Onagraceae ..... 290, 291
*Epilobium latifolium* ..... Onagraceae ..... 290, 291
*Epilobium obscurum* ..... Onagraceae ..... 290, 291, 292
*Epilobium roseum* ..... Onagraceae ..... 290
*Epimedium alpinum* ..... Berberidaceae ..... 67, 69, 71, 72
*Epimedium pinnatum* ..... Berberidaceae ..... 67, 68, 70, 72
*Eranthis hyemalis* ..... Ranunculaceae ..... 352, 353, 354, 357
*Erica arborea* ..... Ericaceae ..... 156
*Erica carnea* ..... Ericaceae ..... 156
*Erica cinerea* ..... Ericaceae ..... 156, 157
*Erica multiflora* ..... Ericaceae ..... 156
*Erica scoparia* ..... Ericaceae ..... 156, 158
*Erica terminalis* ..... Ericaceae ..... 156
*Erica tetralix* ..... Ericaceae ..... 156
*Erica umbellata* ..... Ericaceae ..... 156
*Erica vagans* ..... Ericaceae ..... 156
*Erinacea anthyllis* ..... Fabaceae ..... 176
*Eriobotrya japonica* ..... Rosaceae ..... 383, 392
*Eriogonum fendlerianum* ..... Polygonaceae ..... 332, 336, 337, 338
*Eriogonum inflatum* ..... Polygonaceae ..... 24, 332, 339
*Eriogonum jamesii* ..... Polygonaceae ..... 24, 332, 334, 336, 337, 338
*Eriogonum longifolium* ..... Polygonaceae ..... 332, 335
*Eriogonum ovalifolium* ..... Polygonaceae ..... 20, 332, 335, 336
*Eriogonum pyrifolium* ..... Polygonaceae ..... 332, 335
*Eriogonum trichopes* ..... Polygonaceae ..... 22, 332
*Erodium ciconium* ..... Geraniaceae ..... 17, 205, 207
*Erodium cicutarium* ..... Geraniaceae ..... 205, 207
*Erodium laciniatum* ..... Geraniaceae ..... 205, 206
*Erodium pilosum* ..... Geraniaceae ..... 205, 206
*Erophila verna* ..... Brassicaceae ..... 79, 83
*Eruca sativa* ..... Brassicaceae ..... 79, 82
*Eruca sativa vesicaria* ssp. *sativa* ..... Brassicaceae ..... 79
*Erucastrum gallicum* ..... Brassicaceae ..... 79
*Erucastrum nasturtifolium* ..... Brassicaceae ..... 79, 84
*Erucastrum varium* ..... Brassicaceae ..... 79
*Erysimum asperum* ..... Brassicaceae ..... 29, 79
*Erysimum bicolor* ..... Brassicaceae ..... 79, 80
*Erysimum capitatum* ..... Brassicaceae ..... 79
*Erysimum cheirii* ..... Brassicaceae ..... 79
*Erysimum crepidifolium* ..... Brassicaceae ..... 8, 80
*Erysimum montosicola* ..... Brassicaceae ..... 80
*Erysimum mutabile* ..... Brassicaceae ..... 80
*Erysimum nivale* ..... Brassicaceae ..... 80, 85
*Erysimum ochroleucum* ..... Brassicaceae ..... 80
*Erysimum odoratum* ..... Brassicaceae ..... 80
*Erysimum rhaeticum* ..... Brassicaceae ..... 80
*Erysimum scoparium* ..... Brassicaceae ..... 80
*Erysimum virgatum* ..... Brassicaceae ..... 80
*Eschscholzia californica* ..... Papaveraceae ..... 304, 305, 309
*Eschscholzia minutiflora* ..... Papaveraceae ..... 304
*Euonymus europaeus* ..... Celastraceae ..... 113, 114, 115, 116
*Euonymus latifolius* ..... Celastraceae ..... 113, 115, 116
*Euonymus verrucosus* ..... Celastraceae ..... 113, 115, 116, 117
*Euphorbia acanthothamnos* ..... Euphorbiaceae ..... 164, 167, 168
*Euphorbia albomarginata* ..... Euphorbiaceae ..... 164
*Euphorbia amygdaloides* ..... Euphorbiaceae ..... 164
*Euphorbia aphylla* ..... Euphorbiaceae ..... 164, 167, 171
*Euphorbia armena* ..... Euphorbiaceae ..... 164
*Euphorbia atropurpurea* ..... Euphorbiaceae ..... 164, 165, 168, 171
*Euphorbia balsamifera* ..... Euphorbiaceae ..... 164, 166, 171
*Euphorbia calyptra* ..... Euphorbiaceae ..... 164, 167, 168, 170
*Euphorbia canariensis* ..... Euphorbiaceae ..... 164, 165, 171, 172
*Euphorbia chamaesyce* ..... Euphorbiaceae ..... 164, 168, 171
*Euphorbia characias* ..... Euphorbiaceae ..... 164
*Euphorbia collina* ..... Euphorbiaceae ..... 164
*Euphorbia corollata* ..... Euphorbiaceae ..... 164
*Euphorbia cyparissias* ..... Euphorbiaceae .. 164, 165, 167, 171, 172, 173

*Euphorbia dendroides* ..... Euphorbiaceae ..... 164
*Euphorbia dulcis* ..... Euphorbiaceae ..... 164, 166
*Euphorbia echinus* ..... Euphorbiaceae ..... 24, 164, 166
*Euphorbia esula* ..... Euphorbiaceae ..... 164, 165
*Euphorbia graminifolia* ..... Euphorbiaceae ..... 164, 169
*Euphorbia hadramautica* ..... Euphorbiaceae ..... 164
*Euphorbia helioscopia* ..... Euphorbiaceae ..... 164, 166, 169
*Euphorbia larica* ..... Euphorbiaceae ..... 164, 166
*Euphorbia lathyris* ..... Euphorbiaceae ..... 164, 170
*Euphorbia leptocaula* ..... Euphorbiaceae ..... 164, 168
*Euphorbia maculata* ..... Euphorbiaceae ..... 22, 164, 167
*Euphorbia mellifera* ..... Euphorbiaceae ..... 164, 167, 168
*Euphorbia nicaeensis* ..... Euphorbiaceae ..... 17, 164, 167
*Euphorbia paralias* ..... Euphorbiaceae ..... 164, 168
*Euphorbia piscatoria* ..... Euphorbiaceae ..... 17, 164, 170
*Euphorbia platyphyllos* ..... Euphorbiaceae ..... 164
*Euphorbia prostrata* ..... Euphorbiaceae ..... 164
*Euphorbia pulcherrima* ..... Euphorbiaceae ..... 26, 164, 171
*Euphorbia regis-jubaea* ..... Euphorbiaceae ..... 164, 171
*Euphorbia rigida* ..... Euphorbiaceae ..... 164
*Euphorbia schimperi* ..... Euphorbiaceae ..... 26, 164, 170
*Euphorbia seguieriana* ..... Euphorbiaceae ..... 15, 164, 169
*Euphorbia squamaria* ..... Euphorbiaceae ..... 164
*Euphorbia verrucosa* ..... Euphorbiaceae ..... 164
*Euphorbia villosa* ..... Euphorbiaceae ..... 164, 169
*Euphorbia virgata* ..... Euphorbiaceae ..... 164
*Exochorda racemosa* ..... Rosaceae ..... 383
*Fagonia arabica* ..... Zygophyllaceae ..... 474, 476
*Fagonia cretica* ..... Zygophyllaceae ..... 474, 475
*Fagonia olivieri* ..... Zygophyllaceae ..... 474, 475
*Fagopyrum esculentum* ..... Polygonaceae ..... 332, 335
*Fagopyrum tataricum* ..... Polygonaceae ..... 332, 335
*Fagus grandifolia* ..... Fagaceae ..... 193, 196
*Fagus orientalis* ..... Fagaceae ..... 18, 193, 195, 197
*Fagus sylvatica* ..... Fagaceae ..... 193, 195, 196
*Fallopia convolvulus* ..... Polygonaceae ..... 332, 334, 338, 339
*Fallopia dumetorum* ..... Polygonaceae ..... 332, 338
*Farsetia aegyptica* ..... Brassicaceae ..... 80
*Farsetia ramosissima* ..... Brassicaceae ..... 80
*Ficus carica* ..... Moraceae ..... 268, 269, 270, 271
*Ficus elastica* ..... Moraceae ..... 268
*Ficus salicifolia* ..... Moraceae ..... 268
*Ficus sycomorus* ..... Moraceae ..... 23, 268, 269, 270
*Ficus vasta* ..... Moraceae ..... 268
*Filipendula ulmaria* ..... Rosaceae ..... 383, 385
*Filipendula vulgaris* ..... Rosaceae ..... 383
*Forsskaolea angustifolia* ..... Urticaceae ..... 454, 455
*Forsskaolea tenacissima* ..... Urticaceae ..... 454, 457
*Fortunearia sinensis* ..... Hamamelidaceae & Altingiaceae ..... 217, 218, 219, 220
*Fothergilla gardeni* ..... Hamamelidaceae & Altingiaceae ..... 18, 217, 218, 220
*Fourraea alpina* ..... Brassicaceae ..... 80
*Fragaria vesca* ..... Rosaceae ..... 383
*Fragaria viridis* ..... Rosaceae ..... 383
*Frangula alnus* ..... Rhamnaceae ..... 376, 377, 378, 379, 380
*Frangula azorica* ..... Rhamnaceae ..... 376
*Fumana ericoides* ..... Cistaceae ..... 122, 124, 125
*Fumana procumbens* ..... Cistaceae ..... 122, 124, 125
*Fumana thymifolia* ..... Cistaceae ..... 122
*Fumaria officinalis* ..... Papaveraceae ..... 14, 20, 304, 305, 306, 308
*Fumaria vaillantii* ..... Papaveraceae ..... 304
*Galium album* ..... Rubiaceae ..... 395, 396, 397
*Galium anisophyllum* ..... Rubiaceae ..... 395
*Galium boreale* ..... Rubiaceae ..... 395
*Galium coloradoense* ..... Rubiaceae ..... 395
*Galium laevigatum* ..... Rubiaceae ..... 395
*Galium lucidum* ..... Rubiaceae ..... 395, 396, 399
*Galium luteum* ..... Rubiaceae ..... 395
*Galium megalospermum* ..... Rubiaceae ..... 395
*Galium mollugo* ..... Rubiaceae ..... 395, 396, 399
*Galium obliqum* ..... Rubiaceae ..... 395
*Galium odoratum* ..... Rubiaceae ..... 395
*Galium pusillum* ..... Rubiaceae ..... 395, 398
*Galium rotundifolium* ..... Rubiaceae ..... 395
*Galium rubrum* ..... Rubiaceae ..... 395, 397
*Galium suberosum* ..... Rubiaceae ..... 395
*Galium sylvaticum* ..... Rubiaceae ..... 395
*Galium timeroi* ..... Rubiaceae ..... 395
*Galium verum* ..... Rubiaceae ..... 395
*Galium x pomeranicum* ..... Rubiaceae ..... 395
*Gaultheria shalon* ..... Ericaceae ..... 21, 25, 156, 160, 161
*Genista aethnensis* ..... Fabaceae ..... 176
*Genista anglica* ..... Fabaceae ..... 176
*Genista candicans* ..... Fabaceae ..... 176
*Genista cinerea* ..... Fabaceae ..... 176, 180
*Genista germanica* ..... Fabaceae ..... 176
*Genista hispanica* ..... Fabaceae ..... 176
*Genista pilosa* ..... Fabaceae ..... 176
*Genista pulchella* ..... Fabaceae ..... 176
*Genista purgans* ..... Fabaceae ..... 176
*Genista radiata* ..... Fabaceae ..... 16, 176, 180
*Genista saggitalis* ..... Fabaceae ..... 176
*Genista spartioides* ..... Fabaceae ..... 176
*Genista sphacellata* ..... Fabaceae ..... 176
*Genista tinctoria* ..... Fabaceae ..... 176, 177
*Genista triacanthos* ..... Fabaceae ..... 176
*Genista umbellata* ..... Fabaceae ..... 176
*Gentiana acaulis* ..... Gentianaceae ..... 199, 200, 202
*Gentiana asclepiadea* ..... Gentianaceae ..... 199, 200, 201, 202
*Gentiana bavarica* ..... Gentianaceae ..... 199
*Gentiana campestris* ..... Gentianaceae ..... 199
*Gentiana ciliata* ..... Gentianaceae ..... 199
*Gentiana clusii* ..... Gentianaceae ..... 199
*Gentiana cruciata* ..... Gentianaceae ..... 199, 200, 201, 202
*Gentiana germanica* ..... Gentianaceae ..... 199, 200, 201, 202
*Gentiana insubrica* ..... Gentianaceae ..... 199
*Gentiana lutea* ..... Gentianaceae ..... 199, 201, 202
*Gentiana nana* ..... Gentianaceae ..... 199
*Gentiana nivalis* ..... Gentianaceae ..... 199, 200, 201, 202
*Gentiana orbicularis* ..... Gentianaceae ..... 199
*Gentiana pneumonanthe* ..... Gentianaceae ..... 199
*Gentiana punctata* ..... Gentianaceae ..... 199, 201, 202
*Gentiana purpurea* ..... Gentianaceae ..... 199, 201
*Gentiana ramosa* ..... Gentianaceae ..... 199
*Gentiana tenella* ..... Gentianaceae ..... 199, 200, 201
*Gentiana utriculosa* ..... Gentianaceae ..... 199, 202
*Gentiana verna* ..... Gentianaceae ..... 199
*Geranium caespitosum* ..... Geraniaceae ..... 205, 206, 207
*Geranium canariense* ..... Geraniaceae ..... 205
*Geranium columbinum* ..... Geraniaceae ..... 24, 205, 206, 207, 208
*Geranium dissectum* ..... Geraniaceae ..... 205
*Geranium divaricatum* ..... Geraniaceae ..... 205, 207, 208
*Geranium molle* ..... Geraniaceae ..... 205, 206
*Geranium nodosum* ..... Geraniaceae ..... 205
*Geranium phaeum* ..... Geraniaceae ..... 205, 206, 207, 208
*Geranium pratense* ..... Geraniaceae ..... 205, 206
*Geranium pusillum* ..... Geraniaceae ..... 205, 206, 207, 209
*Geranium pyrenaicum* ..... Geraniaceae ..... 205, 208
*Geranium richardsonii* ..... Geraniaceae ..... 205, 206, 208
*Geranium robertianum* ..... Geraniaceae ..... 205, 208
*Geranium rotundifolium* ..... Geraniaceae ..... 205, 209
*Geranium sanguineum* ..... Geraniaceae ..... 205, 206, 207, 208, 209
*Geranium sylvaticum* ..... Geraniaceae ..... 205, 207, 209
*Gesnouinia arborea* ..... Urticaceae ..... 454, 455, 457
*Geum glaciale* ..... Rosaceae ..... 23, 383, 388
*Geum macrophyllum* ..... Rosaceae ..... 383
*Geum montanum* ..... Rosaceae ..... 383
*Geum reptans* ..... Rosaceae ..... 383, 385, 390, 391
*Geum rivale* ..... Rosaceae ..... 383
*Geum triflorum* ..... Rosaceae ..... 383
*Geum urbanum* ..... Rosaceae ..... 383
*Glaucium flavum* ..... Papaveraceae ..... 304, 306, 308, 310
*Gleditsia triacanthos* ..... Fabaceae ..... 176
*Gomphocarpus fruticosus* ..... Apocyanaceae & Asclepiadaceae ..... 54
*Gossypium herbaceum* ..... Malvaceae ..... 254, 255, 258, 259
*Gossypium stoksii* ..... Malvaceae ..... 254
*Greenovia diplocyla* ..... Crassulaceae ..... 134, 137
*Gypsophila muralis* ..... Caryophyllaceae ..... 103, 107
*Gypsophila repens* ..... Caryophyllaceae ..... 103, 106, 108, 110
*Hagenia abyssinica* ..... Rosaceae ..... 384, 386
*Halimium atriplicifolium* ..... Cistaceae ..... 122
*Halimium halimifolium* ..... Cistaceae ..... 122, 125
*Halimium ocymoides* ..... Cistaceae ..... 122
*Halimium viscosum* ..... Cistaceae ..... 122, 123
*Haloxylon articulatum* ..... Amaranthaceae ..... 38
*Haloxylon persicum* ..... Amaranthaceae ..... 40
*Hamamelis virginiana* ..... Hamamelidaceae & Altingiaceae ..... 217, 218, 219
*Haplopeplis perfoliata* ..... Amaranthaceae ..... 38
*Hedera helix* ..... Araliaceae ..... 22
*Hedysarum arcticu* ..... Fabaceae ..... 176, 188, 189
*Hedysarum gmelinii* ..... Fabaceae ..... 176, 186

*Hedysarum hedysaroides*.....Fabaceae.....176, 177
*Hedysarum zundukii*.....Fabaceae.....176, 190
*Helianthemum album*.....Cistaceae.....122
*Helianthemum almeriense*.....Cistaceae.....122
*Helianthemum alpestre*.....Cistaceae.....122
*Helianthemum apenninum*.....Cistaceae.....122
*Helianthemum canariense*.....Cistaceae.....122
*Helianthemum canum*.....Cistaceae.....122, 123
*Helianthemum caput-felis*.....Cistaceae.....122
*Helianthemum croceum*.....Cistaceae.....122
*Helianthemum hirtum*.....Cistaceae.....122, 124
*Helianthemum italicum*.....Cistaceae.....122
*Helianthemum lavandulifolium*.....Cistaceae.....122
*Helianthemum ledifolium*.....Cistaceae.....122
*Helianthemum leptophyllum*.....Cistaceae.....122
*Helianthemum nummularium*.....Cistaceae.....122
*Helianthemum rufficonum*.....Cistaceae.....122
*Helianthemum squamatum*.....Cistaceae.....122
*Helianthemum umbellatum*.....Cistaceae.....122, 123
*Helleborus foetidus*.....Ranunculaceae.....352, 365, 366
*Helleborus niger* ssp. *niger*.....Ranunculaceae.....352, 353
*Helleborus viridis*.....Ranunculaceae.....13, 352, 365, 366
*Hepatica nobilis*.....Ranunculaceae.....352, 364
*Herniaria alpina*.....Caryophyllaceae.....103, 109, 111
*Herniaria glabra*.....Caryophyllaceae.....103
*Herniaria hirsuta*.....Caryophyllaceae.....103
*Herniaria incana*.....Caryophyllaceae.....103
*Heuchera americana*.....Saxifragaceae.....423, 426
*Heuchera hallii*.....Saxifragaceae.....423, 425
*Hibiscus rosa-sinensis*.....Malvaceae.....254, 256, 258
*Hibiscus syriacus*.....Malvaceae.....254, 255
*Hippocrepis comosa*.....Fabaceae.....176, 177, 186
*Hippocrepis emerus*.....Fabaceae.....176, 178, 189
*Hippocrepis glauca*.....Fabaceae.....176
*Hippophae rhamnoides*.....Eleagnaceae.....26, 152, 153, 154
*Hirschfeldia incana*.....Brassicaceae.....80, 83, 85
*Holboellia coriaceae*.....Lardizabalaceae.....228
*Holodiscus discolor*.....Rosaceae.....384, 386, 392, 393
*Holosteum umbellatum*.....Caryophyllaceae.....103
*Hornungia petraea*.....Brassicaceae.....80
*Hottonia palustris*.....Primulaceae.....344, 346, 347, 351
*Hugueninia tanacetifolia*.....Brassicaceae.....80, 84
*Humulus lupulus*.....Cannabaceae.....93, 95, 96
*Hutchinsia alpina*.....Brassicaceae.....80
*Hybanthus communis*.....Violaceae.....459, 460, 461, 462, 463
*Hypericum androsaemum*.....Clusiaceae.....126, 127
*Hypericum balearicum*.....Clusiaceae.....126
*Hypericum calycina*.....Clusiaceae.....126
*Hypericum canariense*.....Clusiaceae.....126, 127, 128
*Hypericum coris*.....Clusiaceae.....126, 127, 128, 129
*Hypericum empetrifolium*.....Clusiaceae.....126
*Hypericum grandifolium*.....Clusiaceae.....126, 127, 128
*Hypericum hirsutum*.....Clusiaceae.....126, 127
*Hypericum humifusum*.....Clusiaceae.....126, 129
*Hypericum inodorum*.....Clusiaceae.....21, 126, 128, 129
*Hypericum maculatum*.....Clusiaceae.....126
*Hypericum montanum*.....Clusiaceae.....126
*Hypericum perforatum*.....Clusiaceae.....126
*Hypericum polygonifolium*.....Clusiaceae.....126, 127
*Hypericum ptarmicifolium*.....Clusiaceae.....126
*Hypericum reflexum*.....Clusiaceae.....29, 126, 127, 128
*Hypericum revolutum*.....Clusiaceae.....126
*Hypericum richeri*.....Clusiaceae.....126
*Hypericum tomentosum*.....Clusiaceae.....126
*Iberis sempervirens*.....Brassicaceae.....80
*Illecebrum sp.*.....Caryophyllaceae.....104
*Impatiens balfourii*.....Balsaminaceae.....31
*Impatiens noli-tangere*.....Balsaminaceae.....18
*Impatiens parviflora*.....Balsaminaceae.....14
*Isatis tinctoria*.....Brassicaceae.....80, 84
*Ixanthus viscosus*.....Gentianaceae.....13, 27, 199, 200, 201, 202
*Jathropha dhofarica*.....Euphorbiaceae.....164, 166, 168, 172
*Jovibarba arenaria*.....Crassulaceae.....134
*Jovibarba hirta*.....Crassulaceae.....20, 134, 137, 138
*Juglans regia*.....Juglandaceae.....222, 223, 224
*Kalmia angustifolia*.....Ericaceae.....156, 160, 161
*Kalmia latifolia*.....Ericaceae.....157
*Kernera saxatilis*.....Brassicaceae.....80, 81
*Kerria japonica*.....Rosaceae.....384, 388
*Kleinia neriifolia*.....Asteraceae.....19
*Kochia prostrata*.....Amaranthaceae.....38, 40
*Krameria grayi*.....Krameriaceae.....225, 226
*Krascheninnikovia ceratoides*.....Amaranthaceae.....38, 45
*Krascheninnikovia lanata*.....Amaranthaceae.....38
*Laburnum alpinum*.....Fabaceae.....176
*Laburnum anagyroides*.....Fabaceae.....175, 176, 179
*Larrea cuneifolia*.....Zygophyllaceae.....474, 475, 476
*Laserpitium gallicum*.....Apiaceae.....13
*Lathyrus heterophyllus*.....Fabaceae.....176, 191
*Lathyrus niger*.....Fabaceae.....176
*Lathyrus occidentalis*.....Fabaceae.....176
*Lathyrus sylvestris*.....Fabaceae.....176, 186, 190
*Lathyrus venetus*.....Fabaceae.....176
*Lathyrus vernus*.....Fabaceae.....176, 177
*Laurus azorica*.....Lauraceae.....26, 232, 233, 234, 235
*Laurus nobilis*.....Lauraceae.....18, 232, 233, 234
*Lavatera acerifolia*.....Malvaceae.....254, 256, 257, 259
*Lavatera arborea*.....Malvaceae.....254, 255
*Lavatera assurgentiflora*.....Malvaceae.....26, 254, 257
*Lavatera maritima*.....Malvaceae.....254
*Lavatera oblongifolia*.....Malvaceae.....254, 255, 256, 257
*Lavatera olbia*.....Malvaceae.....254, 255
*Ledum decumbens*.....Ericaceae.....21, 156, 160
*Ledum groenlandicum*.....Ericaceae.....156, 158, 159, 162
*Ledum palustre*.....Ericaceae.....156, 162
*Lepidium campestre*.....Brassicaceae.....21, 80
*Lepidium densiflorum*.....Brassicaceae.....80
*Lepidium perfoliatum*.....Brassicaceae.....80
*Leptadenia pyrotechnica*.....Apocyanaceae & Asclepiadaceae.....27, 54, 56, 57
*Leptopus colchicus*.....Euphorbiaceae.....164, 166, 168, 171
*Lespedeza hirta*.....Fabaceae.....176, 185
*Lespedeza virginiana*.....Fabaceae.....176
*Lesquerella alpina*.....Brassicaceae.....80
*Limoniastrum guyonianum*.....Plumbaginaceae.....323, 324, 325
*Limoniastrum monopetalum*.....Plumbaginaceae.....323, 324
*Limonium insigne*.....Plumbaginaceae.....323, 326
*Limonium pectinatum*.....Plumbaginaceae 21, 323, 324, 325, 326, 327
*Limonium vulgare*.....Plumbaginaceae.....323
*Linum alpinum*.....Linaceae.....237, 238
*Linum austriacum*.....Linaceae.....237, 239
*Linum bienne*.....Linaceae.....237, 238, 239
*Linum catharticum*.....Linaceae.....237
*Linum hypericifolium*.....Linaceae.....237, 238, 240
*Linum narbonense*.....Linaceae.....237, 238, 240
*Linum strictum*.....Linaceae.....237, 238, 239
*Linum suffruticosum*.....Linaceae.....237, 238
*Linum tenuifolium*.....Linaceae.....237, 239
*Liquidambar styraciflua*.....Hamamelidaceae & Altingiaceae.....32, 217, 218, 219, 220, 221
*Liriodendron tulipifera*.....Magnoliaceae.....250, 251, 252, 253
*Lobularia canariensis*.....Brassicaceae.....80
*Lobularia libyca*.....Brassicaceae.....80
*Lobularia maritima*.....Brassicaceae.....80
*Lobularia palmensis*.....Brassicaceae.....80
*Loiseleria procumbens*.....Ericaceae.....156, 157, 160, 161
*Lomatogonium carinthiacum*.....Gentianaceae.....199, 200, 201, 202
*Loranthus acaciae*.....Loranthaceae & Viscaceae.....241, 242, 243
*Loranthus aphyllus*.....Loranthaceae & Viscaceae.....13, 241, 242, 243, 244
*Loranthus europaeus*.....Loranthaceae & Viscaceae.....241, 242, 243
*Lotus aragonensis*.....Fabaceae.....176, 189
*Lotus campylocladus*.....Fabaceae.....176
*Lotus corniculatus*.....Fabaceae.....176, 178, 179, 185
*Lotus creticus*.....Fabaceae.....176
*Lotus glaucus*.....Fabaceae.....176, 190
*Lotus maritimus*.....Fabaceae.....176
*Lotus mascaensis*.....Fabaceae.....176
*Lotus sesslilifolius*.....Fabaceae.....176
*Lunaria annua*.....Brassicaceae.....80
*Lupinus albicaulis*.....Fabaceae.....176, 184, 188
*Lupinus argenteus*.....Fabaceae.....176
*Lupinus obtusifolius*.....Fabaceae.....176, 187
*Lupinus tassilicus*.....Fabaceae.....176, 177, 184
*Lygos monosperma*.....Fabaceae.....176
*Lygos retam*.....Fabaceae.....176
*Lysimachia nemorum*.....Primulaceae.....344, 349
*Lysimachia nummularium*.....Primulaceae.....344
*Lysimachia punctata*.....Primulaceae.....344
*Lysimachia thyrsiflora*.....Primulaceae.....14, 344, 349
*Lysimachia vulgaris*.....Primulaceae.....344, 345, 348, 349, 350, 351
*Lythrum acutangulum*.....Lythraceae.....246, 247, 248

*Lythrum hyssopifolia* ..... Lythraceae ..... 246, 247, 249
*Lythrum salicaria* ..... Lythraceae ..... 246, 247, 248
*Maerua crassifolia* ..... Capparaceae ..... 98, 99, 100, 101
*Magnolia acuminata* ..... Magnoliaceae ..... 250, 251, 252, 253
*Magnolia denudata* ..... Magnoliaceae ..... 250, 252
*Magnolia grandiflora* ..... Magnoliaceae ..... 250, 251, 252, 243
*Magnolia soulangiana* ..... Magnoliaceae ..... 250, 251, 252
*Magnolia stellata* ..... Magnoliaceae ..... 250
*Magnolia virginiana* ..... Magnoliaceae ..... 250
*Mahonia aquifolium* ..... Berberidaceae ..... 67, 69, 71
*Mahonia bealei* ..... Berberidaceae ..... 16, 67, 68, 69, 71
*Mahonia fremontii* ..... Berberidaceae ..... 30, 67, 69, 70
*Mahonia nervosa* ..... Berberidaceae ..... 67, 68, 69
*Mairena pyramidata* ..... Amaranthaceae ..... 38
*Malcolmia aegyptica* ..... Brassicaceae ..... 80, 85
*Malva moschata* ..... Malvaceae ..... 17, 254, 256, 259
*Malva neglecta* ..... Malvaceae ..... 254, 259
*Malva parviflora* ..... Malvaceae ..... 254, 256
*Malva sylvestris* ..... Malvaceae ..... 254, 258
*Marcetella moquiniana* ..... Rosaceae ..... 384
*Marrubium alysson* ..... Lamiaceae ..... 30
*Marrubium vulgare* ..... Lamiaceae ..... 29
*Matthiola fruticulosa* ..... Brassicaceae ..... 22, 80
*Matthiola parviflora* ..... Brassicaceae ..... 80
*Matthiola sinuata* ..... Brassicaceae ..... 80
*Maytenus canariensis* ..... Celastraceae ..... 113, 114
*Maytenus dhofarensis* ..... Celastraceae ..... 113, 114
*Maytenus senegalensis* ..... Celastraceae ..... 113, 114
*Meconopsis cambrica* ..... Papaveraceae ..... 304
*Meconopsis robusta* ..... Papaveraceae ..... 305
*Medicago arborea* ..... Fabaceae ..... 176
*Medicago falcata* ..... Fabaceae ..... 176
*Medicago lupulina* ..... Fabaceae ..... 176
*Medicago minima* ..... Fabaceae ..... 176, 187
*Medicago rididula* ..... Fabaceae ..... 176, 186, 188
*Medicago sativa* ..... Fabaceae ..... 176
*Melilotus albus* ..... Fabaceae ..... 176, 177
*Melilotus indica* ..... Fabaceae ..... 176
*Menyanthes trifoliata* ..... Menyanthaceae ..... 31, 264, 265, 266
*Menziesia ferruginea* ..... Ericaceae ..... 156
*Mercurialis annua* ..... Euphorbiaceae ..... 164, 166, 168
*Mercurialis ovata* ..... Euphorbiaceae ..... 164, 168, 170
*Mercurialis perennis* ..... Euphorbiaceae ..... 164, 168
*Mertensia ciliata* ..... Boraginaceae ..... 31
*Mesembryanthemum cristatum* ..... Aizoaceae ..... 36
*Mesembryanthemum crystallinum* ..... Aizoaceae ..... 35, 36
*Mesembryanthemum nodiflorum* ..... Aizoaceae ..... 37
*Mespilus germanica* ..... Rosaceae ..... 384
*Minuartia arctica* ..... Caryophyllaceae ..... 103, 106
*Minuartia capillaceae* ..... Caryophyllaceae ..... 103
*Minuartia cherlerioides* ..... Caryophyllaceae ..... 103
*Minuartia laricifolia* ..... Caryophyllaceae ..... 103, 111
*Minuartia recurva* ..... Caryophyllaceae ..... 103
*Minuartia rostrata* ..... Caryophyllaceae ..... 103, 105
*Minuartia rubella* ..... Caryophyllaceae ..... 103
*Minuartia rubra* ..... Caryophyllaceae ..... 103, 105, 106, 110
*Minuartia sedoides* ..... Caryophyllaceae ..... 103, 111
*Minuartia verna* ..... Caryophyllaceae ..... 103
*Mitella ovalis* ..... Saxifragaceae ..... 423, 425
*Moeringia ciliata* ..... Caryophyllaceae ..... 103
*Moeringia muscosa* ..... Caryophyllaceae ..... 103
*Monanthes brachycaulon* ..... Crassulaceae ..... 134
*Monanthes pallens* ..... Crassulaceae ..... 134
*Moricandia arvensis* ..... Brassicaceae ..... 80
*Morus alba* ..... Moraceae ..... 15, 268, 269, 271
*Morus nigra* ..... Moraceae ..... 268
*Myrica californica* ..... Myricaceae ..... 272, 273, 274
*Myrica faya* ..... Myricaceae ..... 272, 273
*Myrica gale* ..... Myricaceae ..... 272, 273
*Myricaria germanica* ..... Tamaricaceae ..... 30, 434, 435, 436, 437
*Myriophyllum alternifolium* ..... Haloragaceae ..... 214, 215, 216
*Myriophyllum spicatum* ..... Haloragaceae ..... 31, 214, 215
*Myrtus communis* ..... Myrtacaea ..... 275, 276, 277
*Nandina domestica* ..... Berberidaceae ..... 18, 67, 68, 69, 70
*Nasturtium officinale* ..... Brassicaceae ..... 80
*Neatostema apulum* ..... Boraginaceae ..... 19
*Neochamaelea pulverulenta* ..... Ceoraceae ..... 130, 131, 132
*Nepenthes alata* ..... Nepenthaceae ..... 278, 279, 280
*Nepenthes ampullaria* ..... Nepenthaceae ..... 278, 279, 280
*Nerium mascatense* ..... Apocyanaceae & Asclepiadaceae ..... 54
*Nerium oleander* ..... Apocyanaceae & Asclepiadaceae ..... 54, 55, 56, 58
*Neslia paniculata* ..... Brassicaceae ..... 80
*Nigella arvensis* ..... Ranunculaceae ..... 352, 362, 363
*Nigella damascena* ..... Ranunculaceae ..... 352, 362, 363
*Noea mucronata* ..... Amaranthaceae ..... 27, 38
*Nonea erecta* ..... Boraginaceae ..... 19
*Notoceras bicorne* ..... Brassicaceae ..... 80, 83
*Nuphar lutea* ..... Nymphaeaceae ..... 26, 286, 287, 288, 289
*Nuytsia floribunda* ..... Loranthaceae & Viscaceae ..... 244, 245
*Nymphaea alba* ..... Nymphaeaceae ..... 286, 287, 288, 289
*Nymphaea candida* ..... Nymphaeaceae ..... 286, 287, 288, 289
*Nymphoides peltata* ..... Menyanthaceae ..... 15, 264, 265, 266, 267
*Ochradenus baccatus* ..... Resedaceae ..... 372, 373
*Ocotea foetens* ..... Lauraceae ..... 232, 233, 234
*Oemleria cerasiformis* ..... Rosaceae ..... 384, 389
*Oenothera biennis* ..... Onagraceae ..... 290, 291, 292, 293
*Oenothera flava* ..... Onagraceae ..... 290, 293
*Oenothera glazioviana* ..... Onagraceae ..... 290, 291, 292, 294
*Olea europaea* ..... Oleaceae ..... 18
*Onobrychis arenaria* ..... Fabaceae ..... 176
*Onobrychis caput-galli* ..... Fabaceae ..... 176
*Onobrychis montana* ..... Fabaceae ..... 176
*Onobrychis sativa* ..... Fabaceae ..... 177
*Onobrychis viciifolia* ..... Fabaceae ..... 176, 187
*Ononis angustissima* ..... Fabaceae ..... 176, 187, 189
*Ononis aragonensis* ..... Fabaceae ..... 176
*Ononis cristata* ..... Fabaceae ..... 176
*Ononis fruticosa* ..... Fabaceae ..... 176
*Ononis minutissima* ..... Fabaceae ..... 176, 190
*Ononis mitissima* ..... Fabaceae ..... 176
*Ononis natrix* ..... Fabaceae ..... 176, 177
*Ononis repens* ..... Fabaceae ..... 176
*Ononis rotundifolia* ..... Fabaceae ..... 176
*Ononis serrata* ..... Fabaceae ..... 176
*Ononis speciosa* ..... Fabaceae ..... 176, 178
*Ononis spinosa* ..... Fabaceae ..... 176
*Ononis tridentata* ..... Fabaceae ..... 176
*Orobanche canescens* ..... Orobanchaceae ..... 17
*Osmanthus decorus* ..... Oleaceae ..... 20
*Ostrya carpinifolia* ..... Betulaceae ..... 73, 74
*Osyris alba* ..... Santalaceae ..... 415, 416, 417, 418
*Oudneya africana* ..... Brassicaceae ..... 80
*Oxalis acetosella* ..... Oxalidaceae ..... 296
*Oxalis corniculata* ..... Oxalidaceae ..... 296, 297, 298, 299
*Oxalis pres-caprae* ..... Oxalidaceae ..... 296, 297, 298, 299
*Oxalis stricta* ..... Oxalidaceae ..... 296, 297, 298, 299
*Oxalis subacaulis* ..... Oxalidaceae ..... 296, 297, 298, 299
*Oxyria digyna* ..... Polygonaceae ..... 332, 333, 334, 335, 336, 337, 339
*Oxytropis campestre* ..... Fabaceae ..... 176
*Oxytropis coerulea* ..... Fabaceae ..... 176
*Oxytropis helvetica* ..... Fabaceae ..... 176
*Oxytropis jaquinii* ..... Fabaceae ..... 176
*Oxytropis pilosa* ..... Fabaceae ..... 176, 181
*Oxytropis popoviana* ..... Fabaceae ..... 176
*Oxytropis tragacanthoides* ..... Fabaceae ..... 176, 183
*Oxytropis triphylla* ..... Fabaceae ..... 176
*Pachysandra stylosa* ..... Buxaceae ..... 88, 89, 91
*Pachysandra terminalis* ..... Buxaceae ..... 88, 90, 91
*Pachystima myrsinithes* ..... Celastraceae ..... 113, 114, 115, 116
*Paeonia lutea* ..... Paeoniaceae ..... 300
*Paeonia officinalis* ..... Paeoniaceae ..... 300, 301, 302
*Paeonia suffruticosa* ..... Paeoniaceae ..... 19, 300, 301, 302
*Paeonia tenuifolia* ..... Paeoniaceae ..... 300
*Paliurus spina-christi* ..... Rhamnaceae ..... 376, 377, 379, 381
*Papaver alpinum* ..... Papaveraceae ..... 304, 305, 306, 307, 309, 310
*Papaver auranthiacum* ..... Papaveraceae ..... 304, 306, 307, 309
*Papaver dubium* ..... Papaveraceae ..... 304
*Papaver rhoeas* ..... Papaveraceae ..... 304, 307
*Papaver somniferum* ..... Papaveraceae ..... 304, 305
*Papaver variegatum* ..... Papaveraceae ..... 304, 306, 307, 308, 309
*Parietaria debilis* ..... Urticaceae ..... 454, 455, 456, 457
*Parietaria judaica* ..... Urticaceae ..... 454, 455
*Parietaria officinalis* ..... Urticaceae ..... 454, 455, 456
*Parolinia intermedia* ..... Brassicaceae ..... 80, 81, 85
*Parolinia ornata* ..... Brassicaceae ..... 80, 85
*Paronychia canariensis* ..... Caryophyllaceae ..... 103
*Paronychia glabrata* ..... Caryophyllaceae ..... 103
*Paronychia kapela* ..... Caryophyllaceae ..... 103, 109
*Paronychia kapela* ssp. *serpyllifolia* ..... Caryophyllaceae ..... 103
*Parrotia persica* ..... Hamamelidaceae & Altingiaceae ..... 217, 218, 219

*Parthenocissus inserta*.....Vitaceae .....17, 24, 31, 465, 466, 467, 469
*Parthenocissus tricuspidata*.....Vitaceae .....17, 465, 466, 468
*Patellifolia patellaris*.....Amaranthaceae.....38, 45
*Patellifolia procumbens*.....Amaranthaceae.....38, 40
*Peganum harmala*.....Zygophyllaceae.....474
*Peltaria alliacea*.....Brassicaceae.....80
*Peperomia caperata*.....Piperaceae .....314, 315, 317
*Periploca aphylla*.....Apocyanaceae & Asclepiadaceae.....54
*Periploca graeca*.....Apocyanaceae & Asclepiadaceae.....54, 55
*Periploca laevigata*.....Apocyanaceae & Asclepiadaceae....54, 57, 58
*Persea americana*.....Lauraceae .....232, 233, 234, 235, 236
*Persea indica*.....Lauraceae .....232, 233, 234, 235, 236
*Petrophyton caespitosum*.....Rosaceae.....384
*Petrorhagia nanteulii*.....Caryophyllaceae.....103, 107
*Petrorhagia prolifera*.....Caryophyllaceae.....103, 104
*Petrorhagia saxifraga*.....Caryophyllaceae.....103
*Petteria ramentecea*.....Fabaceae.....176
*Peucedanum ostruthium*.....Apiaceae.....32
*Phaseolus angustissimus*.....Fabaceae.....176, 191
*Phaseolus coccineus*.....Fabaceae.....176
*Phoradendron californicum*.....Loranthaceae & Viscaceae.....241, 243, 244
*Phoradendron juniperinum*.....Loranthaceae & Viscaceae.....241, 242, 243, 244, 245
*Phoradendron tomentosum*.....Loranthaceae & Viscaceae.....241, 242, 243
*Phyllis nobla*.....Rubiaceae.....395, 396, 398
*Phyllodoce coerulea*.....Ericaceae.....156
*Physocarpus amurensis*.....Rosaceae.....384, 387
*Phytolacca americana*.....Phytolaccaceae .....30, 311, 312
*Pieris taiwanensis*.....Ericaceae.....156
*Piper methysticum*.....Piperaceae .....314, 315, 316, 317
*Piper nigrum*.....Piperaceae .....28, 30, 314, 315, 316, 317
*Pistacia lentiscus*.....Anacardiaceae.....49, 51, 52
*Pistacia palaestina*.....Anacardiaceae.....49
*Pistacia terebinthus*.....Anacardiaceae.....49, 50, 51
*Plantago aschersonii*.....Plantaginaceae.....14
*Platanus orientalis*.....Platanaceae.....18, 319, 320
*Platanus wrightii*.....Platanaceae.....319, 320, 321
*Platanus x hispanica*.....Platanaceae.....319, 320, 321
*Pleurospermum austriacum*.....Apiaceae.....31
*Plocama pendula*.....Rubiaceae.....395, 396, 397, 398, 399
*Plumbago zeylanica*.....Plumbaginaceae .....323, 324, 325, 326
*Polemonium caeruleum*.....Polemoniaceae.....22
*Polycarpaea aristata*.....Caryophyllaceae.....26, 103, 105
*Polycarpaea carnosa*.....Caryophyllaceae.....103
*Polycarpaea divaricata*.....Caryophyllaceae.....103
*Polycarpaea latifolia*.....Caryophyllaceae.....103
*Polycarpaea nivea*.....Caryophyllaceae.....103
*Polycneum arvense*.....Amaranthaceae.....38, 40, 42, 43
*Polygala alpestris*.....Polygalaceae .....328, 329
*Polygala amarella*.....Polygalaceae .....328
*Polygala chamaebuxus*.....Polygalaceae .....328, 329, 331
*Polygala comosa*.....Polygalaceae .....328
*Polygala myrtifolia*.....Polygalaceae .....328, 329, 330, 331
*Polygala pedemontana*.....Polygalaceae .....328, 329, 330, 331
*Polygala tenuifolia*.....Polygalaceae .....328, 329
*Polygala transcaucasica*.....Polygalaceae .....328, 330
*Polygala vulgaris*.....Polygalaceae .....328
*Polygonum amphibium*.....Polygonaceae.....333
*Polygonum aviculare*.....Polygonaceae.....332
*Polygonum bistorta*.....Polygonaceae.....332, 333, 334, 338
*Polygonum bistortoides*.....Polygonaceae.....332, 335, 336, 338, 339
*Polygonum equisetiforme*.....Polygonaceae.....332
*Polygonum hydropiper*.....Polygonaceae.....332, 335
*Polygonum minus*.....Polygonaceae.....332, 335
*Polygonum mite*.....Polygonaceae.....332, 335
*Polygonum paronychia*.....Polygonaceae.....332, 337
*Polygonum persicaria*.....Polygonaceae.....332
*Polygonum polystachyum*.....Polygonaceae.....332, 334, 336
*Polygonum viviparum*.....Polygonaceae.....332, 333, 334, 335, 338
*Poncirus trifoliata*.....Rutaceae.....401, 402, 403, 404, 405
*Populus canadensis*.....Salicaceae .....406
*Populus nigra*.....Salicaceae .....406, 407
*Populus suaveolens*.....Salicaceae .....16, 406, 408, 409
*Populus tremula*.....Salicaceae .....406, 408, 409, 410, 411
*Populus tremuloides*.....Salicaceae .....406
*Porlieria hygrometrica*.....Zygophyllaceae.....474, 475, 476, 477
*Portulaca oleraceae*.....Portulaccaceae.....341, 342, 343
*Portulaca orientalis*.....Portulaccaceae.....341
*Potentilla argentea*.....Rosaceae.....384
*Potentilla aurea*.....Rosaceae.....384, 385
*Potentilla brauniana*.....Rosaceae.....384
*Potentilla caucasica*.....Rosaceae.....384
*Potentilla caulescens*.....Rosaceae.....384, 391
*Potentilla cinerea*.....Rosaceae.....384, 388
*Potentilla crantzii*.....Rosaceae.....384
*Potentilla erecta*.....Rosaceae.....384
*Potentilla frigida*.....Rosaceae.....384
*Potentilla fruticosa*.....Rosaceae.....384
*Potentilla grandiflora*.....Rosaceae.....384
*Potentilla hippiana*.....Rosaceae.....384
*Potentilla lanuginosa*.....Rosaceae.....384
*Potentilla micrantha*.....Rosaceae.....384
*Potentilla multifida*.....Rosaceae.....384
*Potentilla neumanniana*.....Rosaceae.....384
*Potentilla nitida*.....Rosaceae.....384
*Potentilla nivalis*.....Rosaceae.....384
*Potentilla palustris*.....Rosaceae.....384, 388, 390
*Potentilla pennsylvanica*.....Rosaceae.....384
*Potentilla pusilla*.....Rosaceae.....384
*Potentilla recta*.....Rosaceae.....384, 391
*Potentilla reptans*.....Rosaceae.....384
*Potentilla rubricaulis*.....Rosaceae.....384
*Potentilla sterilis*.....Rosaceae.....384, 388
*Potentilla supina*.....Rosaceae.....384
*Potentilla thuringiaca*.....Rosaceae.....384
*Primula auricula*.....Primulaceae.....344, 346, 347
*Primula elatior*.....Primulaceae.....344
*Primula farinosa*.....Primulaceae.....31, 344, 347
*Primula hirsuta*.....Primulaceae.....15, 344, 347
*Primula integrifolia*.....Primulaceae.....344, 346
*Primula latifolia*.....Primulaceae.....344
*Primula parry*.....Primulaceae.....344
*Primula veris*.....Primulaceae.....344
*Primula woronowi*.....Primulaceae.....344
*Pritzelago alpina*.....Brassicaceae.....80
*Proustia cuneifolia*.....Asteraceae .....27
*Prunus amygdalus*.....Rosaceae.....384, 386, 390, 393
*Prunus armeniaca*.....Rosaceae.....384, 390
*Prunus avium*.....Rosaceae.....384, 389, 390
*Prunus brigantina*.....Rosaceae.....384, 388
*Prunus cerasifera*.....Rosaceae.....384
*Prunus cerasus*.....Rosaceae.....384
*Prunus domestica*.....Rosaceae.....384
*Prunus dulcis*.....Rosaceae.....384
*Prunus fruticosa*.....Rosaceae.....384
*Prunus ilicifolia*.....Rosaceae.....384
*Prunus laurocerasus*.....Rosaceae.....384, 385, 387
*Prunus lusitanica*.....Rosaceae.....384
*Prunus mahaleb*.....Rosaceae.....384
*Prunus padus*.....Rosaceae.....384
*Prunus persica*.....Rosaceae.....384, 386, 391
*Prunus prostrata*.....Rosaceae.....384
*Prunus ramburii*.....Rosaceae.....384
*Prunus sachalinensis*.....Rosaceae.....384
*Prunus spinosa*.....Rosaceae.....384, 393
*Prunus tenella*.....Rosaceae.....384
*Prunus virginiana*.....Rosaceae.....384
*Prunus webbii*.....Rosaceae.....384
*Pseudoerucaria clavata*.....Brassicaceae.....80
*Psoralea bituminosa*.....Fabaceae.....176
*Ptilotrichum spinosum*.....Brassicaceae.....80, 83
*Pueraria hirsuta*.....Fabaceae.....176, 191
*Pulsatilla alpina* ssp. *alpina*.....Ranunculaceae .....352
*Pulsatilla alpina* ssp. *apiifolia*.....Ranunculaceae .....352
*Pulsatilla alpina* ssp. *millefoliata*.....Ranunculaceae .....352, 360
*Pulsatilla montana*.....Ranunculaceae .....22, 352
*Pulsatilla multifida*.....Ranunculaceae .....352
*Pulsatilla patens*.....Ranunculaceae .....352, 359
*Pulsatilla vernalis*.....Ranunculaceae .....352
*Pulsatilla vulgaris* ssp. *vulgaris*.....Ranunculaceae .....18, 352, 353, 360
*Punica granatum*.....Lythraceae.....246, 247, 248, 249
*Purshia tridentata*.....Rosaceae.....384
*Putoria calabrica*.....Rubiaceae.....395, 396, 398, 399
*Pyracantha coccinea*.....Rosaceae.....384
*Pyrola rotundifolia*.....Ericaceae .....156, 157, 162, 163
*Pyrus amygdaliformis*.....Rosaceae.....384
*Pyrus communis*.....Rosaceae.....384
*Pyrus malus*.....Rosaceae.....384, 385, 388
*Pyrus orientalis*.....Rosaceae.....384, 392
*Quercus alba*.....Fagaceae.....193

*Quercus alnifolia* ..... Fagaceae ..... 193
*Quercus cerris* ..... Fagaceae ..... 16, 193, 194, 196
*Quercus coccifera* ..... Fagaceae ..... 193
*Quercus congesta* ..... Fagaceae ..... 193
*Quercus faginea* ..... Fagaceae ..... 193
*Quercus frainetto* ..... Fagaceae ..... 193
*Quercus fruticosa* ..... Fagaceae ..... 193
*Quercus ilex* ..... Fagaceae ..... 193, 196, 197
*Quercus infectoria* ..... Fagaceae ..... 193
*Quercus petraea* ..... Fagaceae ..... 193
*Quercus ponticum* ..... Fagaceae ..... 193
*Quercus pubescens* ..... Fagaceae ..... 193
*Quercus pyrenaica* ..... Fagaceae ..... 193, 195, 197
*Quercus robur* ..... Fagaceae ..... 193, 194
*Quercus rubra* ..... Fagaceae ..... 193, 196
*Quercus suber* ..... Fagaceae ..... 193, 195
*Quercus trojana* ..... Fagaceae ..... 193
*Randonia africana* ..... Resedaceae ..... 372, 373, 374
*Ranunculus aconitifolius* ..... Ranunculaceae ..... 352, 356, 357
*Ranunculus acris* ..... Ranunculaceae ..... 352
*Ranunculus alismifolius* ..... Ranunculaceae ..... 352
*Ranunculus alpestris* ..... Ranunculaceae ..... 352
*Ranunculus bulbosus* ..... Ranunculaceae ..... 352, 356
*Ranunculus circinatus* ..... Ranunculaceae ..... 352, 354, 356, 358
*Ranunculus cortusifolius* ..... Ranunculaceae ..... 352, 356
*Ranunculus ficaria* ..... Ranunculaceae ..... 352
*Ranunculus flammula* ..... Ranunculaceae ..... 352, 355, 358
*Ranunculus glacialis* ..... Ranunculaceae ..... 352
*Ranunculus kuepferi* ..... Ranunculaceae ..... 352
*Ranunculus lanuginosus* ..... Ranunculaceae ..... 352, 354, 355, 357, 358
*Ranunculus montanus* ..... Ranunculaceae ..... 352, 357
*Ranunculus nemorosus* ..... Ranunculaceae ..... 353
*Ranunculus repens* ..... Ranunculaceae ..... 352
*Ranunculus serpens* ..... Ranunculaceae ..... 352
*Ranunculus trichophyllus* ..... Ranunculaceae ..... 352, 354, 356
*Rapistrum rugosum* ..... Brassicaceae ..... 80
*Reseda lutea* ..... Resedaceae ..... 372, 373, 374, 375
*Reseda luteola* ..... Resedaceae ..... 372, 373, 375
*Reseda odorata* ..... Resedaceae ..... 372
*Reseda phyteuma* ..... Resedaceae ..... 372
*Reseda scoparia* ..... Resedaceae ..... 372, 373, 374
*Reseda suffruticosa* ..... Resedaceae ..... 18, 372, 373
*Reseda villosa* ..... Resedaceae ..... 372, 374
*Reynoutria japonica* ..... Polygonaceae ..... 332, 334, 336, 338, 339
*Rhamnus alaternus* ..... Rhamnaceae ..... 376, 378
*Rhamnus alnifolia* ..... Rhamnaceae ..... 376
*Rhamnus alpina* ..... Rhamnaceae ..... 376
*Rhamnus cathartica* ..... Rhamnaceae ..... 376
*Rhamnus crenulata* ..... Rhamnaceae ..... 376, 381, 382
*Rhamnus davurica* ..... Rhamnaceae ..... 376
*Rhamnus fallax* ..... Rhamnaceae ..... 376, 380
*Rhamnus glandulosa* ..... Rhamnaceae ..... 376
*Rhamnus myrtifolius* ..... Rhamnaceae ..... 376
*Rhamnus oleoides* ..... Rhamnaceae ..... 376
*Rhamnus pallasii* ..... Rhamnaceae ..... 376
*Rhamnus pumila* ..... Rhamnaceae ..... 376
*Rhamnus saxatilis* ..... Rhamnaceae ..... 376, 379, 382
*Rhazya stricta* ..... Apocyanaceae & Asclepiadaceae ..... 54, 56
*Rhinanthus glacialis* ..... Orobanchaceae ..... 21
*Rhodiola integrifolia* ..... Crassulaceae ..... 134, 138
*Rhodiola rosea* ..... Crassulaceae ..... 134, 135, 136, 137, 138
*Rhododendron adansoni* ..... Ericaceae ..... 156, 161
*Rhododendron aureum* ..... Ericaceae ..... 156
*Rhododendron caucasicum* ..... Ericaceae ..... 156, 160, 161
*Rhododendron dahurica* ..... Ericaceae ..... 156
*Rhododendron ferrugineum* ..... Ericaceae ..... 156
*Rhododendron hirsutum* ..... Ericaceae ..... 156, 157
*Rhododendron lapponicum* ..... Ericaceae ..... 156
*Rhododendron luteum* ..... Ericaceae ..... 156, 160
*Rhododendron macrophyllum* ..... Ericaceae ..... 156, 160, 162
*Rhododendron myrtifolium* ..... Ericaceae ..... 156
*Rhododendron parviflorum* ..... Ericaceae ..... 156
*Rhododendron ponticum* ..... Ericaceae ..... 156
*Rhododendron virginianum* ..... Ericaceae ..... 156
*Rhodothamnus chamaecistus* ..... Ericaceae ..... 156, 158
*Rhus coriaria* ..... Anacardiaceae ..... 49
*Rhus glabra* ..... Anacardiaceae ..... 49, 51
*Rhus trilobata* ..... Anacardiaceae ..... 49
*Rhus tripartitus* ..... Anacardiaceae ..... 49, 50, 51, 52
*Rhus typhina* ..... Anacardiaceae ..... 49, 50, 52
*Ribes acicularis* ..... Grossulariaceae ..... 210, 211, 212
*Ribes alpinum* ..... Grossulariaceae ..... 16, 17, 210, 211, 212, 213
*Ribes bracteosum* ..... Grossulariaceae ..... 210
*Ribes dikuscha* ..... Grossulariaceae ..... 210
*Ribes glandulosum* ..... Grossulariaceae ..... 210, 212
*Ribes hudsonianum* ..... Grossulariaceae ..... 210
*Ribes lacustre* ..... Grossulariaceae ..... 210
*Ribes laxiflorum* ..... Grossulariaceae ..... 210, 212
*Ribes nigrum* ..... Grossulariaceae ..... 210, 211, 212
*Ribes pauciflorum* ..... Grossulariaceae ..... 210, 212
*Ribes petraeaum* ..... Grossulariaceae ..... 210, 213
*Ribes procumbens* ..... Grossulariaceae ..... 210
*Ribes rubrum* ..... Grossulariaceae ..... 210
*Ribes triste* ..... Grossulariaceae ..... 210, 211
*Ribes uva-crispa* ..... Grossulariaceae ..... 210
*Ricinus communis* ..... Euphorbiaceae ..... 164, 166, 170, 171, 172
*Robinia neo-mexicana* ..... Fabaceae ..... 176
*Robinia pseudoacacia* ..... Fabaceae ..... 176
*Rorippa austriaca* ..... Brassicaceae ..... 80
*Rorippa stylosa* ..... Brassicaceae ..... 80, 82
*Rosa acicularis* ..... Rosaceae ..... 384
*Rosa arkansana* ..... Rosaceae ..... 384, 391
*Rosa arvensis* ..... Rosaceae ..... 384
*Rosa canina* ..... Rosaceae ..... 384
*Rosa elliptica* ..... Rosaceae ..... 384, 393
*Rosa pendulina* ..... Rosaceae ..... 383, 384
*Rosa pomifera* ..... Rosaceae ..... 384, 386
*Rosa rugosa* ..... Rosaceae ..... 384
*Rosa sempervirens* ..... Rosaceae ..... 384
*Rubia fruticosa* ..... Rubiaceae ..... 395, 396, 399
*Rubia peregrina* ..... Rubiaceae ..... 395, 398
*Rubia tenuifolia* ..... Rubiaceae ..... 395, 396
*Rubia tinctoria* ..... Rubiaceae ..... 395
*Rubus caesius* ..... Rosaceae ..... 384
*Rubus chamaemorus* ..... Rosaceae ..... 384, 386, 388, 389, 392
*Rubus fruticosus* ..... Rosaceae ..... 384
*Rubus idaeus* ..... Rosaceae ..... 384, 386, 387
*Rubus saxatilis* ..... Rosaceae ..... 384
*Rubus spectabilis* ..... Rosaceae ..... 384, 386, 388, 389
*Rumex acetosa* ..... Polygonaceae ..... 332, 334, 335
*Rumex acetosella* ..... Polygonaceae ..... 332, 335, 337, 338, 340
*Rumex alpestris* ..... Polygonaceae ..... 332
*Rumex alpinus* ..... Polygonaceae ..... 332, 333, 338
*Rumex conglomeratus* ..... Polygonaceae ..... 332, 338
*Rumex crispus* ..... Polygonaceae ..... 332
*Rumex hydrolapathum* ..... Polygonaceae ..... 332, 336, 338, 339
*Rumex lunaria* ..... Polygonaceae ..... 332, 334
*Rumex maderensis* ..... Polygonaceae ..... 332
*Rumex nivalis* ..... Polygonaceae ..... 332, 335, 336
*Rumex obtusifolius* ..... Polygonaceae ..... 332, 335, 338
*Rumex scutatus* ..... Polygonaceae ..... 332, 334, 337
*Rumex thyrsiflorus* ..... Polygonaceae ..... 332, 338
*Rumex uthaensis* ..... Polygonaceae ..... 332
*Rumex vesicarius* ..... Polygonaceae ..... 332
*Ruta angustifolia* ..... Rutaceae ..... 401, 402, 403
*Ruta chalepensis* ..... Rutaceae ..... 401, 402
*Ruta graveolens* ..... Rutaceae ..... 401, 402
*Ruta montana* ..... Rutaceae ..... 401, 402, 404
*Sagina apetala* ..... Caryophyllaceae ..... 103
*Sagina maritima* ..... Caryophyllaceae ..... 14, 26, 103, 106
*Sagina saginoides* ..... Caryophyllaceae ..... 104
*Salix alba* ..... Salicaceae ..... 406, 407
*Salix appendiculata* ..... Salicaceae ..... 406, 410, 411
*Salix arbuscula* ..... Salicaceae ..... 406
*Salix arctica* ..... Salicaceae ..... 406
*Salix aurita* ..... Salicaceae ..... 406
*Salix berberidifolia* ..... Salicaceae ..... 406
*Salix brachycarpa* ..... Salicaceae ..... 406
*Salix breviserrata* ..... Salicaceae ..... 406
*Salix canariensis* ..... Salicaceae ..... 406
*Salix caprea* ..... Salicaceae ..... 406
*Salix cinerea* ..... Salicaceae ..... 406
*Salix daphnoides* ..... Salicaceae ..... 406
*Salix foetida* ..... Salicaceae ..... 406, 409
*Salix fragilis* ..... Salicaceae ..... 406
*Salix glabra* ..... Salicaceae ..... 406
*Salix glaucosericea* ..... Salicaceae ..... 406
*Salix hastata* ..... Salicaceae ..... 406
*Salix helvetica* ..... Salicaceae ..... 406
*Salix herbacea* ..... Salicaceae ..... 406, 410

*Salix incana* ... Salicaceae ... 406
*Salix lanata* ... Salicaceae ... 406, 411
*Salix myrsinifolia* ... Salicaceae ... 406, 409
*Salix myrtilloides* ... Salicaceae ... 406
*Salix planifolia* ... Salicaceae ... 18, 406, 409, 410
*Salix polaris* ... Salicaceae ... 406, 411
*Salix pulchra* ... Salicaceae ... 406
*Salix purpurea* ... Salicaceae ... 406, 410, 411
*Salix repens* ... Salicaceae ... 406
*Salix reticulata* ... Salicaceae ... 406, 408
*Salix retusa* ... Salicaceae ... 406, 408, 409
*Salix schwerini* ... Salicaceae ... 406
*Salix viminalis* ... Salicaceae ... 406, 410
*Salix waldsteiniana* ... Salicaceae ... 406
*Salsola foetida* ... Amaranthaceae ... 38
*Salsola genistoides* ... Amaranthaceae ... 38, 45
*Salsola kali* ... Amaranthaceae ... 38, 42
*Salsola oppositifoila* ... Amaranthaceae ... 38
*Salsola vermiculata* ... Amaranthaceae ... 38, 42
*Salsola verticillata* ... Amaranthaceae ... 38
*Salvadora persica* ... Salvadoraceae ... 413, 414
*Samolus valerandi* ... Primulaceae ... 344, 348, 349
*Sanguisorba ancistroides* ... Rosaceae ... 384, 387
*Sanguisorba minor* ssp. *magnolii* ... Rosaceae ... 384
*Sanguisorba minor* ssp. *minor* ... Rosaceae ... 384, 387
*Sanguisorba officinalis* ... Rosaceae ... 384, 385, 389
*Saponaria lutea* ... Caryophyllaceae ... 103
*Saponaria ocymoides* ... Caryophyllaceae ... 103, 108
*Saponaria officinalis* ... Caryophyllaceae ... 104, 106, 107
*Sarcococca confusa* ... Buxaceae ... 88
*Sarcococca hookeriana* ... Buxaceae ... 21, 88, 89, 90, 91
*Sarcococca saligna* ... Buxaceae ... 88, 91
*Sarcopoterium spinosum* ... Rosaceae ... 384
*Satureja montana* ... Lamiaceae ... 24
*Saxifraga aizoides* ... Saxifragaceae ... 423
*Saxifraga aspera* ... Saxifragaceae ... 423
*Saxifraga bryoides* ... Saxifragaceae ... 423
*Saxifraga bulbifera* ... Saxifragaceae ... 423, 424, 425, 426
*Saxifraga caesia* ... Saxifragaceae ... 32, 423, 424
*Saxifraga caespitosa* ... Saxifragaceae ... 423
*Saxifraga callosa* ... Saxifragaceae ... 423
*Saxifraga cotyledon* ... Saxifragaceae ... 423
*Saxifraga cuneifolia* ... Saxifragaceae ... 423
*Saxifraga exarata* ssp. *exarata* ... Saxifragaceae ... 423
*Saxifraga moschata* ... Saxifragaceae ... 23, 423, 424, 427
*Saxifraga muscoides* ... Saxifragaceae ... 423
*Saxifraga mutata* ... Saxifragaceae ... 423
*Saxifraga oppositifolia* ... Saxifragaceae ... 423, 424, 425, 427
*Saxifraga paniculata* ... Saxifragaceae ... 423
*Saxifraga rotundifolia* ... Saxifragaceae ... 423
*Saxifraga seguieri* ... Saxifragaceae ... 423
*Saxifraga stellaris* ... Saxifragaceae ... 423
*Saxifraga tridactylites* ... Saxifragaceae ... 423, 424, 426
*Schinus molle L.* ... Anacardiaceae ... 49, 50, 51, 52
*Scleranthus annuus* ... Caryophyllaceae ... 104, 104, 105, 106
*Scleranthus perennis* ... Caryophyllaceae ... 104
*Securigera varia* ... Fabaceae ... 176
*Securinega suffruticosa* ... Euphorbiaceae ... 164, 166, 168, 170, 171
*Sedum acre* ... Crassulaceae ... 135
*Sedum album* ... Crassulaceae ... 15, 134, 136, 137, 138
*Sedum alpestre* ... Crassulaceae ... 134, 137
*Sedum anopetalum* ... Crassulaceae ... 24, 134, 136, 137, 138
*Sedum atratum* ... Crassulaceae ... 134, 137
*Sedum cepaea* ... Crassulaceae ... 134, 137, 138
*Sedum dasyphyllum* ... Crassulaceae ... 134, 137
*Sedum reflexum* ... Crassulaceae ... 25, 134, 137, 138
*Sedum rupestre* ... Crassulaceae ... 134, 136, 137
*Sedum telephium* ... Crassulaceae ... 134, 135, 137, 138
*Sempervivum arachnoideum* ... Crassulaceae ... 134, 137, 138
*Sempervivum montanum* ... Crassulaceae ... 134, 135
*Sempervivum tectorum* ... Crassulaceae ... 24, 134, 137, 138
*Sempervivum wulfenii* ... Crassulaceae ... 134, 137
*Senna armata* ... Fabaceae ... 176
*Senra incana* ... Malvaceae ... 254
*Shepherdia canadensis* ... Eleagnaceae ... 152, 153, 154
*Sherardia arvensis* ... Rubiaceae ... 395, 396, 397
*Sibbaldia parviflora* ... Rosaceae ... 384
*Sibbaldia procumbens* ... Rosaceae ... 384
*Sibiraea altaensis* ... Rosaceae ... 384, 388
*Sideritis hirsuta* ... Lamiaceae ... 32
*Silena adscendens* ... Caryophyllaceae ... 103
*Silene acaulis* ... Caryophyllaceae ... 104, 106, 108
*Silene arctica* ... Caryophyllaceae ... 104
*Silene coronaria* ... Caryophyllaceae ... 104, 110
*Silene dioeca* ... Caryophyllaceae ... 104, 107
*Silene excapa* ... Caryophyllaceae ... 104, 106
*Silene flos-cuculi* ... Caryophyllaceae ... 104
*Silene flos-jovis* ... Caryophyllaceae ... 104
*Silene gallica* ... Caryophyllaceae ... 104
*Silene italica* ... Caryophyllaceae ... 104, 106, 108
*Silene latifolia* ssp. *alba* ... Caryophyllaceae ... 104, 106
*Silene maritima* ... Caryophyllaceae ... 16, 104
*Silene noctiflora* ... Caryophyllaceae ... 104
*Silene nutans* ssp. *nutans* ... Caryophyllaceae ... 104, 106
*Silene otites* ... Caryophyllaceae ... 104, 110
*Silene pauciflora* ... Caryophyllaceae ... 104
*Silene petrarchae* ... Caryophyllaceae ... 104
*Silene pseudovelutina* ... Caryophyllaceae ... 104
*Silene pusilla* ... Caryophyllaceae ... 104
*Silene rupestris* ... Caryophyllaceae ... 104
*Silene saxifraga* ... Caryophyllaceae ... 104
*Silene scouleri* ... Caryophyllaceae ... 104
*Silene suecica* ... Caryophyllaceae ... 104
*Silene tridentata* ... Caryophyllaceae ... 104
*Silene viscaria* ... Caryophyllaceae ... 25, 104
*Silene vulgaris* ... Caryophyllaceae ... 104, 106, 108, 111
*Silene vulgaris* ssp. *canariensis* ... Caryophyllaceae ... 104
*Simmondsia chinensis* ... Simmondsiaceae ... 429, 430
*Sinapidendron angustifolia* ... Brassicaceae ... 80, 83
*Sinapidendron frutescens* ... Brassicaceae ... 80
*Sinapis arvensis* ... Brassicaceae ... 80, 83
*Sinapis flexuosa* ... Brassicaceae ... 80
*Sinofranchetia chinensis* ... Lardizabalaceae ... 19, 228, 229, 230
*Sisymbrium altissimum* ... Brassicaceae ... 80
*Sisymbrium andinum* ... Brassicaceae ... 80
*Sisymbrium austriacum* ... Brassicaceae ... 24, 80, 84
*Sisymbrium irio* ... Brassicaceae ... 80
*Sisymbrium loeselii* ... Brassicaceae ... 80
*Sisymbrium officinale* ... Brassicaceae ... 80
*Sisymbrium orientale* ... Brassicaceae ... 80, 84
*Sisymbrium sophia* ... Brassicaceae ... 80
*Sisymbrium strictissimum* ... Brassicaceae ... 80
*Smelowskia calycina* ... Brassicaceae ... 80, 81, 85
*Soldanella alpina* ... Primulaceae ... 344, 345
*Soldanella pusilla* ... Primulaceae ... 344, 346
*Sonchus pustulatus* ... Asteraceae ... 31
*Sophora japonica* ... Fabaceae ... 176
*Sorbaria sorbifolia* ... Rosaceae ... 384, 388, 390
*Sorbus aria* ... Rosaceae ... 384, 393
*Sorbus aucuparia* ... Rosaceae ... 384, 385
*Sorbus chamaemespilus* ... Rosaceae ... 384, 386, 391
*Sorbus decora* ... Rosaceae ... 384, 388
*Sorbus domestica* ... Rosaceae ... 384
*Sorbus graeca* ... Rosaceae ... 384
*Sorbus sambucifolia* ... Rosaceae ... 384
*Sorbus sibirica* ... Rosaceae ... 384
*Sorbus torminalis* ... Rosaceae ... 384
*Spartium junceum* ... Fabaceae ... 176
*Spartocytisus filipes* ... Fabaceae ... 176
*Spartocytisus supranubicus* ... Fabaceae ... 176
*Spergula arvensis* ... Caryophyllaceae ... 104, 109
*Spergula morisonii* ... Caryophyllaceae ... 104
*Spergularia marina* ... Caryophyllaceae ... 104
*Spergularia media* ... Caryophyllaceae ... 104
*Spergularia rubra* ... Caryophyllaceae ... 104
*Sphaeralcea ambigua* ... Malvaceae ... 254, 257
*Sphaeralcea coccinea* ... Malvaceae ... 254, 255
*Sphaeralcea coulteri* ... Malvaceae ... 254, 255, 257
*Sphaeralcea miniata* ... Malvaceae ... 254, 258
*Spiraea betulifolia* ... Rosaceae ... 384
*Spiraea dahurica* ... Rosaceae ... 384
*Spiraea douglasii* ... Rosaceae ... 384, 388
*Spiraea hypericifolia* ... Rosaceae ... 384
*Spiraea latifolia* ... Rosaceae ... 384
*Spiraea media* ... Rosaceae ... 384
*Spiraea salicifolia* ... Rosaceae ... 384
*Spiraea stevenii* ... Rosaceae ... 384, 386
*Stanleya pinnata* ... Brassicaceae ... 80
*Staphylea colchica* ... Staphyleaceae ... 431, 432, 433
*Staphylea pinnata* ... Staphyleaceae ... 431, 432, 433

*Stauntonia hexapetala* ..... Lardizabalaceae ..... 228, 230, 231
*Staurocanthus boivinii* ..... Fabaceae ..... 176
*Stellaria media* ..... Caryophyllaceae ..... 104, 106
*Styloceras brokawii* ..... Buxaceae ..... 88, 89, 91
*Suaeda fruticosa* ..... Amaranthaceae ..... 38, 44, 45
*Suaeda pruniosa* ..... Amaranthaceae ..... 38, 40
*Suaeda vera* ..... Amaranthaceae ..... 38
*Suaeda vermiculata* ..... Amaranthaceae ..... 28, 38
*Swertia perennis* ..... Gentianaceae ..... 199, 202
*Swertia radiata* ..... Gentianaceae ..... 199, 202
*Sycopsis sinensis* ..... Hamamelidaceae & Altingiaceae ... 22, 217, 218, 219
*Syringa vulgaris* ..... Oleaceae ..... 21
*Tamarix aphylla* ..... Tamaricaceae ..... 434, 435
*Tamarix articulata* ..... Tamaricaceae ..... 25, 26, 434, 435, 436
*Tamarix balanse* ..... Tamaricaceae ..... 30, 434, 435, 436
*Tamarix bovenana* ..... Tamaricaceae ..... 434
*Tamarix canariensis* ..... Tamaricaceae ..... 434, 435, 437
*Tamarix gallica* ..... Tamaricaceae ..... 434, 436, 437, 438
*Tamarix parviflora* ..... Tamaricaceae ..... 434
*Tamarix pentandra* ..... Tamaricaceae ..... 434
*Tasmannia xerophila* ..... Winteraceae ..... 470, 471
*Teline canariensis* ..... Fabaceae ..... 176
*Teline maderensis* ..... Fabaceae ..... 176
*Teline monspessulana* ..... Fabaceae ..... 176
*Teline nervosa* ..... Fabaceae ..... 176
*Tephrosia leptostachya* ..... Fabaceae ..... 176, 186
*Teucrium luteum* ..... Lamiaceae ..... 30
*Thalictrum alpinum* ..... Ranunculaceae ..... 29, 352, 359, 360, 361
*Thalictrum aquilegifolium* ..... Ranunculaceae ..... 352, 353, 359
*Thalictrum foetidum* ..... Ranunculaceae ..... 352
*Thalictrum minus* ..... Ranunculaceae ..... 352, 359, 360
*Thermopsis divaricarpa* ..... Fabaceae ..... 176, 185
*Thesium alpinum* ..... Santalaceae ..... 415
*Thesium arvense* ..... Santalaceae ..... 415, 416
*Thesium bavarum* ..... Santalaceae ..... 21, 415, 416
*Thesium divaricatum* ..... Santalaceae ..... 415, 416
*Thesium humile* ..... Santalaceae ..... 415, 416, 417
*Thesium linophyllon* ..... Santalaceae ..... 415, 416, 417
*Thesium pyrenaicum* ..... Santalaceae ..... 415, 416, 418
*Thlaspi arvense* ..... Brassicaceae ..... 80
*Thlaspi bonariense* ..... Brassicaceae ..... 80
*Thlaspi caerulescens* ..... Brassicaceae ..... 80
*Thlaspi perfoliatum* ..... Brassicaceae ..... 80, 82
*Thlaspi praecox* ..... Brassicaceae ..... 80
*Thlaspi rotundifolium* ..... Brassicaceae ..... 80
*Thlaspi sylvium* ..... Brassicaceae ..... 80, 85
*Thymelaea dioica* ..... Thymelaeaceae ..... 439, 440, 441, 442, 443
*Thymelaea hirsuta* ..... Thymelaeaceae ..... 23, 439, 440, 441, 443
*Thymelaea microphylla* ..... Thymelaeaceae ..... 439, 443
*Thymelaea sanamuda* ..... Thymelaeaceae ..... 439, 440
*Thymelaea tartonraira* ..... Thymelaeaceae ..... 439, 440
*Tiarella cordifolia* ..... Saxifragaceae ..... 423, 425, 427
*Tiarella unifoliata* ..... Saxifragaceae ..... 423, 426, 427
*Tilia amurensis* ..... Tiliaceae ..... 444
*Tilia cordata* ..... Tiliaceae ..... 444, 445
*Tilia platyphyllos* ..... Tiliaceae ..... 444
*Tilia rubra* ..... Tiliaceae ..... 444, 445
*Tilia tomentosa* ..... Tiliaceae ..... 444, 445
*Tolmiea menziesii* ..... Saxifragaceae ..... 423
*Tolpis fruticosa* ..... Asteraceae ..... 17
*Traganum moquinii* ..... Amaranthaceae ..... 28, 38, 44, 45
*Trifolium alpinum* ..... Fabaceae ..... 176
*Trifolium ambiguum* ..... Fabaceae ..... 176, 187
*Trifolium angustifolium* ..... Fabaceae ..... 176
*Trifolium arvense* ..... Fabaceae ..... 176
*Trifolium aureum* ..... Fabaceae ..... 176
*Trifolium badium* ..... Fabaceae ..... 176
*Trifolium dasyphyllum* ..... Fabaceae ..... 176, 188
*Trifolium incarnatum* ..... Fabaceae ..... 176, 184, 187
*Trifolium maciletum* ..... Fabaceae ..... 176
*Trifolium medium* ..... Fabaceae ..... 176
*Trifolium montanum* ..... Fabaceae ..... 176
*Trifolium nanum* ..... Fabaceae ..... 176, 188
*Trifolium pallescens* ..... Fabaceae ..... 176
*Trifolium pratense* ..... Fabaceae ..... 176, 186
*Trifolium repens* ..... Fabaceae ..... 176
*Trifolium rubens* ..... Fabaceae ..... 176, 189
*Trifolium saxatile* ..... Fabaceae ..... 176
*Trifolium thalii* ..... Fabaceae ..... 176
*Trochodendron aralioides* ..... Trochodendraceae ..... 20, 22, 447, 448, 449
*Trollius albiflorus* ..... Ranunculaceae ..... 352
*Trollius europaeus* ..... Ranunculaceae ..... 352, 353
*Tuberaria guttata* ..... Cistaceae ..... 122, 123
*Tuberaria lignosa* ..... Cistaceae ..... 122
*Turritis glabra* ..... Brassicaceae ..... 80
*Ulex baeticus* ..... Fabaceae ..... 176
*Ulex europaeus* ..... Fabaceae ..... 176
*Ulex minor* ..... Fabaceae ..... 176
*Ulex parviflorus* ..... Fabaceae ..... 176
*Ulmus glabra* ..... Ulmaceae ..... 450, 451
*Ulmus laevis* ..... Ulmaceae ..... 16, 450
*Ulmus minor, syn. campestris* ..... Ulmaceae ..... 450, 451, 452
*Umbilicus horizontalis* ..... Crassulaceae ..... 14, 25
*Umbilicus rupestris* ..... Crassulaceae ..... 134
*Urtica dioica* ..... Urticaceae ..... 23, 454, 456
*Urtica membranacea* ..... Urticaceae ..... 454, 456
*Urtica morifolia* ..... Urticaceae ..... 454, 457
*Urtica urens* ..... Urticaceae ..... 23, 454, 455, 457
*Vaccaria hispanica* ..... Caryophyllaceae ..... 104, 107
*Vaccinium angustifolium* ..... Ericaceae ..... 156
*Vaccinium gaultherioides* ..... Ericaceae ..... 156
*Vaccinium maderense* ..... Ericaceae ..... 156
*Vaccinium myrtillus* ..... Ericaceae ..... 156
*Vaccinium ovalifolium* ..... Ericaceae ..... 156
*Vaccinium ovatum* ..... Ericaceae ..... 156, 159
*Vaccinium oxycoccus* ..... Ericaceae ..... 156
*Vaccinium parviflorum* ..... Ericaceae ..... 156
*Vaccinium uliginosum* ..... Ericaceae ..... 156, 162
*Vaccinium vitis-idaea* ..... Ericaceae ..... 156, 157
*Vancouveria planipetala* ..... Berberidaceae ..... 67, 68, 69, 70, 71
*Vella spinosa* ..... Brassicaceae ..... 80
*Vella spinosa* ssp. *lucentina* ..... Brassicaceae ..... 23, 80, 83
*Vicia hirsuta* ..... Fabaceae ..... 14, 176
*Vicia onobrychioides* ..... Fabaceae ..... 176
*Vicia pannonica* ..... Fabaceae ..... 176, 188
*Vicia pisiformis* ..... Fabaceae ..... 176
*Vicia sativa* ..... Fabaceae ..... 176, 184, 191
*Vicia sepium* ..... Fabaceae ..... 176, 177, 185, 191
*Vicia sylvatica* ..... Fabaceae ..... 176
*Vicia villosa* ..... Fabaceae ..... 176
*Vinca major* ..... Apocyanaceae & Asclepiadaceae ... 32, 54, 55, 56, 58, 59
*Vinca minor* ..... Apocyanaceae & Asclepiadaceae ..... 54, 55
*Vincetoxicum officinale* ..... Apocyanaceae & Asclepiadaceae ..... 54, 55
*Viola arborescens* ..... Violaceae ..... 459, 460, 463
*Viola biflora* ..... Violaceae ..... 459, 460, 463
*Viola calcarata* ..... Violaceae ..... 17, 459, 460, 461, 462
*Viola canadensis* ..... Violaceae ..... 459
*Viola canina* ..... Violaceae ..... 459
*Viola chamissoniana* ..... Violaceae ..... 459
*Viola elatior* ..... Violaceae ..... 22, 459, 461
*Viola hirta* ..... Violaceae ..... 459
*Viola labradorica* ..... Violaceae ..... 459
*Viola mirabilis* ..... Violaceae ..... 459, 461
*Viola odorata* ..... Violaceae ..... 13, 459, 462, 463
*Viola palustris* ..... Violaceae ..... 459, 460, 463
*Viola reichenbachiana* ..... Violaceae ..... 459, 460, 463, 464
*Viola rupestris* ..... Violaceae ..... 459
*Viola suavis* ..... Violaceae ..... 459
*Viola tricolor* ..... Violaceae ..... 459, 460, 462
*Viscum album* ..... Loranthaceae & Viscaceae ..... 241, 242, 244, 245
*Viscum cruciatum* ..... Loranthaceae & Viscaceae ..... 241
*Vitis vinifera* ..... Vitaceae ..... 465, 466, 467, 468
*Wisteria sinensis* ..... Fabaceae ..... 176, 191
*Woodfordia uniflora* ..... Lythraceae ..... 246, 247, 248
*Worownia speciosa* ..... Rosaceae ..... 384
*Zellkova carpinifolia* ..... Ulmaceae ..... 450, 451, 452
*Zilla spinosa* ..... Brassicaceae ..... 80
*Ziziphus jujuba* ..... Rhamnaceae ..... 376, 380
*Ziziphus oblongifolius* ..... Rhamnaceae ..... 376, 379, 382
*Ziziphus spina-christi* ..... Rhamnaceae ..... 376, 377, 378, 379
*Zygogynum polyneurum* ..... Winteraceae ..... 470, 471
*Zygophyllum fontanesii* ..... Zygophyllaceae ..... 16, 474, 476, 477
*Zygophyllum gaetulum* ..... Zygophyllaceae ..... 474, 475, 476
*Zygophyllum waterlotii* ..... Zygophyllaceae ..... 474