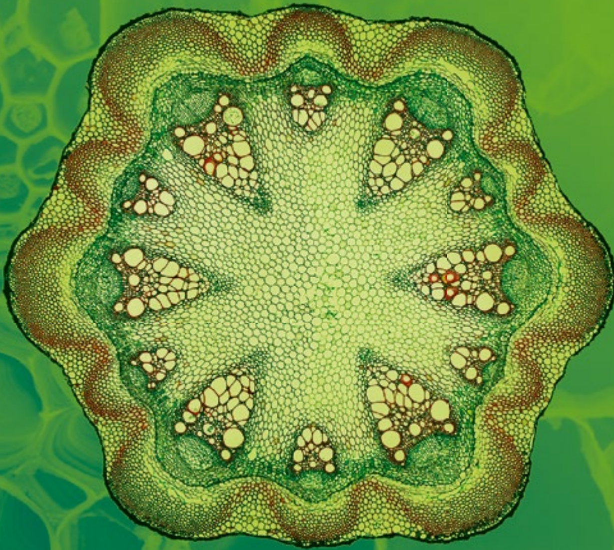

Richard Crang
Sheila Lyons-Sobaski
Robert Wise

Plant Anatomy

A Concept-Based Approach to the Structure of Seed Plants

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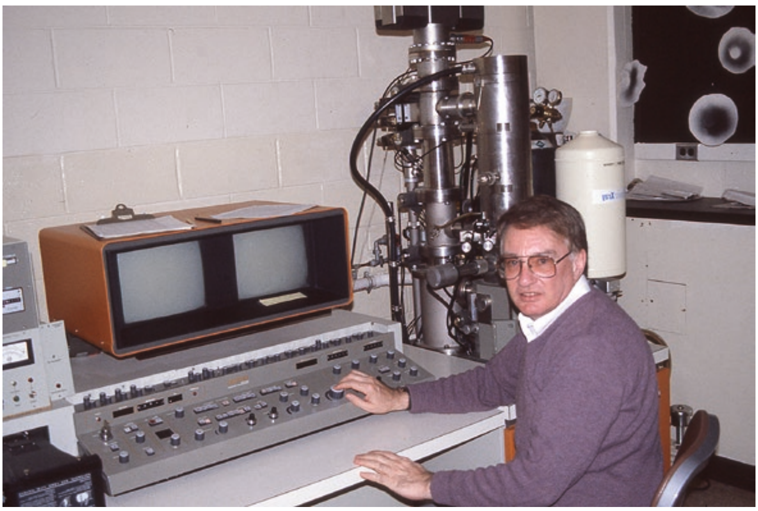

Richard was a vital contributor to this project from its infancy to its final production phase. We take some comfort that he knew the book was essentially complete prior to his passing. We greatly miss our colleague and friend, and so we dedicate this book to Richard who was a courageous and venturesome guy, a brilliant scholar, an innovative teacher, and a kind, thoughtful man.

SLS and RRW

Preface

The science of plant anatomy extends back to the late seventeenth century and, by now, spans over 300 years and encompasses hundreds of thousands of reports in the scientific literature. The early plant anatomy research was summarized in 1899 by Dr. Hans Solereder in his two volume work entitled *Systematische Anatomie der Dicotyledonen: Ein Handbuch für Laboratorien der wissenschaftlichen und angewandten Botanik*. The 1908 English translation by Boodle, Fritsch, and Scott remains as fresh, informative, and useful today as when it was published over 100 years ago. Several important texts were published in the 1950s. The two-volume work of Metcalfe and Chalk, *Anatomy of the Dicotyledons* (1950) with second editions in 1979 (Volume 1) and 1983 (Volume 2), is a thorough survey of anatomical traits and features arranged by family. Some of the taxonomy has been rearranged, but the anatomical references remain accurate and valuable. The year 1953 saw the publication of the first edition of the classic *Plant Anatomy* by Katherine Esau. Encyclopedic in its coverage, insightful in interpretation, and complete in its synthesis, "Esau" (as it has been referred to by several generations of botanists) remains a go-to reference to this day. A second edition was released in 1977 and Dr. Ray Evert authored the third, revised edition, published in 2006. Additionally, the 1988 *Plant Anatomy* by Dr. James Mauseth and Dr. Avraham Fahn's 1967 *Plant Anatomy* (4th edition in 1990) belong on every plant anatomist's book shelf as valuable references.

In 2018, plant anatomy continues to play key roles in studies of molecular plant biology, forestry, plant pathology, plant physiology, horticulture, agronomy, and a host of related botanical disciplines. Therefore, the authors of this plant anatomy resource – printed book and *e*-book – have made a substantial effort to update the subject matter, reveal new ways in which aspects of plant anatomy play a key role in a variety of related disciplines in plant biology, and present the topics in an understandable and interesting manner to the student and instructor. Heavy reliance was made on original light and electron micrographs, and color has been used extensively. Literature citations were kept to a minimum because, in today's electronically searchable world, a wealth of knowledge on any topic is a mere click or two away.

This effort was started over two decades ago when a collaboration between Prof. Richard Crang of the University of Illinois at Urbana-Champaign and Prof. Andrey Vassilyev of the Komarov Botanical Institute in St. Petersburg, Russia, identified the need for novel approaches to the teaching of plant anatomy. This led to the development that used modern educational technologies in a searchable, compact disk format that presented a traditional view regarding the anatomy of temperate seed plants, their place in evolution, and taxonomic relations, with a novel approach in subject delivery. Although Prof. Vassilyev died in 2012, his significant contributions to botany must not be overlooked. Educated in dendrology, he devoted his life to plant anatomy, specializing in plant secretory structures. Dr. Vassilyev worked at the Komarov Botanical Institute and Garden in St. Petersburg (formerly Leningrad), Russia, and rose to the position of Lead Scientist at that institute. His contributions in the field of plant anatomy, and to the beginnings of this project, must be noted.

It has been felt for some time that a new and more extensive approach to the teaching of plant anatomy should be developed. Such plans began in 2013 and grew to include two established plant biologists with extensive backgrounds in plant anatomy. Prof. Robert Wise of the University of Wisconsin at Oshkosh and Dr. Sheila Lyons-Sobaski from Albion College in Michigan each bring new ideas and experiences to this effort in publishing. Prof. Wise integrates anatomy and electron microscopy with a full background in plant physiology, and Dr. Lyons-Sobaski has added strength in ecology and evolution with relevance to plant anatomy. Prof. Emeritus Crang conveyed a lengthy background in microscopy applications as well as years of experience in teaching courses and research in plant anatomy to this effort.

May the concepts of plant structure and development help open our minds to a better understanding of the interrelationship of life in its various forms throughout the Earth and, perhaps, beyond. And may this text help, in a limited way, to aid in that fuller understanding.

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Plants as Unique Organisms; History and Tools of Plant Anatomy

Photograph of an 1879 Zeiss compound light microscope. (Timo Mappes, Wikimedia Commons), drawing of a moss (*Polytrichum commune*) sporophyte (Lukas Hochenleitter), drawing of a fern (*Asplenium ebeneum*) sporophyte (Thomas Meehan), drawing of a pine (*Pinus* sp.) cone and needles (Aylmer Bourke Lambert), drawing of a scarlet cordia (*Cordia sebestena*) stem with flowers (Henry Charles Andrews)

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Introduction

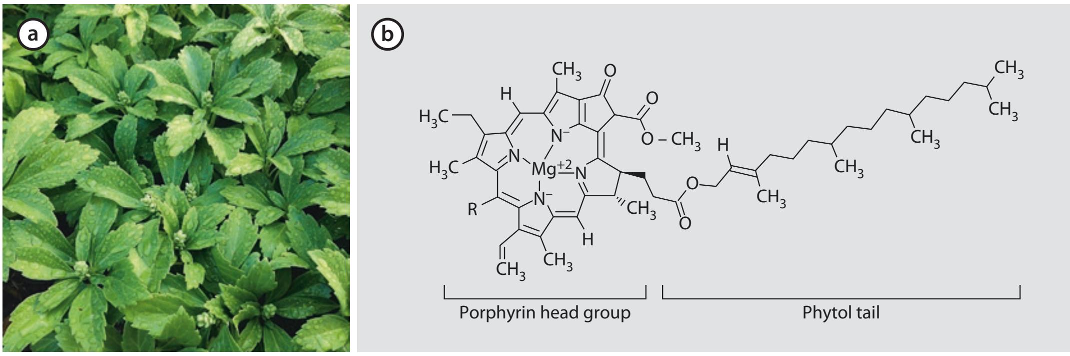
Plants possess unique properties that distinguish them from all other living things. The "green" plants comprise a very diverse group of organisms from algae that are formally not plants, but are protists, to bryophytes, gymnosperms, and angiosperms that are considered true plants. On a cellular level, the vast majority of plants contain the pigment, chlorophyll, and are the primary producers on planet Earth, on land, and in water. These organisms have life cycles that encompass an alternation of generations from a haploid generation to one that is diploid. The complexity associated with these groups can be attributed to the evolution of land plants from ancestral ties to the blue-green algae (cyanobacteria) and algae (protists).

In this text, we are primarily going to focus on the properties of seed plants, particularly flowering plants, in the study of plant anatomy—i.e., the microscopic study of cells, tissues, and organs. As such, we must come to the recognition that while it is possible to make general statements about their distinguishing characteristics, there are, from time to time, exceptions that do not fit the rules. Nevertheless, the rules are usually accurate, and the collective set of rules certainly states notable properties. This text begins by introducing basic concepts associated with plants to set the stage for learning about the anatomy of land plants.

1.1 Plants Have Multiple Pigments with Multiple Functions

Plants possess a unique set of **pigments**. Among the pigments, the light-trapping **chlorophylls** (e.g., chlorophyll *a* and chlorophyll *b*) are typically widespread in foliar structures and young stems (▣ Fig. 1.1a, b). The ability of such green-pigmented plants to trap light and to utilize it in the production of carbohydrates (simple sugars in particular) makes them **photoautotrophs**. That is, they are capable of synthesizing their own food in the presence of light, requiring only water, minerals, and air from their natural surroundings to survive. This property separates the green plants from **heterotrophs**, which require an external source of carbon-based food materials for survival. Practically all life on the planet Earth is dependent, either directly or indirectly, on the photosynthate produced by green plants.

Additionally, plants use other pigments such as **anthocyanins**, **carotenoids**, **phytochrome**, and **cryptochrome**. The different colors of light the pigments absorb may attract fruit dispersers and guide **pollinators** (▣ Fig. 1.1c, d). The pigments may also determine the direction, brightness, and color of light, as well as track the time of day and the season of the year. For instance, the pigment phytochrome is used to measure the length of the dark period (i.e., nighttime) and that information is retained for several days. If last night was longer than the night before, that indicates to the plant that autumn is approaching (shortening days). If last night was shorter than the night before, then spring is nearing. This information is used by many plants to indicate flowering time.



◘ Fig. 1.1 **a** A dew-covered pachysandra (*Pachysandra* sp.) leaf exhibits a typical green of photosynthetic tissues. **b** Both chlorophyll *a* and *b* are present in the leaf, in a ratio of about 3:1. Chlorophyll *a* has a methyl group (-CH_3) in the R position; chlorophyll *b* has an aldehyde (-CHO). The 20-carbon hydrophobic phytol tail is embedded in the thylakoid membrane for stability, while the porphyrin ring with its central magnesium atom acts as an antenna to capture photons of light energy (**a**, **b** RR Wise)

◘ Fig. 1.1 Monkey flower (*Mimulus* sp.) photographed in visible light **c** and ltraviolet light **d** showing a dark nectar guide visible to bees but not to humans. The nectar guide facilitates visitation to flowers by pollinators that can see in the UV (usually insects or birds). Scale bar = 1 cm (**c** Images by Plantsurfer—Own work, CC BY-SA 3.0; **d** Plantsurfer, CC BY-SA 3.0)

1.2 Plants Use Water, and the Properties of Water, in Unique Ways

All life-forms, including plants, need water to survive. Indeed, most living organisms are 80–90% H_2O. Plants, however, are unique in their use of water as a hydraulic tool. Lacking force-generating contractile muscle cells, plants have evolved to take advantage of the physical properties of water and the laws of physics to generate force that drives a circulatory system, growth, and movement.

As water evaporates from a leaf (via a process called **transpiration**), that water is replaced by water in the petiole, which

Fig. 1.2 **a** A young redwood tree (*Sequoia sempervirens*) already quite tall. **b** Concrete sidewalk buckled and cracked by the growth of tree roots. **c** Venus flytrap plant (*Dionaea muscipula*) prior to feeding. (**a** N Gabel, UW Oshkosh; Image **b** by Ildar Sagdejev (Specious)—Own work, CC BY-SA 3.0; **c** RR Wise)

pulls water from the stem, in turn from the roots and eventually the soil. Thus, water is pulled from the soil to the atmosphere much like soda is sucked up by a straw. The difference in the available energy held by the water in the soil, versus that of the water in the air, is sufficient to pull water to the top of a 100-m-tall tree, via the xylem tissue (Fig. 1.2a). The water-conducting cells in the xylem tissue are not merely tubes through which water flows. Their structure and design facilitates and controls the several hundred gallons of water that move through a medium-sized tree on a typical summer day.

Hydraulics is defined as the use of a fluid (water in this case) to perform work. By the physiological manipulation of solute concentrations in selected cells, and using the adjustable properties of cell walls, plants can generate the force needed to drive cell expansion, growth, and directed movement. Pressures well in excess of 200 psi are common (automobile tires are typically 32–34 psi), allowing stomata to open and close and plant roots to split rocks and crack concrete sidewalks (Fig. 1.2b). Insectivorous plants close their traps on their unsuspecting meals by rapid water movements; Venus flytraps (Fig. 1.2c) close in about one-tenth of a second. While animals use muscle cells to contract and pull, plants use water to expand and push.

1.3 Plants Use Anabolic Metabolism to Manufacture Every Molecule Needed for Growth and Produce Virtually No Waste

Plants are **photoautotrophic**, meaning they use the energy of sunlight to manufacture their own food. What is often not as well recognized is that, in addition to making the carbohydrates to supply basic energy and structural needs, plants make 100% of the amino acids, proteins, lipids, nucleic acids, vitamins, and other biomolecules they need for growth and development. Most plants need light, water, and approximately 20 elements to manufacture themselves, and most of that anabolic machinery is in the plastids (Wise and Hoober 2016).

Plants are literally rooted in one place and therefore are easy prey for herbivores. To protect themselves, plants have evolved biosynthetic pathways that synthesize a veritable cornucopia of toxic compounds, many of which are used by humans as flavorings, spices, herbals, dyes, preservatives, medicines, and recreational drugs (◘ Fig. 1.3). The course of history has been shaped by these compounds, which are called plant secondary metabolites. For example, Christopher Columbus was not searching for the New World in 1492 (his first of four excursions to the Caribbean and South America). He and his crew were seeking a westward route to the lucrative south Asian spice trade, but, alas, he returned empty-handed as the newfound region was essentially devoid of the highly sought spices.

Due to the uniqueness of plants, they can grow, develop, and complete their life cycle while producing a minimum of toxic wastes. For example, almost all animals have extensive digestive and excretory systems responsible for eliminating food wastes and removing metabolic toxins that are the by-products of their digestion (mostly nitrogen in the form of urea). Animals ingest a wide variety of foods, metabolize what they need, and dispose of the rest.

◘ **Fig. 1.3** Many prescription and natural drugs are synthesized by and isolated from plant tissues (RR Wise)

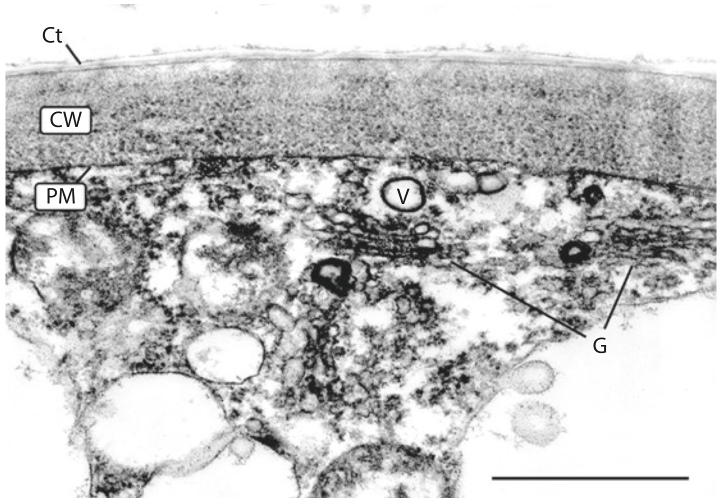
Upon kidney failure, a person will typically live less than a week before they poison themselves to death. In contrast, because plants manufacture all their needed organic molecules, they typically only make what they need for growth, development, reproduction, and defense. The concept of toxic metabolic wastes is foreign to plants, yet a central theme in the study of animals.

Box 1.1 Plants Are Important Sources of Anticancer Drugs
Secondary plant compounds are compounds synthesized within a plant that are often used in plant defense, but not produced via primary metabolic pathways such as photosynthesis or respiration that are necessary for life. Due to the defensive nature of secondary compounds, it isn't surprising that they are toxic to other organisms. Thus, secondary defensive compounds can be used to combat illnesses such as cancer within vertebrates, particularly humans. However, host toxicity and the evolution of tumor resistance are problems associated with traditional chemotherapy treatments. Plant compounds are often probed for anticancer properties to provide less toxic, yet effective alternatives to traditional chemotherapies.

One study isolated compounds from the inner bark of Pau D'Arco (*Tabebuia avellanedae)*, examining them for toxicity to non-small lung cancer cells. Two new furanonaphthoquinone compounds with cytotoxic effects were discovered that affected the replication of DNA and also impaired the growth and division of cells. Apoptosis, or programmed cell death, can reduce the proliferation of cancer cells. Thus, these compounds increased apoptosis rates and, thus, showed promise as a potential drug to combat cancer cells.
Reference: (Zhang et al. 2015).

1.4 Cell Walls Are Nonliving Matrices Outside the Plant Cell Membrane that House and/or Perform a Variety of Functions

As will be evident in the succeeding chapters, plant cells possess a nonliving but often biologically active **cell wall** that encloses the protoplasmic cell contents (◘ Fig. 1.4). Evolution of the plant cell wall relied on some components that were used by prokaryotic ancestors and others that arose more recently (Sørensen et al. 2010). The cell wall may be simple or complex, thin or thick, or have unique properties and associated components. In all cases, it possesses **cellulose** as a building structure. Cellulose, in turn, is composed of multiple units of simple sugars (glucose) in a unique linear or branching organization. While cellulose is the most characteristic polymeric substance comprising cell walls, there are also a variety of unique compounds found only in plants that are incorporated into cell walls to a greater or lesser extent. The cell wall is also a site of active cell secretion that frequently contains enzymes of living cells as well as strengthening



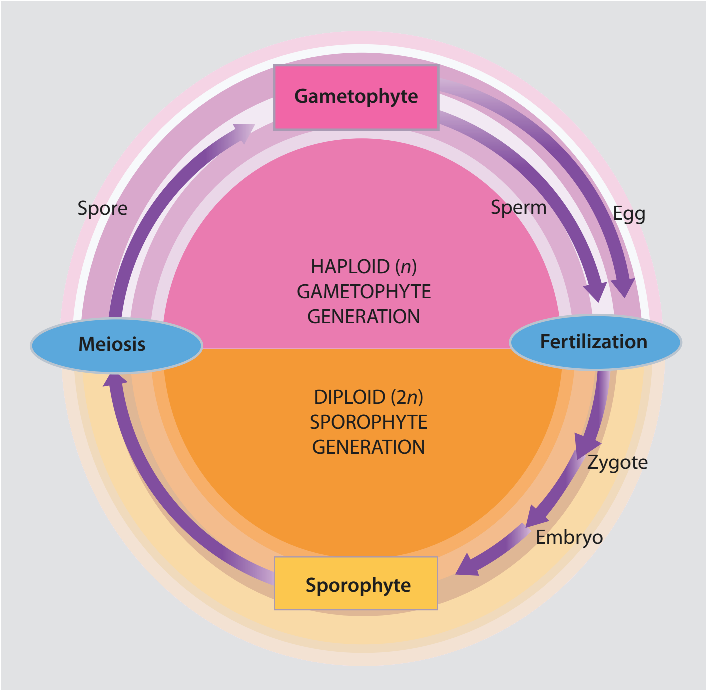
◘ Fig. 1.4 Primary cell wall synthesis in an epidermal cell of a blackjack oak (*Quercus marilandica*) leaf. Golgi bodies (G) produce vesicles (V) that deliver precursors to the developing cell wall (CW). Note also cuticle (Ct) to the exterior and plasma membrane (PM) to the interior or of the cell wall. Scale bar = 1 μm (Crang and Vassilyev 2003)

polymers in living and nonliving cells. Unlike the exoskeleton of insects and other arthropods, the plant cell wall can grow, expand, and adjust to mechanical stress. It is a marvel of flexible packaging. Cell walls will be discussed in more detail in ► Chap. 5.

1.5 The Plant Life Cycle Alternates Between a Haploid Gametophyte Stage and a Diploid Sporophyte Stage

All plants that carry out sexual reproduction possess an alternation of generations (◘ Fig. 1.5), which is characteristically different from the life cycle of animals. In most green algae, and in bryophytes (e.g., mosses), the dominant phase of the life cycle is the **gametophyte**, which is haploid and which gives rise to gametes by means of mitotic divisions. The haploid gametes fuse at fertilization and produce a zygote, which is then diploid, and subsequent division by mitosis gives rise to the sporophyte generation. Ferns and fern allies, as well as seed plants, possess a dominant sporophyte (diploid) generation, which is the evident plant. By means of meiosis, chromosome reduction results in the formation of haploid cells that now are a part of the gametophyte generation. Technically, meiosis produces haploid spores while mitosis produces gametes in plants. These two distinct phases of the life cycle are referred to as an "**alternation of generations**".

The type of life cycle that plants possess is known as a sporic life cycle, because the products of meiosis are spores. This contrasts with the zygotic life cycle of many protists and the gametic life cycle of animals that directly produce gametes by means of meiosis.



◘ **Fig. 1.5** Events (in a clockwise manner) that define an alternation of generations (Redrawn from Crang and Vassilyev 2003)

1.6 Meristematic Activity Continues Throughout the Life of a Plant

Throughout the life of the plant, there is continuous growth. In seed plants this takes place in zones called meristems. This is in contrast with most animals, which have a set size and form of development that once reached is not exceeded. While a plant may be dozens or even hundreds of years old, it will always have a continual supply of new, juvenile tissues produced by meristems. Even bristlecone pine trees (*Pinus longaeva*) at over 5000 years old have newly formed tissues every year (◘ Fig. 1.6a).

There are two basic types of meristems—**apical** and **lateral** (◘ Fig. 1.6b). Apical meristems are found at the shoot tip and the root tip. They are responsible for the cell division that results in growth along the long axis and thus leads to an increase in length. This growth is also called **primary growth**, because it produces new organs (new shoots, leaves, and roots). In contrast, cells produced by divisions in the lateral meristems contribute to an increase in stem or root girth, and this type of growth is called **secondary growth**. No new organs are produced, but existing organs become larger in diameter. In most plants, both types of growth continue for the lifetime of the plant. The detailed and unique features of meristems and their derivatives will be examined in ► Chap. 4.

Fig. 1.6 **a** These 4000-year-old bristle cone pine trees (*Pinus longaeva*) have some cells that were produced in the most recent growing season (Image by Rick Goldwaser from Flagstaff, AZ, USA—GnarlyUploaded by Hike395, CC BY 2.0)

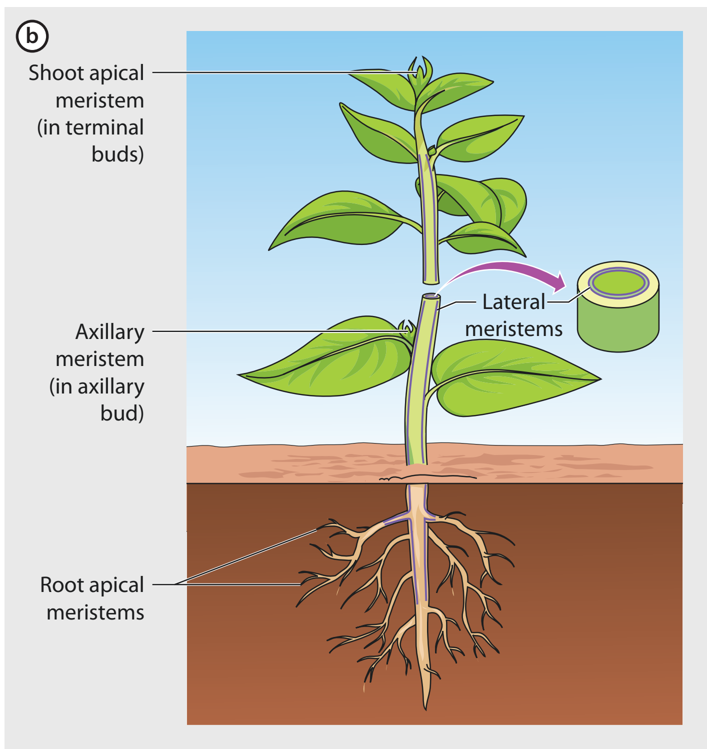


Fig. 1.6 **b** Meristems are found at the shoot and root tips and within the cylinder of the stem and root (Redrawn from Crang and Vassilyev 2003)

1.7 Fruits Disperse Seeds Through Space: Dormancy Disperses Seeds Through Time

Because animals are mobile, their offspring can, and typically must, disperse to new territory. Plants are usually considered to be **sessile**, or fixed in one place, incapable of movement. However, they too must disperse the next generation to access new territory and prevent overcrowding. In angiosperms, this is the job of the **fruit**.

Fruits are usually thought of as being tasty and sweet. However, to a botanist a fruit is the tissue surrounding the seed that is derived (usually) from the wall of the ovary (◘ Fig. 1.7a–f). In broad terms, anything with a seed inside is a fruit. Thus, true botanical fruit can be hard, soft, fibrous, winged, or, even in some cases, sweet and edible. The fruit is the unit of seed dispersal, allowing plants to distribute their offspring over a wide geographic area.

In addition, and unlike most animals, the plant **embryo** can stay **dormant** for extended periods of time, allowing dispersal of the next generation through time. The record is held by 32,000-year-old campion (*Silene* sp.) seeds recovered from the Siberian permafrost in 2007. Scientists surgically removed the embryos from the seeds and were able to culture them to become mature, adult, seed-bearing plants (◘ Fig. 1.7g). In terms of viable, intact seeds, a 2000-year-old date palm seed recovered from Herod's palace in Israel was germinated and grown to a mature plant in 2005 (◘ Fig. 1.7h).

◘ **Fig. 1.7** Fruit of the **a** peanut plant (*Arachis hypogaea*), **b** various peppers (*Capsicum* sp.), **c** maple tree (*Acer saccharinum*), **d** tomato (*Solanum lycopersicum*), **e** dandelion (*Taraxicum officinale*), and **f** bean plant (*Phaseolus vulgaris*) (**a**–**f** RR Wise)

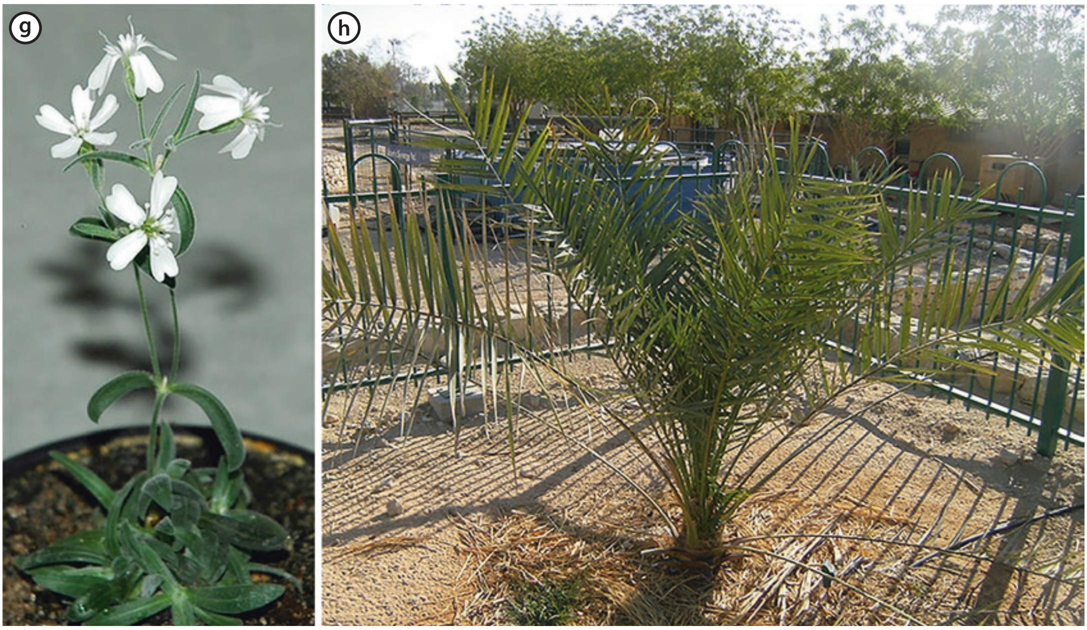


Fig. 1.7 Two plants germinated from long-dormant seeds. **g** Campion (*Silene stenophylla*) and **h** King Herod's palm (*Phoenix dactylifera*). **g** (Image **g** from Yasina, S. et al. 2012, with permission. Image **h** by Benjitheijneb, CC BY-SA 3.0; via Wikimedia Commons)

While these examples represent extremes in history, it is not uncommon for seeds of some species to remain dormant in a soil seed bank for as many as 20 years and for a few even longer than 120 years.

Box 1.2 The Complementary Nature of Seed Dispersal Mechanisms

Angiosperms have evolved a variety of ways to disperse seeds including using wind (anemochory), water (hydrochory), gravity (barochory), and ballistic means (ballochory), as well as by transport internally (endozoochory) or externally by an animal (epizoochory or ectozoochory) ("-chory" means "to place," as in choreography). Reynolds and Cumming (2016) studied seed dispersal by six species of African waterfowl to quantify and determine the germination success of seeds dispersed by way of epizoochory and endozoochory. They discovered that seeds dispersed following consumption and defecation had higher germination success than those attaching to feathers or legs of birds. Interestingly, while seeds were found more often on animals than in feces, seed germination was highest in samples from feces. Species diversity observed from samples obtained from feces and external brushing of birds was significantly different indicating that the seed dispersal mechanisms complement one another and are important in determining species composition within plant communities.

Reference: Reynolds and Cumming (2016)

1.8 Earth's History Is Divided into Four Major Time Periods

Animals tend to fossilize better than plants, leading the early geologists to name the major geological time divisions after zoological fossils (Paleo-, Meso-, and Cenozoic eras) rather than the algae and plants upon which they depended for survival. Practically all the eras and eras are demarcated by, and named for, changes in the animal fossil record.

The Earth is thought to be approximately 4.55 billion years old. If that age were represented as a month of time divided into 30 days, each "day" would equal 150 million years. It would be only on day 8 that the first life-forms—types of prokaryotic cells—would have likely appeared, and the first fossils of these cells (bacteria and blue-green algae) date to day 10. However, the first eukaryotic cells would not have appeared until day 24.

The first land plants would have appeared on day 28, and cycads and gymnosperms would have appeared on day 29. It would not be until the latter half of day 30 that both flowering plants and mammals would have appeared through evolution. Humans (*Homo sapiens*) would have appeared late in the last day. Modern humans would have evolved at 11:50 pm on the 30th day of the month.

1.8.1 The Precambrian: 4550 to 542 mya

The Precambrian encompasses the great majority of Earth's geologic history, stretching from the formation of our planet about 4550 million years ago (mya) to the appearance of shelled marine life 542 mya. It is technically a supereon and is composed of two eons, seven eras, and ten periods. Highlights include the formation of the oceans, the initial evolution of life, and the development of the atmosphere (largely by the addition of oxygen produced by photosynthesis). The first simple life-forms are thought to have been **chemoautotrophic** bacteria, which appeared about 3600 mya.

The evolution of cyanobacteria, which first appeared perhaps 3400 mya, gradually enriched the atmosphere with life-sustaining oxygen and, eventually, led to the development of the vital, protective ozone layer. Without the photosynthetically derived, oxygen-containing atmosphere (fully developed by ~2000 mya), aerobic life could not have evolved. Photosynthetic bacteria were the planet's primary producers until about 659–645 million years ago, until they were replaced by the rise of eukaryotic algae. Being eukaryotes, algae were able to evolve more complex anabolic pathways, thus producing the molecules **eumetazoans** ("true animals") needed for their evolution and leading to the origination of early animals such as sponges (Brocks et al. 2017). Animals, therefore, established early on their basic metabolic strategy of catabolism as a means of survival, relying entirely on the anabolic prowess of the preceding algae. By the end of the Precambrian, complicated eukaryotic algae were the dominant primary producers in the oceans and fresh water ecosystems (Knoll et al. 2007).

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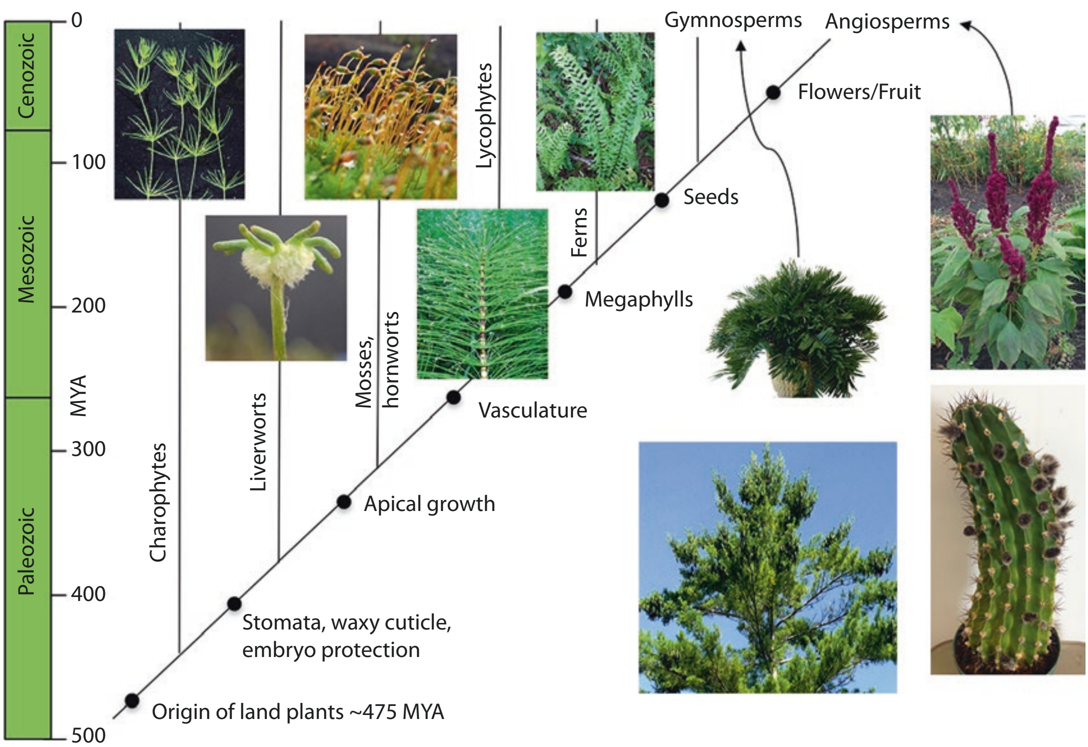
1.8.2 The Paleozoic Era: 542 to 251 mya

The Paleozoic era stretches from the appearance of shelled marine life (542 mya) to the evolution of mammal-like reptiles (251 mya). The first land plants, which were similar to the extant liverworts, evolved from advanced marine algae and appeared in the late Silurian or early Devonian periods, about 430 mya (Gensel 2008), although earlier dates are possible. The Paleozoic also saw the appearance of bryophytes (hornworts and mosses), club mosses, ferns, and gymnosperms along with important structures needed to survive on land— embryo protection, apical growth, **lignin**, vasculature, stomata, complex leaves, and the seed (◘ Fig. 1.8). The colonization of terrestrial ecosystems by plants was of critical importance to the evolution of life. Without land plants, there could be no land animals because, being heterotrophs, animals needed the plants to serve as a food source. The fern forests of this era would later yield the vast coal deposits that fed the industrial revolution and supply much of the world's energy needs even today. Periods within this era include the Cambrian, Ordovician, Silurian, Devonian, Carboniferous, and Permian.



◘ **Fig. 1.8** A *cladogram* depicting some of the major groups and events in plant evolution. From left to right: *Chara* sp., *Marchantia* sp., moss, *Equisetum* sp., fishtail fern (*Nephrolepis falcata*), *Zamia pumila*, *Pinus* sp., fox tail amaranth (*Amaranthus caudatus*), cactus. Image of *Chara* courtesy of Missouri Department of Conservation (CC0-public domain) (Image of *Equisetum* courtesy of Max Pixel (CC0-public domain))

1.8.3 The Mesozoic Era: 251–66 mya

The Mesozoic era, also called the Age of Conifers, is defined as being dominated by early gymnosperms and covering the reign of dinosaurs. Periods within the Mesozoic are the Triassic, Jurassic, and Cretaceous. *Ginkgo biloba*, and the genus *Sequoia* (redwoods), both ancient, extant (still living) gymnosperms, arose during this era (Ryberg et al. 2012). Fossil evidence indicates that flowering plants diverged from gymnosperms over 200 mya, and evidence of true angiosperms appears at about 140 mya (Royer et al. 2010). Angiosperms dominated by the end of the era. Grasses arose toward the end of the Cretaceous, becoming the most widespread plant group today. Other new life-forms include turtles, crocodiles, ancestral birds, snakes, lizards— leading to the alternative name "Age of Reptiles." Primitive mammals arose during the Jurassic and were able to fill empty niches created by the extinction of the dinosaurs. The Mesozoic era is thought to have ended with the impact of a large meteor off the Yucatan Peninsula 66 mya, forming the Chicxulub Crater (Morgan et al. 2016). An estimated 65–75% of all species went extinct at the end of the Mesozoic era (Vajda and Bercovici 2014; Nichols and Johnson 2008), opening up numerous ecological niches for rapid evolution of the survivors.

1.8.4 The Cenozoic Era: 66 mya to Present

The Cenozoic era, which continues today, began about 66 mya. This can be thought of as the age of flowering plants and mammals, both of which expanded greatly after the mass extinctions at the end of the Mesozoic. Flowering plants conscripted many of the evolving animal groups to serve as pollination vectors. The coevolution of plant/animal mating systems is described in the next section.

Modern humans did not appear until about 125,000 years ago. The last 10,000 years of the Cenozoic, following the end of the Pleistocene Ice Age, have witnessed the rise of human culture, the cultivation of plants, the domestication of animals, the development of industry, and the human's widespread impact on the ecosystems of our planet. Periods within the Cenozoic include the Paleogene, Neogene, and Quaternary.

1.9 Life on Earth Has Experienced Five Mass Extinctions: A Sixth Is in Progress

There have been five major mass extinctions events in the history of Earth (◘ Fig. 1.9), and we are now experiencing a sixth. The sixth is different from the others in that it is primarily due to **anthropogenic** causation. The first four mass extinctions were caused by severe climate changes, while the fifth (at the end of the Cretaceous) is believed to have been largely brought about by a meteor striking the Earth in the region of the Yucatan Peninsula in what is now Mexico. The heavy atmospheric dust of soil and metals obscured light and growth of

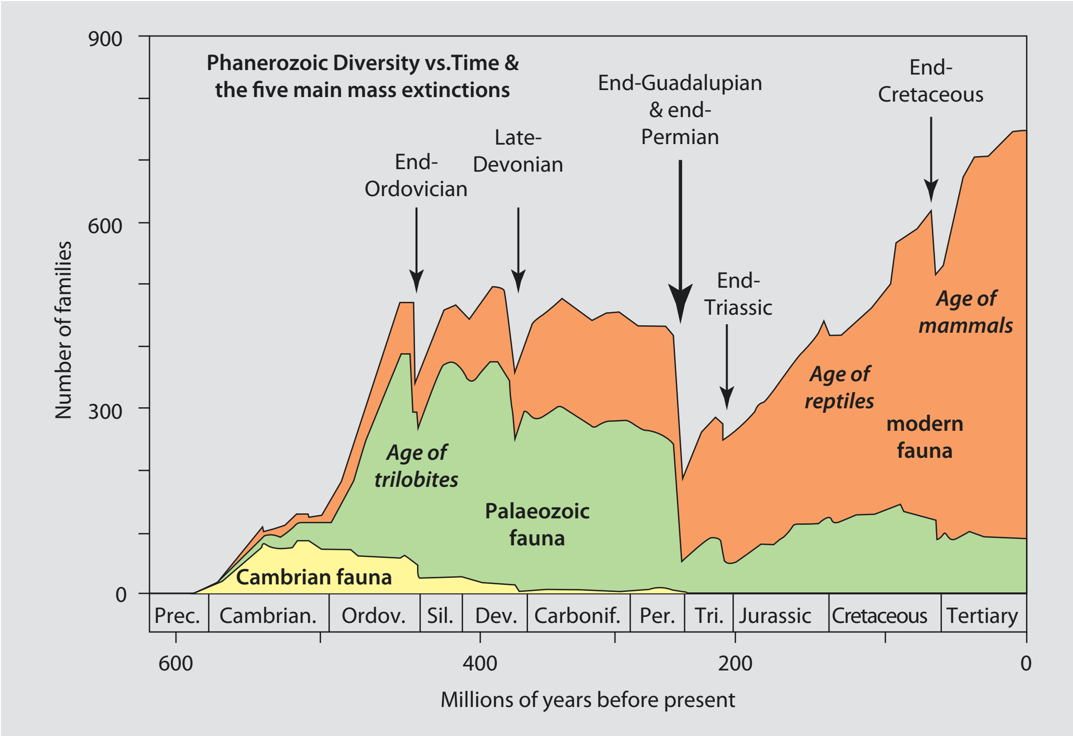


Fig. 1.9 An illustration of the geological periods, mass extinctions, and the relative numbers of animal families before and after the times of mass extinctions. Fossil spores indicate that land plants may have arisen as early as 470 mya, during the Ordovician Period. (Redrawn from Sepkoski (1984))

plants. It is commonly believed to have also brought about the demise of dinosaurs which required exceptionally long times for eggs to hatch.

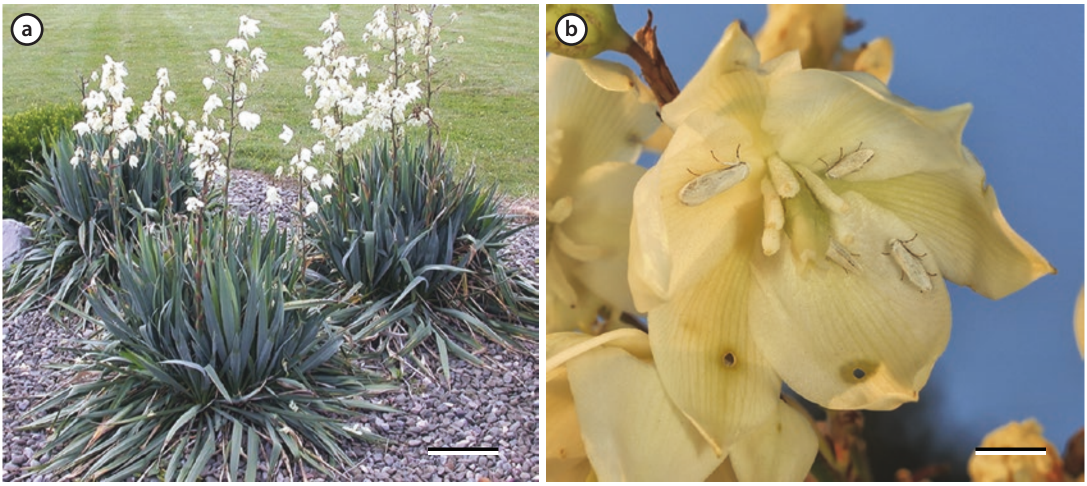
The latest mass extinction (in progress) is likely to surpass any of the others in the loss of species. Currently, the rate of extinction of species is 1000–10,000 times greater than “background extinction” (that extinction which is due to normal forces of natural selection). The increase is almost entirely due to humans via our negative impact on nature via habitat destruction and global climate change.

1.10 Many Plants and Animals Have Coevolved

Species that have mutually influenced one another’s evolution are said to have **coevolved**. Many plant families have intricate reproductive strategies that have coevolved with animals, particularly insects. Plants reward their animal partners with food, shelter, a place to lay eggs (ovipositories), or even the (false) lure of sex by mimicking insect pheromones.

Sometimes the coevolution is general, as in the case of the nectar guides shown in Fig. 1.1c, d. Because such guides do not necessarily involve a specific species of insect or plant, they are therefore an example of diffuse coevolution.

Coevolution may also be species-specific. The Spanish bayonet (*Yucca filamentosa*) and other yucca species are pollinated only by



◘ **Fig. 1.10** **a**, **b** Species-specific coevolution. **a** The Spanish bayonet (*Yucca filamentosa*) is pollinated by only one species of **b** Yucca moth (*Tegeticula yuccasella*). Scale bars = 10 cm in **a** and 1 cm in **b**. (**a** Image courtesy of Kevin Nixon (Copyright © 2004 by Kevin C. Nixon, Cornell University); **b** Image courtesy of Alan Cressler, US Geological Survey)

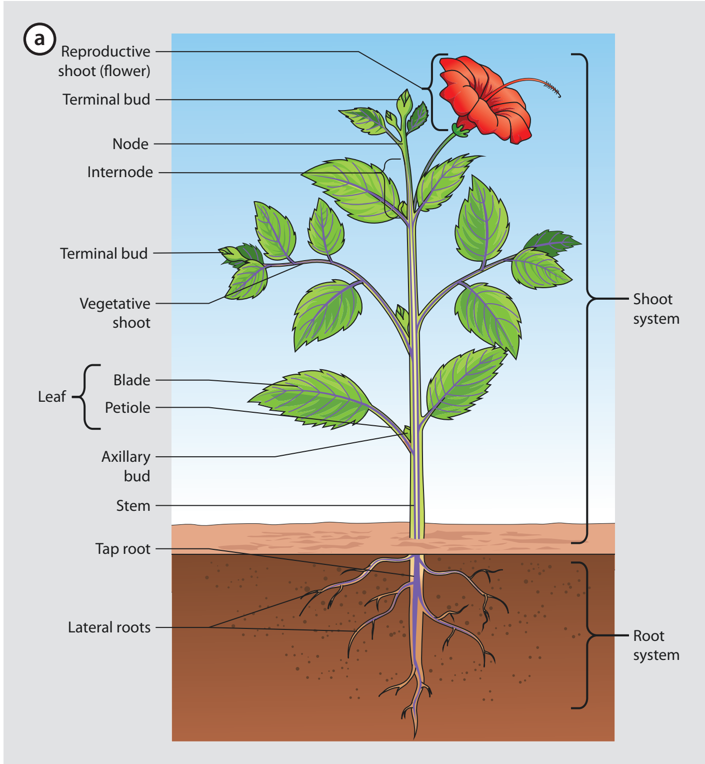
the yucca moth (genus *Tegeticula*; ◘ Fig. 1.10). The female moth lays her eggs in the ovules of yucca flowers and then scrapes up pollen from the flower's anthers into a ball. The pollen ball is then carried to another yucca plant where it is placed on the stigma of a flower and where another batch of eggs is deposited. When the eggs hatch, the larvae feed upon some of the developing yucca seeds, seeds that will only develop if pollination is successful. Yucca has no other pollinators, and the *Tegeticula* larvae eat no other food, so the relationship developed between the plant and insect is an example of species-specific coevolution. In instances such as this, the loss of one partner will lead to the extinction of the other.

1.11 The Plant Body Consists of Four Organs

During the approximately 475 million years of land plant evolution, there has been significant diversification of plant species and modification of the plant body. The basics of flowering plant anatomy will be sketched in this section; variations present in other taxa will be addressed in following chapters of this book. The four angiosperm organs are the root, stem, leaf, and flower (◘ Fig. 1.11a).

1.11.1 Roots

Roots (◘ Fig. 1.11b, c) anchor the plant in the soil and supply the shoot with water and minerals absorbed from the soil. They also rely on materials produced by photosynthesis in the leaves and shoot. An extensive vascular system connects the roots with all parts of the shoot, leaves, and flowers. Roots are resource-acquisition organs, for water and minerals, and carbon-utilization organs (heterotrophic).

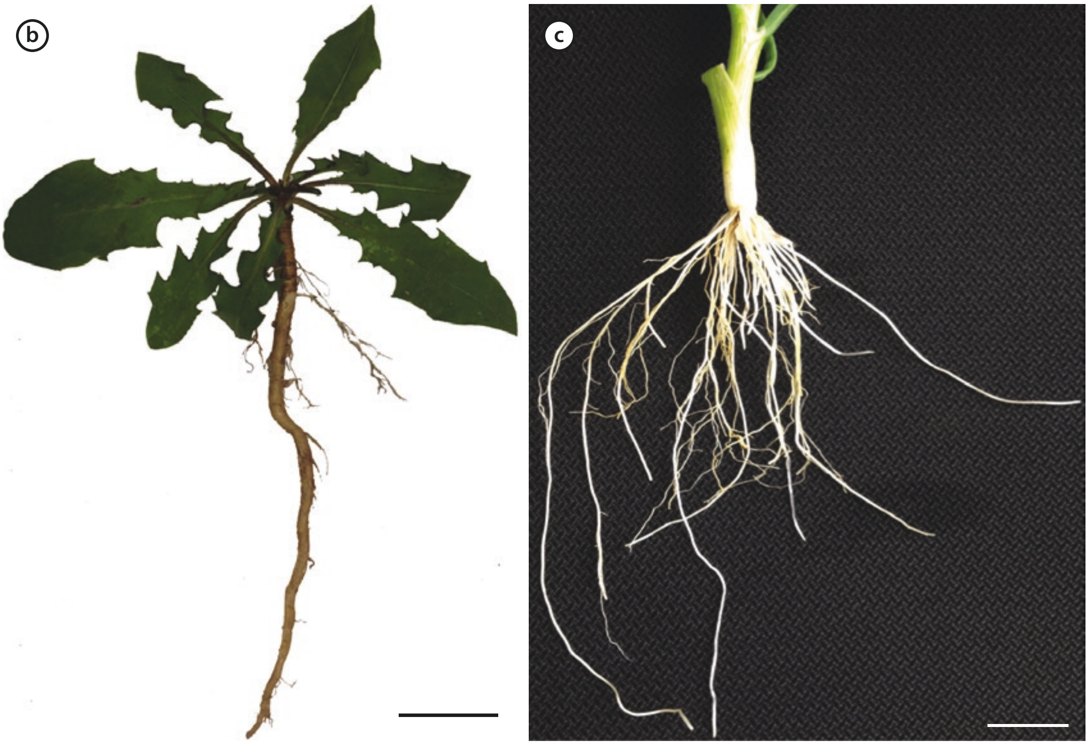


◘ **Fig. 1.11** **a** Illustration of a typical plant body of a flowering plant an angiosperm (Redrawn from Crang and Vassilyev 2003)

Eudicots and monocots have distinctly different root system architectures. The **taproot** system of a dandelion plant is shown in ◘ Fig. 1.11b. Being a eudicot, the taproot developed from the embryonic root (radicle) in the seed, and all branching lateral roots developed from the taproot. ◘ Figure 1.11c shows a **fibrous** root system of onion, a monocot plant. All of the fibrous roots shown are **adventitious** and have developed from stem tissue. In monocots, the main root does not survive the early seedling stage. It dies; thus, all further roots develop directly from the stem. Roots will be explored further in ► Chap. 10.

1.11.2 Stems

The stem supports the aerial portions of the plant, namely, the leaves and flowers (◘ Fig. 1.11d). One of the main resources plants need for survival—light—is obviously only present above ground. Therefore, a major role for the stem is to support the leaves and distribute them in space to maximize light absorption (**phyllotaxis** is the specific, genetically controlled, nonrandom arrangement of leaves on a stem). A second "resource" stems acquire for a plant is access to pollinators, such as wind, insects, birds, or mammals. Thus, the stem presents the flowers in space to maximize pollination success. Stems are resource utilization organs (water, minerals,



◻ **Fig. 1.11** **b** Taproot system of a typical eudicot (dandelion, *Taraxacum officinale*). **c** Fibrous, adventitious roots on a monocot (green onion, *Allium cepa*). Scale bar in (**c**) = 2 cm and applies to both panels (**b**, **c** RR Wise)

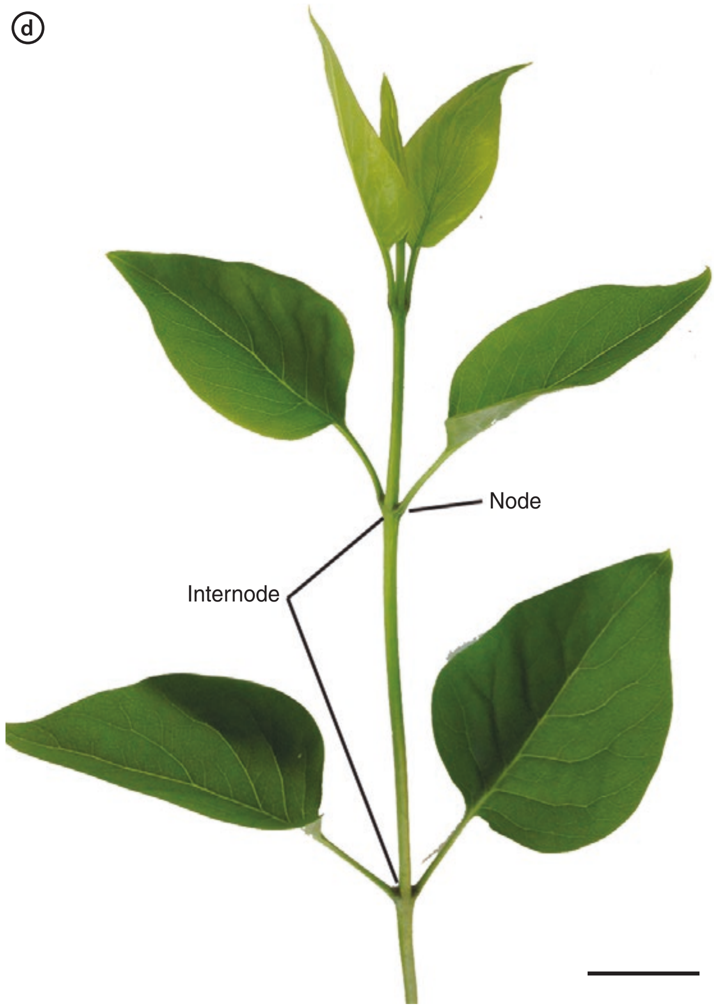
and light), and carbon-acquisition organs (autotrophic), and will be discussed in detail in ► Chap. 11.

1.11.3 Leaves

Leaves are the photosynthetic organs of the plant. Their morphology and anatomy have been adapted over evolutionary time to optimize light absorption and carbon dioxide uptake. A typical plant leaf is seen in ◻ Fig. 1.11e. It is essentially flat (to optimize solar absorption), green (due to tens of thousands of chloroplasts), and slightly transparent (some light penetrates each leaf to supply energy to those lower in the canopy). Many variations on leaf anatomy and function exist, and those will be addressed in ► Chap. 12.

1.11.4 Flowers and Fruit

Most plants under consideration in this book (refer to ► Sect. 1.13 for definition of "plant") reproduce sexually. However, only the angiosperms do so with the use of flowers and fruit. The flower's role is to ensure successful pollination, by being exposed to the wind or attractive to an animal pollinator. The fruit is responsible for seed dispersal—on the wind, in the water, stuck to an animal, or otherwise.



■ **Fig. 1.11** **d** Stem from a lilac bush (*Syringa* sp.). Scale bar = 5 mm (RR Wise)

Stamens produce pollen grains (containing the male gamete) (▶ Chap. 17). Flowers contain one or more ovaries, which house egg cells (female gametes) within ovules (▶ Chap. 18). The pear flower shown in ■ Fig. 1.11f has multiple stamens and an ovary containing multiple ovules; other species, such as corn, have flowers with exclusively male or female parts. Petals, often showy and brightly colored, are responsible for pollinator attraction, while the sepals wrap around and protect the young floral bud from insects and desiccation prior to flowering.

Pollination is the process of transferring pollen grains to the stigma, where they germinate and send a pollen tube through the style to the ovary. Sperm cells are transferred from the pollen grain via the pollen tube to the ovary where they fertilize the ovule. Upon successful fertilization, the petals often die and fall off, their job being done. Now the ovary enlarges and develops

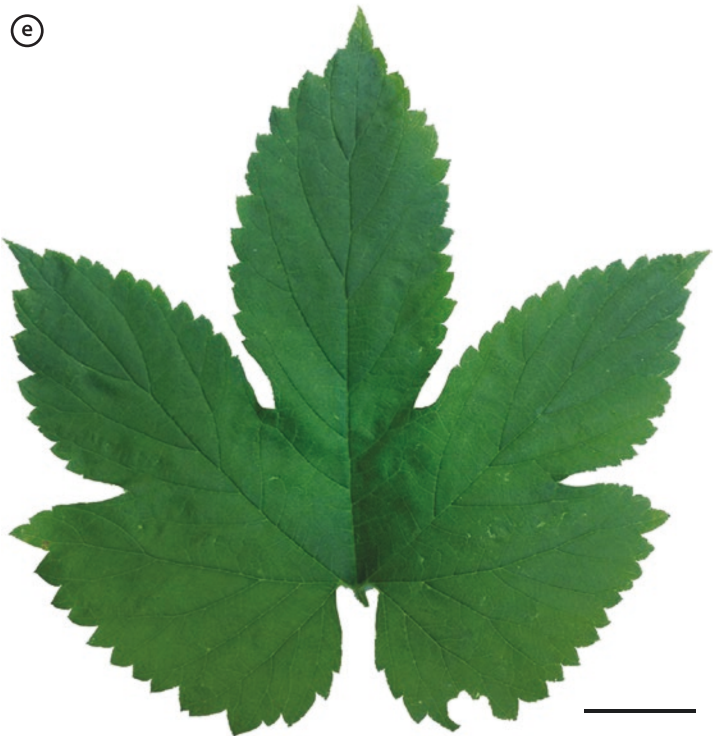


Fig. 1.11 **e** Leaf of hops (*Humulus lupulus*). Scale bar = 5 cm (RR Wise)

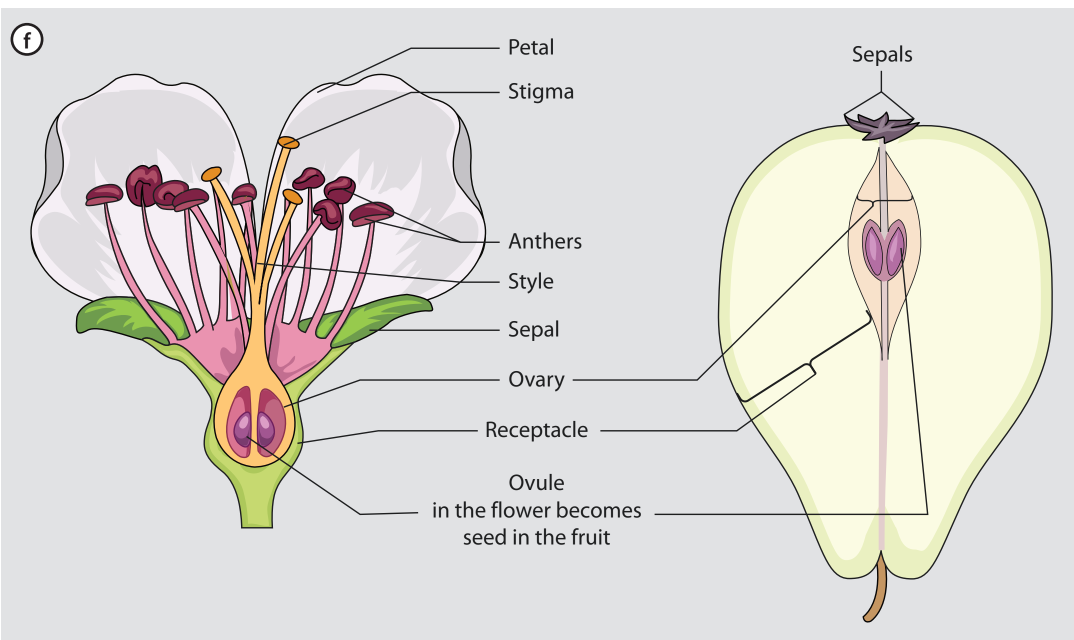


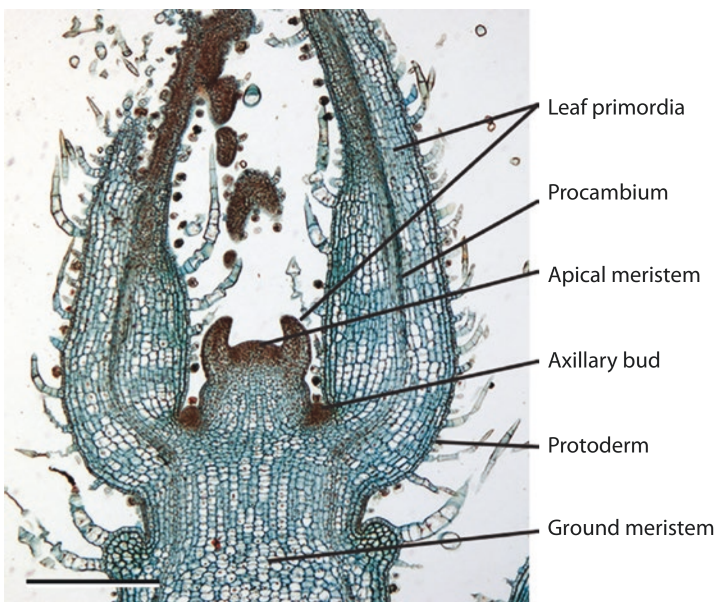
Fig. 1.11 **f** Cutaway drawings of a pear flower and the fruit that develops from the receptacle and ovary wall (Redrawn from Crang and Vassilyev 2003)

into the fruit. In the case of pear (◘ Fig. 1.11f), the true fruit is what we call the core, which is usually discarded. The sweet, fleshy part of a pear which we eat is actually the expanded receptacle or base upon which the flower is mounted. Hence, pear is called an accessory fruit (► Chap. 19).

1.12 Plant Organs Are Initially Made of Three Tissues

Plant tissues are produced by **meristems**—either apical or lateral (refer to ► Sect. 1.6 and ► Chap. 4)—and four different meristems are needed to generate the three tissues of a stem.

The **apical meristem** gives rise to the leaves, seen in their initial stage as leaf primordia, and three additional meristems (also called **histogens**) (◘ Fig. 1.12). At the surface of the new leaves, the **protoderm** lays down epidermal cells (► Chap. 9). Inside each leaf primordium, the **procambium** produces cells that will differentiate into and connect with the xylem (► Chap. 7) and phloem (► Chap. 8) tissues of the vascular system. Further back on the growing stem tip, the **ground meristem** produces the nonspecialized cells that fill the interior of the stem, regions called the cortex, pith, and conjunctive tissue (► Chap. 11).



◘ **Fig. 1.12** Apical meristem in a coleus (*Plectranthus* sp.) shoot tip. Scale bar = 0.5 mm (RR Wise)

1.13 "Plant" Can Be Broadly Defined

What, exactly, are plants? Who are the members of the kingdom Plantae? Defined broadly (and with the inevitable exceptions), a plant is any eukaryotic organism that relies on photosynthesis as a method of acquiring food (also called autotrophs) and any evolutionarily related lineages in that clade (a clade is a group of organisms that includes a common ancestor and all of its descendants). Opinions vary among scientists, but by using such a broad definition, the major groups of "green plants" are the algae, bryophytes, ferns and fern allies, gymnosperms, basal angiosperms, and angiosperms.

Algae, as eukaryotic photosynthesizers, first arose approximately 1.6 billion years ago when a proto-eukaryote engulfed, or endosymbiosed, a photosynthetic, prokaryotic cyanobacterium in a process called **primary endosymbiosis**. Some lines of algae began by endosymbiosing a green bacterium; other lines endosymbiosed a red bacterium. Other lineages arose by endosymbiosing one of the first lineages (**secondary endosymbiosis**). There is even significant molecular evidence of tertiary endosymbiotic events. As one can see, algae are polyphyletic, i.e., arose from multiple lines, and the classification is rather complicated. ◘ Table 1.1 lists some representative algal taxa but is by no means comprehensive or complete (see examples in ◘ Fig. 1.13a–d). Algal taxonomy is currently in a state of flux and will probably not be well-resolved for several more decades. The other major groups will be discussed in the following sections.

Box 1.3 Peptidoglycans surround moss plastids
Peptidoglycan is a sugar amino acid polymer that is considered to be unique to the bacterial domain as a component of the bacterial cell wall. Recent research indicates that peptidoglycan may be associated with plastids of some basal plant lineages such as the Charophytes and the bryophytes but not the angiosperms. Antibiotics that target bacterial cell walls with peptidoglycan do not impact animal cells as they lack the polymer but did interfere with plastid division in the moss, *Physcomitrella patens*. Interestingly, TEM micrographs failed to detect the presence of peptidoglycan within cell walls of *P. patens*. Was peptidoglycan synthesis occurring in plants but not being detected? If so, this would be a truly surprising discovery.

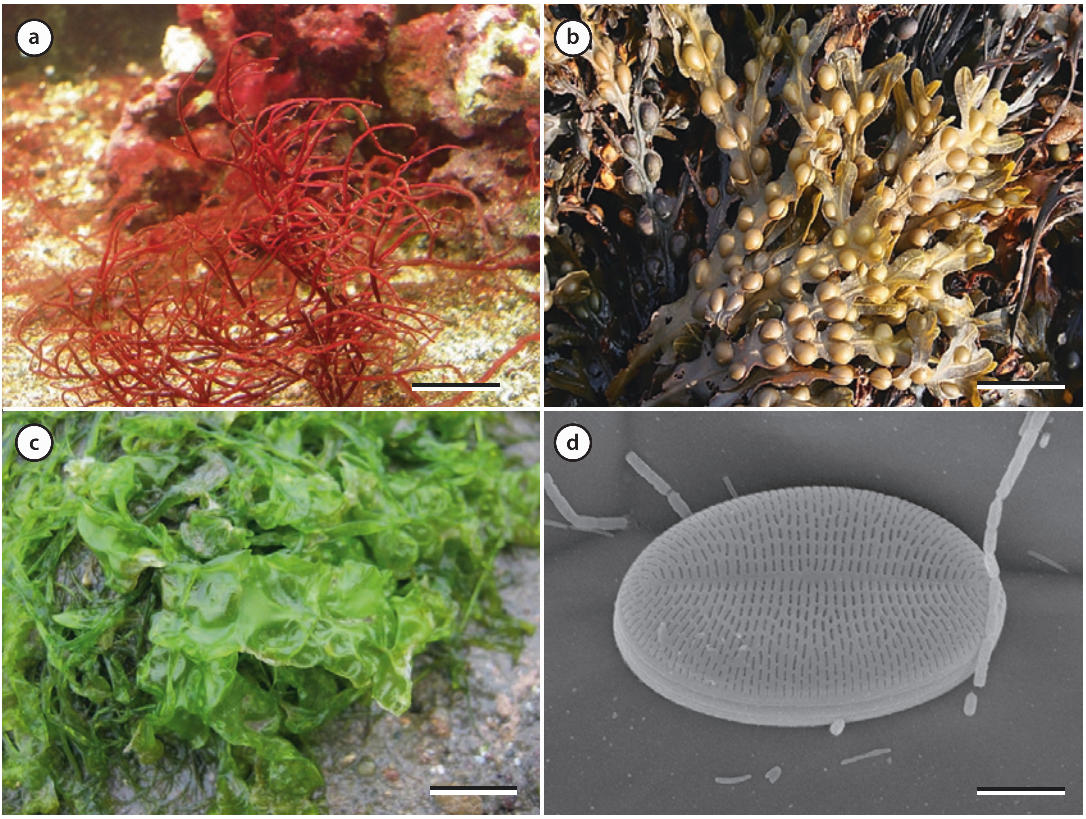
The *P. patens* genome does contain homologs of *Mur* genes that are associated with the synthesis of peptidoglycan in bacteria, such as the D-alanine:D-alanine ligase (DDL) gene. DDL

1

knockout lines that removed this DDL *Mur* gene yielded cells with few, large chloroplasts in comparison to wild type plants where cells had many small chloroplasts, indicating that plastid division was inhibited in the absence of DDL. Using fluorescent techniques, Hirano et al. (2016) observed a layer of peptidoglycan around a dividing plastid. These data provide support that the peptidoglycan pathway is involved in plastid division in *P. patens*. From an evolutionary standpoint, these findings support the bacterial origin of chloroplasts via endosymbiosis. Reference: Hirano et al. (2016)

Table 1.1 A brief comparison of various plant taxa. While dozens or even hundreds of individual characters are used in plant systematics, only four have been used here—ploidy level of the dominant life cycle stage (diploid vs. haploid) and the presence or absence of vasculature, seed, and fruit. The total number of named plant species is approximately 364,000, although by some estimates there may be as many as two million diatom species alone, most undiscovered and unnamed

	Representative taxa (not all inclusive)	**Estimated # of species**	**Dominant stage**	**Vasculature**	**Seed**	**Fruit**
Algae	Red algae – Rhodophyta Brown algae –Phyaeophyceae Green alga – Chlorophyta Diatoms – Bacillariophyceae Glaucophytes – Glaucophyta	72,500	Gametophyte (n)	No	No	No
Bryophytes	Hornworts – Anthocerotophyta Liverworts – Marchantiophyta Mosses – Bryophyta	100 9000 15,000	Gametophyte (n)	No	No	No
Ferns and allies	Psilophyta – whisk ferns Sphenophyta – horsetails Lycophyta – club mosses Pterophyta – ferns	15 15 1200 11,350	Sporophyte ($2n$)	Yes	No	No
Gymnosperms and allies	Ginkgophyta – *Ginkgo* Gnetophyta – gnetophytes Cycadophyta – cycads Coniferophyta – conifers	1 70 130 630	Sporophyte ($2n$)	Yes	Yes	No
Basal angiosperms	*Amborella* Nymphaeales Austrobaileyales	1 70 100	Sporophyte ($2n$)	Yes	Yes	Yes
Angiosperms	*Ceratophyllum* Chloranthales Magnoliids Monocotyledonae – monocots Eudicotyledonae – eudicots	6 70 9000 70,000 175,000	Sporophyte ($2n$)	Yes	Yes	Yes
Total		364,300				



■ **Fig. 1.13** **a**–**d** Representatives of four major algal groups: **a** red algae (*Gracilaria* sp.), **b** brown algae (*Fucus vesiculosus*), **c** green algae (*Ulva lactuca*) and **d** an unidentified freshwater diatom. Scale bars = 2 cm in a and b, 1 cm in c and 2 µm in d. (**a** Eric Moody CC BY 3.0; **b** Anne Burgess, CC BY-SA 2.0, **c** Kristian Peters CC BY 3.0, **d** RR Wise)

1.14 Bryophytes Lack Vasculature and Produce Spores

Bryophytes, hornworts, liverworts, and mosses, (■ Fig. 1.14) are the simplest of the land plants and have many features in common with the first terrestrial plants of some 450 million years ago. Mosses (a representative bryophyte) lack vasculature and do not produce seeds. Photosynthesis takes place in a flattened, green, gametophytic tissue called a **thallus**. The gametophyte is haploid and produces egg and sperm by means of mitosis, which fuse to form the sporophyte plant phase, which is diploid. Spores are formed within the sporophyte capsule by means of meiosis. The haploid spores subsequently germinate and grow into the gametophyte phase. Thus, there are no seeds or fruit. While small in size (usually 2–4 cm inches in height), some mosses in Australia and New Zealand have reached heights of up to 40+ cm. Modern-day bryophytes occupy some of the most extreme environments on earth, from dry desert crusts to Antarctic lakeshores.

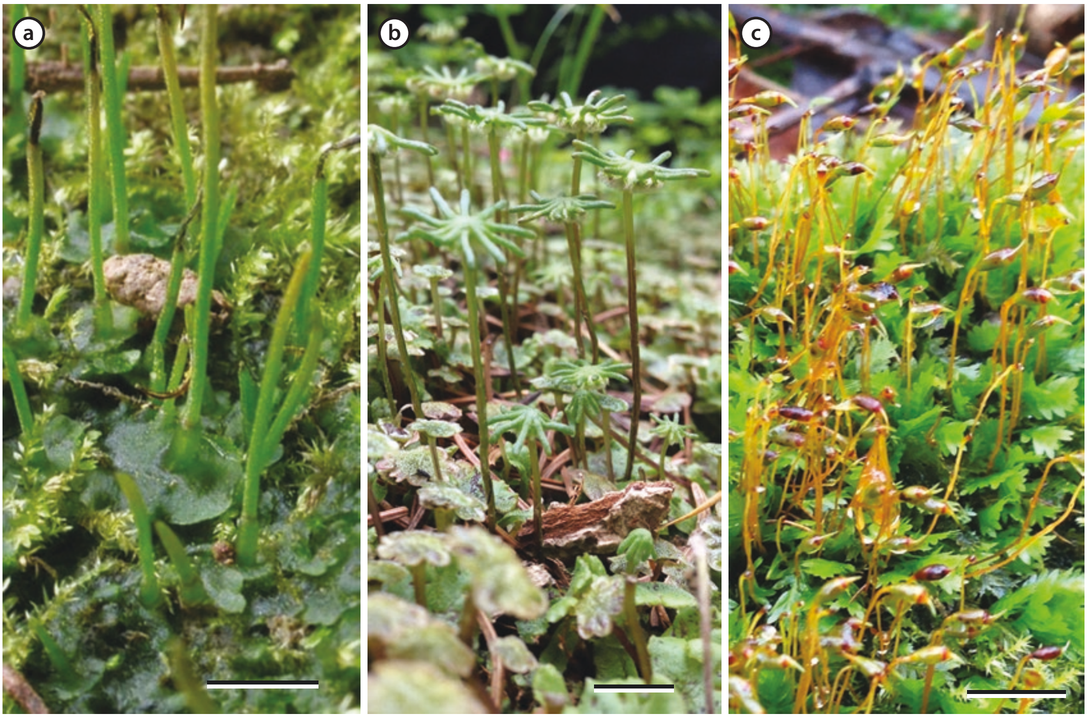


Fig. 1.14 Representative bryophytes. **a** The hornwort (*Phaeoceros laevis*) is so-named because of the horn-like sporophytes arising from the flattened thalli of the gametophyte. **b** The liverwort (*Marchantia* sp.) has male and female sporophytes. The flattened thalli lay on the ground while the male antheridia and female archegonia point upwards. **c** A moss (unidentified) shows both gametophyte stage (the "leafy" green phase) and the sporophyte stage (stalked reddish phase with terminal capsules). Scale bars in all images = 1 cm. (Image **a** courtesy of Li Zhang, Shenzhen & Chinese Academy of Sciences. Images **b** and **c** by RR Wise.)

1.15 Ferns and Fern Allies Are Seedless Tracheophytes

Plants that contain vasculature (xylem and phloem) are called tracheophytes (literally, "vascular plants"), and ferns and their close relatives are the simplest tracheophytes (Fig. 1.15a–c). Club mosses and horsetails have **microphylls**, the simplest leaves, while ferns possess megaphylls. **Megaphylls** are believed to have evolved from lateral branching systems that were gradually filled in with additional tissue of chlorophyllous cells. Megaphylls possess a complex vein system, and contemporary angiosperm leaves (and most gymnosperm leaves) are essentially developed megaphylls.

The fern life cycle is similar to the moss life cycle, with the alternation of generations between a gamete-producing gametophyte and a spore-producing sporophyte. The main difference is in the relative sizes of the sporophytic and gametophytic stages. In mosses, the gametophyte is the leafy green stage (refer to Fig. 1.14c), whereas in ferns it is the sporophyte that is larger (Fig. 1.15c). Some modern-day ferns can reach 5 m in height.

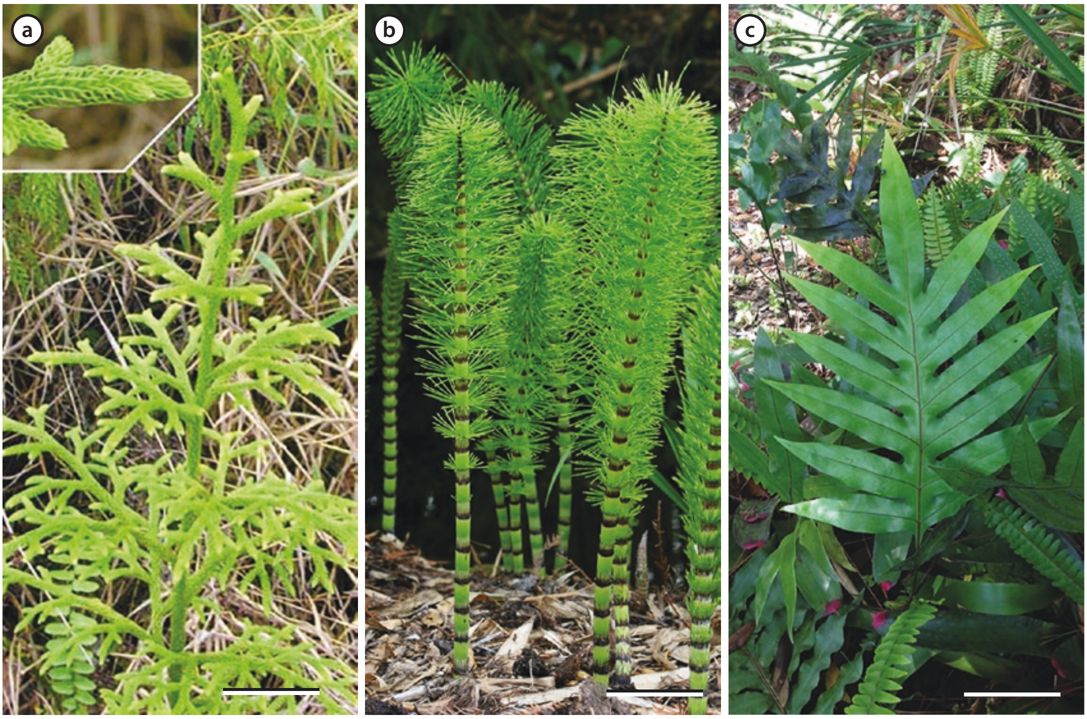


Fig. 1.15 Typical **a** club moss (*Lycopodiella cernua*), **b** horsetail (*Equisetum telmateia*) and **c** wart fern (*Microsorum scolopendrium*), the simplest vascular plants. Scale bars = 10 cm in **a**, 2 cm in **b,** and 10 cm in **c**. (Image **a** by Eric Guinther, CC BY-SA 3.0), image **b** by Rror—Own work. Licensed under CC BY-SA 3.0 via Commons, image **c** by RR Wise.

1.16 Gymnosperms Are Seed-Producing Tracheophytes that Lack Flowers and Fruit

While being an approximation, seed plants are typically divided into two primary groups—gymnosperms and angiosperms. In both of these groups of seed plants, the gametophyte (gamete-producing) generation has been much reduced from that in non-seed plants. (In bryophytes such as mosses, the vegetative plant is the gametophyte and thus, is homologous with the pollen grain or embryo sac of seed plants.) Ovule parts (specifically, integuments) develop into a seed coat, and food reserves are deposited in the **endosperm** of the seed or **cotyledons** of the embryo. Because of the protective coat, seeds may survive cold and drought, as well as journeys by water, wind, or animal coats, which may disperse the plant population.

The four living divisions of gymnosperms (Fig. 1.16a–d) are the Cycadophyta, Ginkgophyta, Gnetophyta, and Coniferophyta. Evidence indicates they evolved separately and earlier than other seed plants, the angiosperms (flowering plants), and they do not have ovaries to protect the developing seed. Today, there remain about 830 known extant gymnosperm species (Conway 2013).

Conifers (Coniferophyta) reproduce via a woody structure called a cone, of which there are both male and female cones. The male cones produce pollen, which is carried by the wind to the female cone, where the seed development takes place (Fig. 1.16e, f).

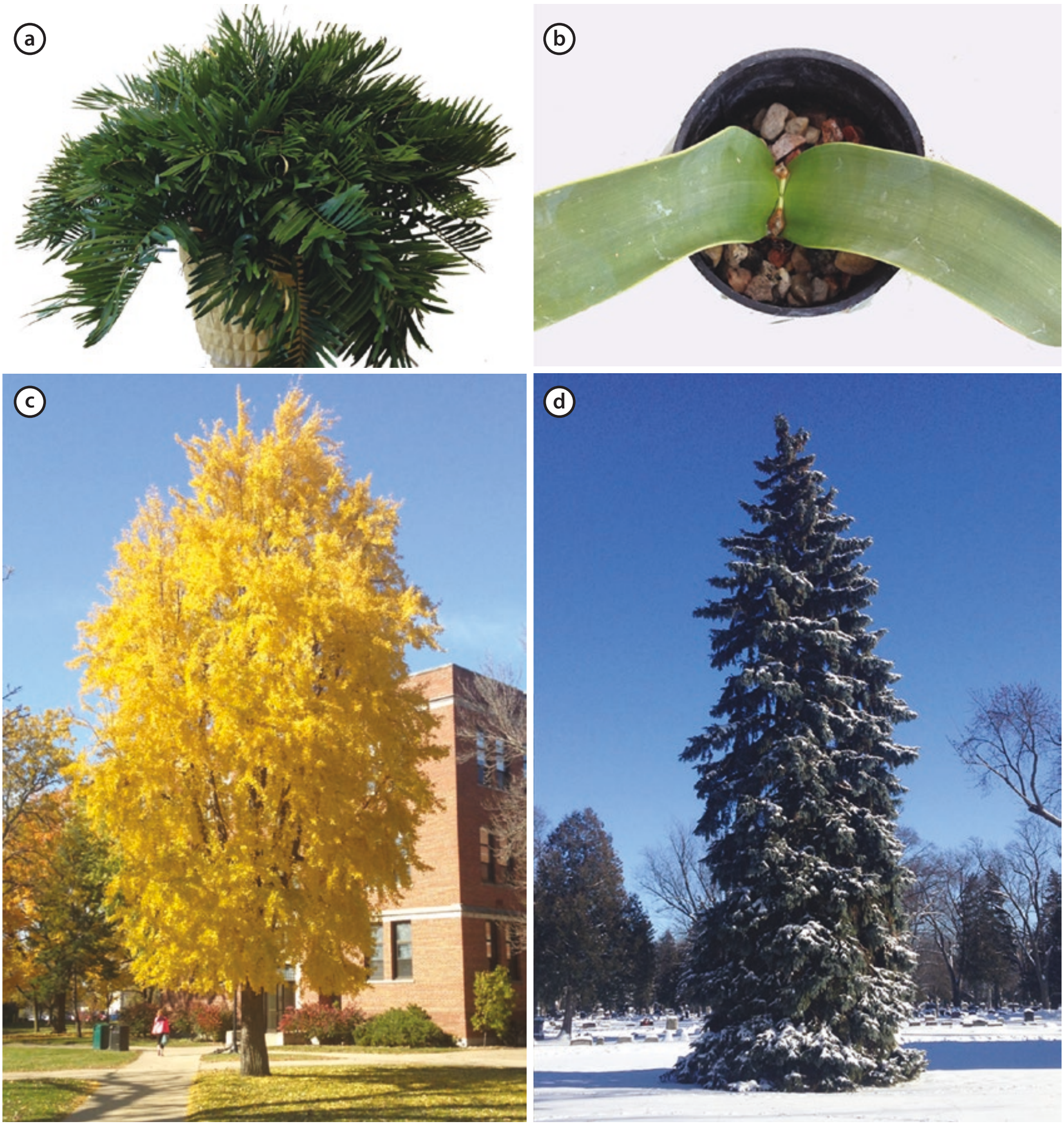


Fig. 1.16 Representative gymnosperms: **a** coontie (*Zamia pumila,* Cycadophyta) **b** welwitschia (*Welwitschia mirabilis*, Gnetophyta), **c** maidenhair tree (*Ginkgo biloba*, Ginkgophyta) in fall foliage, and **d** white spruce (*Picea glauca*, Coniferophyta) (RR Wise)

Conifers are gymnosperms; most species of which are typically evergreen and keep their leaves all year. However, such gymnosperms as larch, tamarack, and bald cypress are **deciduous**. Retention of foliage by the evergreen conifers enables them to adapt to warmer, sunny winter days, as well as allowing them to take advantage of early spring sunshine when deciduous trees are just putting out their new leaves. Because conifers do not need to produce all of the photosynthetic needles in one season, there is a considerable energetic savings in not being deciduous. These characteristics help conifers live at higher latitudes (more northern in Canada, for example) and higher elevations where the growing season is shorter.

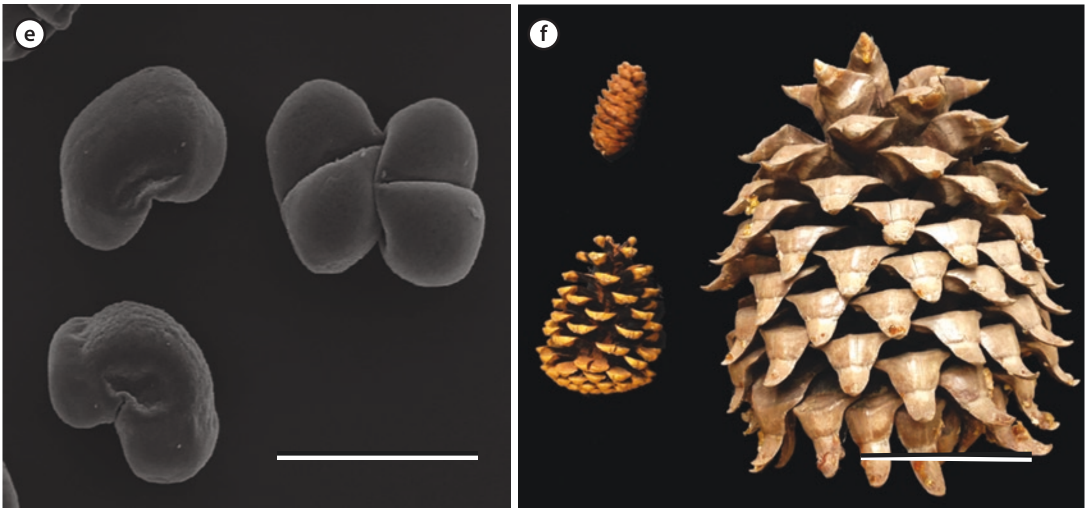


Fig. 1.16 **e** Pollen grains from blue spruce (*Picea pungens*) male cones and **f** several gymnosperm female cones, each of which bears exposed seeds. In pine, there are two seeds with papery wings on the upper surface of each scale of the female cone. Scale bars: (**e**) = 100 µm, (**f**) = 5 cm (**e**, **f** RR Wise)

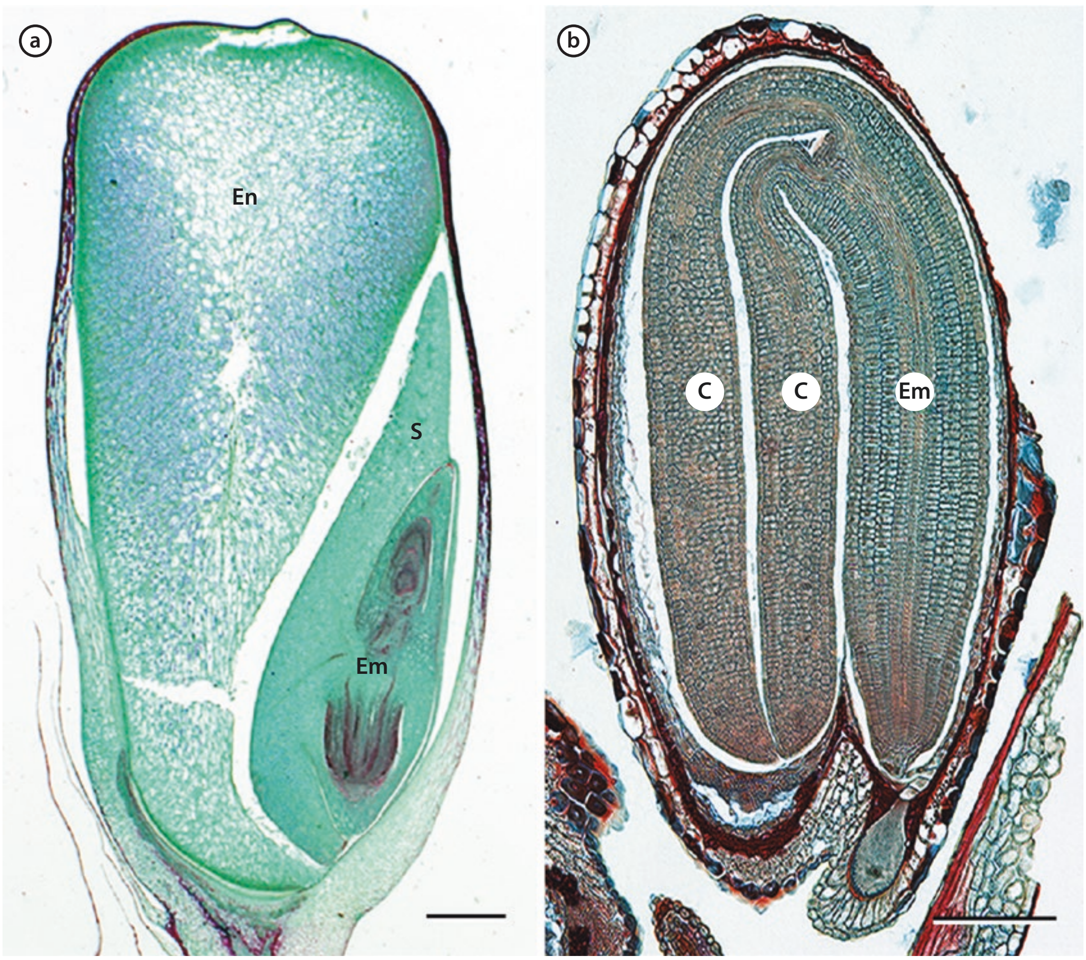
The needle-shaped leaves are also resistant to drought. Conifer woods contain tracheids to conduct water. Tracheids are long tapered cells with overlapping ends. They are believed to be ancestors of elongated cells that became modified for water transport at the center of the stem. In an evolutionary sense, tracheids are also thought to have given rise to the shorter and wider cells called vessel elements, which combine with fibers, tracheids, and parenchyma cells to make up xylem or water-conducting tissue in angiosperms.

1.17 Monocots and Eudicots Are the Two Largest Groups of Angiosperms

Currently, there are five recognized groups of angiosperms (refer to Table 1.1). The *Ceratophyllum* (six species), Chloranthales (70 species), and Magnoliids (9000 species) are relatively small clades and collectively account for less than 4% of known angiosperm species. The remaining 96% are distributed between the class Monocotyledonae (70,000 species) and the class Eudicotyledonae (175,000 species), commonly called monocots and eudicots. Those two latter clades of plants will be the main focus of this text.

When comparing monocot and eudicot traits, not all features will be clear-cut, and some are even shared with certain gymnosperms; but in most cases the characteristic features that distinguish the two classes are useful to remember, even if there are occasional exceptions.

The cotyledon is an absorptive or storage structure found in the seed with a vascular connection to the embryo. Monocots have a single cotyledon (also called the scutellum) that serves as an absorptive structure, and their food reserves are stored elsewhere, in the endosperm. During seed germination, the endosperm food reserves are broken down, absorbed by the scutellum, and transported to the embryo via the vascular connection of xylem and phloem tissues. In contrast, eudicots have two cotyledons. Some eudicots, like monocots, store the seed food reserves in an endosperm. In those cases, the two cotyledons perform the same function as the monocot's scutellum. Many other dicots, however, store seed reserves within the cotyledons themselves and have very little endosperm in the seed. So, the number of cotyledons—one or two—a major trait distinguishing monocots from eudicots (◘ Fig. 1.17a, b). Other main traits are parallel vs. net-like leaf venation pattern (◘ Fig. 1.17c, d), **vascular bundles** appear in an apparent scattered pattern throughout the stem vs. being arranged in a ring at the periphery of the stem (◘ Fig. 1.17e, f), and the number of floral parts. Monocots typically have three sepals, petals, and anthers (or multiples of three), while eudicots typically have floral parts in multiples of five (◘ Fig. 1.17g, h).



◘ **Fig. 1.17** Comparison of monocot with eudicot. **a** Maize (*Zea mays*) seed showing embryo (Em), scutellum (Sc), and endosperm (En). **b** Shepherd's purse (*Capsella bursa*) seed with embryo (Em) and cotyledons (C). **c** Maize (*Zea mays*) leaf clearing demonstrating parallel venation. **d** Apple (*Malus pumila*) leaf with netted venation. **e** Cross-section of Sprenger's asparagus (*Asparagus aethiopicus*) stem. **f** Cross-section of sunflower (*Helianthus* sp.) stem. **g** Daylily (*Hemerocallis* sp.) flower. **h** White browallia (*Browallia* sp. hybrid) flower. Scale bars: **a**, **b** = 200 µm, **c**, **d** = 100 µm, **e** = 0.5 mm, **f** = 1 mm, **g** = 5 cm, **h** = 1 cm (**a**–**h** RR Wise)

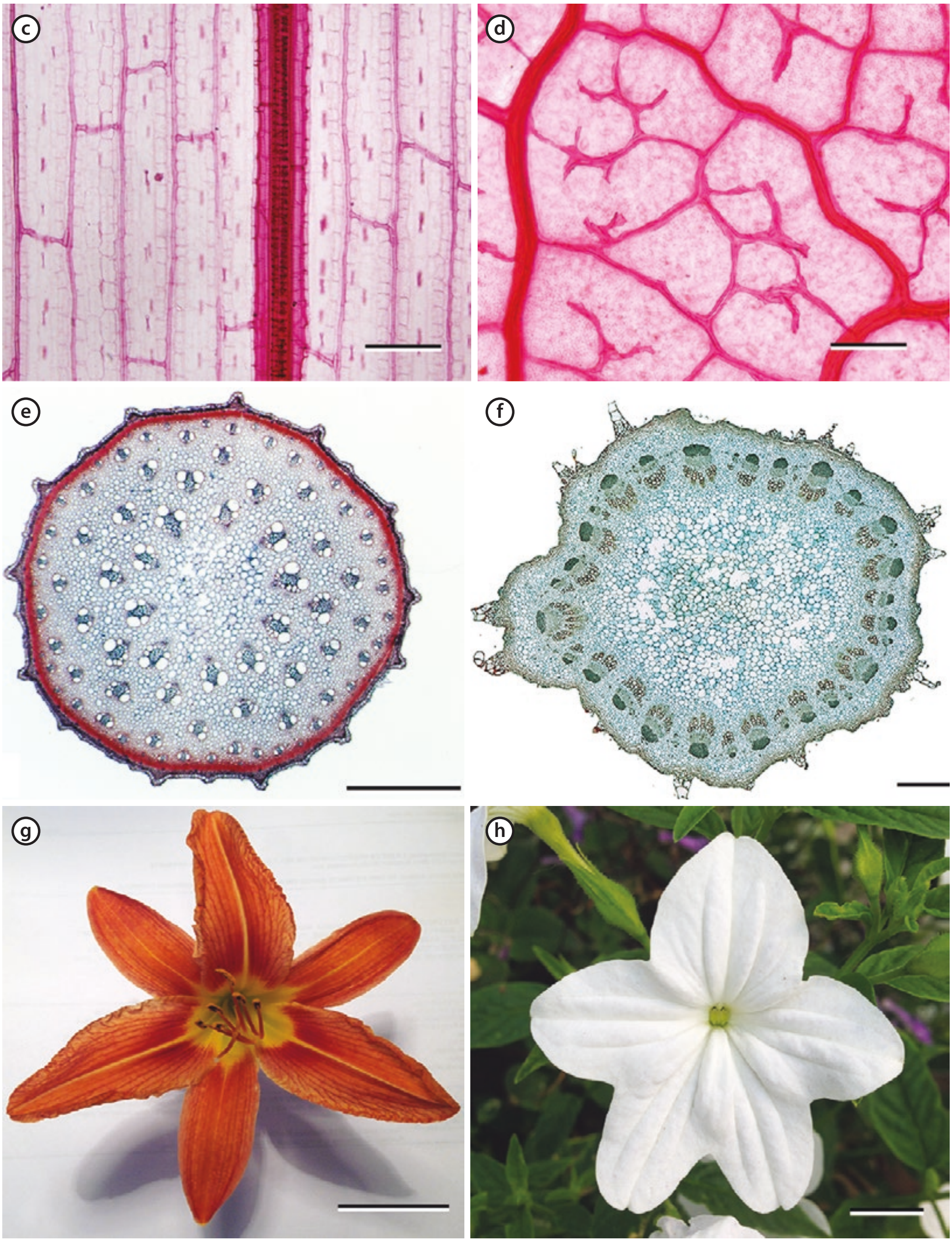


Fig. 1.17 **c–h** (continued)

1.18 Understanding Plant Structure Requires a Sense of Scale

The International System of Units (called SI units) uses the meter (m) and multiples or fractions thereof, to denote length. Structures of interest to plant anatomists range in size over 10 or 11 orders of

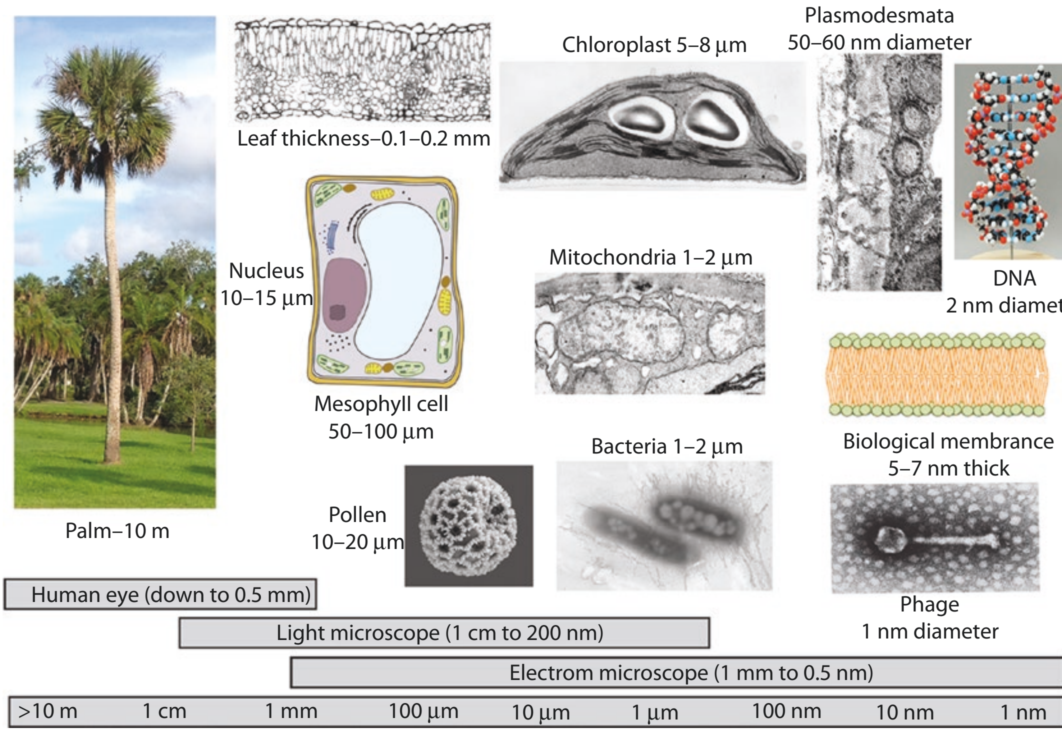


Fig. 1.18 A pictorial depiction of various plant structures and their sizes. The ability to visualize the size of each component is given by the bars across the bottom of the figure (Palm tree courtesy of J.F. Wise, DNA model courtesy of Molecular Models Corporation, Beloit, WI, phage courtesy of RV Cyrus)

magnitude, from the tallest trees (over 3×10^2 m tall) to the thickness of a biological membrane ($5–7 \times 10^{-9}$ m). Standard meter-based units are the centimeter (cm, $1 \mathrm{x} 10^{-1}$ m), millimeter (mm, 1×10^{-3} m), micrometer (or micron, μm, 1×10^{-6}), and nanometer (nm, 1×10^{-9} m). Figure 1.18 gives examples of some of the plant structures and their approximate size that will be discussed throughout this book.

1.19 "Primary" and "Secondary" Are Important Concepts in Plant Anatomy

Students of plant anatomy will frequently encounter the adjectives "primary" and "secondary" throughout this and other textbooks, which can be confusing. A firm grasp of these two terms is fundamental to understanding plant anatomy as well as growth and development.

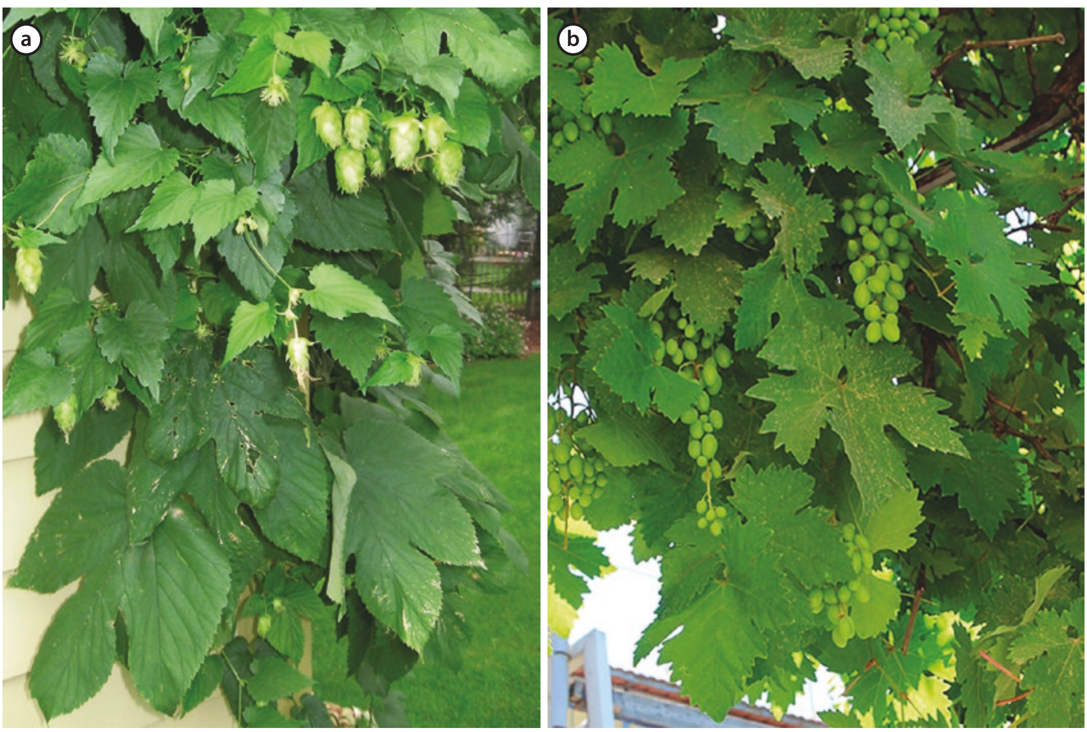
1.19.1 Primary Versus Secondary Growth and Meristems

Primary growth is the initial growth of a shoot or root and the generation of leaves and flowers. Many plants, particularly monocots and annual eudicots, only engage in primary growth (Fig. 1.19a).

They tend to be short-lived (seasonal, **annuals**, or **biennials**) or have other mechanisms to generate more permanent structures. [Refer to ► Sect. 11.9 on secondary thickening in monocot stems for a full explanation of the exceptions.] “Herbaceous” is a term used to describe eudicots that are limited to primary growth only.

Primary growth is produced by the **primary meristems**, of which there are two types—the **shoot apical meristem** (SAM) and the **root apical meristem** (RAM). SAMs and RAMs are found at the shoot tips and root tips; therefore, primary growth results in longer shoots and roots. Primary growth allows plants to explore and occupy a greater above-ground volume, which is vital to their ability to compete for light, and a greater belowground volume, from which they extract water and minerals. Refer to ► Chap. 4 (Mitosis and Meristems).

Secondary growth, on the other hand, increases the girth of existing stems and roots and produces more permanent structures (◘ Fig. 1.19b). Leaves and flowers, while sometimes containing sclerenchyma tissues (with secondary cell walls), do not exhibit true secondary growth. Secondary growth is produced by two secondary meristems, the **vascular cambium** and the **phellogen**. Each growing season, the vascular cambium produces xylem to the interior and phloem to the exterior. The xylem, which is dead at maturity, accumulates in annual growth rings, while the phloem is replaced

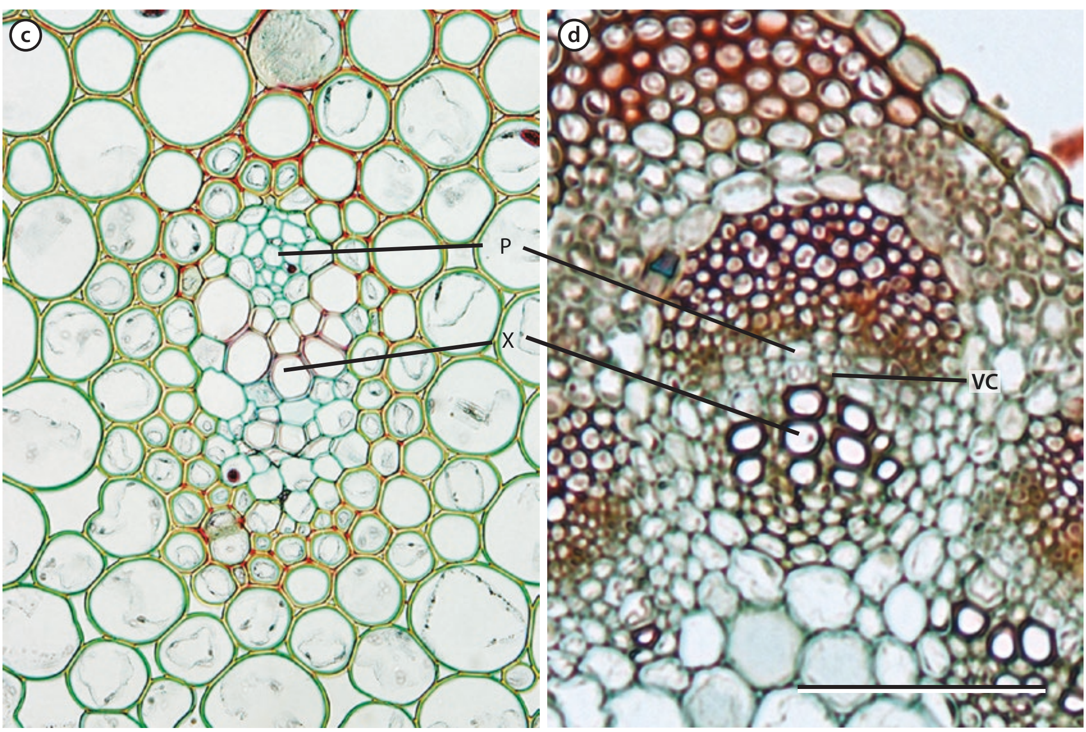


◘ **Fig. 1.19** **a** Although hops (*Humulus lupulus*) stems may grow 10 m or more in a growing season, they are herbaceous, annual organs displaying only primary growth. They die back to the ground in the autumn and grow anew from underground rhizomes in the spring. **b** Grapes (*Vitis riparia*) produce woody, secondary growth. They are perennial vines that increase in length and girth and may live for dozens of years. Leaves may be shed in the autumn, but the woody vines persist. (Image **a** by RR Wise. Image **b** courtesy of Sara Rivka Dahan, Israel) with new tissue because the increasing diameter of the xylem cylinder pushes outward and crushes last year's phloem. Exterior to the phloem, the phellogen continuously generates the tissues that become the periderm or bark of a tree. Refer to ► Chaps. 14 (Vascular Cambium) and 16 (Periderm).

Because secondary growth can only arise in existing tissues, all woody plants start as a seedling and engage in primary growth during their first growing season. Once a basic body plan has been established (and with many variations on the theme), the vascular cambium and the phellogen develop and generate secondary growth. Thus, plant anatomists sometimes speak of a plant or organ being "in the primary state of growth," in the "secondary state of growth," or of the "primary to secondary transition." They also may distinguish between the primary plant body (monocots, herbaceous eudicots, and first-year woody eudicots) and the secondary plant body (gymnosperms and woody eudicots).

1.19.2 Primary Versus Secondary Xylem and Phloem

The primary meristems—SAM and RAM—generate the primary vascular bundles, which contain primary xylem and phloem. The vascular bundles of herbaceous plants lack a cambium, cannot develop further, and thus are called **closed vascular bundles** (◘ Fig. 1.19c). **Open vascular bundles** are those with a vascular



◘ **Fig. 1.19** **c** A closed vascular bundle in a lily (*Lilium* sp.) stem. **d** An open vascular bundle in a clover (*Medicago* sp.) stem. P = phloem, VC = vascular cambium, X = xylem. Scale bar = 50 μm for both panels (**c**, **d** RR Wise) cambium (a secondary meristem) (◘ Fig. 1.19d). They transition from the primary state to the secondary state upon the activation of the vascular cambium which then produces secondary xylem and phloem. These concepts will be given more meaning in ► Chaps. 7 (Xylem), 8 (Phloem), and 11 (Stem).

1.19.3 Primary Versus Secondary Cell Walls

Primary and secondary cell walls are not conceptually related to primary and secondary growth, meristems, or vasculature (◘ Table 1.2). However, primary walls are laid down first and are then followed by the deposition of a secondary wall, in those cells that have a secondary cell wall (◘ Fig. 1.19e). The cell wall is unique to plants and covered in detail in ► Chap. 5 (Cell Walls).

◘ Table 1.2 "Primary" versus "Secondary" terminology used in plant anatomy

Primary growth Initial growth of a plant organ Generated by primary meristems Results in an increase in organ length Found in monocots and annual eudicots—a.k.a. herbaceous plants	*Secondary growth* Subsequent growth of a shoot or root Generated by secondary meristems Results in an increase in organ girth Found in perennial eudicots—a.k.a. woody plants
Primary meristem Located at the shoot and root tip. Two types—shoot apical meristem (SAM) and root apical meristem (RAM) Both in ► Chap. 4	*Secondary meristem* Located at the shoot and root periphery. Two types—vascular cambium (generates xylem and phloem, ► Chap. 14) and phellogen (generates periderm/bark, ► Chap. 16)
Primary xylem or phloem Generated by a SAM or RAM ► Chapters 8 (xylem) and 9 (phloem)	Secondary xylem or phloem Generated by the vascular cambium ► Chap. 10
Primary cell wall Laid down first Thin, cellulosic, and rarely lignified ► Chapter 5 Nonliving but contains active enzymes and capable of expanding All plant cells (parenchyma, collenchyma, and sclerenchyma) have a primary cell wall ► Chapters 5 (Cell Wall) and 6 (Cell Types)	*Secondary cell wall* Laid down after primary cell wall Thick, multilayered, impregnated with lignin Nonliving and incapable of expansion Only sclerenchyma cells have a secondary cell wall (with a few exceptions) ► Chapters 5 and 6
Primary pit field—a hole in a secondary cell wall that exposes an area of primary cell wall that has many plasmodesmata ► Chapter 5	

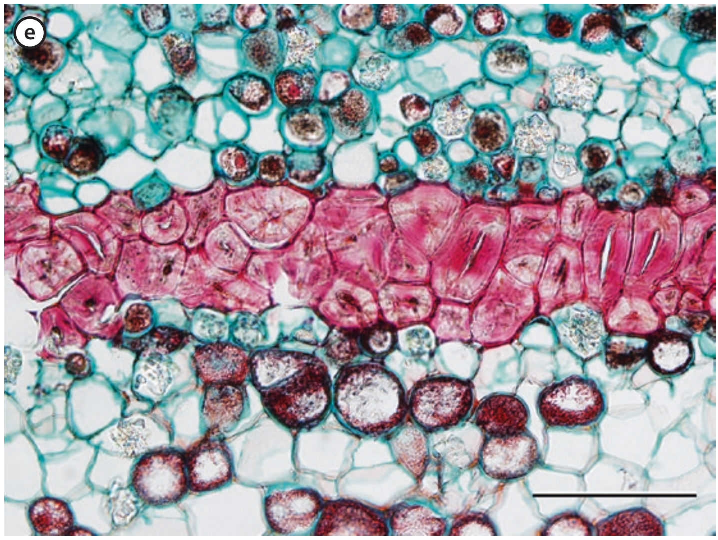


Fig. 1.19 **e** Primary and secondary cell walls in a young black walnut (*Juglans nigra*) stem. Parenchyma cells with thin primary walls (*green*) lie to either side of a band of brachysclereids with thick secondary walls (*red*). Many of the parenchyma cells contain reddish-brown tannin deposits. Scale bar = 50 µm (RR Wise)

1.20 Chapter Review

Concept Review

1.1 *Plants have multiple pigments with multiple functions*. Plant uses chlorophylls to harvest sunlight energy via photosynthesis, carotenoids and anthocyanins to attract and reward pollinators and they track the time of day, day length, and season of the year by using the phytochrome system.

1.2 *Plants use water, and the properties of water, in unique ways*. Hydraulics, the laws of physics and the physical properties of water are used to drive water movement and generate the force needed for growth and movement in plants.

1.3 *Plants use anabolic metabolism to manufacture every molecule needed for growth and produce virtually no wastes*. Plants make 100% of the amino acids, proteins, lipids, nucleic acids, vitamins, and other biomolecules they need for growth and development using sunlight, water, and about 20 elements. Plastids are the organelle in which all the major anabolic pathways take place. Spices and drugs, produced primarily as antiherbivory defenses, are some of the secondary products made by plants.

1.4 *Cell walls are nonliving materials outside the plant cell membrane that house and/or perform a variety of functions*. The cell wall was a major evolutionary advancement needed for plants to colonize the land. It is composed of cellulose and other organic polymers and may contain active enzymes. Many plant cell walls can expand, grow, and adjust to mechanical stresses.

1.5 *The plant life cycle alternates between a haploid gametophyte stage and a diploid sporophyte stage*. In plant sexual reproduction, gametophytes produce haploid male (sperm) and female (egg) gametes. Fertilization unites the two gametes to form a diploid zygote, which develops into the mature sporophyte via mitosis. Using meiosis, the sporophyte produces haploid spores that germinate and become the gametophytic stage.

1.6 *Meristematic activity continues throughout the life of a plant*. Plants produce new cells in meristems. A growing plant, even 100 of years old, has new, juvenile cells at each meristem. Apical meristems at the shoot tip and root tip increase plant length via primary growth. Lateral meristems increase the girth of stems and roots, which is called secondary growth.

1.7 *Fruit disperses seeds through space; dormancy disperses seeds through time*. Fruit (which may or may not be edible) is the tissue surrounding the seed in angiosperms and is responsible for fruit dispersal via wind, water, and gravity or with the help of animals. Seeds may remain dormant for years, decades, or even centuries and still germinate, allowing the next generation of plants to "time travel" into the future.

1.8 *Earth's history is divided into four major time periods*. Earth's history has been divided into the Precambrian (4550–542 mya), the Paleozoic era (542–251 mya), the Mesozoic era (251–66 mya), and the Cenozoic era (66 mya–present). Earth is approximately 4.55 billion years old. If expressed as a month-long calendar, life appeared on day 8, cyanobacteria on day 10, eukaryotic cells on day 24, land plants on day 28, gymnosperms on day 29, and angiosperms on the afternoon of day 30.

1.9 *Life on Earth has experienced five mass extinctions; a sixth is in progress*. Natural disasters such as climate change or meteor impact lead to five major extinctions in Earth's history. Human activity is currently driving a sixth mass extinction. Anthropogenic habitat destruction and global climate change are the major drivers in this mass extinction.

1.10 *Many plants and animals have coevolved*. Coevolution occurs when the evolution of one species influences that of another. Many plant reproductive strategies have coevolved with animals and involved rewards of food, shelter, ovipositories, or pheromones. The relationship may be general or species-specific.

1.11 *The plant body consists of four organs*. The four plant organs (and their basic functions) are the root (anchorage, storage, and water uptake), stem (support, storage), leaf (photosynthesis), and flower/fruit (reproduction, seed dispersal). Each has a unique and characteristic anatomy. All are interconnected by a vascular system consisting of xylem and phloem.

1.12 *Plant organs are initially made of three tissues*. All plant organs have an epidermis (produced by a meristem called the protoderm), a vascular system (produced by the procambium), and a filling tissue (produced by the ground meristem).

1.13 *"Plant" can be broadly defined*. Members of the kingdom Plantae are defined as photosynthetic eukaryotes. With very few exceptions, they are autotrophic and exhibit an alternation of generations. Major plant groups include algae, bryophytes, ferns and fern allies, gymnosperms, basal angiosperms, and angiosperms.

1.14 *Bryophytes lack vasculature and produce spores*. Bryophytes (hornworts, liverworts, and mosses) are simple land plants that resemble the first plants to colonize land. The gametophyte ($1n$) generation is dominant and represented by a green photosynthetic organ called a thallus. Bryophytes that lack vasculature do not produce seeds or fruit. They reproduce via spores.

1.15 *Ferns and fern allies are seedless tracheophytes*. Ferns (including club mosses and horsetails) are vascular plants that do not produce seeds, flowers, or fruit. Photosynthesis takes place in the stem, in microphylls, or in megaphylls. Reproduction is via spores and the sporophyte ($2n$) generation is dominant.

1.16 *Gymnosperms are seed-producing tracheophytes that lack flowers and fruit*. The four groups of gymnosperms (*Ginkgo*, gnetophytes, cycads, and conifers) are seed-producing vascular plants, but they lack flowers and fruit. The sporophyte ($2n$) generation is dominant. Photosynthesis is in the leaves which may be needle- or scalelike. Conifers, the largest gymnosperm group, produce their seeds in cones, are typically evergreen, and have needle- or scale-shaped leaves.

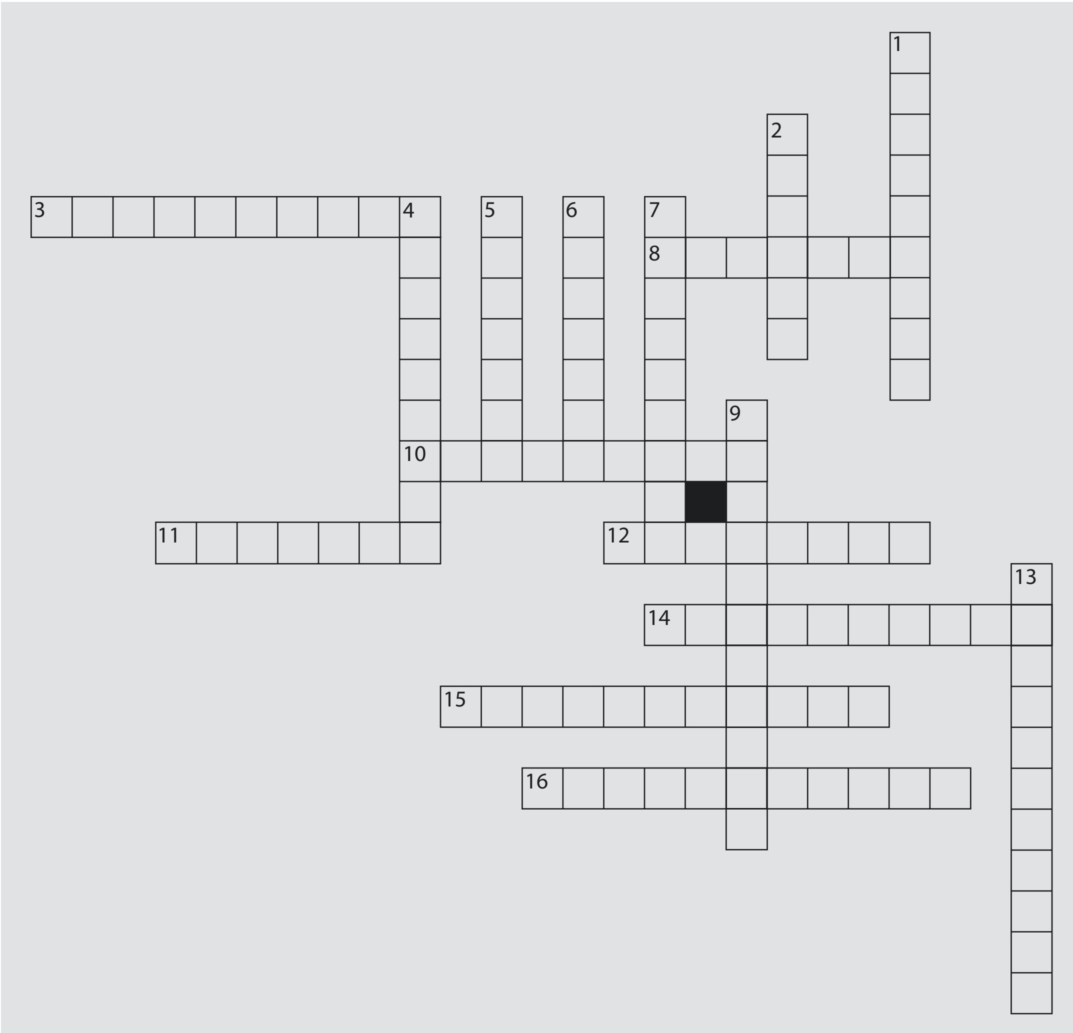
1.17 *Monocots and eudicots are the two largest groups of angiosperms*. Angiosperms, roughly divided into the monocots and the eudicots, are the dominant and most diverse group of modern plants. Monocots and eudicots have vasculature, flowers, seeds, and fruit but differ from each other in many ways including leaf venation, numbers of floral parts, and basic anatomy. The sporophyte ($2n$) generation is dominant. Photosynthesis may be in the stem or leaf.

1.18 *Understanding plant structure requires a sense of scale*. Plant anatomists use SI units for length measurements, which is based on multiples or fractions of the meter (m). Most images presented in this text use scale bars displaying the micron (μm, 1×10^{-6} m) as a reference unit.

1.19 *"Primary" and "secondary" are important concepts in plant anatomy*. These terms are used in multiple, and sometimes confusing, ways to describe such things as plant growth, meristems, xylem, phloem, and cell walls.

- **Concept Connections**

1. Complete the crossword puzzle with the most appropriate term.



Across

3. Leaves thought to have evolved from lateral branching systems.
8. Vascular system of stems arranged in a ring.
10. Self-feeder.
11. Growth that leads to formation of new organs.
12. Modern-day era.
14. This generation gives rise to haploid spores.
15. This generation can produce gametes via mitosis.
16. Two species evolving in response to one another.

Down

1. Rapidly growing part of plant containing undifferentiated cells.
2. Important for the dispersal of angiosperm seeds.
4. This type of growth allows for the development of wood.
5. Reflects light at certain wavelengths.
6. Floral structures in threes and leaves with parallel venation.
7. Porous substance found within cell walls.
9. Pigment important in photosynthesis.
13. Obtains nutrients and energy from other organisms.

■ Concept Assessment

2. Plants have multiple pigments that are used to
   a. trap sunlight energy.
   b. attract pollinators.
   c. determine light direction.
   d. measure the time of day and time of year.
   e. all of the above.

3. Hydraulics is defined as
   a. the movement of water throughout the plant body.
   b. pumping water from the soil to the atmosphere.
   c. using a fluid to do work.
   d. the evaporation of water from the leaf surface.
   e. the force behind muscle contraction.

4. In terms of metabolism, plants and animals differ in that
   a. most animals are autotrophs.
   b. plants produce copious metabolic wastes.
   c. plants use anabolic pathways to manufacture all molecules needed for growth.
   d. animal secretions are the source of many spices and medicines.
   e. plants must be supplied with vitamins and other biomolecules to grow and reproduce.

5. The geological period in which we live is termed the
   a. Paleozoic.
   b. Devonian.
   c. Jurassic.
   d. Cambrian.
   e. Quaternary.

6. Flowering plants and mammals became dominant during the past _______ million years.
   a. 1
   b. 23
   c. 66
   d. 195
   e. 500

7. Which is not a characteristic of plant cell walls?
   a. plant cell walls are found only in the sporophyte phase of the life cycle.
   b. plant cell walls contain molecules built of simple sugars.
   c. plant cell walls may contain enzymes that are biologically active.
   d. plant cell walls often contain strengthening polymers.
   e. plant cell walls are a site of active secretion.

8. The broad definition of "plants" includes all
   a. heterotrophic eukaryotes.
   b. bacteria, fungi, and angiosperms.
   c. photoautotrophic eukaryotes.
   d. chemotropic bacteria.
   e. life-forms that perform metabolism.

9. The plant life cycle alternates between
   a. a haploid gametophyte generation and a diploid sporophyte generation.
   b. an egg phase and a sperm phase.
   c. a sexual reproductive phase and an asexual reproductive phase.
   d. a zygotic phase and a meiotic phase.
   e. fertilization and mitosis.

10. Which choice ranks the SI units of length from smallest to largest?
   a. cm, mm, μm, nm, m
   b. mm, μm, m, nm, cm
   c. m, cm, mm, μm, nm
   d. nm, μm, mm, cm, m
   e. nm, mm, μm, cm, m

11. Which tissue gives rise to secondary growth?
   a. apical meristem.
   b. adventitious roots.
   c. germinating seed.
   d. terminal buds.
   e. vascular cambium.

Concept Applications

12. Plants use carbon dioxide, sunlight, and minerals to produce the molecules that serve as the basis of the food chain. Sketch a design of an agricultural system that astronauts might use in a closed spaceship to provide food for a multi-year space flight.

13. Almost all spices used in cooking are derived from plant leaves, stems, roots, or flowers. Why would plants make so many flavor compounds? Of what value are spices to the plants that produce them?

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Microscopy and Imaging

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R. Crang et al., *Plant Anatomy*, https://doi.org/10.1007/978-3-319-77315-5_2

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Introduction

Plant anatomy is typically regarded as the microscopic study of plant tissues and cells, and the development of light and electron microscopes has had a major impact in elucidating our knowledge of structure. It is, therefore, important that we have some understanding of the development, design, and use of these types of instruments. How did microscopy develop, and what has been its significance in the understanding of plant anatomy? This chapter will begin by getting to know some key individuals significant in the developing of microscopy and its relevant applications in plant biology. However, we begin this section, not by focusing on early microscopists, such as Zacharias Jansen who is credited with inventing the first **compound microscope**, but rather, we also explore the key individuals whose work ultimately led to advancements in the field of plant anatomy. Thus, we are starting with those scientists such as Hooke and van Leeuwenhoek who made discoveries and innovations with early microscopes.

2.1 Robert Hooke, 1635–1703, Described a Cell as the Basic Unit of Life by Studying the Bark of the Cork Oak Tree, *Quercus suber*

The Englishman, Robert Hooke (◘ Fig. 2.1a), first described biological matter, including plant material, from its microscopic perspective using an instrument of his own design (◘ Fig. 2.1b). His famous treatise, *Micrographia*, was published in 1665. He used the term "cellulae" to describe the tiny compartments of bottle cork (bark of the cork oak or *Quercus suber*), which reminded him of room-like compartments similar to the small, identical rooms of monasteries which were called cells (◘ Fig. 2.1c). The name "cell" has, of course, remained. A direct count of some 60 cells per one-eighteenth of an inch led him to calculate that there must be over a billion cells in a cubic inch of cork.

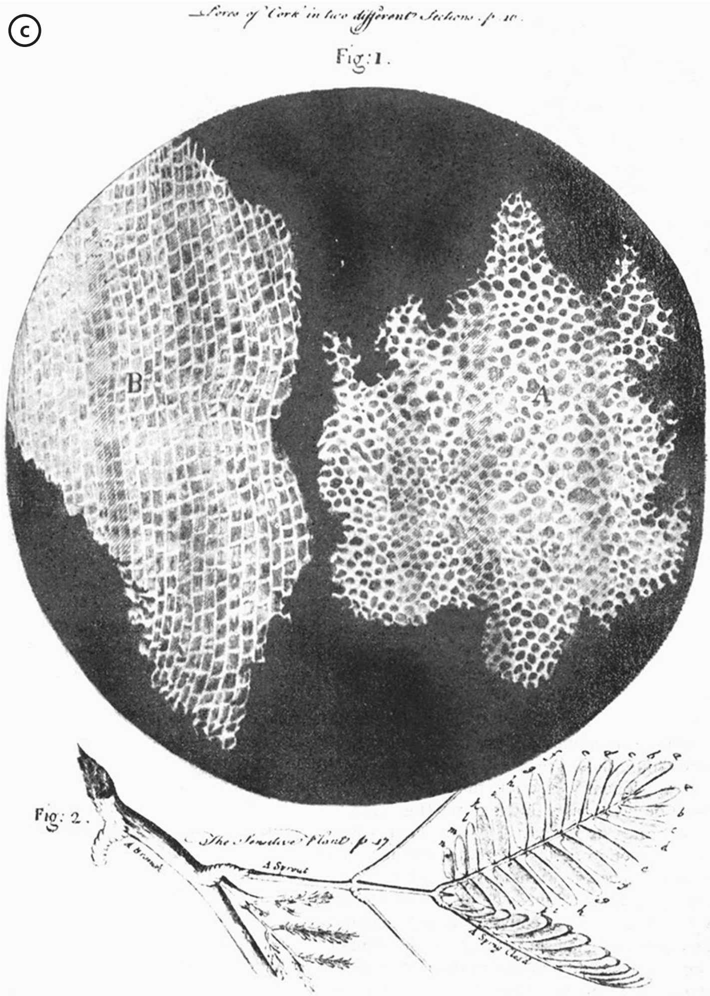
Hooke was a remarkable individual, but reportedly plagued with ill health and, according to all accounts, physically unattractive with long, untidy hair, with a stooping gait, and with a pallid complexion. However, besides microscopy, among his other accomplishments, Hooke studied problems in celestial mechanics; invented the vacuum pump, the first respirator, and the iris diaphragm; and developed an early balance spring used in watches. He was one of the most gifted inventors of his day, though not as well recognized as he might have been due to his antagonistic relationship with Sir Isaac Newton. Hooke's life and scientific contributions have received considerable attention by historians. See Jardine (2005) as an example.

Fig. 2.1 **a** A recent interpretation of the appearance of Robert Hooke by artist Rita Greer. The only known portrait of Hooke was destroyed or lost shortly after his death when Isaac Newton became president of the Royal Society of England. (Image courtesy of Rita Greer). **b** Drawing of a microscope designed and used by Hooke (public domain)

2.2 Antoni Van Leeuwenhoek, 1632–1723, Was the First Scientist to Observe Microorganisms

In the mid- and late 1600s, Antoni van Leeuwenhoek (Fig. 2.2a) published many letters to the Royal Society of London regarding his observations of different microorganisms observed with his hand-ground, single-lens microscopes (Fig. 2.2b). Van Leeuwenhoek's lens qualities were outstanding, and it is still not known how he designed them so perfectly, as he appeared to have closely guarded the technique.

Modern microscopes use multiple lenses to achieve maximum magnification and resolution. However, at lesser magnifications, the single-lens microscope of van Leeuwenhoek was quite successful. Thus, Leeuwenhoek made many pioneering discoveries of single cells from plants, animals, and microorganisms (Schierbeek 1959; Ford 1992).



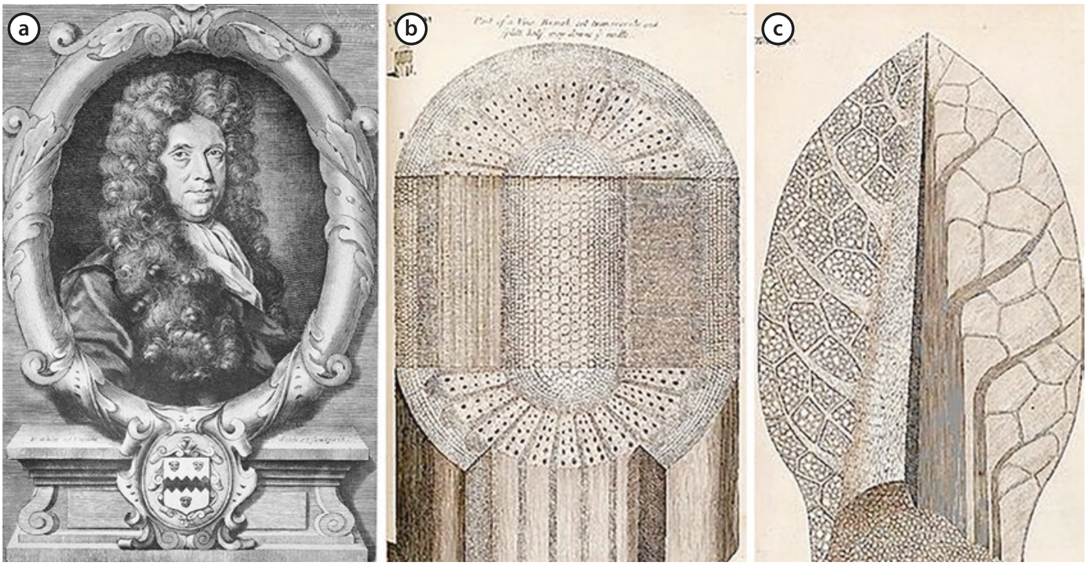
■ **Fig. 2.1** **c** Hooke's most famous image of cork as he drew it from viewing with his light microscope. In it, he saw small compartments, which he referred to as "cells" (public domain)

Among the microorganisms first described were bacteria, protozoa, and rotifers. It is believed that van Leeuwenhoek made at least 500 microscopes during his career, but only nine are known to currently exist. The highest magnification obtainable was approximately 275×.

◘ **Fig. 2.2** **a** Antoni van Leeuwenhoek, a well-to-do Dutch draper, developed a strong interest in science and in the art of microscopy. His most famous instruments were designed to employ only a single lens. **b** A replica of Leeuwenhoek's single-lens microscope is shown above, with the single lens indicated by the red arrow. The microscope is quite small, with the brass back plate only being approximately 2 × 5 cm. (**a** RR Wise; Image **b** by Jeroen Rouwkema. Licensed under CC BY-SA 3.0 via Wikimedia Commons)

2.3 Nehemiah Grew, 1641–1712, Was the Father of Plant Anatomy

In 1682 Nehemiah Grew (◘ Fig. 2.3a) published the first of two well-illustrated volumes with the Royal Society on the microscopic anatomy of plants entitled: *The Anatomy of Plants: With an Idea of a Philosophical History of Plants.* in which he described minute "vesicles" (the cells that were earlier described by Hooke). While some of his work was more morphology than anatomy, he did make considerable use of light microscopy in his investigations, and Grew was the first microscopist who limited his investigations to the anatomy



◘ **Fig. 2.3** **a**–**c** Nehemiah Grew, an English scientist and doctor, is often referred to as the "father of plant anatomy." **b**, **c** Two of the anatomical illustrations developed by Grew using an early compound microscope. **b** A eudicot stem and **c** different paradermal sections (cut parallel with the leaf surface) through a eudicot leaf (**a**–**c** public domain)

of plants (◘ Fig. 2.3b, c). Although the compound light microscope had been around for over a half century, Grew and a few other individuals simultaneously described general plant microscopic structure for the first time during the end of the seventeenth century and the early eighteenth century.

Grew was a doctor of medicine, having studied at Cambridge University in England. Not unlike other botanists of his time, although his training was in medicine, his interest in plant structure developed from microscopic work in his medical practice.

2.4 Robert Brown, 1773–1858, Discovered the Nucleus of the Cell by Studying Orchid Petals

In 1831 Robert Brown (◘ Fig. 2.4a, b) described the cell nucleus during a study of orchids. He is also credited with first observing **Brownian movement** (named for him and illustrating molecular motion he observed by studying pollen grains) and the process of **cytoplasmic streaming**. Although he practiced medicine as a surgeon for 5 years, he later abandoned this and turned all his efforts toward botanical science, publishing dozens of books and articles. He was distinguished in making a series of anatomical studies involving the process of reproduction and in the study of pollen and reproduction of gymnosperms (Brown 1828).

Fig. 2.4 **a** Robert Brown, a Scottish surgeon and botanist. **b** The microscope with which he made many of his observations that was made prior to 1820. It is a compound light microscope because it uses both objective and ocular lenses. (**a** public domain; Image **b** courtesy of Dr. Brian Ford)

2.5 Katherine Esau, 1898–1997, Advanced the Field of Plant Anatomy with Her Influential Textbooks

Born in the Ukraine, a daughter of the mayor of Yekaterinoslav, Katherine Esau (Fig. 2.5a) was educated at the Women's Agricultural College in Moscow, Russia. In 1917 her studies were interrupted due to the revolution, and she returned to her home, which had not been occupied by the Bolsheviks. She remained there until the end of the First World War when her family immigrated to Germany and later (1922) to America. They settled in Reedley, California, near Fresno.

In California, she was hired by a sugar company to develop a sugar beet that would be resistant to curly top disease caused by a virus. Her work drew the attention of researchers at the University of California, Davis, where she was recruited to study botany. Her dissertation research discovered that the curly top virus was spread within plants via the phloem. Upon graduation, she was offered the position of instructor of botany in the College of Agriculture at Davis where she taught plant anatomy, systematic botany, morphology of crop plants, and microtechnique (Fig. 2.5b, c). She achieved the rank of full

Fig. 2.5 **b** A transmission electron micrograph by Katherine Esau showing a portion of a tobacco leaf infected by the tobacco mosaic virus (V). Scale bar = 10 µm. **c** A longitudinal section of a Pinus sp. needle seen in the light microscope and prepared by Katherine Esau. Scale bar = 500 µm. (**b**, **c** Cheadle Center for Biodiversity and Ecological Restoration, UC Santa Barbara)

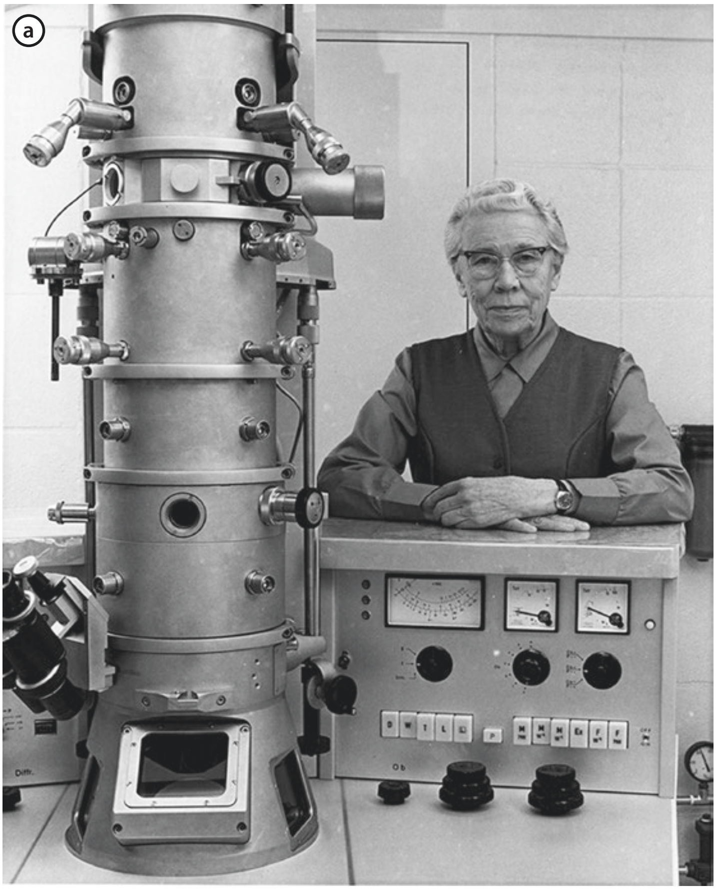
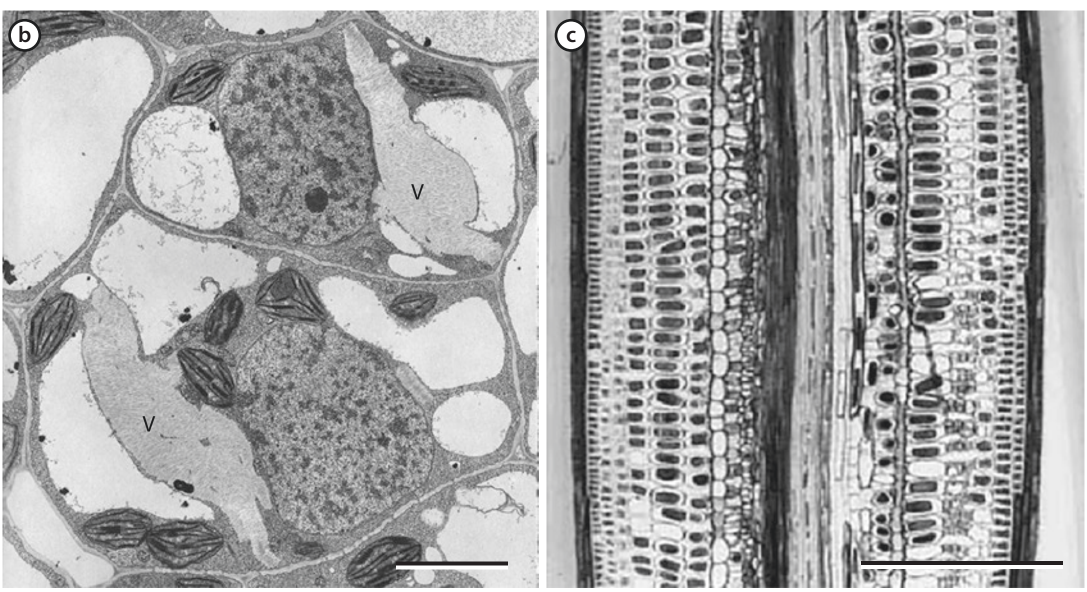


Fig. 2.5 **a** Katherine Esau, a Ukrainian botanist, plant pathologist, and plant anatomist. (Image courtesy of Cheadle Center for Biodiversity and Ecological Restoration, UC Santa Barbara)



professor in 1949 at the age of 51. Her research became increasingly involved with the anatomy of phloem, as she was concerned about plant pathways in disease, and for chemicals in weed control.

Dr. Esau was elected to the National Academy of Sciences in 1957. In the early 1960s she became interested in electron microscopy involving the study of phloem tissue—an area of study she pursued throughout the rest of her career. In 1989, US President George H.W. Bush awarded her the National Medal of Science. She is most noted for her highly read textbooks that established a modern foundation for the field of plant anatomy (Esau 1953, 1961, 1969, 1977).

2.6 Light Microscopy: The Most Useful Tool of the Plant Anatomist

Resolution is the ability to distinguish a gap between two adjacent lines or objects. The smaller that gap, the higher the resolution, which allows for greater detail at higher magnifications. Light microscopy enables us to resolve structures of about 0.2 μm and achieve magnifications of about 2000×, which is not fine enough to visualize cell membranes and many subcellular units. However, in the range in which it works, and given the use of color and special imaging techniques which are possible, it has been the most valuable tool of the plant anatomist for almost four centuries. Realizing that, it is useful to understand some basics of light microscopy, starting with image formation.

How a compound light microscope works can be related to some simple optical principles. To start with, we may imagine making simple images, even without a glass lens. Prior to the popularity of digital photography, many students in elementary or secondary school designed and built pinhole cameras (◘ Fig. 2.6). These are very simple devices which have a small circular pinhole in a piece of foil through which light rays pass and are projected onto the back of a light-tight box where there is a piece of photographic film attached. An image of a well-lighted scene can be projected onto the film through the pinhole due to the rectilinear propagation of light (that means that light travels in straight lines). The size of image points produced on the film depends on the diameter of the pinhole and the distance between the hole and the film. The larger the hole, the more blurred is the image. If the hole is too small, brightness and diffraction become limiting factors.

Now suppose that you are photographing a tree at some distance. The light travels from any point on the plant in all directions, but a certain solid angle of the light is intercepted by the pinhole (or lens) of the camera, refracted (bent), and recombined at the film plane. Normally, the image on the film plane will be much smaller than the original object, and the distance from the center of the pinhole (or lens) to the image is much shorter than the distance from the object to the pinhole (or lens) center. Actually, this sets up a consistent ratio in which we can say that $A/a = B/b$ where A is the height of the object (the tree) and where a is the distance to the pinhole (or lens) from the object. B is the height of the image on the film plane, and b is the distance from the center of the pinhole (or

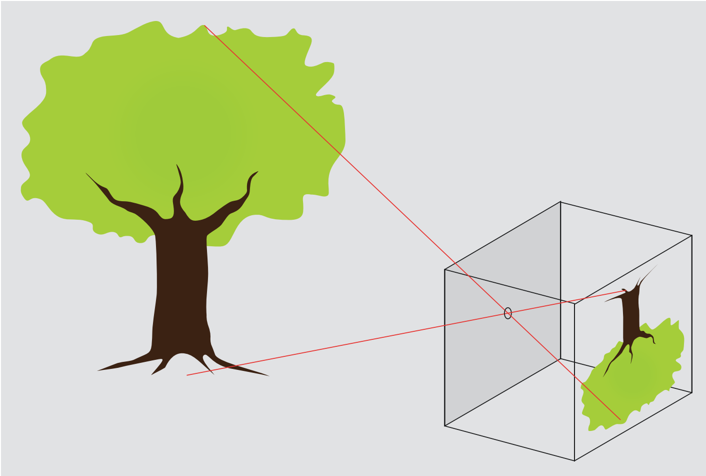


Fig. 2.6 An example of how images are formed using a pinhole camera (Redrawn from Crang and Vassilyev 2003)

lens) to the film plane. Thus, the ratio of A to a is always equal to the ratio of B to b when the image is in focus.

The image produced on the piece of film can be greatly improved by using a glass lens in place of the pinhole. A lens has the extremely valuable property of refracting light, thus counteracting the principle of the rectilinear propagation of light. It also can be of much larger diameter than a pinhole and thereby capable of collecting much more light to make a much shorter exposure time on the film.

2.7 The Compound Light Microscope Uses Multiple Lenses to Form and Capture Images

In the case of the single-lens microscope, such as the early instruments designed by van Leeuwenhoek, greater magnification is obtained by increasing the curvature of the surface of the lens. In theory, the greatest magnification would result from a perfectly spherical lens. However, the focal length of the lens would be on the surface of the lens, and the field of view would be infinitely small, making the device impractical.

There are several advantages to using a compound microscope over a single-lens instrument. First, using two or more lenses in tandem enables magnification to be viewed as the product of the combined magnifications of the individual lenses. Second, it is easy to obtain variable magnification by simply changing objectives lenses. Third, the compound microscope allows for a relatively wide field of view at all magnifications. Additional advantages in using a compound scope include brighter imaging as well as the ability to work greater distances from a specimen than when using a single lens.

The modern compound light microscope (Fig. 2.7) possesses two or more magnifying lenses. Light travels from a light source in

Fig. 2.7 The basic components of a modern compound light microscope (Olympus CX23). (Image courtesy of Jennifer Reed, Olympus Instruments)

the base of the microscope, through a condenser underneath the microscope stage, through the specimen, objective lens, and then to the ocular lenses. Various magnifications are selected by rotating the revolving nosepiece and inserting a different objective lens into the light path. Unlike the single-lens microscope, it also permits a greater working distance from a specimen by allowing for finite focal lengths outside of the lens itself.

2.8 The Resolving Power of a Lens Places Limits on Resolution and Magnification

The physicist Ernst Abbé, working with the master lens maker Carl Zeiss in Jena, Germany, during the latter part of the eighteenth century, defined the rules of light optics and determined the theoretical limits of resolution. To their amazement, it was found in the 1880s that Zeiss had already produced (through his own skills) microscopes that had essentially reached the limits of resolution (approximately 0.2 μm). Abbé later founded the lens-making company named after Carl Zeiss, which continues today.

Resolution, introduced above, is usually meant to represent the unitless concept of the amount of detail available at high magnifications. The **resolving power**, or R.P., on the other hand, is the mathematical expression of the resolution and is determined by the equation shown below. Lambda (λ) is the average wavelength of light used in imaging, and N.A. represents the numerical aperture of the objective lens ($N.A._{obj}$) plus that of the condenser lens ($N.A._{cond}$) in the microscope.

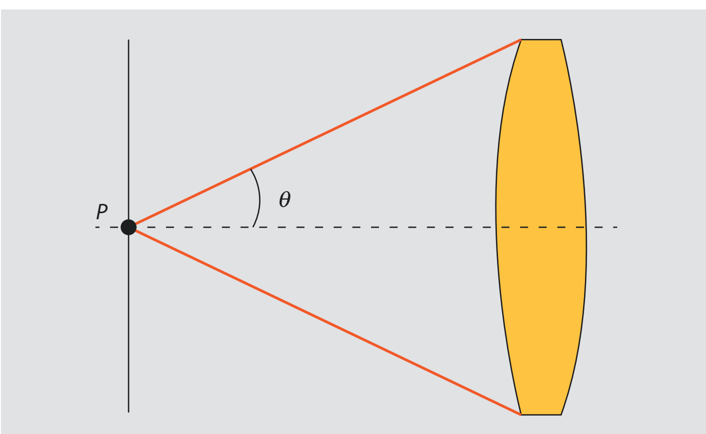
$$\text{R.P.} = \frac{\lambda}{\text{N.A.}_{\text{obj}} + \text{N.A.}_{\text{cond.}}}$$

The **numerical aperture** is a function of n (the index of refraction of the medium being used) and of the sine of the half angle that light rays would take from a specimen in focus through the objective lens (◘ Fig. 2.8). It is represented by the formula shown here.

$$\text{N.A.} = n \sin\theta$$

The index of refraction (n) is the ratio of the speed of light in a vacuum to the speed of light in a medium such as air, water, or oil. The value is always equal to or greater than 1.0. Air has a **refractive index** of 1.0, thus in this case, the numerical aperture is dependent upon the half angle of the light cone (θ).

Numerical apertures are values that can be found inscribed on the housing of the objective lens or on the condenser lens. Some representative values for objective lenses are as follows (there may be variation due to different manufacturers). A 4× lens may have a N.A. = 0.1, a 9× lens may have a N.A. = 0.25, a 40× lens may have a N.A. = 0.65, and an oil immersion 100× lens may have a N.A. = 1.3. There is a rule of thumb, which says that the maximum magnification obtainable that yields good resolution is not greater than 1000× the N.A. of an objective lens. Thus, this sets a limit on how much magnification can be obtained by the corresponding ocular lens of the microscope. Therefore, a microscope with a 10× ocular lens and a 4× objective lens would have a total magnification of 40×. This is lower than 100× magnification (1000 * 0.1) and thus, would be expected to yield a high-resolution image.



◘ **Fig. 2.8** Diagrammatic representation of numerical aperture. The numerical aperture of a microscope lens in alignment with a point (P) depends on the half-angle (θ) of the maximum cone of light that either enters or exits the lens. The N.A. has no units of measurement. The blue object to the right represents a lens, which parallel light rays enter from the right (Redrawn from Crang and Vassilyev 2003)

Box 2.1 How Low Can You Go? Achieving Maximum Image Quality by Post-imaging Processing

Light and electron microscopes are some of the plant anatomist's most basic tools. Both use lenses to manipulate a beam of photons or electrons. Strict manufacturing tolerances allow for the production of high quality lenses. However, there are technological and physical limits to maximum magnification and resolution, and the image produced by even the finest lens will always have a certain amount of built-in "aberration." The advent of digital cameras, coupled with inexpensive and powerful personal computers, has allowed microscope manufacturers to partner with computer scientists to develop software-based approaches to markedly improve images generated by microscopists. While theoretical resolution is limited by the physics of the light or electron beam, sophisticated mathematically-based methods such as energy loss spectroscopy and image deconvolution are being used to greatly enhance the quality, and scientific value, of modern imaging techniques.

References: Ramasse (2017) and Storath et al. (2017).

2.9 The Confocal Microscope Allows for Sharper Detail, Computer Control, and 3-D Imaging with a Modified Compound Microscope

During the mid-to-late 1980s, commercial microscopes began to appear that made use of the principle of confocal imaging (◘ Fig. 2.9a).

a

◘ **Fig. 2.9** **a** A confocal laser scanning microscope (Nikon A1R CLSM) with computerized functions and display. (Image courtesy of Eric Flem, Nikon Instruments, Inc.)

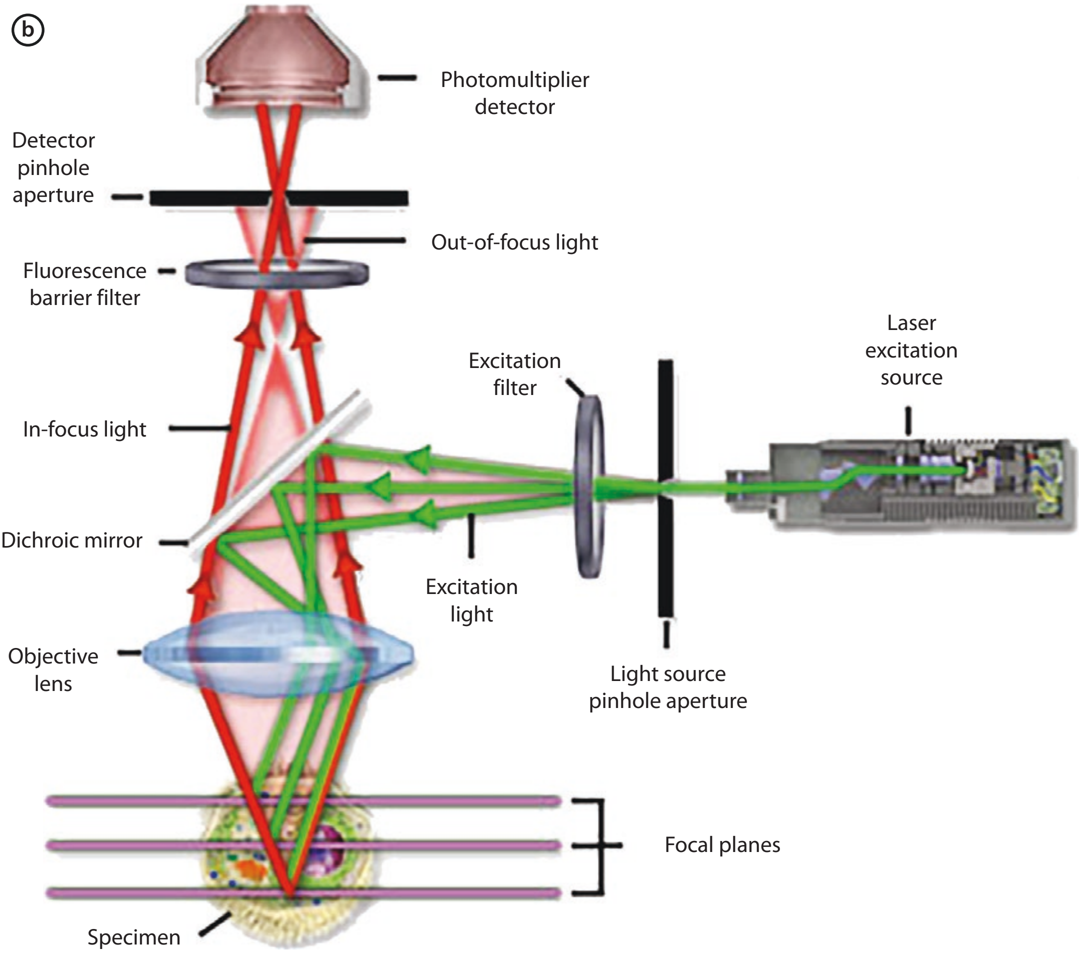
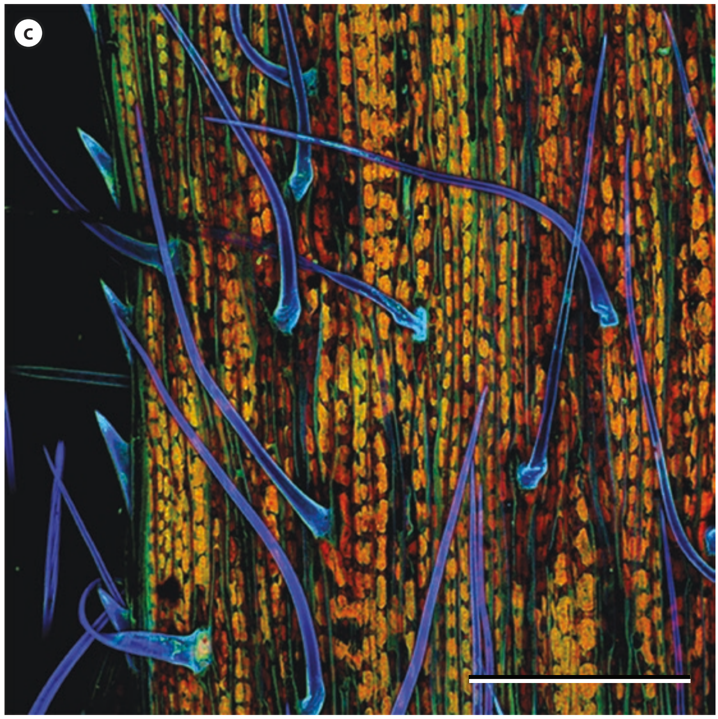


Fig. 2.9 **b** Schematic diagram of a confocal microscope. A rastered light pathway is projected onto a specimen by epiluminescence. Reflected or fluoresced light is imaged back through the objective lens. (Image courtesy of Carl Zeiss Microscopy, LLC, with modification)

This type of microscopy utilizing the confocal laser scanning microscope (CLSM) is very powerful in that it is a versatile instrument that allows scientists to study gene expression and protein movements within specific plant structures. By fluorescently tagging genes, plant geneticists can observe protein expression as well as how substances move within plants. Thus, while the CLSM isn't necessarily used for classic plant anatomy per se, it is a powerful tool for plant cell biologists and geneticists.

Both full-color visible light instruments and laser instruments have been designed and are useful in different applications. Both have similar principles of design, however (Fig. 2.9b). A beam of light is passed through a small opening and may be deflected in a series of lines that constitute a raster which is projected from above the objective lens of a light microscope, through that lens, and onto the surface of a specimen located in the front focal plane of the lens. The pathway of the light will be at its smallest diameter as determined by the point of light source and its crossover on the surface of the specimen. Since the excitation light is coming from above the specimen, it is said to represent **epiluminescence**.



■ **Fig. 2.9** **c** A CLSM image of autofluorescence of a blade of grass. Trichomes are shown in blue, and epidermal cells appear mostly orange. Scale bar = 200 µm. (Image courtesy of Dr. Donna Stolz University of Pittsburgh School of Medicine)

The object being illuminated may be a section or, more often, a layer (or multiple layers) of the specimen. The crossover light, being in a raster, will be projected one point at a time in rapid sequence. Either reflected or fluoresced light can be captured by the objective lens and be conveyed back up the image tube of the light microscope to a dichroic mirror (a glass surface coated with a special metal film that reflects certain colors of light while allowing others to pass through), that, in turn, projects the radiant image toward a pinhole aperture plate. Any light that was received from either above or below the focal plane of the objective lens will strike the aperture plate away from the pinhole and will be blocked. Only those light paths that have come from the exact focal plane on the specimen will be focused through the aperture. Such light is then picked up by a photomultiplier tube and used to create a point of some brightness (depending on the amount of light captured through the aperture) on a cathode ray tube or computer monitor screen. The position of each point of light displayed will correspond with the position of the rastered laser beam on the specimen. Thus, a confocal laser scanning image can be generated (■ Fig. 2.9c).

Since the operation of the confocal laser scanning microscope is controlled by computer inputs, and its images are electronically stored, it can then assemble the various images from the specimen and reconstruct a three-dimensional image, which can be rotated and/or analyzed for structural composition.

2.10 Electron Microscopy Allows a View into the World of Cellular Ultrastructure

It remained well into the twentieth century before resolution greater than that of the light microscope could be achieved. This depended upon employing illumination with a vastly shorter wavelength than that possible in the light optical range. Electrons, discovered by the British physicist, J.J. Thompson, in 1898, were shown by L. de Broglie in 1924 to possess wave properties nearly a thousand times shorter than that of visible light. Since it was recognized that the resolution of the light microscope was limited mostly by the wavelength of visible light, electrons seemed to offer an outstanding possibility for vastly improved resolution (and therefore also magnification).

With the work of physicists, such as H. Busch, M. Knoll, and E. Ruska from 1925 through 1934, strong electromagnetic lenses were developed that enabled electron beams to be focused in much the same manner as glass lenses direct the pathway of visible light. In fact, the basic design of early transmission electron microscopes (and even today's instruments) follows similar optical pathways as that of light microscopes. Electrons, however, can be deflected by the presence of air; hence the electron microscope needed to have a vacuum system for the pathway of the electron beam.

There are two basic types of electron microscope (and many variations thereof). The transmission electron microscope (TEM) was invented in the early 1930s by the German physicist Ernst Ruska (◘ Fig. 2.10a), for which he shared the 1986 Nobel Prize in Physics (Hawkes 1990). The first electron micrograph of a biological sample followed almost immediately and coincidentally in the field of plant anatomy. L.L. Marton published a shadowy outline of a sundew leaf in 1934 (◘ Fig. 2.10c). However, the TEM did not become commercially available until the late 1940s after the end of the Second World War. In addition to the interruption caused by the war, the TEM was invented by physicists, not biologists, and it took the 1940s and 1950s for biologists to develop the sample preparation techniques necessary to prepare and image biological samples to the level of resolution with which we are familiar today. The invention of those techniques and protocols, coupled with the resolving power of the TEM, revolutionized cellular biology in the mid-twentieth century (Rasmussen 1997). The micrograph atlas of plant cell ultrastructure produced by Myron Ledbetter and Keith Porter remains a classic to this day (Ledbetter and Porter 1970). ► Section 2.11 covers the TEM in more detail.

True to its name, the TEM works by transmitting a beam of electrons through a thin slice of tissue. Organelles and molecules in the tissue section selectively block the incident electrons, which projects a pattern on a viewing screen or film negative much like a slide projector sends an image to a viewing screen. Thus, cellular internal detail is revealed. The image can be collected directly on film.

The scanning electron microscope (SEM) was developed in 1937 (◘ Fig. 2.12b) by Manfred von Ardenne, another German physicist. Just as there was a 20–30-year lag between the invention of the TEM and the generation of useful micrographs of biological specimens,

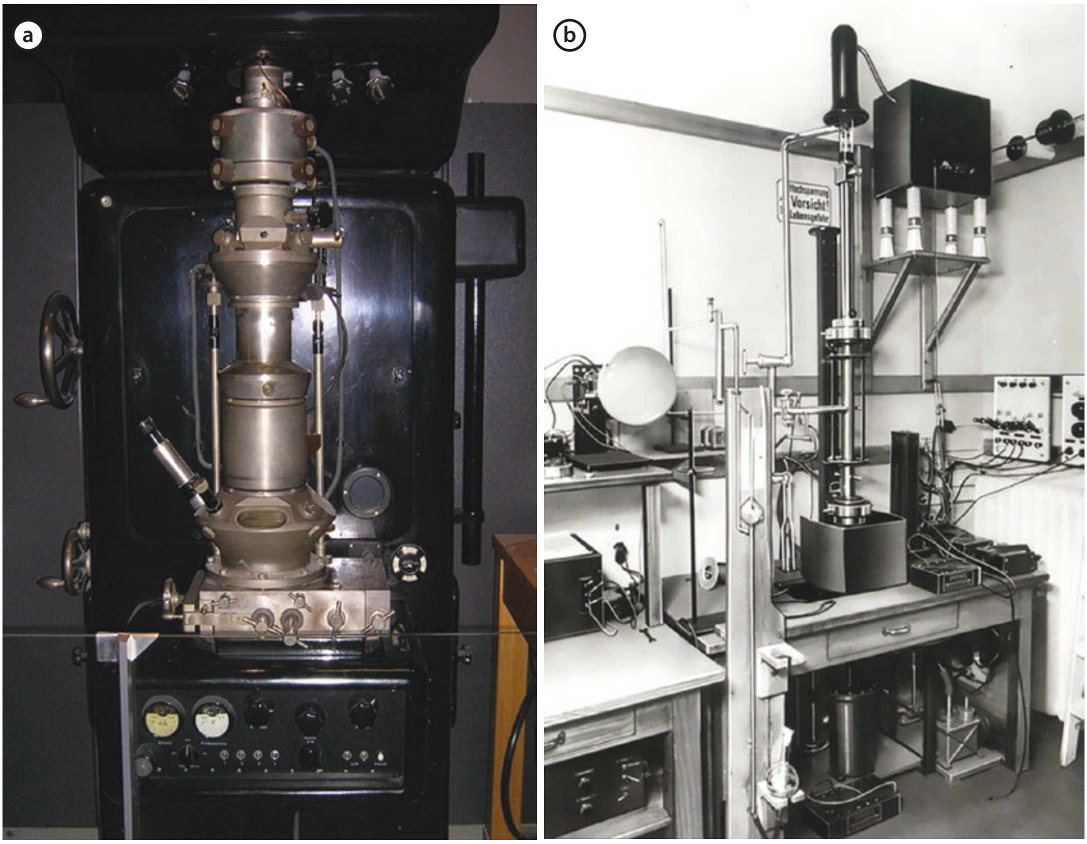


Fig. 2.10 Early electron microscopes. **a** A prototype transmission electron microscope built in 1933 by German physicist Ernst Ruska. (J Brew, CC BY-SA 3.0). **b** The first SEM capable of high-magnification imaging, built in 1937 by Manfred von Ardenne. (A von Ardenne, CC BY-SA 3.0). (Image **a** by J Brew, licensed under CC BY-SA 3.0 via Wikimedia Commons. Image **b** by Rechteinhaber: Dr. rer. nat. Alexander von Ardenne, by inheritance from his father Prof. Dr. h. c. mult. Manfred von Ardenne, C licensed under C BY-SA 3.0)

the SEM was not immediately made available to the scientific community either. In the case of the TEM, the lag was largely due to the development of suitable sample preparation techniques. SEMs were not commercially available until the mid 1960s because of the need for high quality electronics and a viable method for collecting images. Cambridge Scientific Instrument Company of Cambridge, England, sold the first SEM in 1965, the so-called Steroscan model.

A SEM scans a very narrow beam of electrons over the outside of a specimen to reveal surface detail point by point (a pattern referred to as a raster), not internal detail. The interaction of the beam with the specimen can produce reflected electrons, electrons knocked off the surface, photons, X-rays, and other signals. Different detectors pick up those signals and produce an image on a computer monitor screen that replicates the signal from each point of the raster. Notable SEM plant anatomy reference volumes include O'Brien and McCully (1969) and Lott (1976).

Compared to the maximum resolution and magnification achievable by light microscopes (about 0.2 μm and 2000×), electron microscopes can achieve theoretical resolutions of roughly 50 picometers (0.00005 μm) and magnifications of up to 10 million-fold. While

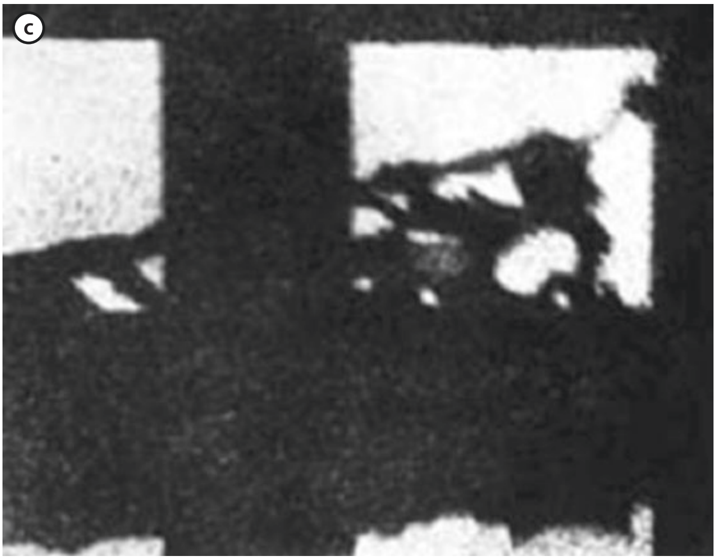
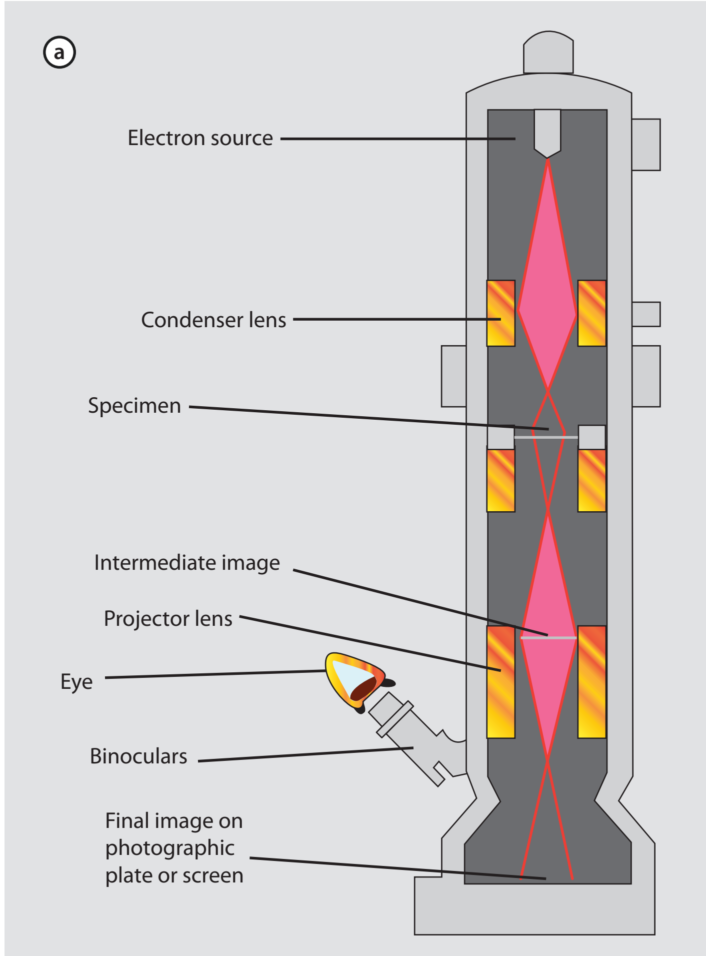


Fig. 2.10 **c** The first transmission electron micrograph of a biological specimen ever published was a hand-cut section of sundew (*Drosera intermedia*) leaf prepared by L.L. Marton 1934, in Belgium. Dark areas illustrate where the electrons could not penetrate the screen within the TEM. (Image from Marton (1934), reprinted in Süsskind (1985))

such extremes are useful for physicists and materials scientists, biological electron microscopists typically operate in the 100× to 10,000× range because biological structures, even viruses, are fairly "large" as compared to crystals and atoms.

2.11 The Transmission Electron Microscope Reveals Internal Cellular Detail

The designers of the transmission electron microscope used the same optical principles as used in light microscopy. However, electrons will not penetrate through any significant mass, including air, and therefore must be projected within a vacuum. This also means that glass lenses cannot be employed. Instead, hollow electromagnetic lenses are used in the electron microscope since electrons, being charged particles, can be refracted by circular magnetic fields in much the same way as glass lenses influence the pathway of light photons. In a transmission electron microscope, the design is similar to that of an inverted light microscope with the illumination source (an electron gun assembly) at the top of an optical column (Fig. 2.11a, b). The emitted and accelerated electrons are projected by one or two condenser lenses through a very thin specimen (remember that electrons cannot penetrate through very thick objects) and into the field of an objective lens where focusing of the electron beam takes place and projection of a real image some distance away occurs. Then, one or more projector lenses cast a final magnified image onto a sheet of film, electronic camera, or a viewing screen. When electrons strike objects, they give up their energy



■ **Fig. 2.11** **a** A diagrammatic representation of the basic function of the electron beam and the electromagnetic lenses in producing a shadow-type image on a fluorescent screen or electronic detection camera (Redrawn from Crang and Vassilyev 2003)

by generating X-rays that can be damaging to the operator. Thus, the operator must observe images through a thick leaded glass window, which also separates the vacuum of the column from the room outside of the microscope. Electrons cannot be directly visualized, so they can only be observed on a viewing screen (within the vacuum) that is coated with a phosphorescent paint that glows when excited by the energy of the electrons, on photographic film (again, within the vacuum) or, on modern instruments, with a digital image sensor (as in ■ Fig. 2.11b).

Transmission electron microscopes form images based on the selective absorption of electrons by various parts of the specimen. The specimen lies above the fluorescent screen, and hence, the electrons that make a mark on the screen are the ones able to pass through the specimen. The parts that absorb the electrons prevent their passage to the screen and thus appear dark. The parts that allow the electrons to pass through appear bright (■ Fig. 2.11c).

Fig. 2.11 **b** A modern transmission electron microscope (Hitachi HT-7700) with many refinements is shown. Although appearing quite different, it uses essentially the same optical plan as the instrument from 1933. Note the lack of a viewing port. All imaging is done digitally and displayed on the computer monitor. (Image courtesy of Roger Teppert, Hitachi High Technologies America, Inc.)

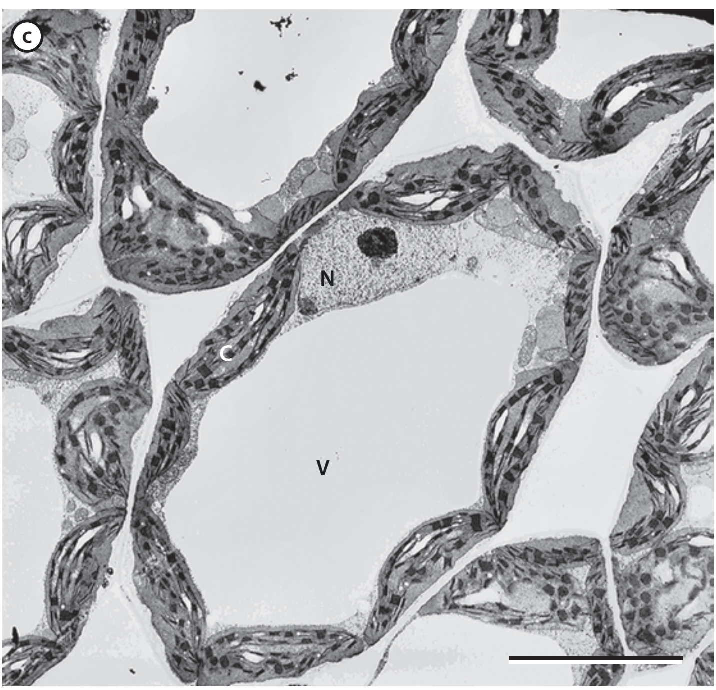


Fig. 2.11 **c** Transmission electron micrograph of a cucumber (*Cucumis sativus*) leaf cell. Note vacuole (V), nucleus (N) and chloroplasts (C). Scale bar = 20 µm (RR Wise)

2

2.12 The Scanning Electron Microscope Resolves Surface Detail

The scanning electron microscope has many features similar to the transmission electron microscope, up to a point. To a degree, it may be thought of as the "top half" of a transmission electron microscope column. In essence, the electron beam is reduced in size by one or more condenser lenses producing a very narrow beam diameter, and then it is electronically deflected in a raster pattern across a solid specimen surface in a series of lines, each of which is composed of many image points. The electron beam dwells for a very short time at each image point (e.g., a millionth of a second or less), during which time it excites outer shell electrons out of the specimen (called secondary electrons). These are low-energy electrons (typically <50 electron volts of energy), and are therefore capable of being attracted to a positively charged (usually ~ + 250 eV) detector, where they create an electrical signal that is proportional to their numbers from any given site on the specimen. The strength of this signal regulates the intensity

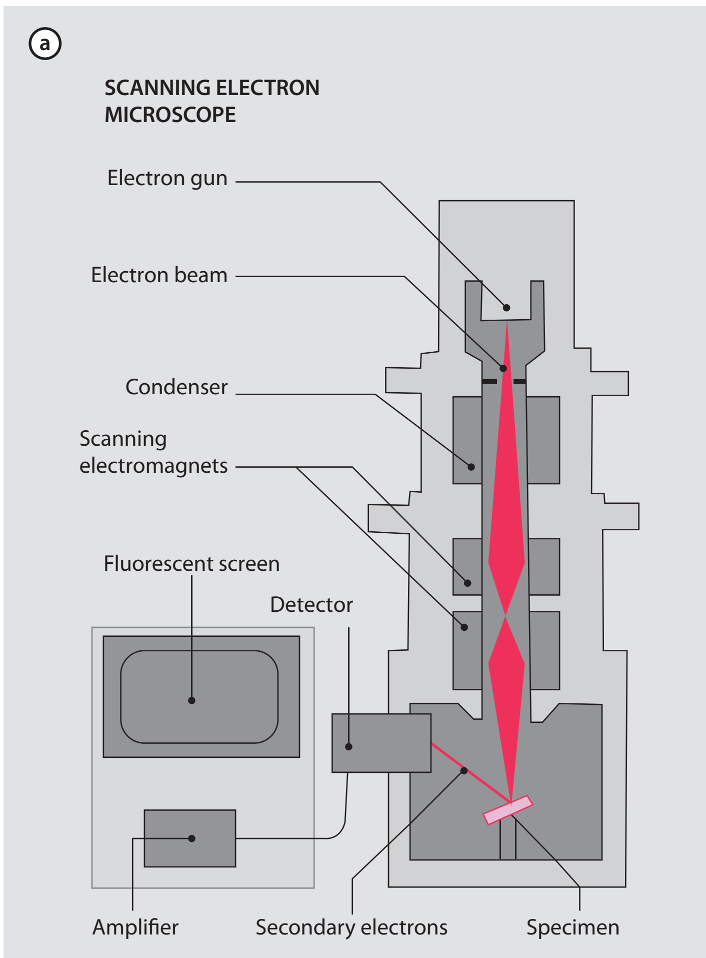


Fig. 2.12 **a** Diagram of the beam path in an SEM (Redrawn from Crang and Vassilyev 2003)

Fig. 2.12 **b** A modern scanning electron microscope with ultra-high-resolution capabilities (SU-3500). It is capable of resolving structures 0.8 nm at 15 eV beam acceleration. (Image courtesy of Roger Teppert, Hitachi High Technologies America, Inc.)

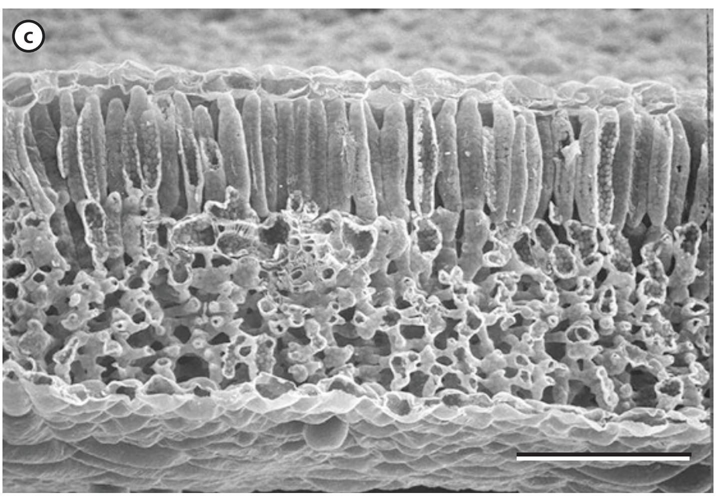


Fig. 2.12 **c** Upland cotton (*Gossypium hirsutum*) leaf in cross-section. The specimen was frozen and then fractured along a cross-sectional plane, which was then prepared for observation with the SEM. Scale bar = 100 µm (RR Wise)

(brightness) of a corresponding electron beam in a television or monitor-like screen. Thus, the number of electrons emitted from the surface of a specimen at any one point determines the intensity of the signal on the electronic viewing screen (Fig. 2.12a–c).

The electron beam of the microscope and the raster display both move in synchrony. However, the ratio of the length of the electron beam scan across the specimen, to the scan of the one across the viewing screen, determines image magnification. The smaller the sweep across the specimen, the greater the displayed magnification. Thus, this instrument is more like an image mapping system compared to the optical projection of the transmission electron microscope.

Box 2.2 An Atomic-Resolution Microscope Without Lenses

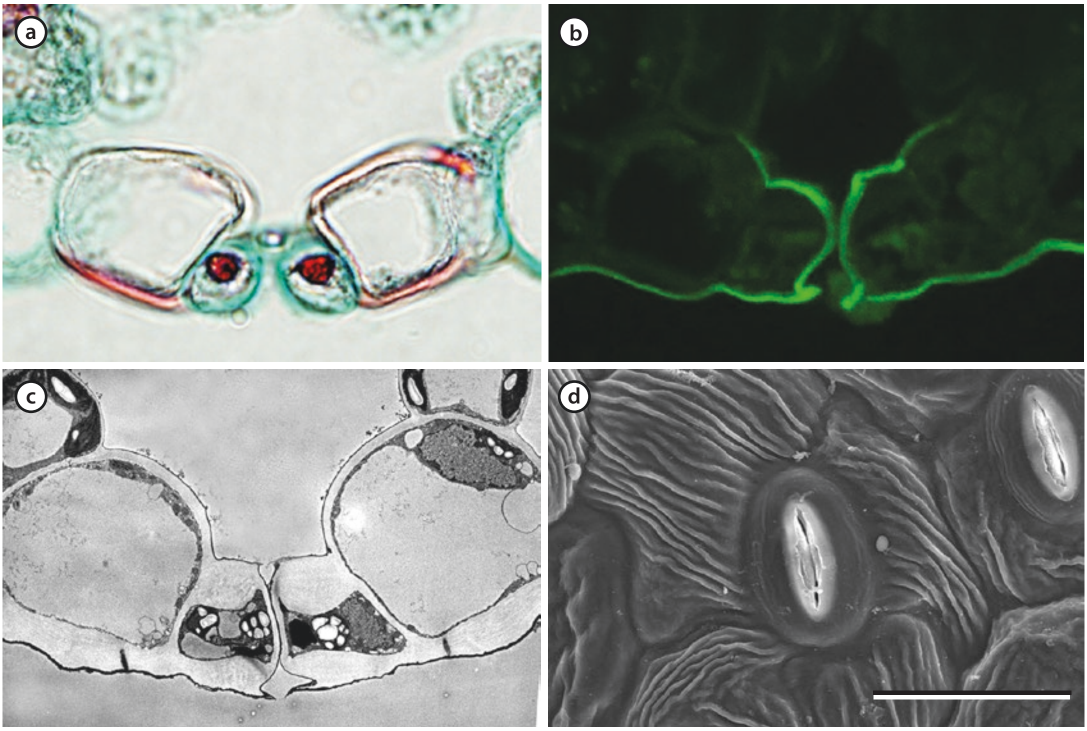
Light and electron microscopes use lenses, either glass or electromagnetic, to manipulate an illuminating beam of photons or electrons to produce the image of a specimen. Alternatively, an atomic force microscope (AFM), physically scans the surface of a specimen with a very small and highly sensitive probe capable of measuring atom-to-atom interactions. In effect, the AFM "feels" its way across the surface and generates a three-dimensional map of surface features. Resolutions of 30 nm (1×10^{-9} m) in the horizontal direction and 1 nm in the vertical direction can be achieved. The plant cuticle is a layer of lipids, largely wax, that coats the leaves and stems of terrestrial plants (refer to ► Chap. 9). By gently removing the cuticle from living plant leaves, and then using AFM to monitor the redeposition of waxes, researchers have been able to determine the timing and rate of various stages of cuticle formation. This information is useful in understanding the basic biology of cuticle formation at an extremely high "magnification."

Reference: Koch et al. (2004).

2.13 Different Microscopies Produce Different Images of the Same Specimen

Below are four images of the same specimen—stomata from cotton (*Gossypium hirsutum*). All have been adjusted to the same magnification, yet note the different kinds of visual information conveyed by each. The light micrograph (◘ Fig. 2.13a) shows a flat appearance and low resolution due to the very shallow depth of focus of the instrument. For the CLSM image (◘ Fig. 2.13b), the leaf was stained with Auramine O, which fluoresces only in the presence of lipids and waxes. It is used to highlight the layer of epicuticular wax that covers the exterior of the leaf and extends into the **substomatal cavity**. The transmission electron micrograph (◘ Fig. 2.13c) is of a section that shows internal structure of the guard cells. The scanning electron micrograph (◘ Fig. 2.13d) shows a three-dimensional like view, which quickly gives the observer a feel for the surface properties of the leaf and stomatal complex.

The transmission electron microscope, like the light microscope, projects an optical image on a viewing or recording plane from a thin specimen. On the other hand, the scanning electron microscope generates an image map of the surface of a specimen. It



■ **Fig. 2.13** Comparative micrographs of upland cotton (*Gossypium hirsutum*) stomata revealed in cross-sectional view using **a** light microscopy, **b** confocal laser scanning microscopy (stained green to reveal epicuticular wax), **c** transmission electron microscopy, and **d** in surface view using scanning electron microscopy. Scale bar in (**d**) = 20 µm and applies to all panels (**a**–**d** RR Wise)

can readily be calculated that the limit of resolution of the light microscope is approximately 0.2 µm (200 nm), that of the scanning electron microscope is approximately 1.0 nm, and that of the transmission electron microscope normally is approximately 0.1 nm. Thus, based on these resolution potentials, the highest useful magnification of the transmission electron microscope is about 500× greater than the light microscope and 10× greater than that of the scanning electron microscope.

2.14 Chapter Review

■ Concept Review

2.1 *Robert Hooke, 1635–1703, was the first to describe a cell as the basic unit of life*. Hooke was the first to describe biological materials under microscopes and discover the cell as the simplest unit of life.

2.2 *Antoni van Leeuwenhoek, 1632–1723, was the first scientist to observe microorganisms*. Van Leeuwenhoek had a deep interest in science and microscopy which lead to innovations in single-lens microscopes. He is also known for his work in describing microorganisms.

2.3 *Nehemiah Grew, 1641–1712, was the father of plant anatomy*. Grew is most noted for his pivotal work on two illustrated books focused solely on plant anatomy.

2.4 *Robert Brown, 1773–1858, discovered the nucleus of the cell*. While Brown's work is exciting for any cell biologist, his discovery of the nucleus in orchid cells earns him notoriety in the field of plant anatomy. Other notable discoveries include Brownian movement and cytoplasmic streaming.

2.5 *Katherine Esau, 1898–1997, advanced the field of plant anatomy with her influential textbooks*. Esau's work in plant anatomy is so thorough that no other books on plant anatomy have been as detailed or complete. Her life's work in plant anatomy led to many honors including the National Medal of Science.

2.6 *Light microscopy: The most useful tool of the plant anatomist*. Light microscopy provides relatively high magnification and resolution and continues to be a vital tool for the modern plant anatomist.

2.7 *The compound light microscope uses multiple lenses to form and capture images*. Compound light microscopes use two or more lenses, which allow for both variable and greater magnification of images, wider fields of view, and brighter images. It also allows the observer to work at greater distances from the specimen.

2.8 *The resolving power of a lens places limits on resolution and magnification*. The resolving power of a microscope is a function of the wavelength divided by the sum of the numerical aperture of the objective and condenser lenses.

2.9 *The confocal microscope allows for sharper detail, computer control, and 3-D imaging with a modified compound microscope*. Confocal microscopy provides greater detail in the anatomy, structure, function, and gene expression within plants using fluorescence.

2.10 *Electron microscopy allows a view into the world of cellular ultrastructure*. Using electron beams, scientists can view exceptionally small structures due to the greater resolution and magnification afforded by electron microscopy.

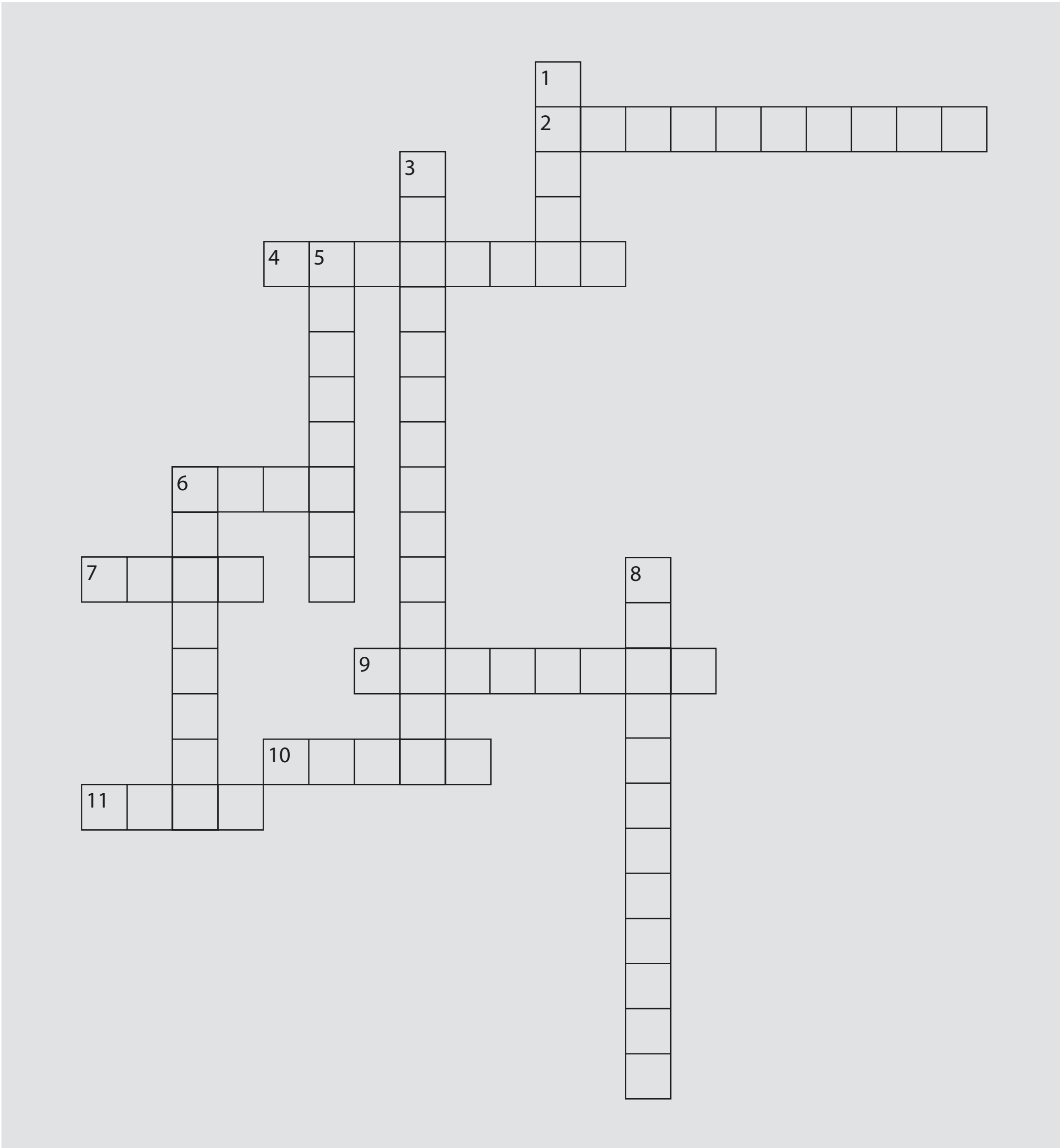
2.11 *The transmission electron microscope reveals internal cellular detail*. Electrons have a very limited ability to penetrate substances. When looking at a TEM image, the parts that are dark represent those areas where the electrons were absorbed, while the parts that allowed the passage.

2.12 *The scanning electron microscope resolves surface detail*. SEM scans electrons over the outside surface of a specimen. When internal structures are to be visualized, the specimens are frozen and fractured to allow for the surfaces of the internal components of the cell to be imaged.

2.13 *Different microscopies produce different images of the same specimen*. This chapter discusses a variety of different microscopy techniques, which are all valuable at the level of detail that they can capture from light microscopy to the exceptionally high resolution of the electron microscopes.

■ Concept Connections

1. Complete the crossword puzzle with the most appropriate term.



Across

2. When this is high, gaps between adjacent objects are small
4. Type of electron microscopy that details surfaces
6. Famous plant anatomist who began studying how viruses travel through phloem
7. Father of plant anatomy
9. Uses fluorescence to build 3-D plant structures
10. First described the cell as cellulae
11. Magnifies a specimen

Down

1. Determined that a nucleus was in a cell
3. An excellent lens maker
5. Type of light microscope that has more than a single lens
6. Type of microscopy that can provide highly magnified images using electron beams
8. Type of electron microscopy that can detail the inner details within a cell

▪ Concept Assessment

2. __________ is credited with the discovery of the cell.
   a. Robert Hooke.
   b. Robert Brown.
   c. Katherine Esau.
   d. Nehemiah Grew.
   e. Zacharias Jansen

3. Antoni van Leeuwenhoek was very important in the field of microscopy. What advances he credited with?
   a. high-quality single-lens microscopes.
   b. cytoplasmic streaming.
   c. initial descriptions of many types of microorganisms.
   d. both a and c.
   e. a, b, and c.

4. The most noteworthy plant anatomist of the twentieth century was
   a. Zacharias Jansen.
   b. Robert Hooke.
   c. Katherine Esau.
   d. Nehemiah Grew.
   e. Robert Brown.

5. One primary advantage of a lens in a camera over a pinhole is
   a. greater light-gathering power.
   b. a fixed focal length.
   c. a small numerical aperture.
   d. greater empty magnification.
   e. lower cost.

6. The physical principles of microscope resolution were first determined by
   a. Ernst Abbé.
   b. Katherine Esau.
   c. J. J. Thompson.
   d. Robert Brown.
   e. Carl Zeiss.

7. Resolution in a microscope is primarily determined by which lens?
   a. ocular.
   b. condenser.

c. objective.
d. projector.
e. intermediate.

8. The compound microscope is more powerful than a single-lens microscope because
   a. it reduces the amount of light necessary to view the specimen.
   b. it allows for a narrow field of view to enhance magnification.
   c. two lenses allow for increased magnification of the specimen.
   d. the multiple lenses allow the microscopist to work closer to the specimen.
   e. the multiple lenses have little to no effect on the brightness of the image.

9. In its optical design, the transmission electron microscope is most like a (n)
   a. scanning electron microscope.
   b. atomic force microscope.
   c. single-lens microscope.
   d. confocal microscope.
   e. compound light microscope (brightfield).

10. How does the scanning electron microscope differ from the transmission electron microscope? It
    a. uses electromagnetic lenses.
    b. operates with a vacuum.
    c. uses an electron beam.
    d. maps images rather than optically projecting them.
    e. produces monochrome images.

11. Which instrument is best used to view the structure of viruses?
    a. single-lens microscope.
    b. confocal microscope.
    c. scanning electron microscope.
    d. transmission electron microscope.
    e. compound light microscope (brightfield).

Concept Applications

12. If you want to investigate the expression of a gene in the root of an oak tree, what type of microscopy would you use? Why? Could you use this same type of microscopy in a leaf, why or why not?

13. You have been charged with understanding the leaf anatomy of a plant in the desert in contrast to a plant from a tropical rain forest. What types of microscopy would you use to investigate similarities or differences associated with the leaves?

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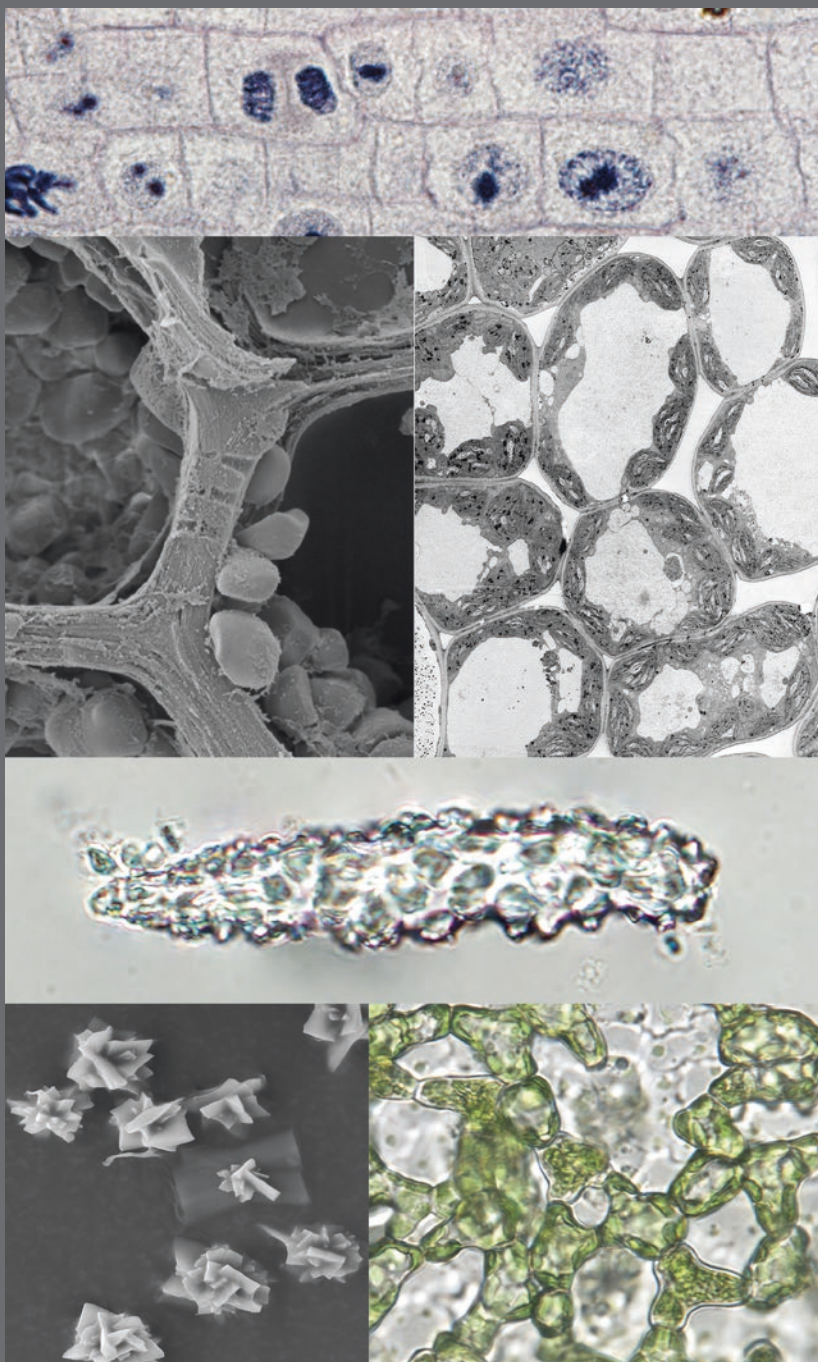
Cellular Plant Anatomy



Light micrograph of an onion (*Allium* sp.) root tip in longitudinal section. Scanning electron micrograph of several plasmodesmata in the cell walls of Katsura (*Cercidiphyllum japonicum*) stem pith. Transmission electron micrograph of a thale cress (*Arabidopsis thaliana*) leaf mesophyll cell. LM of a cystolith isolated from a Mexican petunia (*Ruellia simplex*) leaf. SEM of druse crystals in American basswood (*Tilia americana*) wood. LM of European hornbeam (*Carpinus betulus*) leaf mesophyll cells. (All images by RR Wise.)

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Plant Cell Structure and Ultrastructure

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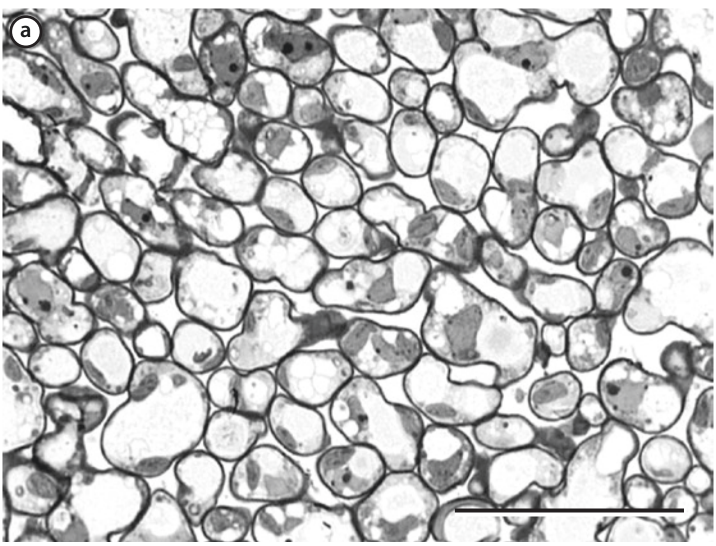
Introduction

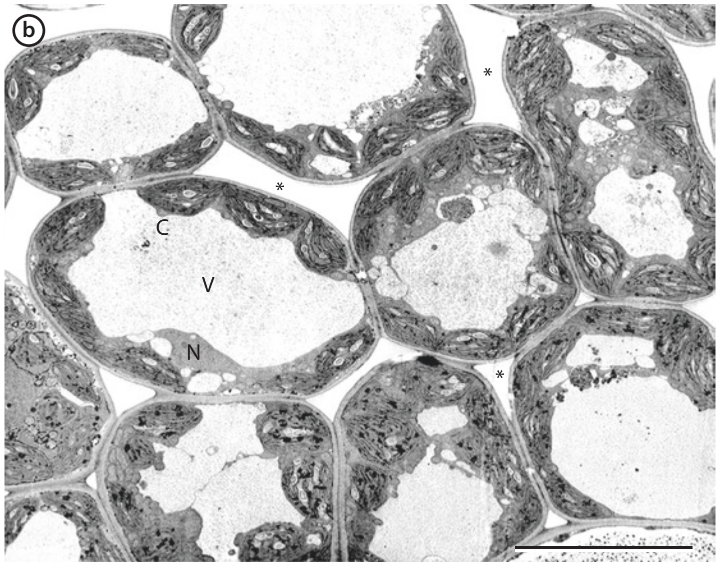
Plants typically contain millions of cells and a wide variety of cell types (cells are discussed in ► Chap. 6: Parenchyma, Collenchyma, and Sclerenchyma). Plant cells are composed of cell walls (► Chap. 5), a cytoplasm, and vacuoles, which are primarily water sacs that contain storage and waste products of metabolism and which provide turgor pressure for the cell. While the vacuole physically takes up the most space in the cell, the cell contains many **organelles** within the protoplasm that are pushed up against the cell wall. Protoplasmic organization includes nuclear structure and the cytoplasmic contents of the cell. The most basic to the organization of cells are membranes which represent the limiting boundary of the living components, being organized into various unique functional bodies called organelles. Such organelles are usually thought of as membrane-bound bodies that have a specific function and identifiable structural organization. The exceptions are certain elements of the cytoskeleton, which are considered to be organelles but are not limited by a membrane.

3.1 Plant Cells Are Complex Structures

With the development of the transmission electron microscope in the mid-twentieth century, plant biologists were able to visualize for the first time the organization of cells at a level much finer than that seen with the light microscope (◘ Fig. 3.1a, b). Hence, the terms *ultrastructure* and *fine structure* came about in reference to



◘ **Fig. 3.1** **a** Light microscopy (LM) showing a **paradermal** section (i.e., cut parallel with the surface) of a leaf from the lyre-leaved sand cress (*Arabidopsis lyrata*). Scale bar = 50 µm (RR Wise)



■ **Fig. 3.1** **b** TEM of several leaf cells from *Arabidopsis thaliana*. Each cell contains a large central vacuole (V), nucleus (N), and numerous chloroplasts (C). Note the intercellular air spaces (*). Other organelles are too small to be seen at this magnification. Scale bar = 10 µm (RR Wise)

the detailed cellular structure shown with the electron microscope. The information learned from the use of the electron microscope in plant anatomy has revealed that cells are primarily composed of membrane-bound organelles associated with specific functions. Here, we consider the major structural entities and their functions. In recent years, a variety of techniques have been developed which enable investigators to identify elemental composition, localize functional (usually enzyme) activities, and quantify cellular structure. These techniques extend our observations beyond merely descriptive ones.

3.2 Plant Cells Synthesize an External Wall and Contain a Variety of Internal Compartments

Plant cells vary greatly in the numbers and types of organelles they contain. That is why textbooks usually show a drawing and not a micrograph of a "typical plant cell"—there is no such thing in real life. ■ Figure 3.2 is, therefore, a "convenient fiction" showing all the organelles neatly arranged in a prototypical plant parenchyma cell. The four basic components are (from the outside in) cell wall (a primary wall in this case), plasma membrane, cytoplasm (which contains many and varied organelles), and vacuole.

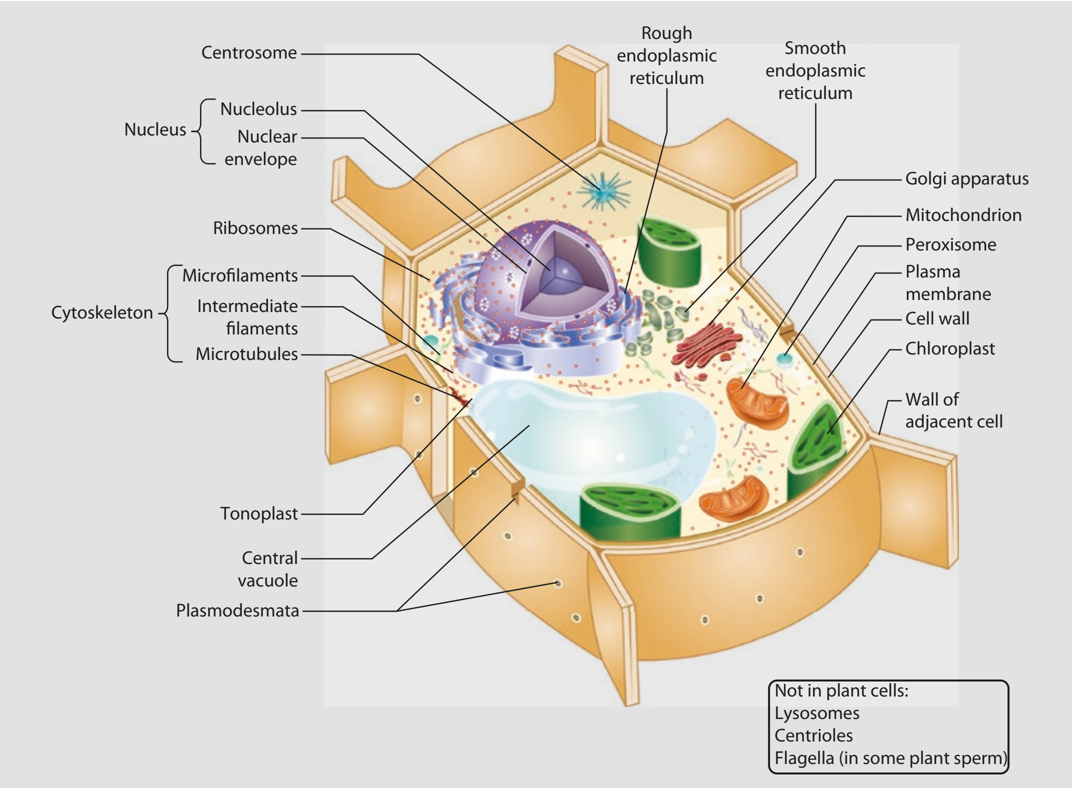


Fig. 3.2 Basic components of a plant cell. The individual organelles are discussed throughout this chapter (Redrawn from Wikipedia)

3.3 Cells and Cell Organelles Are Typically Bound by Lipid Bilayer Membranes

The biological **membrane** is a ubiquitous and remarkable boundary of all living cells and most cell organelles. All membranes share a common structure and function (Fig. 3.3a, b), although the individual components and the precise roles played by membranes can vary greatly. The cell membrane (a.k.a. **plasma membrane**) will be discussed in this section. Membranes of organelles such as those in the chloroplast, nucleus, or Golgi apparatus share many of the same basic characteristics.

Observed with very high-resolution transmission electron microscopy, membranes often appear as two tracks or dense lines when observed in a distinct cross-sectional plane (Fig. 3.3a). That phenomenon occurs because of the deposition of osmium and associated stains (all contain heavy metals that do not transmit the electron beam of the microscope). The density appears to take place primarily towards each side of the membrane, leaving a somewhat translucent region in the center where the hydrophobic “tails” of lipids are in contact from the two layers. Some investigators have designated this type of pattern as a “unit membrane” image.

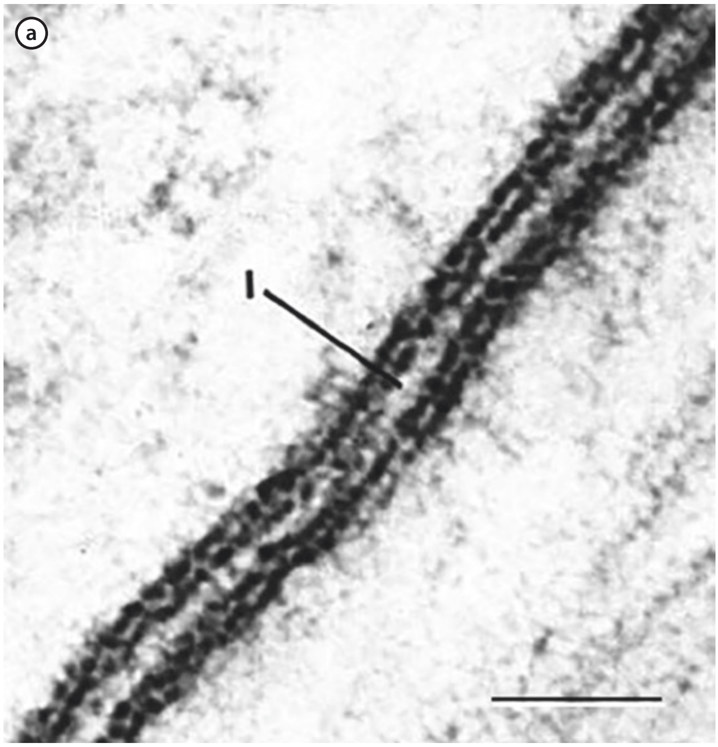


Fig. 3.3 **a** Unit membrane structure of **nuclear envelope** observed with very high-resolution transmission electron microscopy. Two unit membranes are found closely opposed to each other, with an intervening space (I), which is similar to the nuclear envelope or outer double membrane of chloroplasts. The magnification of this micrograph is close to 350,000×, and the thickness of each membrane is approximately 10 nm (i.e., 100 Å). Scale bar = 50 nm. (Image from Macleod (1973) Cytology: The Cell and Its Nucleus, The Upjohn Co, with permission)

Biological membranes are called a "fluid mosaic lipid bilayer." The latter term, "lipid bilayer," obviously means that the membrane is composed of two layers of lipids (Fig. 3.3b). The individual lipid molecules are amphipathic, meaning they have a hydrophilic head group and (usually two) hydrophobic tails. In the bilayer structure, the hydrophilic head groups are oriented towards the outsides of the membrane, exposed to the aqueous milieu on either side of the membrane, while the hydrophobic tails face each other in the membrane's interior. Individual lipid molecules are free to rotate or diffuse sideways within the plane of the membrane, hence the modifier "fluid." Phospholipids are a common membrane lipid, although many other molecular species contribute to the diversity of membrane structure and function across the plant and animal kingdoms. Cholesterol, when present, helps maintain membrane structure and fluidity. Cholesterol is common in animal membranes but relatively scarce in plant membranes. Membranes may also contain other lipids such as chlorophyll, carotenoids, and the lipid-soluble, redox-active quinones of the chloroplast and mitochondrion (plastoquinone and ubiquinone).

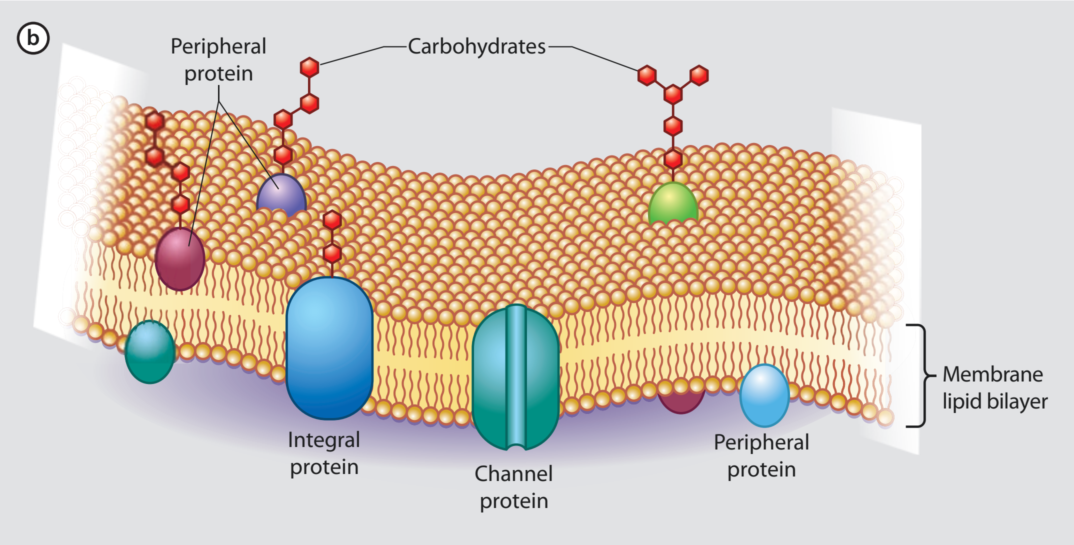


Fig. 3.3 **b** Basic components of a plant cell membrane. The amphipathic lipids face each other creating two hydrophilic surfaces and a hydrophobic interior. Different proteins may be on the surface of, or embedded within, the membrane (Redrawn from Crang and Vassilyev 2003)

The term "mosaic" refers to the fact that membranes are a mixture of lipids and proteins occurring in varying proportions, depending on the role that the membrane plays in the plant cell. Proteins can make up a significant portion of the membrane and play key roles in membrane functions. In fact, the energy-transducing membranes in chloroplasts and mitochondria are approximately 85% protein by weight and only 15% lipid. Proteins may be associated with the surface of the membrane (peripheral proteins) or embedded within and even span the membrane from one side to the other (integral protein). Many membrane proteins are free to diffuse throughout the membrane (like lipids), while others, particularly proteins in the limiting cell membrane, are anchored to cytoskeletal elements lying close to the cytoplasmic (inside) surface of the cell. The cellulose-synthesizing protein complex is actually dragged through the plane of the membrane by the cytoplasmic cytoskeleton during cell wall synthesis (► Chap. 5). Short chains of carbohydrates may be covalently attached to proteins (glycoproteins) or lipids (glycolipids) and facing the outer surface of the plasma lemma. By facing the exterior, the sugars, their number and subunit structure, carry important information for neighboring cells.

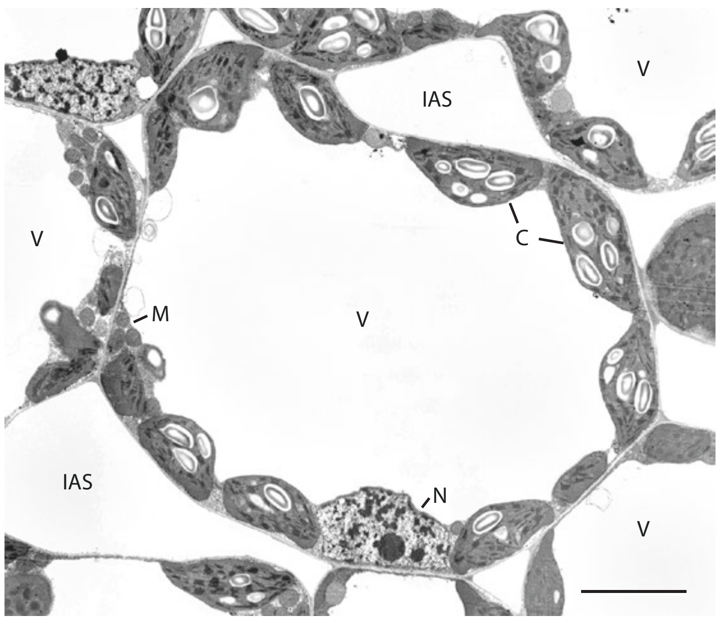
Biological membranes are selectively permeable, implying that some substances cross the membrane more easily and rapidly than others. Membranes can fuse one with another, and they also can grow by adding new molecules. They can form bubble-like **vesicles**, which segregate certain products that are moved to different sites in the cytoplasm.

Membranes play many important roles. First, and foremost, they create a boundary between the inside and outside of a cell or organelle, which allows for the compartmentalization of metabolism. Catabolic processes can take place in the mitochondrion, while anabolism may simultaneously proceed in the chloroplast or endoplasmic reticulum. Second, membranes, specifically the membrane proteins, control the transport of water, ions, and molecules into and out of the cell or organelle. Third, because membranes are basically two-dimensional, the proteins involved in metabolic or electron transport pathways can be arranged side-by-side, thus allowing metabolites or electrons to be passed directly from one protein molecule to the next.

3.4 Vacuoles Play a Role in Water and Ion Balance

A large central **vacuole** as seen in ◘ Fig. 3.4 is a key characteristic of almost every mature plant cell. Once thought of as merely empty space fillers ("vac" is Latin root for "empty"), vacuoles are now seen as fully functional cellular organelles that play crucial roles in cell homeostasis, water balance, metabolite, ion and pigment storage, and detoxification and lysis of unwanted compounds.

The vacuole is bounded by a single membrane called the **tonoplast**, which at 10 nm (0.01 µm) in thickness is too thin to be visible in ◘ Fig. 3.4. The tonoplast contains **transport proteins** that control the movement of water and molecules into and out of the vacuole, which is critical to controlling the movement of water throughout the plant and the maintenance of turgor (refer to ► Sect. 1.2). Water-soluble pigments such as anthocyanins accumulate in vacuoles in epidermal cells and impart the purple, red, and blue colors



◘ **Fig. 3.4** TEM of a **mesophyll** cell from a pea (*Pisum sativum*) leaf with a large central vacuole (V) and a thin rim of cytoplasm. Organelles such as a nucleus (N, with nucleolus), chloroplasts (C), and mitochondria (M) occupy the majority of the cytoplasm volume. Intercellular air spaces (IAS) are situated between the cells. Scale bar = 10 µm (RR Wise) of many flower petals and leaves, whereas seed vacuoles are adapted for protein storage. Vacuoles are also sometimes used to store the end products of catabolism.

3.5 Plastids Are a Diverse Family of Anabolic Organelles

Chloroplasts are photosynthetic organelles found in plant cells. Indeed, the very definition of what it means to be a plant is largely predicated on their photoautotrophic abilities, which reside exclusively in the chloroplast. However, chloroplasts are only one member of the **plastid** family, a large, closely related and diverse group of organelles (Kirk and Tilney-Bassett 1967). Depending on the breadth of the definition, there are as many as 20 distinctly different types of plastids found in both plants and (in a few surprising cases) animals (Wise 2006, Table 3.1).

Plastids are sometimes categorized based on their color. In such a scheme, the nonpigmented plastids such as proplastids, etioplasts, amyloplasts, and elaioplasts are called leucoplasts. Red and orange plastids (chromoplasts and gerontoplasts) are grouped together as chromoplasts. Green plastids (C_3, dimorphic C_4, and guard cell) are

Table 3.1 Summary of plastid forms and functions

Plastid type	Function(s)	Distinctive features
Proplastid	Source of other plastids	Found in egg, meristematic and embryonic cells; source of all other plastids in the plant
Etioplast	Transitionary stage	Develops in dark-grown tissue; site of gibberellin synthesis; converts to chloroplast in light
Amyloplast	Starch synthesis and storage	Also functions in gravisensing
Elaioplast	Oil synthesis and storage	Supplies lipids and oils to exine upon pollen grain maturation
Chromoplast	Fruit and flower coloration	Rich in carotenoids; used to attract pollinators and seed/fruit-dispersing animals
Gerontoplast	Catabolism	Controls the dismantling of the photosynthetic apparatus during senescence
Chloroplasts		
C_3	Photosynthesis, etc.	Also functions in fatty acid, lipid, amino acid and protein synthesis, N and S assimilation
C_4	Photosynthesis, etc.	**Dimorphic chloroplasts** provide a CO_2-rich, O_2-poor environment for enhanced Rubisco activity (enzyme for early carbon fixation)
Sun/shade	Photosynthesis, etc.	Dimorphic forms develop under different light conditions in order to optimize photosynthesis
Guard cell	Stomatal functioning	Senses light and CO_2; signals and metabolically drives opening and closing of stomata

called chloroplasts. Because this system merely focuses on common color, and not distinct structure or function, it is not relied upon in this text.

Substantial evidence exists to support an **endosymbiotic** origin for plastids, with the original endosymbiont being a photosynthetic cyanobacterium. Two processes took place during the ensuing 1.6 billion years of evolution: (1) approximately 90% of the plastid genome was transferred to the nucleus and (2) the proto-chloroplast radiated and evolved into the other plastid types. Thus, all plastids share the same basic characters of a double-membrane envelope; a separate and third internal membrane system of greater (chromoplast, chloroplast) or lesser (proplastid, amyloplast) complexity; a complete prokaryotic-like genetic machinery consisting of organellar DNA, transcription factors, and ribosomes (► Sect. 3.9); and division by fission (again, very prokaryotic-like). Unlike mitochondria, which were also derived endosymbiotically, plastids did not surrender the anabolic abilities of their free-living ancestors. In fact, the power to manufacture all the biomolecules needed for complete growth and development has enabled plants to use plastids as the central organelle for anabolism, catabolism, energy regulation, and environmental sensing. The seven main plastid types found in green plants are described as follows.

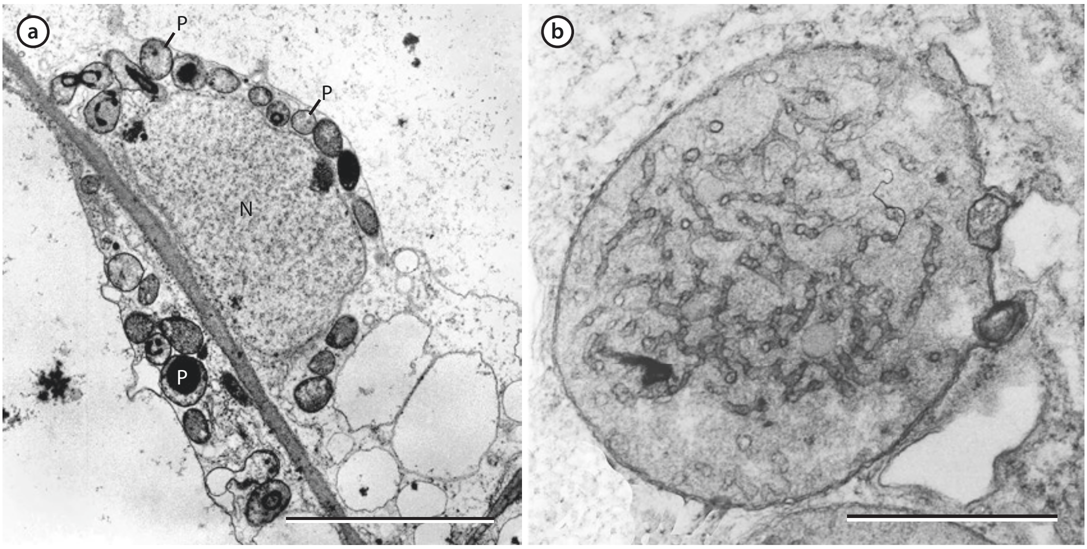
3.5.1 Proplastid

Plants begin with an egg cell, and the egg cell is the primary source of organelles for the zygote that eventually leads to an adult plant (► Chap. 18). Egg cell plastids, of which there may be 50–100 per egg, are called "**proplastids**" and are the progenitors of all the other plastids (regardless of type) found in the mature plant. Subsequent mitosis and the generation of new tissues in plants take place in meristems (► Chap. 4), and meristematic plant cells also contain proplastids. Most plants continue to grow throughout their entire life to support shoot and root expansion. Therefore, they may have hundreds to thousands of meristems at any given time and thus a large population of proplastids.

Unlike the other plastid types, proplastids as a group are defined by their appearance and location, and not by any specific metabolic function. Characteristically, they are small, relatively non-differentiated with few internal membranes and only found in young, undifferentiated cells (◘ Fig. 3.5a, b).

3.5.2 Etioplast

Etioplasts develop in complete darkness in shoot tissue and are a transitional stage between the proplastid and the chloroplast during the process of greening (◘ Fig. 3.5c, d). The reverse process—degreening (chloroplast to etioplast)—is also possible as evidenced by the pale color that results under any light barrier laid on a green lawn (board, tarp, garden hose, etc.). In this process, the green grass undergoes chlorosis (the controlled, enzymatic loss



■ **Fig. 3.5** **a** Proplastids (P) surrounding the nucleus (N) in a cell from a mangrove (*Rhizophora mangle*) embryo. Scale bar = 10 µm (RR Wise). **b** A single proplastid from sweet potato (*Ipomea batatas*) root tip. Scale bar = 0.5 µm (**a**, **b** RR Wise)

of chlorophyll) and becomes pale green upon the imposition of darkness. Removing the obstruction allows the greening process to resume. Thus, the etioplast-to-chloroplast-to-etioplast transition is quite dynamic and under strict genetic control in response to environmental conditions.

Etioplast ultrastructure is dominated by the prolamellar body (PLB), a large, ordered lattice of membranes (■ Fig. 3.5e). While the exact function of the PLB remains obscure, it probably represents a "holding pattern" for the large amount of membrane and protein that will ultimately be utilized in formation of the thylakoid system (see chloroplast below). Interestingly, etioplasts only form in dark-grown cells of the leaves and stems, tissues that under normal conditions will eventually be exposed to light. They never form in roots or tissues that are insensitive to light. The plant growth regulator **gibberellic acid** (GA) is synthesized in the etioplast. Because GA helps direct many early developmental processes, such as those in an expanding and greening leaf, the etioplast probably contributes directly to the light-to-dark transition.

3.5.3 Elaioplast

Lipid synthesis in animal cells is localized to the smooth endoplasmic reticulum (refer to ► Sect. 3.9). However, SER is rarely seen in plant cells because most plant lipids are made in the proplastid, chloroplast, or elaioplast. **Elaioplasts** (■ Fig. 3.5f) are plastids that specialize in oil synthesis and storage and are found primarily in the layer of cells in the anther that surrounds developing pollen grains (called the tapetum or tapetal layer; refer to ► Chap. 17). After meiosis and just prior to pollen release, the tapetal layer degrades and releases the elaioplasts, which contribute their oils to the exine, the outermost, waterproof pollen wall (■ Fig. 3.5g).

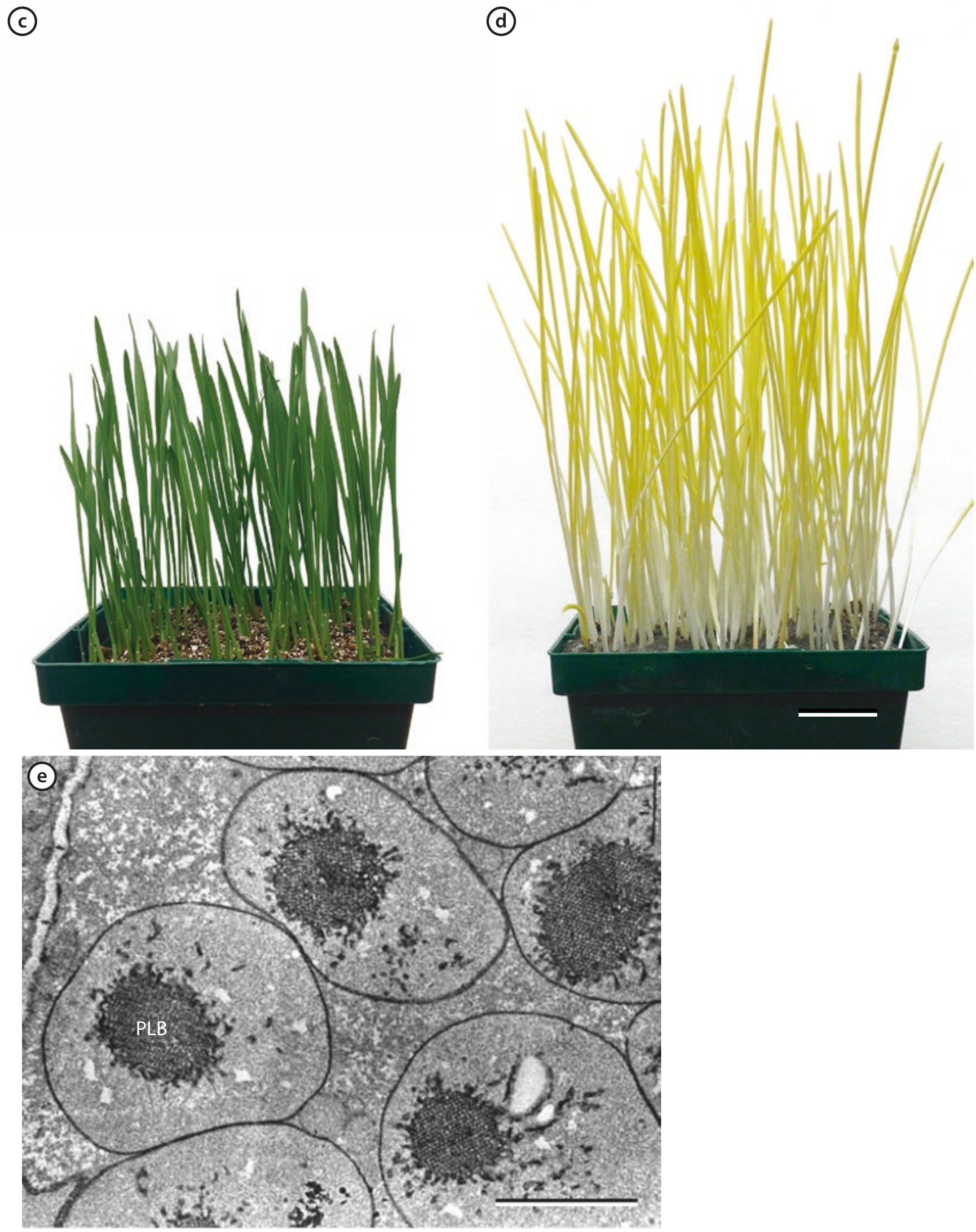


Fig. 3.5 **c**–**e** Wheat (*Triticum aestivum*) seedlings grown either in the light **c** or dark **d**. Note how etiolated growth (*right*) results in pale, long, weak plants. Scale bar = 2 cm (RR Wise). **e** TEM of four etioplasts from the dark-grown plants similar to those seen in **d**. Note large prolamellar bodies (PLB) inside each etioplast. Scale bar = 0.5 μm (**c**, **d** RR Wise, **e** Crang and Vassilyev 2003)

3.5.4 Amyloplast

Starch is a macropolymer of several thousand repeating glucose units. All starch synthesis occurs inside a plastid, and large starch granules can be found in proplastids, chloroplasts, and amyloplasts.

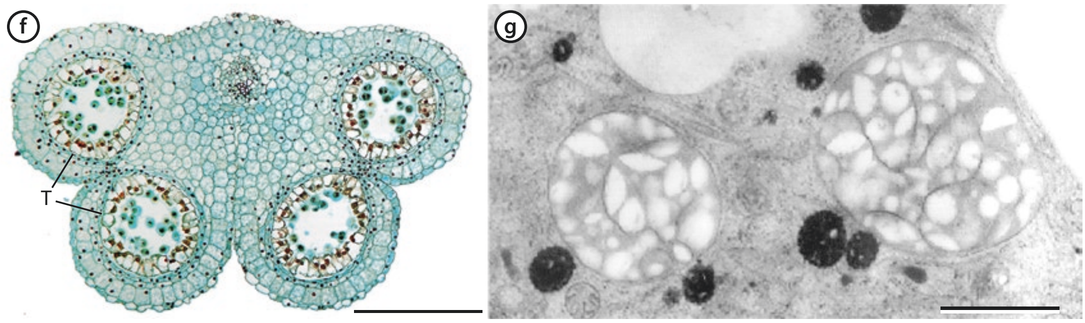


Fig. 3.5 **f** LM of lily (*Lilium* sp.) anther in cross-section. The tapetum (T) lines the cavity (loculus) in which the pollen grains develop. Cells of the tapetum contain dense bodies of oil-rich elaioplasts. Scale bar = 0.5 mm (RR Wise). **g** TEM of two elaioplasts in *Arabidopsis thaliana* anther, showing light oil inclusions. Scale bar = 1 µm. (Image courtesy of Dr. Denis Murphy, University of South Wales)

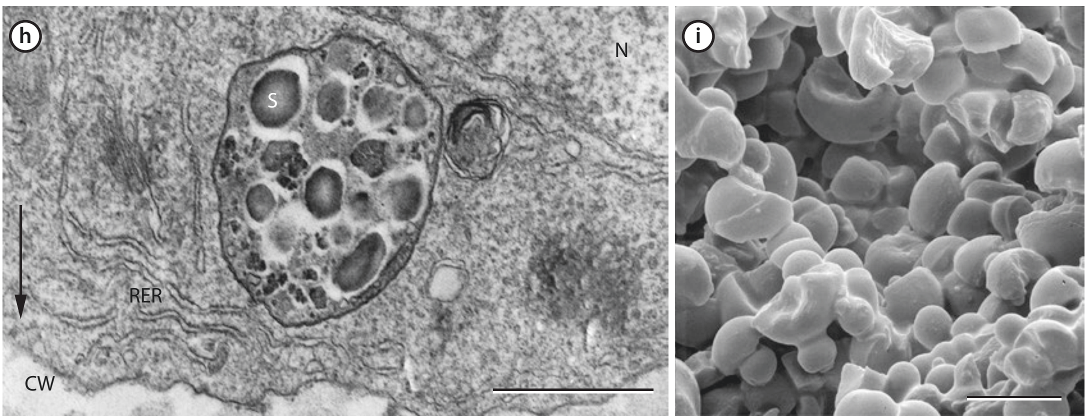


Fig. 3.5 **h** TEM of an amyloplast from root tip (columella) of mung bean (*Vicia faba*). Note starch granules (S) in the amyloplast, nucleus (N), rough endoplasmic reticulum (RER), and cell wall (CW). The direction of the gravitational field is indicated by the arrow. Scale bar = 1 µm (Image courtesy of Dr. Denis Murphy, University of South Wales). **i** SEM of storage starch granules isolated from pea (*Pisum sativum*) amyloplasts. These starch grains are considerably larger than those shown in Fig. 3.5h. Scale bar = 5 µm (**h, i** RR Wise)

Chloroplasts make short-term transitory starch with the entire pool being synthesized during the day and degraded and exported at night. Proplastids and, in particular, amyloplasts make long-term storage starch that may persist for weeks, months, or even years.

While most plastid types can contain starch, **amyloplasts** are unique because of the copious amounts of starch they synthesize in the form of large grains (Fig. 3.5h, i). In another example of plastid versatility, amyloplasts play two uniquely different roles. The function of amyloplasts in starch storage has already been noted. A second, separate function is in **gravisensing** (a positive response to the force of gravity). Starch is heavy, and starch-filled amyloplasts settle toward the pull of gravity on a minute time scale, even within plant cells. Amyloplasts in special tissues in the stem (the endodermis—refer to ► Sects. 10.4 and 11.5) and the root (the columella— ► Sect. 10.4) perform a mechanical, not a metabolic, function as they sink to the bottom of the cell, contact the **rough endoplasmic reticulum** (RER), and signal an upper/lower cell polarity that initiates a gravitropic growth response through a plant growth regulator **indoleacetic acid** (IAA). Shoots therefore exhibit negative gravitropism and grow away from the signal, or up, while roots exhibit positive gravitropism and grow towards the signal, or down.

3.5.5 Chromoplast

Chromoplasts (◘ Fig. 3.5j) contribute the bright red, orange, and yellow colors to many fruits that serve to attract and conscript animals to act as seed dispersers. They originate as chloroplasts, and the chloroplast-to-chromoplast transition (refer to ◘ Fig. 3.6) is tightly coordinated with the complex process of leaf and fruit ripening. In developing tobacco (*Nicotiana tabacum*) nectaries, an amyloplast-to-chromoplast transition is the source of the carbohydrate used for nectar production (Horner et al. 2007).

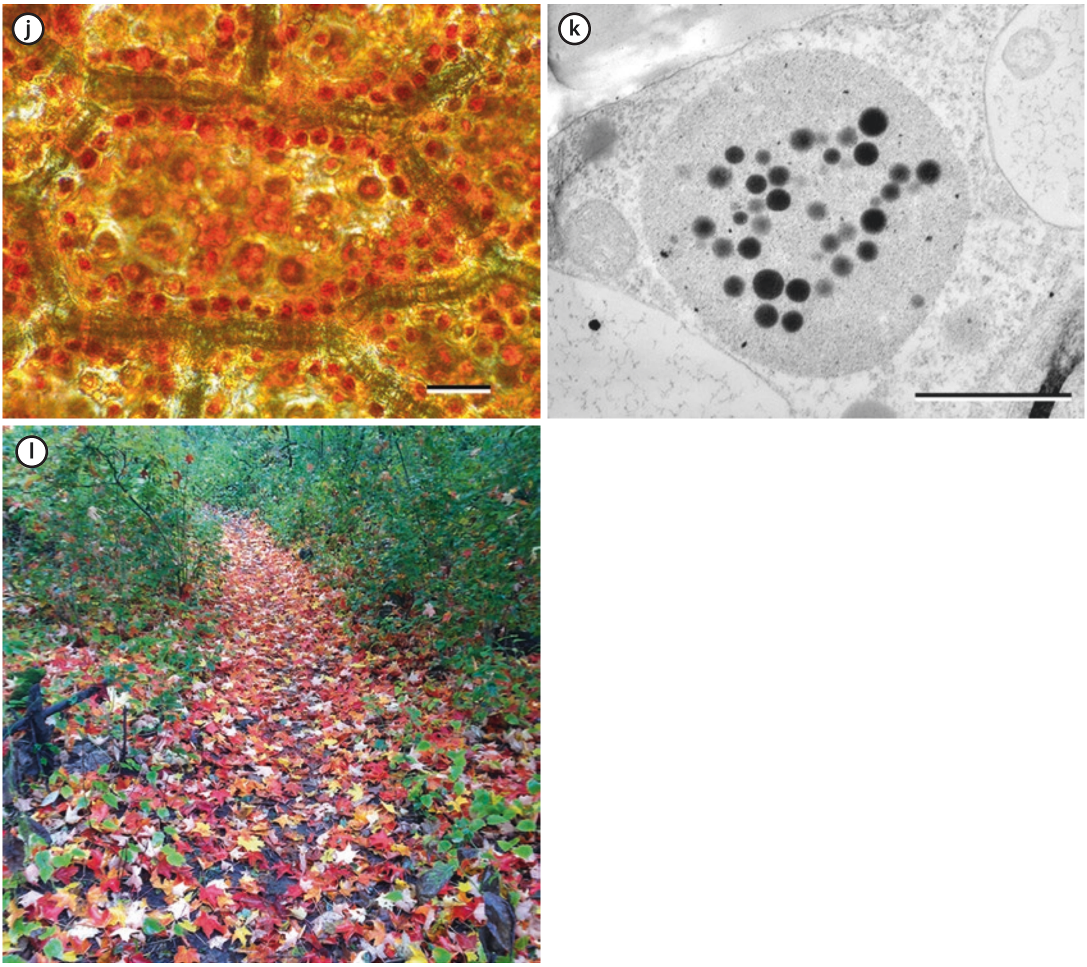
The colors of chromoplasts come from large accumulations of carotenoid pigments of which there are two types: β-carotenes (carbon and hydrogen only) and xanthophylls (C, H plus oxygen). In addition to functioning as animal visual attractants, the carotenoids are also precursors for vitamin A biosynthesis in animals, thus rewarding seed dispersers with an essential nutrient. During the chloroplast-to-chromoplast transition, the chlorophyll-containing thylakoid membranes of the chloroplast are degraded and replaced with outsized pigment-protein droplets called **plastoglobuli** (◘ Fig. 3.5k). The protein, fibrillin, which has many other functions in plant cells, helps maintain plastoglobus structure.

3.5.6 Gerontoplast

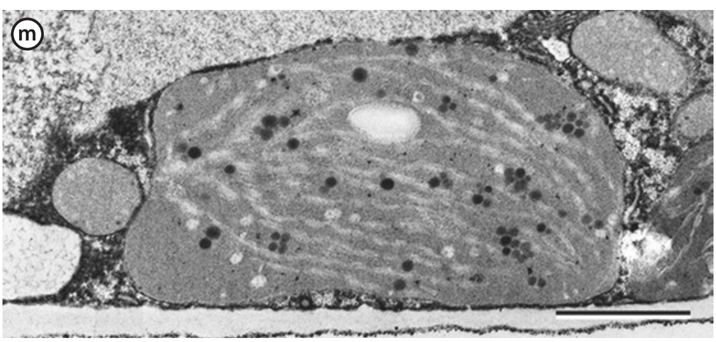
Leaf cells each may have up to a hundred individual chloroplasts, and each chloroplast is rich in the proteins needed for photosynthesis. **Autumnal senescence** ("fall colors") is a genetically programmed, step-by-step dismantling of the chloroplast with the sole purpose of recovering that leaf protein (◘ Fig. 3.5l). Cell walls and chloroplast lipids, including the lipid chlorophyll, are not recovered and remain in the leaves that are eventually shed. As senescence proceeds, thylakoid membranes are degraded, lipids and pigments form large droplets, and the chloroplast is slowly converted to a **gerontoplast** (◘ Fig. 3.5m). Gerontoplasts have few internal membranes and many plastoglobuli—lipid accumulations that represent the catabolic end product of resource recovery.

3.5.7 Chloroplast

These common chlorophyll-containing organelles are found in leaves and stems of eukaryotic plants and in algae. They utilize carbon dioxide and water in the presence of sunlight to initially produce simple sugars that build up food for the plant.



▪ **Fig. 3.5** **j** Cells of a red bell pepper (*Capsicum annuum*) fruit containing many chromoplasts. **k** A single chromoplast from tomato (*Solanum lycopersicum*) fruit containing numerous dark, carotenoid-containing plastoglobuli. Scale bars = 10 µm in **j** and 1 µm in **k**. **l** Maple leaves at the final stage of autumnal senescence (**j**–**l** RR Wise)



▪ **Fig. 3.5** **m** TEM of a gerontoplast from a senescing leaf of hydrangea (*Hydrangea* sp.). Note the numerous, small dark plastoglobuli (refer to ► Sect. 3.5.5), which result from the breakdown of the photosynthetic membranes. Scale bar = 1 µm (RR Wise)

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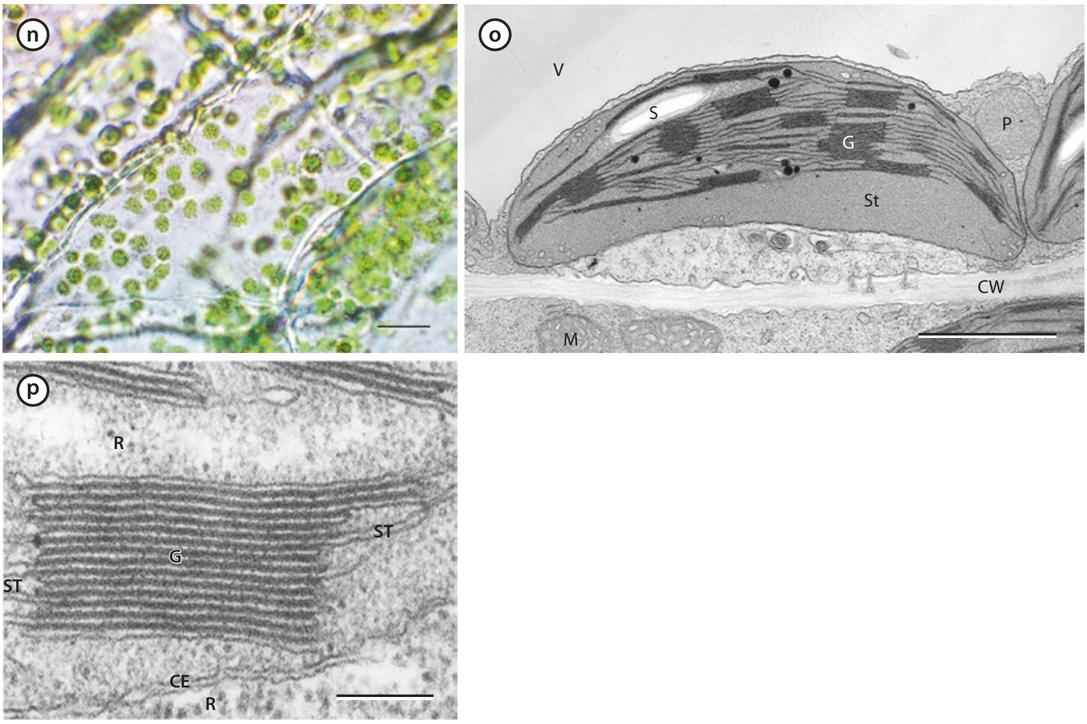

◘ **Fig. 3.5** **n** LM of chloroplasts from the outer layer of a green bell pepper (*Capsicum annuum*) fruit. The dark specks inside the chloroplasts are grana. Scale bar = 10 µm (RR Wise). **o** TEM of spinach (*Spinacia oleracea*) chloroplast situated between the vacuole (V) and cell wall (CW). Internally, chloroplasts have stacks of granal thylakoid (G) and starch grains (S) suspended in the stroma (St). Scale bar = 3 µm (RR Wise). **p** This single granum (G) from a spinach (*Spinacia oleracea*) chloroplast is composed of 15 thylakoid membranes stacked (appressed) on top of each other. Stromal thylakoids (ST) are unstacked (unappressed) and extend from the edges of the granum. Note the two membranes of the chloroplast envelope (CE) and ribosomes (R). Cytoplasm, also with many ribosomes (R), is to the bottom of the image. Scale bar = 0.5 µm (**n**–**p** RR Wise)

The typical **C_3 chloroplast** is a round, plano-convex organelle approximately 5 to 10 µm in length (◘ Fig. 3.5n; see below for definition of the C_3 photosynthetic pathway). They have a double-membrane envelope and a third, internal system of membranes, **thylakoids**, that is suspended in a protein-rich fluid, the stroma (◘ Fig. 3.5o). In a functional chloroplast, thylakoids form a closed, flattened volume, with the stroma to the outside and the lumen to the inside. Two categories of thylakoids are recognized: (1) Granal thylakoids are pressed together in stacks called grana in which an individual granum may contain 2–30 or more thylakoids. (2) Intergranal thylakoids (a.k.a. stromal thylakoids) are unappressed and span the stroma to interconnect grana (◘ Fig. 3.5p).

3.5.8 Chloroplast Functions

Because chloroplasts have a constant supply of reduced carbon, NADPH, and ATP and originated from free-living prokaryotic endosymbionts, they have evolved over time to be capable of performing a large array of anabolic functions in a plant cell. Some of those functions are given here.

Chloroplasts use photosynthesis to manufacture low-molecular-weight, reduced carbon compounds, commonly called sugars. In brief, photosynthesis can be divided into two distinct sets of reactions:

1. The light-dependent reactions harvest light energy and use that energy to transport electrons through an electron transport chain embedded in the thylakoid membrane. Chlorophyll is the primary photosynthetic pigment; hence, thylakoid membranes are deep green in color. The light-dependent reactions synthesize ATP and the reductant NADPH.
2. The light-independent reactions subsequently use that NADPH and ATP to reduce and phosphorylate oxidized atmospheric carbon to the level of a sugar phosphate. The light-independent reaction occurs in the liquid stroma of the chloroplast and converts CO_2 and other compounds to glucose.

Nitrogen and sulfur are two of the 20 essential elements plants need for growth and development. Both are rather scarce in the environment, at least in bioavailable forms. While different pathways are responsible for the uptake of nitrogen and sulfur (and will not be discussed here), once in the plant, both elements must be assimilated into safe, transportable, and usable forms such as amino acids.

As a class of chemical compounds, there are about 500 amino acids, of which only 20 are used to make proteins. These are the so-called proteinogenic (or proteinaceous) amino acids. Humans can only make 11 of the 20 proteinogenic amino acids. In contrast, plants can synthesize all 20 proteinogenic amino acids (as well as hundreds of others), and plastids are the site for the synthesis for the 9 essential amino acids that humans need. Lacking plastids, humans must acquire these nine "essential" amino acids via their diet, by eating plants or other animals that feed on plants.

Glyphosate (Roundup©) is a potent inhibitor of a key plastid enzyme in the aromatic amino acid pathway (phenylalanine, tyrosine, and tryptophan), and, thus, it is a powerful and specific herbicide. Synthesis of the branched-chain amino acids (isoleucine, leucine, and valine) is also plastid localized and can be the subject of specific herbicide inhibition.

Plastids, in one form or another, synthesize chlorophylls, carotenoids, fatty acids, phospholipids, sulfolipids and galactolipids, tocopherols, and quinone lipids. Plant cells only rarely possess smooth endoplasmic reticulum, the site of most lipid synthesis in animals.

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Box 3.1 Where Are Tannins Made?

Tannins are a type of polyphenol that serve many purposes for plants, including protection from predators (due to a bitter taste), regulating plant growth, and protecting plants from ultraviolet radiation. They are what give things like tea, pomegranates, and under-ripe raspberries their "dry" effect.

Tannins form bonds with proteins, cellulose, starches, and even minerals to create substances that resist decomposition. In fact, tannins from trees like oak, maple, and mangrove were used by ancient and indigenous cultures to preserve animal skins for clothing and blankets. Hence the terms "tanned leather" and "suntan."

When you drink green tea, beer, wine, or even fruit juices, the bitter taste in your mouth results from the presence of condensed tannins. Condensed tannins are substances that are produced in a wide variety of plants and are located within leaves, fruits, and bark. Tannins provide plants with protection against herbivores and even from the UV rays of the sun. People utilize tannins for their antioxidant properties, often consuming them for anticancer, anti-inflammatory, and anti-allergenic benefits (Frazier et al. 2010). But how and where are tannins produced within plant cells?

Light, epifluorescence, and confocal microscopy have elucidated that tannins accumulate in **tannosomes**, small bodies found within the central vacuole. Tannosomes contain both tannins and chlorophyll, linking the tannosomes with chloroplasts. By employing TEM, Brillouet et al. (2013) further identified that tannins, and the tannosomes, are produced within differentiated chloroplasts. These specialized chloroplasts are larger than normal chloroplasts and contain unstacked grana that generate small, membrane-bound structures in a process the authors called "pearling." The pearls thus produced are filled with tannins, concentrate together at the chloroplast membrane, and are encapsulated in a membrane. This structure and the tannosomes within are shuttled from the chloroplast, through the cytoplasm and to the central vacuole.

3.5.9 The Dimorphic Chloroplasts of C_4 Photosynthesis

The photosynthetic pathway described above results in the generation of a three-carbon compound, glyceraldehyde-3-phosphate. Hence, plants that use this pathway are called **C_3 plants**. Other plants, most notably grasses such as maize and sugar cane, produce a four-carbon acid as the first stable product of photosynthesis. That form of photosynthesis is called the **C_4 pathway**.

C_4 plants differ from C_3 plants on biochemical, physiological, anatomical (refer to ► Sect. 12.5), and ultrastructural bases. In C_4 photosynthesis, carbon dioxide is initially fixed in chloroplasts in the mesophyll cells of the leaf. Mesophyll cell chloroplasts contain grana stacks and are termed "granal." A four-carbon compound is transported to the bundle sheath cells where it is decarboxylated to a three-carbon molecule and CO_2. The released CO_2 is then fixed again in the **bundle sheath chloroplast**, which lacks grana ("agranal") (◘ Fig. 3.5 q, r). Different ultrastructures arise because the enzyme responsible for the secondary fixation in the bundle sheath chloroplast, ribulose-*bis*phosphate carboxylase/oxygenase (a.k.a. Rubisco, an acronym for the enzyme ribulose *bis*phosphate carboxylase/oxygenase), is inhibited in the presence of oxygen. Unlike C_3 chloroplasts and C_4 mesophyll cell chloroplasts, the C_4 agranal bundle sheath chloroplasts are non-oxygenic; thus, the O_2 inhibition of Rubisco is alleviated.

◘ **Fig. 3.5** **q** TEM of portions of a maize (*Zea mays*) mesophyll cell (*left side*) containing an agranal chloroplast and a bundle sheath cell (*right side*) with a granal chloroplast. Scale bar = 2 µm (RR Wise). **r** Higher magnification of the two plastids in **q** showing granal (*top*) and agranal chloroplast (*bottom*) structure in more detail. V = vacuole, CW = cell wall, M = mitochondrion. Scale bar = 1 µm (**q**, **r** RR Wise)

3.5.10 Guard Cell Chloroplasts

Stomata (stoma = sing.) are minute, adjustable pores on the leaf surface that allow for CO_2, H_2O, and O_2 gas exchange between the leaf and the atmosphere. Specialized pairs of epidermal cells, called **guard cells**, inflate with water and then bend and open the stomatal pore. Subsequent loss of water causes the guard cells to deflate and close the pore. In most plants stomata are closed at night (when photosynthesis cannot operate) and open during the day. The signals to open and close come from environmental cues and an internal circadian clock. The energy to drive the opening and closing comes from guard cell chloroplasts that respond to osmotically driven water movements.

Guard cell chloroplasts (GCC) are, in all respects, the same as C_3 chloroplasts. They contain thylakoids, grana, chlorophyll, and all the components needed to perform both the light-dependent and the light-independent reactions of photosynthesis. They fix carbon and make starch. What sets GCCs apart from other chloroplasts is that they contribute nothing to the carbon economy of the leaf. GCCs function solely to provide the energy and osmotic pressure changes needed to drive stomatal opening and closing (◘ Fig. 3.5s–u).

Guard cell chloroplasts are an impressive example of the evolutionary flexibility of plastids. Plants evolved from green algal ancestors and began land colonization during the Silurian period (approximately 440 million years ago). One of the many adaptations needed for a terrestrial life was a waxy, water impervious outer cuticle, which drove the need for stomatal openings in that cuticle. As guard cells evolved, plastids were enlisted to serve as the power plant for stomatal functioning. They are sensitive to light (and light is a major signal for stomatal opening) and can generate the ATP and the low-molecular-weight ions needed to support osmotically driven stomatal opening and closing.

3.5.11 Sun Versus Shade Chloroplasts

Chloroplast development is light-dependent, and different ultrastructures and physiologies can result as a consequence of the light environment during development. Because light is limiting in the shade, chloroplasts in leaves that develop in the interior of a tree canopy develop to favor the light-dependent reactions over the light-independent reactions. **Shade-type chloroplasts** are optimized for light capture with larger grana, more thylakoids per granum and more chlorophyll per antenna (or light-harvesting) complex. Stromal volume is concomitantly reduced. **Sun-type chloroplasts**, which develop at the exterior of the canopy where light is not limiting, have smaller grana, less chlorophyll (reduced capacity for the light-dependent reactions), and more stromal volume (increased capacity for the light-independent reactions). Both chloroplast types can be found on the same plant; thus, these two different developmental outcomes are driven solely by the light environment experienced during leaf expansion (◘ Fig. 3.5v, w).

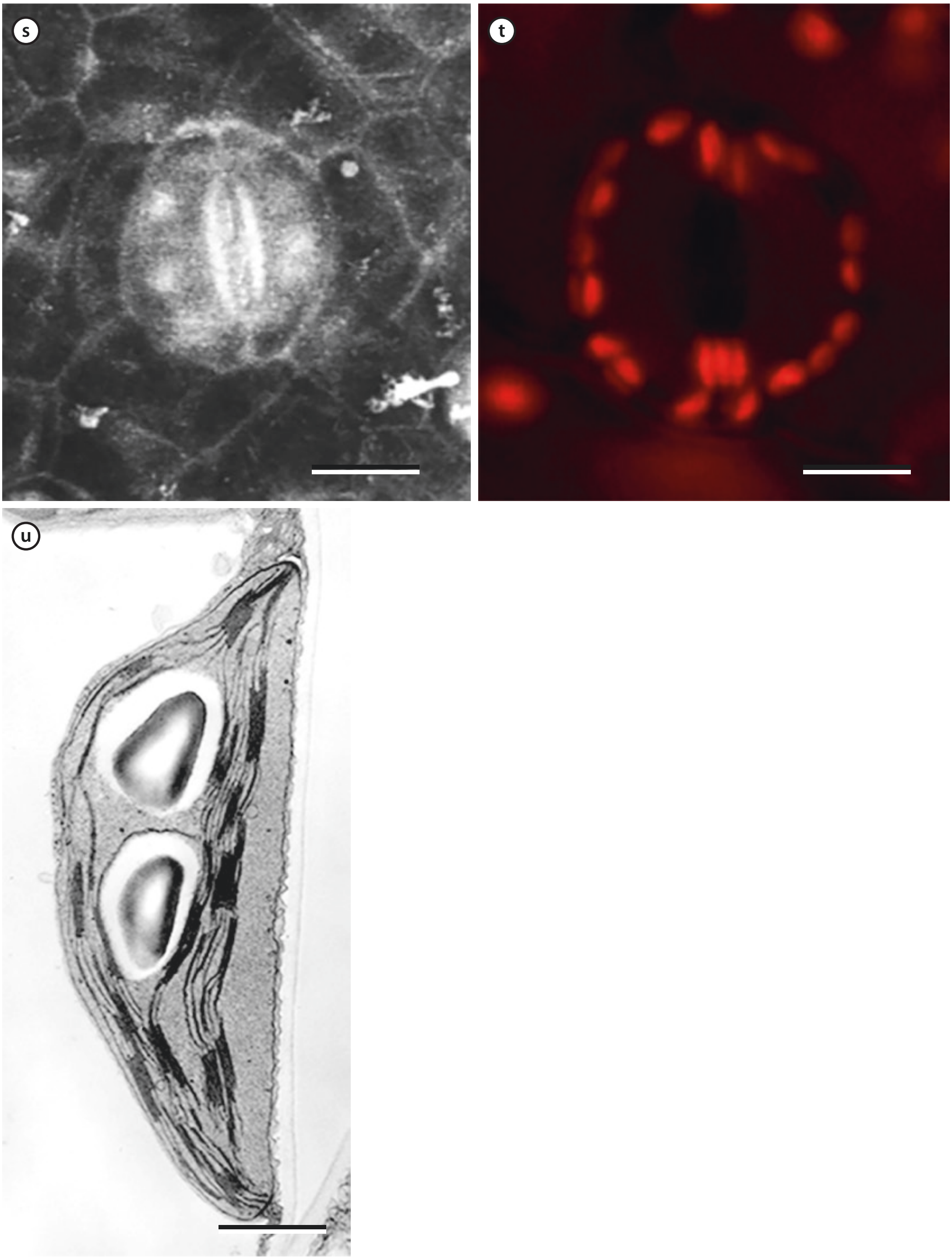

Fig. 3.5 **s** SEM image of an upland cotton (*Gossypium hirsutum*) guard cell pair. Chloroplasts appear as white spots within the guard cells. **t** Confocal laser scanning microscopy (CLSM) fluorescence image of a *Nicotiana benthamiana* guard cell pair. Chloroplasts appear as red spots in guard cells due to chlorophyll fluorescence. **u** TEM of guard cell chloroplast of spinach (*Spinacia oleracea*). Scale bars = 10 µm in **s** and **t**, 1 µm in **u** (**s**–**u** RR Wise)

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Box 3.2 Can Plants Absorb Green Light?

Chloroplasts of most land plants capture blue and red wavelengths of light for photosynthesis and reflect green wavelengths, giving plants a green color. However, species that grow in deep shade are challenged in their ability to capture sufficient light as the intensity and quality of light have been filtered by canopy leaves. Jacobs et al. (2016) have discovered that some species of understory *Begonia* have evolved a unique light-capturing adaptation, specifically the iridoplast, which results in blue iridescent leaves.

Iridoplasts are plastids located within the epidermal cells of some tropical *Begonias*; these plastids are unique in two ways. First, most plants lack epidermal chloroplasts. Second, iridoplasts enable plants to utilize green and red wavelengths for photosynthesis, contrasting with most terrestrial plants that utilize blue and red. This feat is accomplished by having highly structured, multilayered thylakoid membranes within the iridoplasts. The multilayered structure greatly increases the absorption of green light, which is enriched in the understory because the canopy plants depleted the incoming light of the red and blue wavelengths. This allows the plant to increase the quantum yield when in the deep shade of the tropical forests. Thus, by utilizing green light and increasing quantum yield, iridoplasts are important structures in the evolution of understory tropical begonias.

Reference: Jacobs et al. (2016)

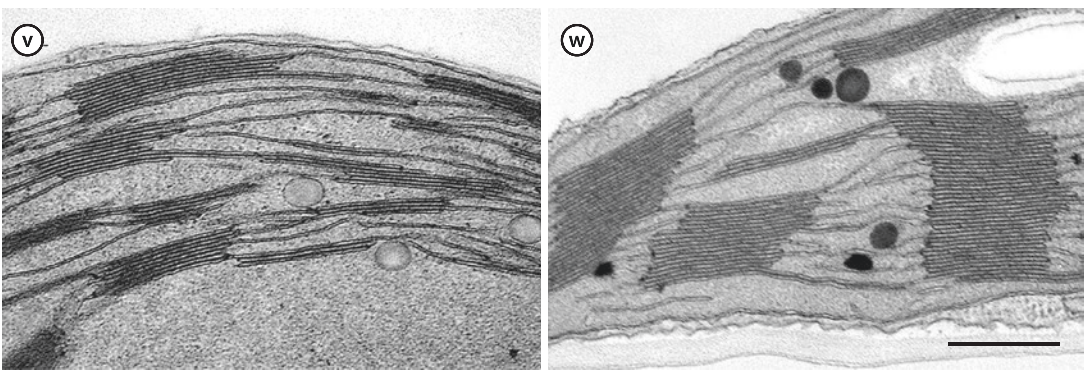
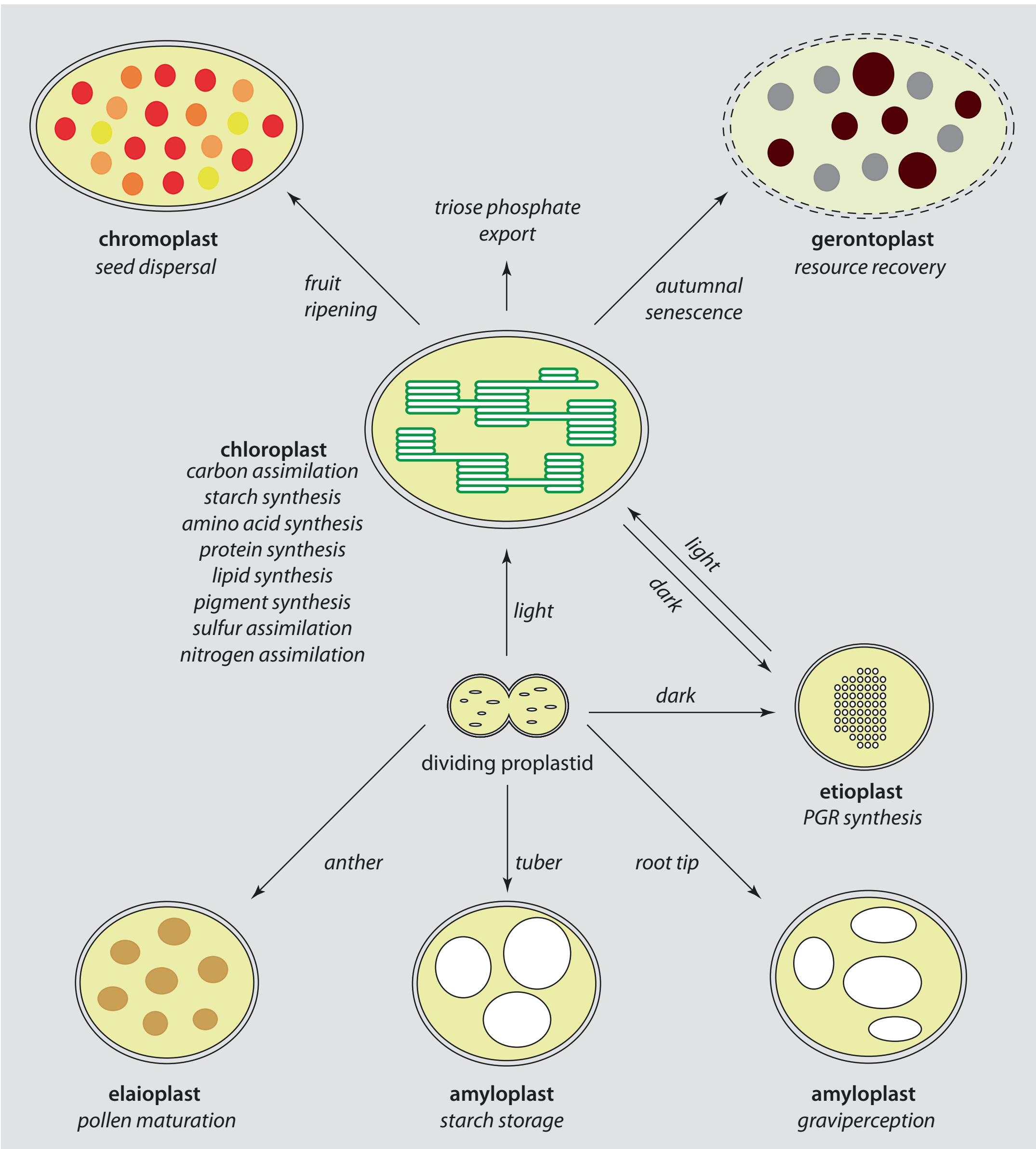


Fig. 3.5 TEM of **v** high-light and **w** low-light chloroplasts from spinach (*Spinacia oleracea*) leaves. **v** The high-light leaves were treated with 1000 µmol photons m^{-2} s^{-1} irradiance for 4 h prior to sampling. **w** The low-light chloroplast is from a leaf on the same plant that received 4 h of high light and then 10 min of 50 µmol photons m^{-2} s^{-1}. Scale bar in (b) = 0.5 µm and applies to both panels. (**v**, **w** Philip Rozak)

3.6 All Plastids Are Developmentally Related

All plastids in a plant are descendants of the hundred or so proplastids provided by the egg cell in angiosperms. ◘ Figure 3.6 shows the development of the various plastid types starting with the proplastid on the left side of the figure. Plastids in anthers, roots, and etiolated tissues develop in the dark (or near dark) and do not turn green. Those plastids become elaioplasts in the tapetum, starch storage or gravisensing amyloplasts in the root, or etioplasts if shoot tissue develops in the dark. Once tissues are



◘ **Fig. 3.6** The different pathways of plastid development depicted in the drawing are both light- and tissue-dependent. The function(s) of each plastid type is given in italics (RR Wise) exposed to the light, either through leaf development or by placing the plant in the light, etioplasts convert to chloroplasts. C_3, C_4, guard cell, and sun/shade chloroplasts follow different developmental pathways depending on their host tissue. Chloroplasts in leaves typically go through the gerontoplast stage as leaves proceed through the senescence process. Chloroplasts in developing fruit, such as those in a green tomato, convert to chromoplasts during ripening.

3.7 Mitochondria Synthesize ATP and Small Carbon Skeletons

Mitochondria are the sites of two of the three phases of respiration: the citric acid cycle and oxidative phosphorylation. Those two stages are preceded by glycolysis, which takes place in the cytoplasm. Respiration takes the low-molecular-weight, reduced carbon compounds produced by photosynthesis, extracts the high-energy electrons (some during glycolysis, most during the citric acid cycle), and feeds those electrons into the mitochondrial electron transport chain to drive ATP synthesis (phosphorylation). In addition to ATP production, mitochondria also export two- to five-carbon skeletons for use by many other metabolic pathways in the cytoplasm.

Mitochondria have two membranes. The outer membrane serves as a barrier between the cytoplasm and the mitochondrial interior. In composition, it is more like the other native cell membranes, i.e., plasmalemma, vacuolar membrane, and many membrane-limited vesicles. The inner membrane has numerous folds called **cristae** that are the site of the mitochondrial electron transport chain, which culminates with ATP synthesis via chemiosmosis. The enzymes of the citric acid cycle reside in the fluid-filled interior, the matrix. The number of mitochondria per cell can vary from only a few to fifty or a hundred, depending on cell type and activity level (◘ Fig. 3.7a–c). However, recent research has demonstrated that mitochondria and the endoplasmic reticulum interact in strikingly dynamic ways in response to light and oxygen deprivation, fusing and splitting on a short time scale (Jaipargas et al. 2015).

Like plastids (refer to ► Sect. 3.5), mitochondria were derived endosymbiotically and have retained the machinery needed to code for and manufacture some of their own proteins.

3.8 Microbodies Are the Site of Specific Biochemical Pathways

In contrast to plastids and mitochondria, **microbodies** are bounded by a single membrane, have no internal membrane structure, lack DNA, and are amorphous internally or, in some cases, may have internal protein crystals, which represent enzymes such as catalase. Like plastids and mitochondria, microbodies multiply by a type of fission division.

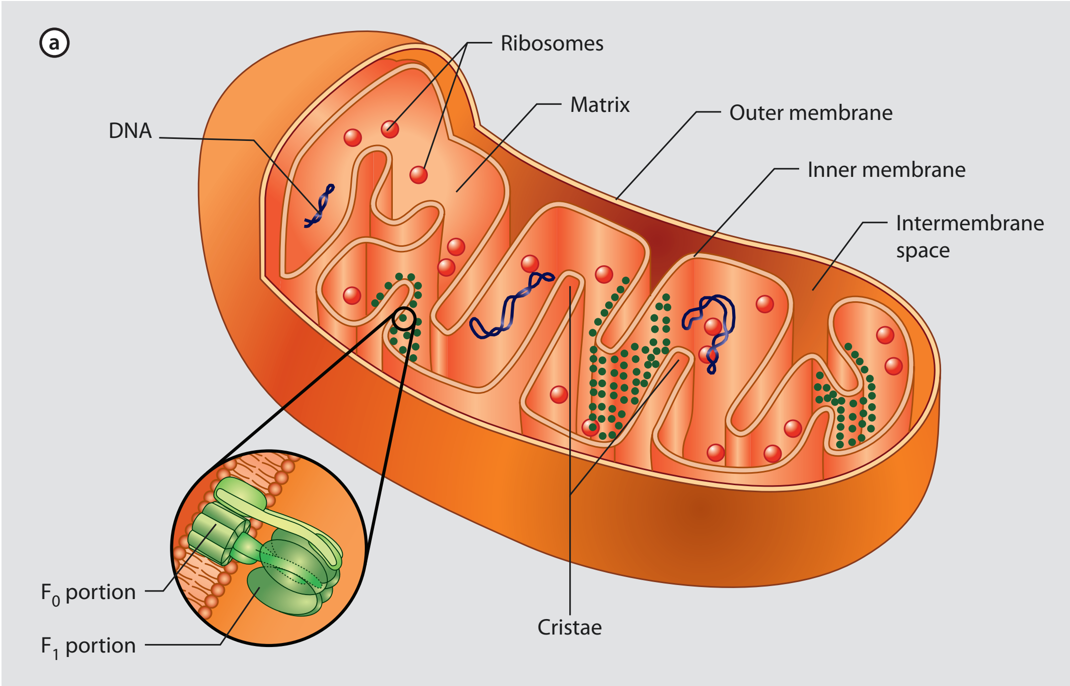


Fig. 3.7 **a** Drawing of a typical plant mitochondrion (Redrawn from Crang and Vassilyev 2003)

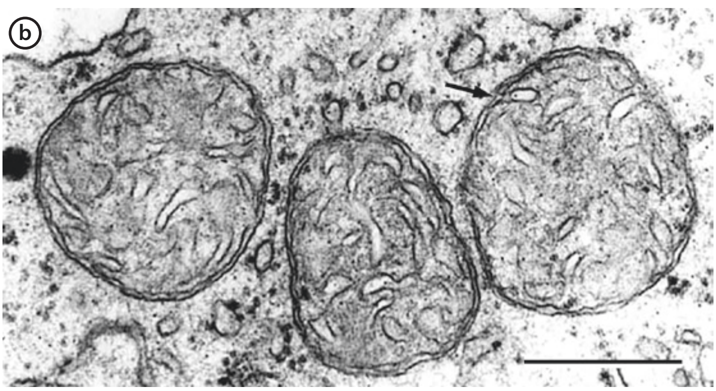


Fig. 3.7 **b** TEM of three mitochondria from a secretory cell in the digestive gland of *Drosophyllum lusitanicum*, a carnivorous plant. Note the continuity of cristae with the inner mitochondrial membrane (*arrow*). Scale bar = 1 µm (RR Wise)

There are two types of microbodies, and both received their name due to their small size and simple structure. Microbodies in leaf cells are called **peroxisomes**, and they participate in the oxidation of glycolate to glyoxylate that produces H_2O_2 (hydrogen peroxide), which in turn is destroyed by the enzyme catalase (Fig. 3.8a). This process is called photorespiration because it consumes oxygen, generates CO_2, and occurs only in the light. It represents an inefficiency of **Rubisco**, which accepts oxygen instead of the normal substrate CO_2 when O_2 accumulates to high concentrations. The oxygen-rich Rubisco is tricked into releasing CO_2.

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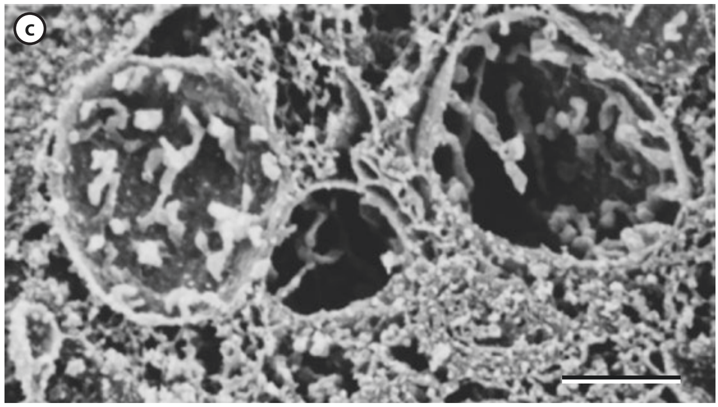


Fig. 3.7 **c** Scanning electron microscopy (SEM) of mitochondria from a spinach (*Spinacia oleracea*) leaf using a frozen and fractured surface. Cristae are visible as outgrowths of the inner membrane. Scale bar = 1 µm (RR Wise)

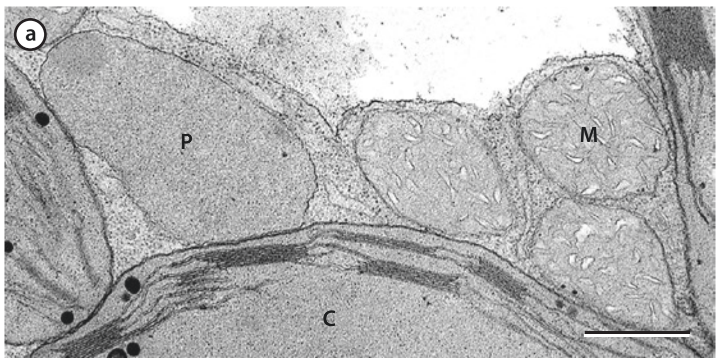
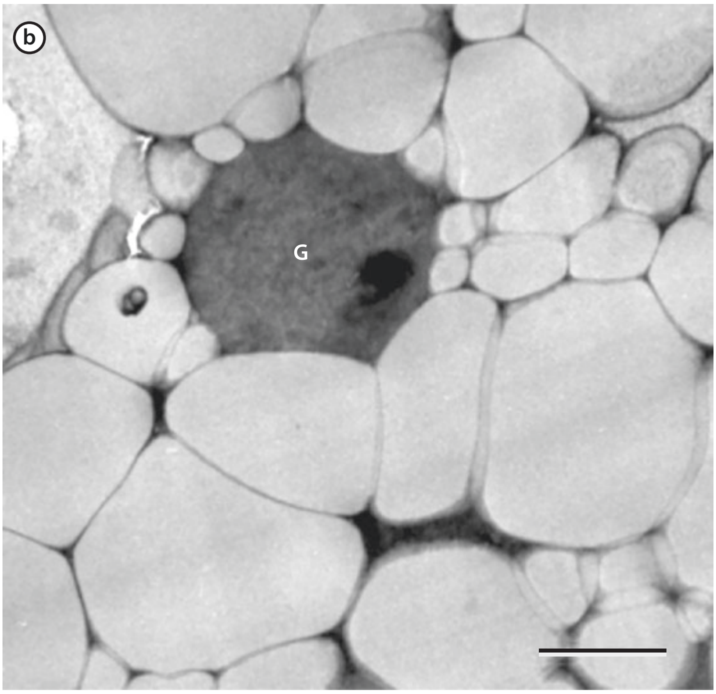


Fig. 3.8 **a** This TEM image shows one peroxisome (P) and several mitochondrion (M) tightly appressed to a chloroplast (C) in a spinach (*Spinacia oleracea*) leaf mesophyll cell. The image reflects the metabolic cooperation of these three organelles. Scale bar = 1 µm (RR Wise)

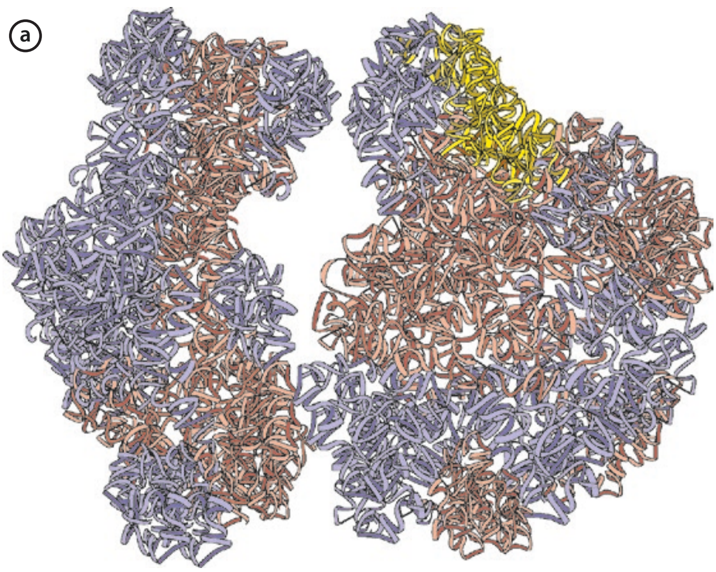
Glyoxysomes, the second type of microbody, are key organelles in oil-storing cells of seeds where they work together with mitochondria to catabolize the long carbon chains on storage oils and lipids into smaller carbon skeletons for respiration and growth (Fig. 3.8b).

3.9 The Endoplasmic Reticulum Synthesizes Proteins and Some Lipids

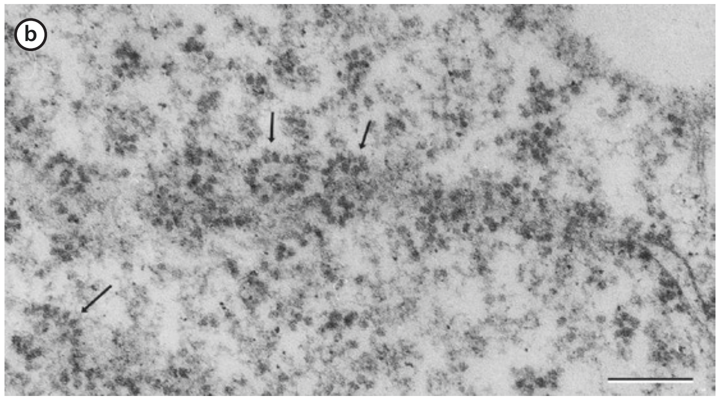
Plant cells are capable of synthesizing every biomolecule needed for complete growth, development, and reproduction; proteins and lipids are two major cellular components, and the endoplasmic reticulum (ER) plays a role in the synthesis of both. The ER is an interconnected series of tubules and sacs that lie in the cytoplasm and comes in two forms, smooth and rough. Rough endoplasmic reticulum (RER) is studded with ribosomes (refer to RER in Fig. 3.9c). Ribosomes are composed of a large and a small subunit (Fig. 3.9a), and there may be thousands of individual ribosomes in a cell that are actively producing proteins.



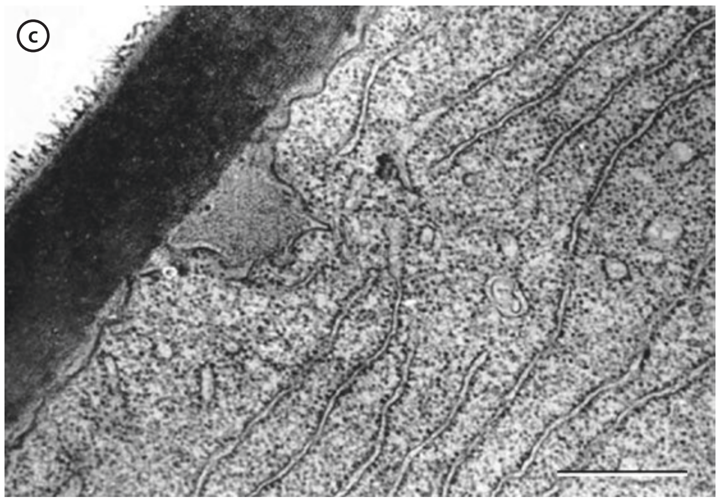
◘ **Fig. 3.8** **b** TEM of glyoxysome (G) in the endosperm of a lyre-leaved sand cress (*Arabidopsis lyrata*) seed surrounded by lighter lipid bodies. Scale bar = 1 µm (RR Wise)



◘ **Fig. 3.9** **a** The two ribosome subunits showing rRNA (*brown and yellow*) and protein (*blue*) molecules. Scale bar = 10 nm (Protein data base, public domain)



■ **Fig. 3.9** **b** Polysomes (*arrows*) in the cytoplasm of a thale cress (*Arabidopsis thaliana*) root. Scale bar = 0.5 µm. (Image courtesy of Dr. Harry Horner)



■ **Fig. 3.9** **c** TEM image of rough endoplasmic reticulum in a rhizodermal cell of the water plant, *Limnobium bogotense* (a member of the grass family). Scale bar = 0.2 µm (Image courtesy of Dr. Harry Horner)

Plant cells have three sets of ribosomes. Those in the cytoplasm may be attached to the endoplasmic reticulum, forming rough ER (■ Fig. 3.9b), or they may be free-floating and not attached to any membrane. A single molecule of mRNA may be bound by multiple ribosomes, each at different position along the message, in a structure called a polysome. When seen in the TEM, polysomes appear as strings of beads (■ Fig. 3.9b). The other two sets of ribosomes are found in the chloroplast stroma (► Sect. 3.5) and the mitochondrial matrix (► Sect. 3.7).

Proteins synthesized by the ribosomes attached to the RER are inserted into the RER membrane or injected into the interior space (lumen). In ultrathin sections for transmission electron microscopy, RER appears as double-membrane profiles covered with bumps (■ Fig. 3.9c). The RER is involved in the synthesis and storage of

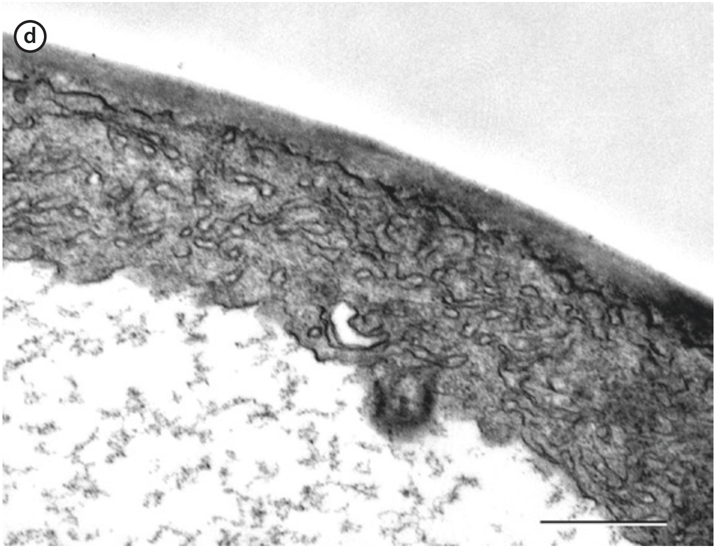


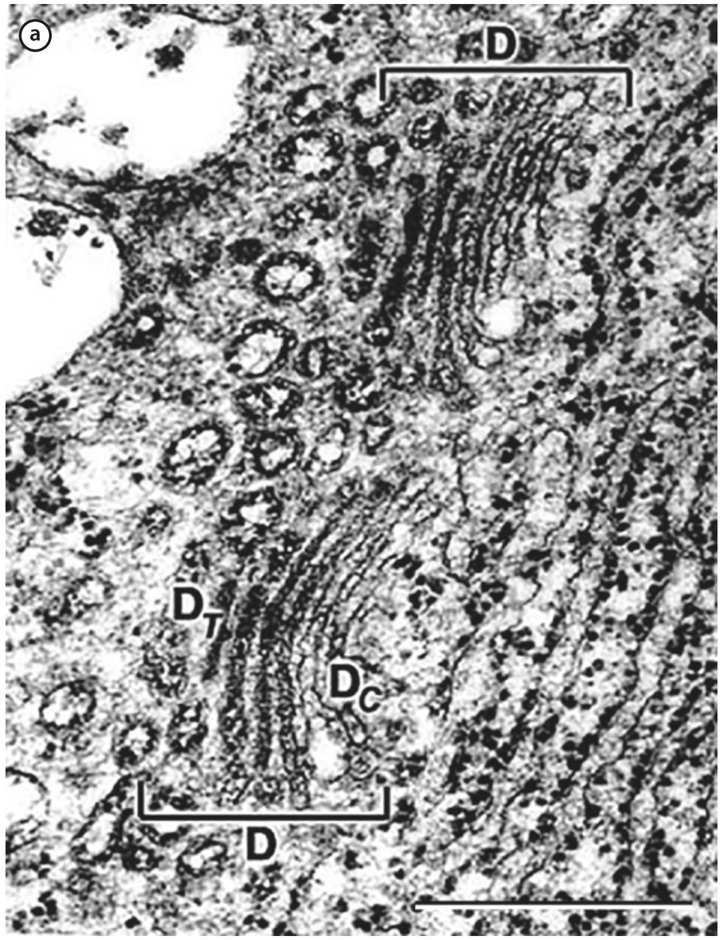
Fig. 3.9 **d** TEM of a portion of a leaf mesophyll cell from the thale cress (*Arabidopsis thaliana*) experiencing a bacterial infection. As a response to the infection, the cells are induced producing callose, via the tubules shown. Scale bar = 1 µm (RR Wise)

specific proteins (hydrolytic enzymes, membrane, storage, and secretory proteins). **Smooth ER** is more vesicular and tubular than the thinner and flatter RER. In animal cells, SER plays a large role in lipid synthesis, a function that plants mainly perform using plastids. In plants, the SER is active in the synthesis and secretion of specific lipophilic substances such as oils and terpenes. Therefore, SER is rarely seen in plant cells and usually is only prominent in plant secretory structures such as oil seed tissues, nectaries, and leaf glands. Smooth ER is also seen in leaf cells that have been infected by bacteria. Such cells often synthesize and secrete copious amounts of callose via the SER (Fig. 3.9d).

3.10 The Golgi Apparatus Processes and Packages Polysaccharides and Proteins for Secretion

The **Golgi apparatus** is the sum of all of the dictyosomes with common function in a plant cell. The dictyosomes are membranous organelles in the cell cytoplasm engaged in the processing and export of materials to the cell exterior. In animal cells, glycosylated proteins are the major export product. However, in plant cells, the Golgi system is primarily used to manufacture and export the non-cellulose polysaccharides used in cell wall synthesis or root cap slime (Rose and Lee 2010). Only in rare instances, such as the digestive traps of carnivorous plants, does the plant Golgi apparatus secrete proteins.

3



◘ **Fig. 3.10** **a** The plant Golgi apparatus consists of an array of dictyosomes (D), two of which are shown here using TEM from a secretory cell of poplar (*Populus* sp.) leaf gland. Note the *cis* (D_C) and *trans* (D_T) faces of a dictyosome. Scale bar = 0.5 µm (Crang and Vassilyev 2003)

The Golgi apparatus consists of dictyosomes and vesicles (◘ Fig. 3.10a, b). Dictyosomes are stacks of (usually) 5–7 membrane cisternae, which exhibit polarity. Membrane vesicles containing proteins and carbohydrate precursors are trafficked from the ER to the ***cis*** **face** (or regenerative pole). Those materials are enzymatically modified as they travel through the dictyosome and then are eventually secreted in vesicles from the ***trans*** **face** (or secretory pole). In micrographs, the polarity is generally obvious inasmuch as the thickness and contents of the cisternae change from the *cis* (D_C) to the *trans* (D_T) side of the stack. Dictyosomes represent functional units of a Golgi apparatus, so that all dictyosomes in a given cell that have similar functionality represent a single Golgi system. Thus, there may be one or more Golgi systems per cell.

Fig. 3.10 **b** Root cap cell of timothy grass (*Phleum pratense*) observed with transmission electron microscopy. Dictyosome cisternae mature from *cis* (D*C*) to *trans* (D*T*) face where they become large secretory vesicles (X) which move polysaccharides to the cell periphery where they fuse with the plasma membrane and discharge their contents into the periplasmic space. Small protein-coated vesicles are also shown. *Arrows* indicate the sites of intercisternal fibrils. CW = cell wall, RER = rough endoplasmic reticulum. Scale bar = 1 μm. (Image from Ledbetter and Porter (1970), with permission)

Carnivorous plants typically occupy ecological niches with low nutrient availability such as bogs and swamps. As such, these plants acquire much of their nitrogen and phosphorous by capturing and digesting insects in tubular traps (pitcher plants), sticky pads (sundew), or closable claws (Venus flytrap). The plant then secretes enzymes into the trap, which digest the prey and releases the nutrient from absorption through the trap surface. In such plants, enzyme secretion is meditated by the Golgi apparatus. Refer to ► Chap. 13 for more information on secretory structures.

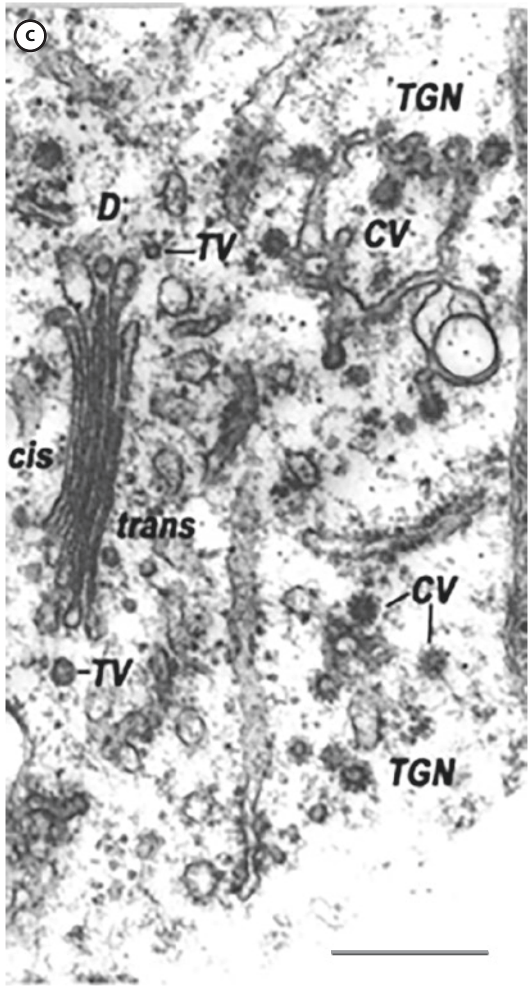


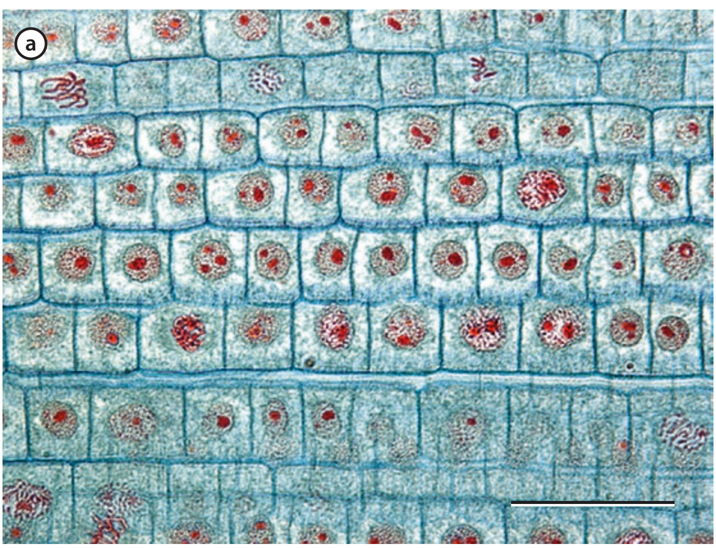
Fig. 3.10 **c** Shown here are a dictyosome (D) and *trans*-Golgi network (TGN), (a.k.a. *trans*-Golgi reticulum) which is the site of protein sorting. Note the clathrin-coated vesicles (CV) and the transport vesicles (TV). Such cells synthesize and secrete digestive enzymes involved in the digestion of captured insects. TEM. Scale bar = 0.5 µm (Crang and Vassilyev 2003)

Figure 3.10c shows details of a cell from a secretory cell of the digestive gland of *Drosophyllum lusitanicum*, a carnivorous plant. Unlike cells secreting polysaccharides, in cells producing proteins, there is no shifting of cisternae in the dictyosomal stack from *cis* to *trans* sides. On the contrary, cisternae in the stack remain stationary, and the exchange of the maturing protein among them occurs through small transport vesicles (TV) that successively pinch off and fuse with neighboring cisternae in the trans-direction. Finally, the transport vesicles fuse with the trans-Golgi network (TGN), an irregular body, where sorting of different proteins and their packing in different secretory vesicles occurs. The digestive enzymes are packed in clathrin-coated vesicles (CV). The name of these vesicles is derived from a spiny coat made of a specific type of protein called clathrin. The coated vesicles bud off the TGN, lose their coat, and move to the plasmalemma. After the fusion of their membrane with the plasma lemma, their cargos, hydrolases, are then released from the cell.

3.11 The Nucleus Houses the Cell's Genetic Material and Participates in Ribosome Synthesis

The **nucleus** is the site of storage of the cell's genetic information, in the form of chromosomes. Recall that plants have three genomes: the plasmid genome contains approximately 100 genes, the mitochondrial genome has 40 or fewer, while the nuclear genome holds between about 26,000 in the thale cress (*Arabidopsis thaliana*, Arabidopsis Genome Initiative, 2000) to 45,550 in black cottonwood (*Populus trichocarpa*; Tuskan et al. 2006). The nucleus is also where the components of cytoplasmic ribosomes are synthesized and partially assembled.

Just as the vacuole is the dominant structure in leaf mesophyll cells, the nucleus is normally the predominant protoplasmic organelle of the cell and thus is one of the largest cellular organelles. In small meristematic cells, such as those shown in ◘ Fig. 3.11a, the nucleus can easily be visualized with the light



◘ **Fig. 3.11** **a** Light micrograph of dividing cells in an onion (*Allium cepa*) root tip. Each cell has a prominent nucleus. Scale bar = 50 µm (RR Wise)

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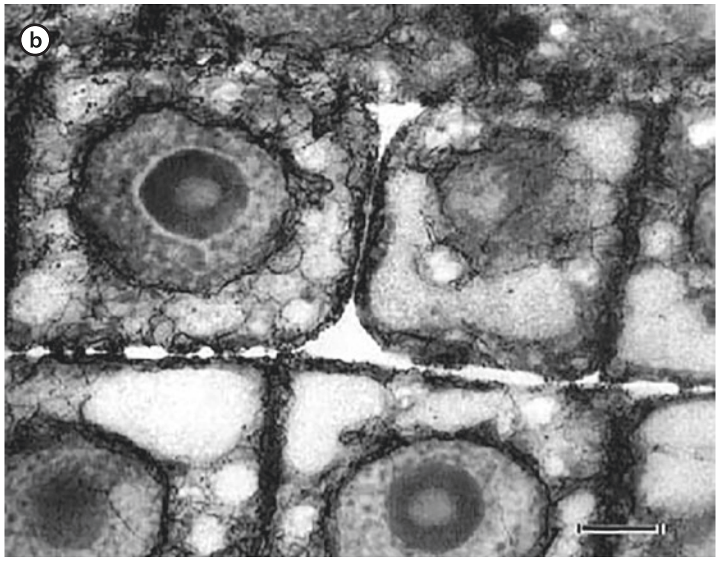


◘ **Fig. 3.11** **b** A TEM micrograph showing two rows of cells from a meristematic region of a root with prominent nuclei and their nucleoli and scattered membranes about the cytoplasm with some prominent vacuolated areas. This TEM image is of a thick (one micron) section and therefore shows more cellular structure. Scale bar = 10 µm (Crang and Vassilyev 2003)

microscope and can be seen to occupy a major portion of the cell's volume when viewed in more detail in the electron microscope (◘ Fig. 3.11b).

Nuclei in cells that are actively engaged in protein synthesis typically contain a large **nucleolus**, a substructure within the nucleus that participates in ribosome synthesis. The transmission electron micrograph in ◘ Fig. 3.11c illustrates a nucleus from an African violet. The nucleolus is the center of production for ribosome precursors (rRNA and imported proteins), which constitute the granular component. These particles are smaller than ribosomes in the cytoplasm, and only after they pass through the nuclear pores do they acquire the remaining proteins to become full-sized and mature ribosomes.

The nucleus is bounded by a double-membrane envelope that is perforated with numerous nuclear pores (◘ Fig. 3.11d, e). Nuclear pores are gateways, which regulate the exchange of RNA and proteins between the nucleus and cytoplasm. More than merely a hole in the envelope, the pores are actually a complicated protein complex that spans the two membranes and selectively regulates the trafficking of molecules into and out of the nucleus.

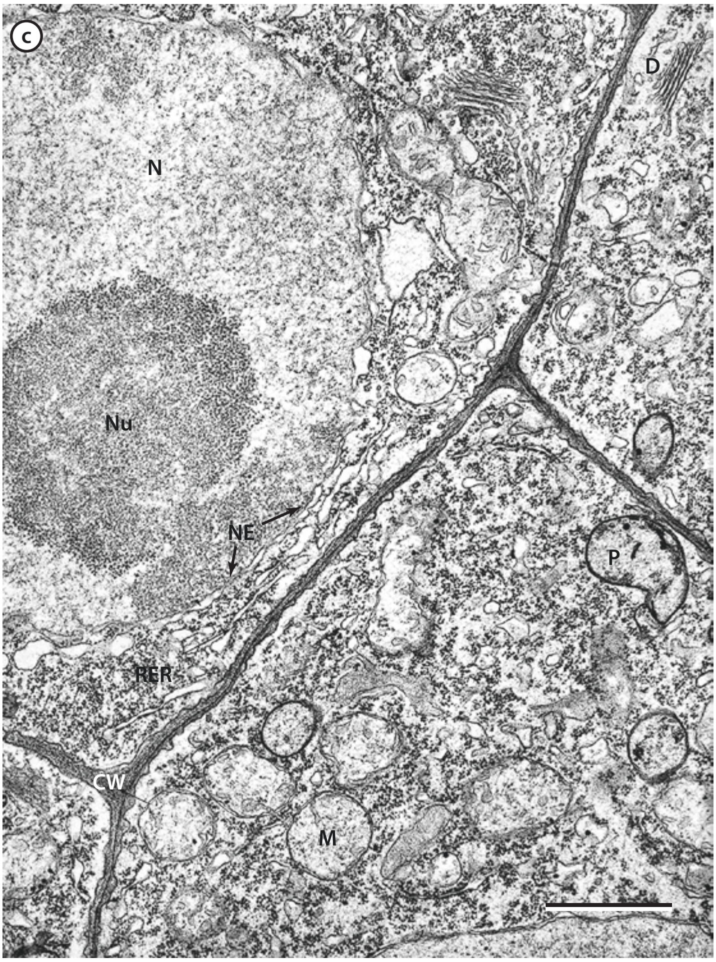
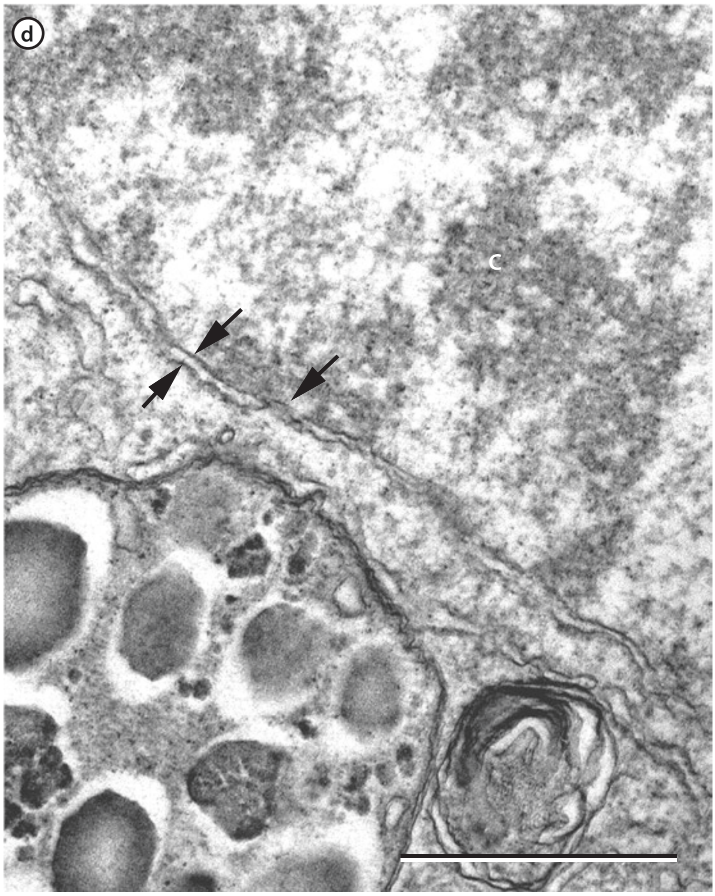


Fig. 3.11 **c** TEM image of a portion of a nucleus from undifferentiated sporogenous tissue of African violet (*Saintpaulia ionantha*). The nucleus (N) occupies a major portion of the cell volume. The genetic material of this interphase nucleus is formed of diffuse (most active) and condensed (least active) chromatin. The large nucleolus (Nu) consists of intermingled granular and fibrillar components which are responsible for assembling ribosomes. NE = nuclear envelope, CW = primary cell wall, D = dictyosome, P = plastid, M = mitochondrion, RER = rough endoplasmic reticulum. Scale bar = 5 µm. (Image from Ledbetter and Porter (1970), Introduction to the Fine Structure of Plant Cells, Springer-Verlag, with permission)

3.12 The Cytoskeleton Organizes the Cell and Helps Traffic Organelles

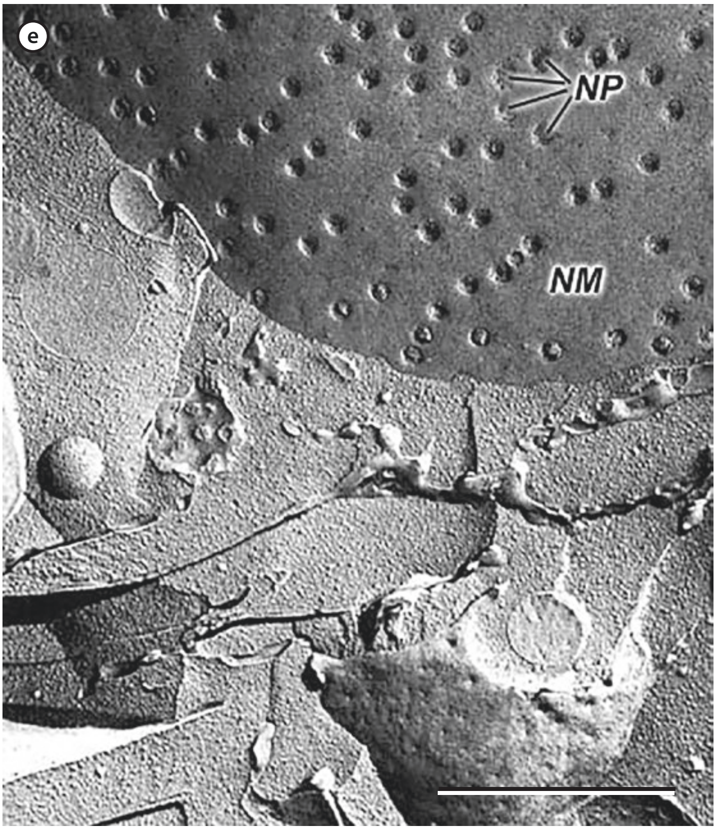
The **cytoskeleton** is an architectural framework of protein strands found in the cytoplasm of all eukaryotic cells. It is composed of two types of components: structural and force-generating. All eukaryotes have a cytoskeleton, but recent research has shown that there are significant differences between the cytoskeletal proteins of plant and animal cells.



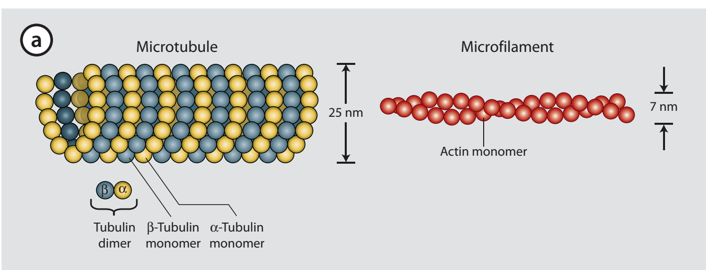
◘ **Fig. 3.11** **d** TEM image showing a portion of a nucleus (*top right*) and amyloplast (*bottom left*) in a mung bean (*Vicia faba*) root tip. Note the two membranes of the nuclear envelope (*between the two arrows*), nuclear pore (*single arrow*), and condensed chromatin (C). Scale bar = 5 μm (RR Wise)

In plants, microtubules and microfilaments (◘ Fig. 3.12a) are the two structural fibers that form the scaffolding of the cytoskeleton while individual motor proteins generate force and move vesicles and organelles along the fibrous scaffold. A third class of cytoskeletal proteins which are purely structural, the so-called **intermediate filaments**, are present in animal cells but are not found in plant cells. Intermediate filaments play multiple roles in animals and are a main component of hair, nails, and skin. They also form a supportive network to the interior of the nuclear membrane. While hair, skin, and nails are not found in plants, analogous structural proteins can be found in plant nuclei.

Microtubules (MT) are polymers of the globular protein **tubulin**, which occurs as dimers of α- and β-tubulin subunits. The subunits are packed in a spiral manner with a hollow core. In cross section, the tubule diameter is approximately 25 nm and typically



■ **Fig. 3.11** **e** A freeze-fracture TEM image of the surface of a nuclear envelope membrane (NM) in face view with numerous nuclear pores (NP). Scale bar = 5 µm. (Illustration modified from Jensen and Park 1967, Cell Ultrastructure, Wadsworth Publishing Co., Inc.)



■ **Fig. 3.12** **a** The two classes of structural proteins found in plant cell cytoskeletons (Redrawn from Crang and Vassilyev 2003)

shows 13 subunits (■ Fig. 3.12b). Microtubules play numerous important roles in the plant cell (refer to Hepler et al. 2013 for a historical perspective). Microtubules are primarily known for their role in the movement of chromosomes during nuclear division and in the formation of the cell plate during cytokinesis, but in interphase cells they are usually confined to the cell periphery. Such cortical microtubules are involved in orienting and depositing

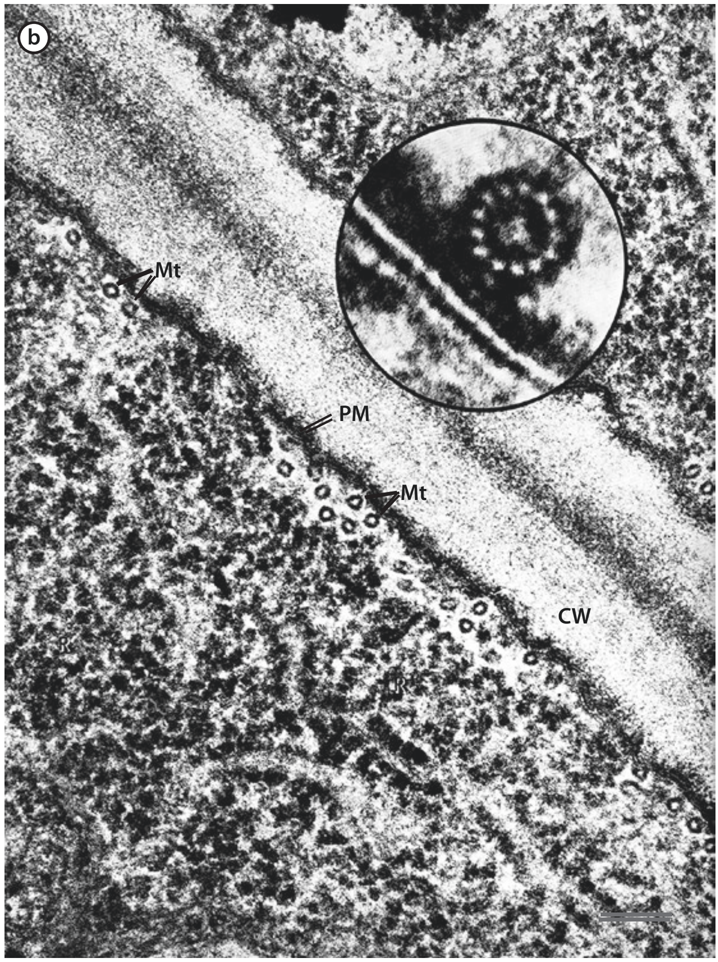
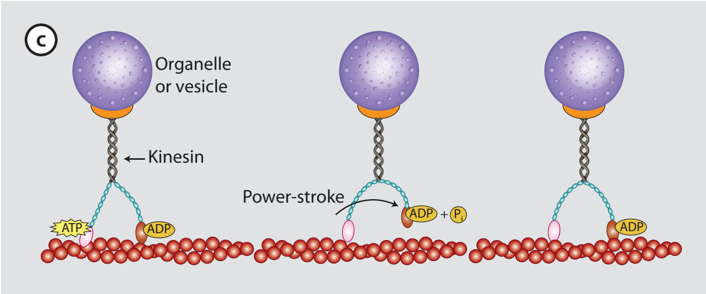


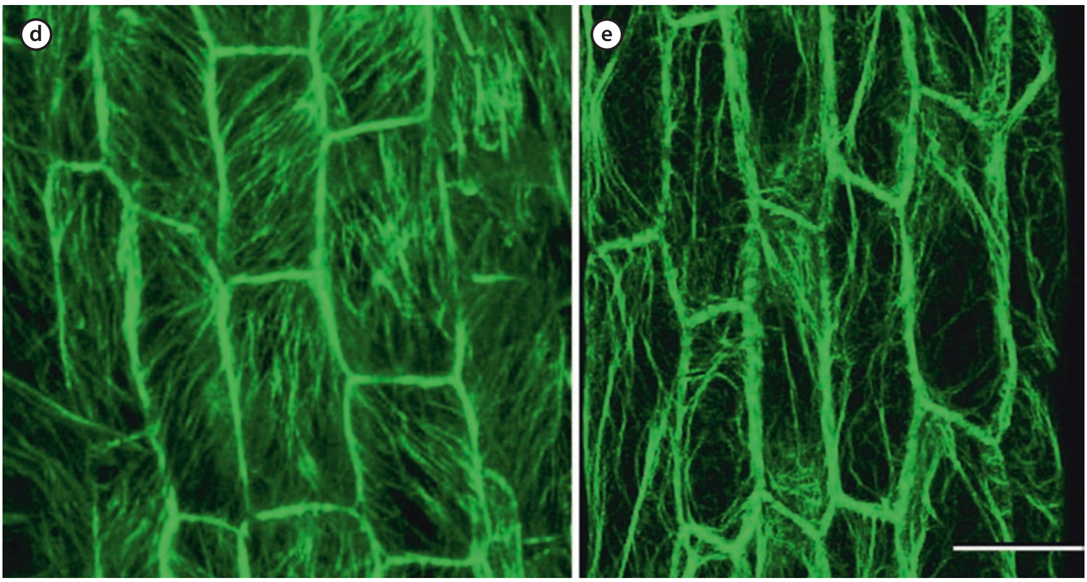
Fig. 3.12 **b** Plant microtubules are shown here in close association with the plasma membrane. The inset demonstrates a very high-resolution TEM image of a single microtubule from a root tip cell of juniper (*Juniperus chinensis*) in cross section revealing 13 subunits of structure around a hollow core. CW = cell wall, Mt = microtubules (in cross section), PM = plasma membrane. Scale bar = 1 μm. (Image from Ledbetter and Porter (1970), Introduction to the Fine Structure of Plant Cells, Springer-Verlag, with permission)

cellulose of plant cell walls, and some give shape to the cell prior to the deposition of the cell wall.

In animal cells, the motor protein **kinesin** is responsible for force generation and vesicle trafficking along microtubule tracks. However, the motor kinesins of plant play a much reduced role, as compared to animal cells. Instead, vesicle trafficking, organelle orientation, and cytoplasmic streaming are all mediated in plant cells by an actomyosin system. **Microfilaments** (MF) are polymers of the protein actin and are smaller than MTs, typically, solid rods about 7 nm in diameter. Microfilaments provide the tracks along which cytoplasmic streaming and the independent movement of organelles and vesicles occur. The motor protein myosin is attached at one end to a vesicle, mitochondrion, or chloroplast. It uses the energy in ATP molecules to travel along



■ **Fig. 3.12** **c** Organelle movement driven by the plant cell actomyosin system (Redrawn from Crang and Vassilyev 2003)



■ **Fig. 3.12** **d** Green fluorescent protein-labeled microtubules in alfalfa (*Medicago sativa*) root cells. The diagonal and diffuse orientation of the MTs probably relates to the direction of primary cell wall synthesis. **e** GFP-labeled microfilaments from Arabidopsis roots. Note that the microfilaments are thinner than the microtubules and arranged at the periphery of the cells. Scale bar in **e** = 50 µm for both panels. (**d**, **e** Images courtesy of Nobel Foundation, Ardmore, OK)

the MFs in a stepwise fashion dragging the cargo vesicle or organelle along with it (■ Fig. 3.12c). The rate and extent of cytoplasmic streaming can be quite impressive with speeds reaching 10 µm sec^{-1} and the entire cell contents swirling when viewed in the microscope.

Over the life of the cell, the MT and MF networks repeatedly disassemble (depolymerize) and reform (polymerize) to accommodate changes in cell shape or in response to stress. In a mature, nondividing cell, the microtubule system forms a network throughout the cytoplasm that aligns primarily with the orientation of the cellulose synthetic machinery used for primary cell wall production (■ Fig. 3.12d), as described in ► Chap. 5. Microfilaments, on the other hand, are arranged in the cytoplasm where they direct the movement of organelles during cytokinesis (■ Fig. 3.12e).

3.13 Chapter Review

Concept Review

3.1 *Plant cells are complex structures*. Many structural details of plant cells can be revealed through the use of electron microscopy that can employ both descriptive and quantitative information.

3.2 *Plant cells synthesize an external wall and contain a variety of internal compartments*. Surrounded by an external cell wall and an adjacent interior plasma membrane, the cellular cytoplasm contains many varied organelles.

3.3 *Cells and cell organelles are typically bound by phospholipid bilayer membranes*. High-resolution transmission electron microscopy reveals that membranes often appear as two parallel dense lines due to the preparatory stain deposit at the site of hydrophilic phosphate groups from a lipid bilayer. Membranes are designated as being "mosaic" due to various proteins that may be anchored at specific sites or mobile on either side of the lipid bilayer and play a large number of important roles in structural and metabolic functioning.

3.4 *Vacuoles play a role in water and ion balance*. Vacuoles, a major characteristic of plant cells, exchange water and ions with the cytoplasm to help maintain cellular water balance. Toxic substances, pigments, and waste products as well as hydrolytic enzymes may also be stored in the vacuoles of some cells.

3.5 *Plastids are a diverse family of anabolic organelles*. There are approximately a dozen different types of plastids found in various plant tissues and organs. As a group, they function to synthesize all the biomolecules needed for plant life and play additional roles in sensing and responding to the environment.

3.6 *Plastids are developmentally related*. All types of plastids are derived from proplastids and are found in virtually all parts of the plant. Many different developmental patterns are found in the conversion to specific types of plastids at all stages of the plant life.

3.7 *Mitochondria synthesize ATP and small carbon skeletons*. Mitochondria are organelles with two membranes that carry out advanced stages of aerobic respiration. The outer membrane is functionally similar to other cell membranes, whereas the inner membrane functions to produce ATP by means of chemiosmosis on a folded surface. Enzymes of the citric acid cycle are only found in the matrix. Mitochondria assume many three-dimensional forms and may vary from a few to approximately 100 per cell.

3.8 *Microbodies are the site of specific biochemical pathways.* These organelles are bounded by a single membrane and lack internal membranes and DNA. They often contain high levels of enzymes or proteins, sometimes in a crystalline form. In leaves, they are designated as peroxisomes and oxidize glycolate to produce peroxides that in turn is decomposed by catalase, a process termed photorespiration. A second type of microbody designated as glyoxysomes functions with mitochondria to break down long chain oils for respiration and growth.

3.9 *The endoplasmic reticulum synthesizes proteins and some lipids*. Rough endoplasmic reticulum (with ribosomes attached to the membrane) produces, stores, and transports proteins. Smooth endoplasmic reticulum (without attached ribosomes) is relatively rare in plants, but when found in secretory structures, it may synthesize oils or terpenes.

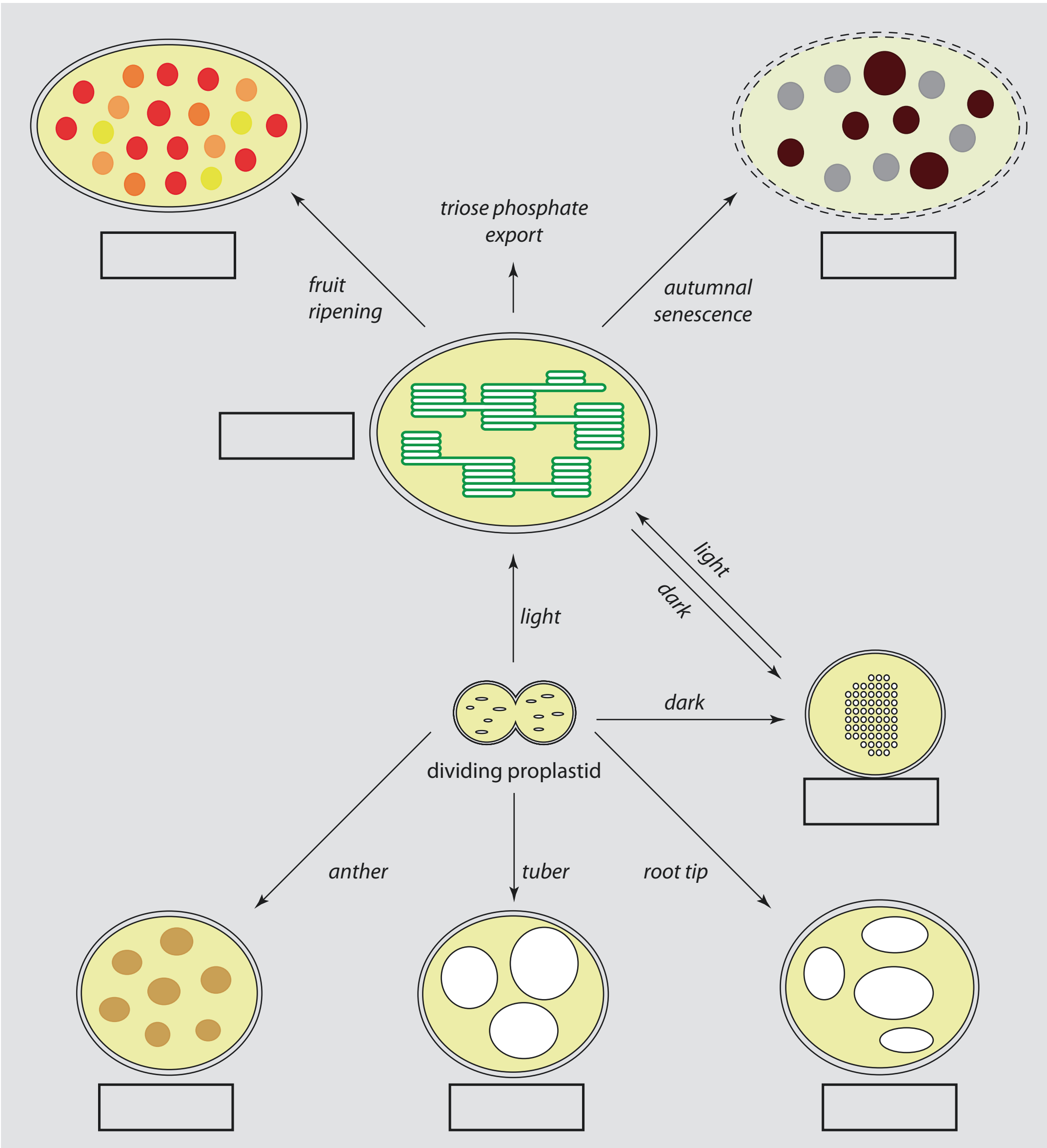
3.10 *The Golgi apparatus processes and packages polysaccharides and proteins for secretion*. The Golgi apparatus is comprised of functionally similar distinctive dictyosomes that transport certain proteins and carbohydrates in vesicles and subsequently to the cell surface for possible discharge. Based on function, there may be one to several Golgi apparatuses per cell. Dictyosomes play a significant role in the secretion of enzymes as found in carnivorous plants.

3.11 *The nucleus houses the cell's genetic material and participates in ribosome synthesis*. In addition to storing the genetic material, the nucleus contains a nucleolus which functions in the synthesis of ribosomes which come to full size after being transported through nuclear pores and into the surrounding cell cytoplasm.

3.12 *The cytoskeleton organizes the cell and helps traffic materials*. A plant cytoskeleton is a framework of protein strands composed of both structural and force-generating components. Microtubules and actin filaments give rise to the shape of the cell and the formation of the cell wall, whereas microtubules direct the movement of chromosomes during mitosis and meiosis. Motor proteins (forms of kinesin) move vesicles from Golgi trans face to cell surface and in other building processes driven by energy from ATP.

Concept Connections

1. On a separate sheet of paper, identify a name and at least one function for each of the plastid types shown in the figure below.



Concept Assessment

2. The cytoskeleton of a cell is comprised of
   a. cell wall and membranes.
   b. nucleus and cytoplasm.
   c. intrinsic and extrinsic proteins.
   d. microtubules and microfilaments.
   e. organelles and crystals.

3. Photorespiration is primarily a function of
   a. chloroplasts.
   b. microbodies.
   c. microtubules.
   d. mitochondria.
   e. dictyosomes.

4. In membranes, sugar groups are most likely associated with
   a. inner phospholipid layer.
   b. outer phospholipid layer.
   c. intrinsic proteins.
   d. intercalated cholesterol.
   e. hydrophobic unsaturated lipid chains.

5. The organelle most responsible for cellular water balance is the
   a. nucleus.
   b. chloroplast.
   c. vacuole.
   d. cell wall.
   e. cytoskeleton.

6. If the mitochondrion is the cell's powerhouse, the ________ is the cell's blueprint library.
   a. tannosome.
   b. ribosome.
   c. gerontoplast.
   d. nucleus.
   e. nucleolus.

7. To synthesize a protein and secrete it to the cell wall, a cell would need to use the
   a. nucleus.
   b. ribosomes.
   c. rough endoplasmic reticulum.
   d. golgi apparatus.
   e. all of the above.

8. What is the main anabolic organelle of the plant cell?
   a. nucleus.
   b. golgi apparatus.
   c. rough endoplasmic reticulum.
   d. vacuole.
   e. plastid.

9. What is the function of the cytoskeleton?
   a. organize the cell interior.
   b. synthesize ATP and small carbon skeletons.
   c. traffic vesicles through the cytoplasm.
   d. photosynthesis and photorespiration.
   e. a and c.

10. Ribosomes are found in the
    a. cytoplasm.
    b. chloroplast.
    c. vacuole.
    d. mitochondrion.
    e. a, b, and d.

11. Respiration involves the
    a. glyoxysome.
    b. gerontoplast.
    c. golgi apparatus.
    d. peroxisome.
    e. guard cell chloroplast.

Concept Applications

12. Plants have the ability to synthesize 100% of the biomolecules and high-energy molecules needed for life. If you were to genetically engineer a cat or a dog to do the same, what processes or organelles would you need to put into your pet?

13. Use the internet to search for the term "kleptoplast." How are kleptoplasts related to other plastid types? How are they different?

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Mitosis and Meristems

4.1 The Plant Cell Cycle Includes Interphase, Mitosis, and Cytokinesis – 125

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Introduction

Unlike animals, plants continue to grow and produce new tissues and organs throughout their lives. It is their adaptation to a stationary and autotrophic life habit. In order to maintain their supply of water and nutrients, plants must grow continuously, expanding the surface of their interaction with the environment. There are two principal types of plant growth, the growth in height or length (primary growth of stems, leaves, roots, and flowers) and the subsequent growth in thickness (secondary growth of stems and roots). Each type of growth takes place by both cell division (mitosis) and cell enlargement, and the cell divisions are primarily concentrated in specific zones called meristems, which contain structurally similar, undifferentiated (embryonic-like) parenchyma cells.

Primary growth is achieved mainly through the activity of apical meristems. Shoot apical meristems occupy the tips of the shoots, and root apical meristems are found at the tips of the roots. In addition, primary growth is found in some plants (mostly monocots) due to the activity of **intercalary meristems** (which was originally derived from the apical meristem but becomes located at some distance with non-meristematic tissues in between; refer to ► Sects. 4.13 and 11.2). In some cases, intercalary meristems may be located at each node of the stem, but each site is isolated with non-meristematic tissues. Secondary growth is found in some eudicot stems and roots and results in an increase in girth. Secondary growth will be addressed in detail in the chapters on xylem (► Chap. 7), phloem (► Chap. 8), stems (► Chap. 11), the vascular cambium (► Chap. 14), and wood (► Chap. 15). From that list, it can be seen that secondary growth is a large part of what makes a plant a plant.

4.1 The Plant Cell Cycle Includes Interphase, Mitosis, and Cytokinesis

The plant **cell cycle** (◘ Fig. 4.1) begins with a single cell and results in the production of two identical copies called daughter cells. Much of the time, a cell is in **interphase**. Interphase may be brief in an actively growing tissue, or it may last weeks or years in a dormant tissue. The portion of interphase indicating the growth period prior to duplication of the chromosomes is called G1 (meaning Gap 1). The signal to divide comes during interphase and initiates chromosome duplication, also called the S phase of interphase for DNA synthesis. The cell may then enter a second growth phase (designated as G2) or proceed directly to mitosis.

Mitosis is division of the single nucleus into two daughter nuclei, and it is usually followed by **cytokinesis**, which is division of the **cytoplasm** into two daughter cells. Mitosis and cytokinesis, key stages in the cell cycle, will be examined in detail in the next few

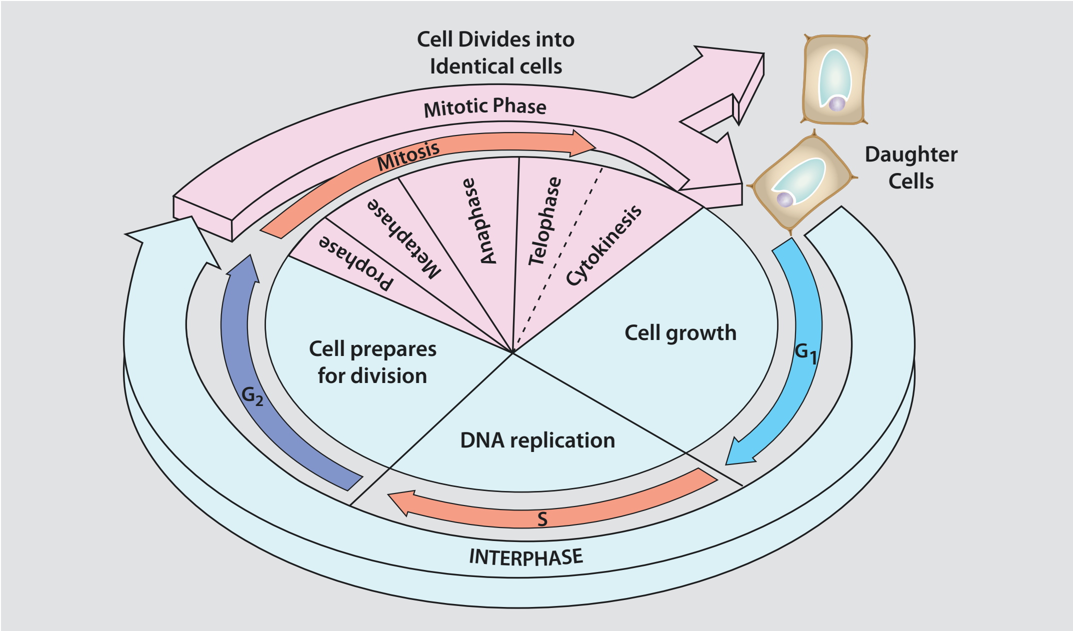


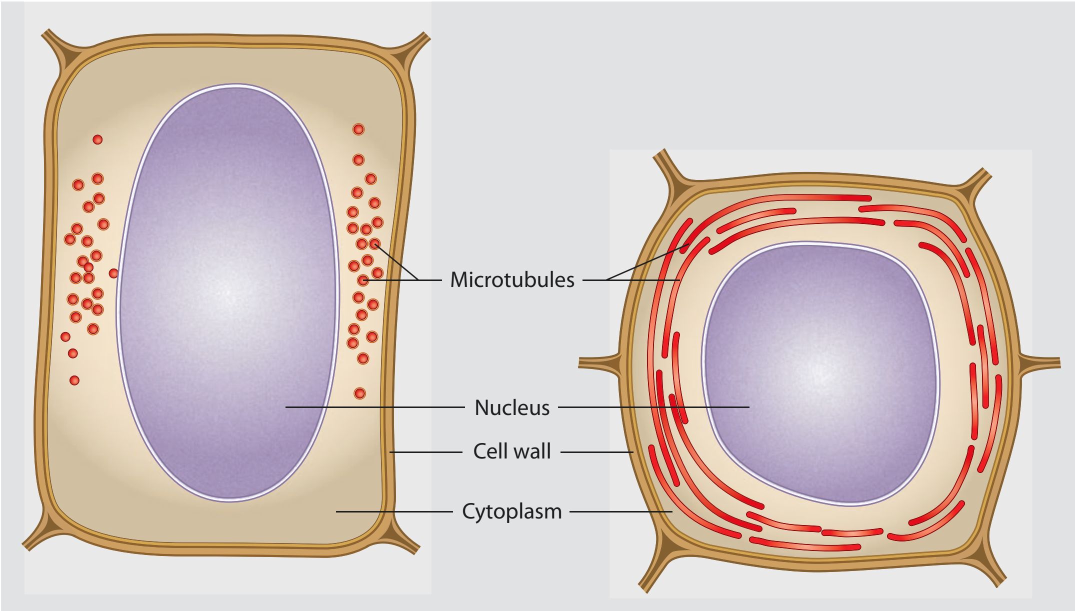
Fig. 4.1 The plant cell cycle: interphase, mitosis, and cytokinesis. Throughout the process of interphase, the cell produces proteins and grows. In G_1, proteins degrade lipids and carbohydrates to form energy. In G_2, prior to mitosis, the more proteins are formed, and mitochondria grow and divide. Follow the diagram in a clockwise direction (Redrawn from Crang and Vassilyev 2003)

sections. The production of egg and sperm cells via **meiosis** will be discussed in ► Chap. 17 (Flowers and Male Reproductive Structures) and 18 (Female Reproductive Structures and Embryogenesis).

4.2 A Pre-prophase Microtubule Band Precedes Mitosis and Defines the Plane of Cell Division

The first sign of incipient mitosis in plants is the clustering of cortical cytoplasmic microtubules in a **pre-prophase band** of microtubules (◘ Fig. 4.2). It is formed at the site where the new cell wall between two daughter cells appears at the end of cytokinesis and coincides with the future metaphase plate. This phase is short-lived, inasmuch as the microtubules become reassembled into the mitotic spindle at prophase of mitosis.

The pre-prophase band determines the division plane of the cell, which determines the relative sizes of the two daughter cells (Rasmussen et al. 2011). In many instances, the daughter cells are equal in size (symmetric), and function, as for the parenchyma of ground tissues. However, in instances in which the daughters have decidedly different developmental fates, the plane of division may be asymmetric. A phloem sieve tube element (large) and its companion cell (small) are the two daughters of a single progenitor and result from the asymmetric placement of the pre-prophase band (see ◘ Fig. 8.4 a–d).



■ **Fig. 4.2** Pre-prophase microtubule band seen in side view (left) and top view (right) (Redrawn from Crang and Vassilyev 2003)

4.3 Mitosis May Be Divided into Distinct, but Continuous, Stages

Division of the nucleus—via the processes of mitosis or meiosis—always precedes the origin of new cells, which occurs by cytoplasmic division (cytokinesis). Unlike plastids and mitochondria, the nuclei never divide into two by simple constriction. Such a method could not provide equal distribution of chromosomes between daughter nuclei. An exact distribution is achieved by a complex and very precise mechanism known as mitosis, the universal form of nuclear division common to all eukaryotes. Four phases of mitosis are recognized: prophase, metaphase, anaphase, and telophase (■ Fig. 4.3a). Interphase is the portion of the cell cycle between mitotic events.

■ ■ *Prophase*

Chromatin condenses and **chromosomes** begin to appear. Near the beginning of prophase, the pre-prophase band of microtubules and nucleolus (a prominent nuclear structure where ribosome synthesis occurs) disappear, and the nuclear envelope disintegrates. A set of microtubules, called the spindle apparatus, is formed. Early mitosis and spindle formation are quite different between plant and animal cells. Plants lack centrosomes, structures in animals that serve as the nucleation point and control center for spindle formation. In its place, other proteins, particularly *Ran* (*Ra*s-related *n*uclear) proteins and the kinetochore, direct spindle formation (Zhang and Dawes 2011). The plant spindle apparatus begins at the poles of the cell and extends to the center of the cell. Some, but not all, of the

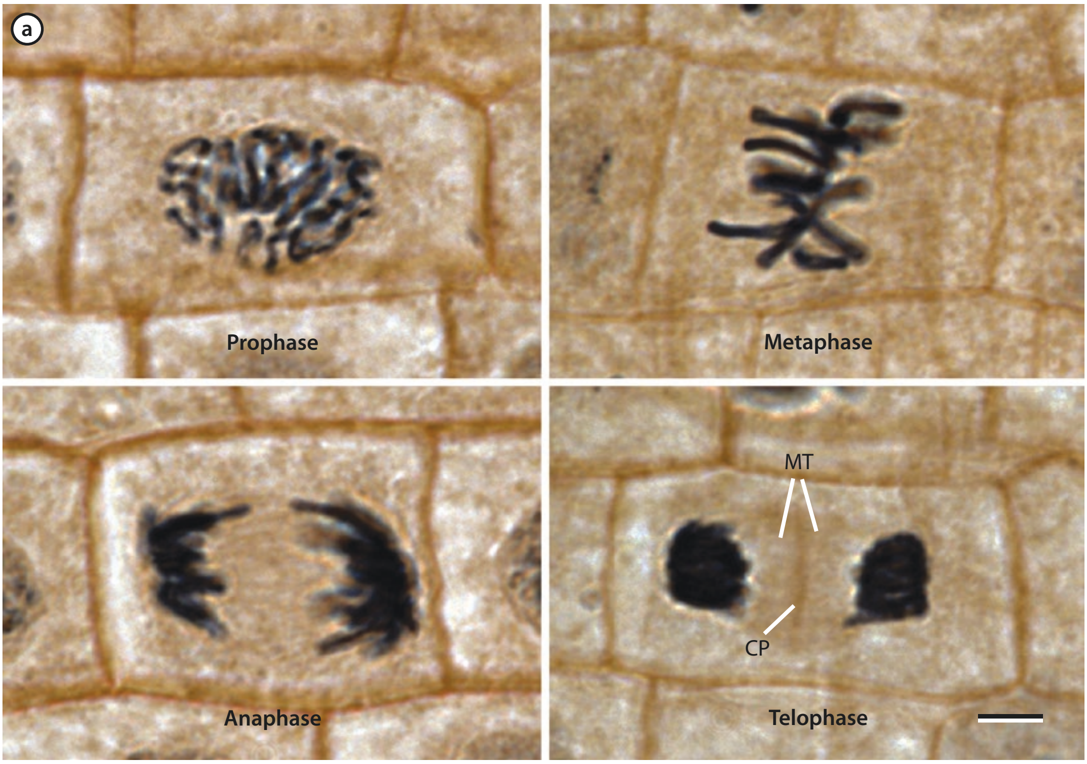


Fig. 4.3 **a** The four phases of mitosis in an onion (*Allium cepa*) root tip: prophase, metaphase, anaphase, and telophase. Microtubules (MT) and the forming cell plate (CP) can be seen in the telophase panel. Scale bar = 10 µm (RR Wise)

spindle microtubules are attached to chromosomes at the centromeres. It becomes apparent that each duplicated chromosome is composed of a pair of identical threads, or sister chromatids.

Metaphase

The duplicated chromosomes aggregate in the equatorial plane of the cell, a site determined earlier by the pre-prophase band of microtubules. The spindle microtubules are responsible for the movement, and both push (via polymerization) and pull (by depolymerization or using motor proteins) the chromosomes to the cell equator. The unattached microtubules of the spindle may aid in formation of new wall plasmodesmata connecting the cytoplasm of the daughter cells with each other.

Anaphase

Sister chromatids separate from each other and move to opposite poles of the spindle as individual chromosomes. In addition to the chromosomes, it is also believed that some organelles may be segregated to the cell poles by the action of microtubules, either as a part of the spindle apparatus or separately (Nebenführ et al. 2000).

Telophase

The individual chromosomes reach the poles of the cell, and two new nuclear envelopes begin to reform. Each daughter nucleus gets

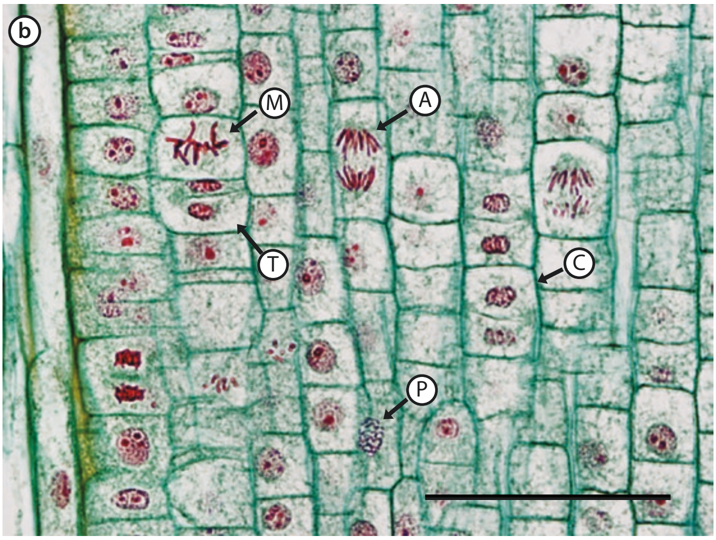


Fig. 4.3 **b** The stages of mitosis and cytokinesis may be seen in a single longitudinal onion (*Allium cepa*) root meristem section. P = prophase, M = metaphase, A = anaphase, and T = telophase with a developing cell plate. C marks two cells in which cytokinesis and cell plate formation have completed. Scale bar = 50 µm (RR Wise)

a set of chromosomes genetically identical to one another and to that of the parent nucleus. Finally, chromatids de-condense and nucleoli (plural for nucleolus) are restored.

Shoot and root apical meristems (discussed in subsequent sections in this chapter) are regions of active mitosis. Figure 4.3b shows an area of approximately 50 cells in an onion root tip. All stages of mitosis can be seen in different cells of the field of view.

Box 4.1 Kinesin-5 Protein Is Important in Spindle Formation and Microtubule Organization in Plants

Kinesin-5 proteins are called motor proteins because they physically move along microtubules and can transport substances from the center of the cell to the poles via filaments (Vale 2003). Kinesin-5 proteins have been documented to influence spindle formation in both animals and yeast. To discover if these proteins were conserved in plants, Bannigan et al. (2007) used a temperature-sensitive arabidopsis mutant (*rsw7*; *radially swollen 7*) to investigate if the kinesin-5 gene was conserved in plants. This mutant contained a single-nucleotide mutation (SNP) where one nucleotide was substituted for another, leading to a change in the amino acid sequence, and ultimately, it changed the structure of the protein. The research indicated that spindle formation was modified in the mutant as compared to the wild-type plant. Similar to animals and fungi, when the allele is mutated in plants, the spindle didn't function properly. Thus, the kinesin-5 protein appears to be conserved over the course of evolution among at least three major groups of eukaryotes.

Kinesin-5 genes also are involved with microtubule organization during interphase. Bannigan et al. (2007) also grew wild-type and *rsw7* mutant plants at 19 °C and at 30 °C and observed microtubule organization during interphase using confocal microscopy. No differences were noted in the plant root meristems at 19 °C. However, at 30 °C, the microtubules of the cells of the mutant plants showed disorganization during interphase, whereas the wild-type plants were normal with microtubules arranged in parallel. Thus, the data indicate that kinesin-5 of the *rsw7* gene is also involved in the organization of microtubules during interphase.

References: Vale (2003) and Bannigan et al. (2007)

4.4 Cytokinesis Begins with Initiation of the Cell Plate and Grows by the Deposition of Callose

Cytokinesis follows telophase and starts with the initiation of a **cell plate** (the developing cell wall) in the equatorial plane between the two daughter nuclei that was defined by the pre-prophase band (Verma 2001). The cell plate is disc-like and grows centrifugally from the center outward toward the walls of the mother cell. ◘ Figure 4.4a shows a cell plate forming in a dividing onion root tip cell. The cell plate has not reached the cell wall on the left but has on the right side.

Cell plate growth occurs by the fusion of dictyosome vesicles and is associated with the **phragmoplast**, an aggregation of microtubules and other proteins with their orientation perpendicular to the expanding cell plate (◘ Fig. 4.4b, c). Vesicles of cell wall precursors produced by the Golgi apparatus are trafficked to the developing cell plate by the microtubules of the phragmoplast and fuse to the developing cell plate. The vesicle contents contribute to the cell wall, and the vesicle membranes contribute to the plasma membrane. The actual vesicle trafficking along the microtubules is mediated by an array of proteins including molecular motors, tethering proteins, fusion proteins, and regulatory elements (McMichael and Bednarek 2013). Cell plate growth is initiated by the deposition of **callose**, a polysaccharide which is soon replaced by cellulose (Samuels et al. 1995). Eventually, the cell plate grows to the wall of the mother cell (◘ Fig. 4.4d), the microtubules of the phragmoplast depolymerize, and the separation of daughter cells is complete. Additional cell wall material is then laid down all around the cell walls—not only at the cell plate—as the two new daughter cells expand.

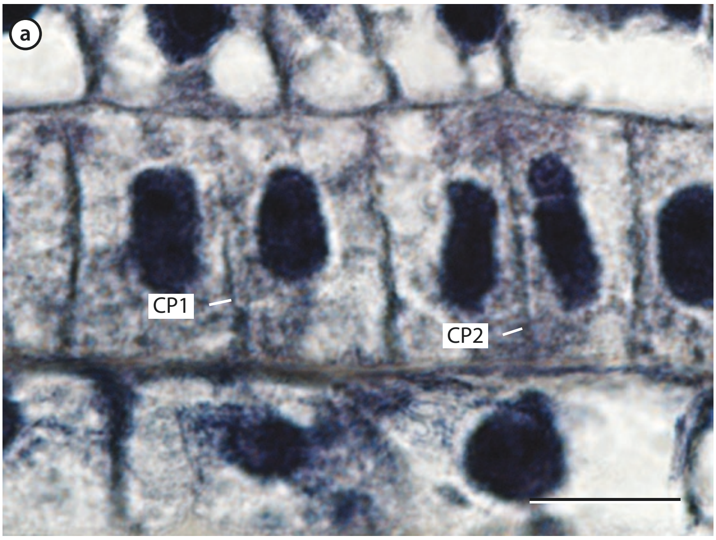


Fig. 4.4 **a** Cell plate formation in onion (*Allium cepa*) root tip. Two developing cell plates are shown. Cell plate #1 (CP1) is at a slightly earlier stage of development than CP2. Scale bar = 10 µm (Crang and Vassilyev 2003)

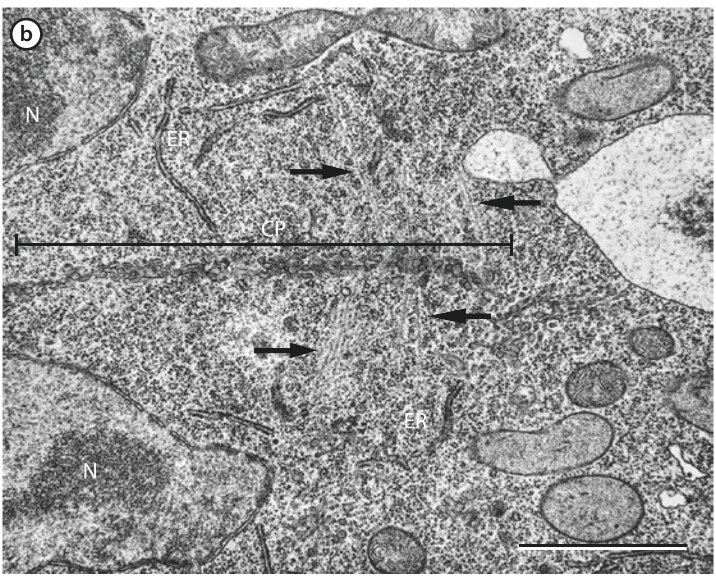


Fig. 4.4 **b** Cell plate in an early stage of initiation in *Arabidopsis thaliana*. A TEM view of a forming cell plate (CP) with an aggregation of phragmoplast microtubules (*arrows*) and endoplasmic reticulum (ER) near the aligned vesicles. The two daughter nuclei are labeled N. Scale bar = 1 µm. (Image from: Ledbetter and Porter (1970), with permission)

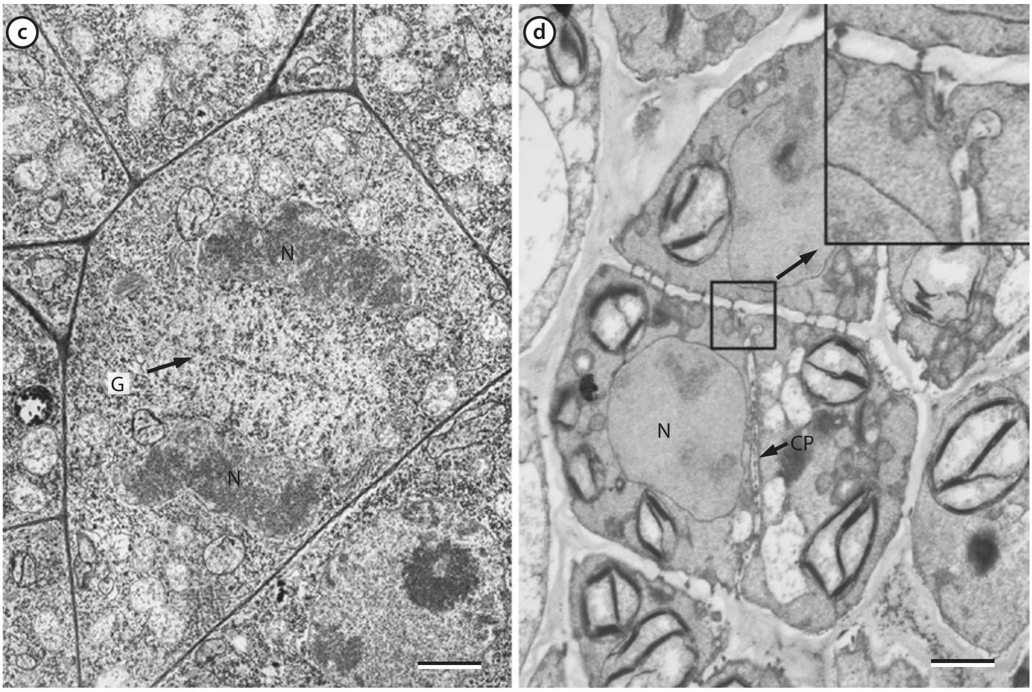


Fig. 4.4 Cell plate formation at the telophase stage of mitosis. **c** Early cell plate formation in a cell from sporogenous anther tissue of the African violet (*Saintpaulia ionantha*). An accumulation of microtubules and Golgi vesicles (G) aligned in the equatorial plane between reforming daughter nuclei (N, with condensed chromatin) mark the site of the future cell plate. **d** Late cell plate (CP) formation in a dividing leaf cell of water lettuce (*Pistia stratiotes*). Inset shows the cell plate dividing the two daughter cells is not quite fused with the mother cell wall. The envelope surrounding the nucleus (N) has reformed, and the chromatin has de-condensed. Scale bars = 2 µm in both panels. (**c** Image from Ledbetter and Porter (1970), with permission. **d** Image courtesy of Dr. Gayle Volk; GM Volk and VR Franceschi, Washington State University)

4.5 Microtubules Play a Critical Role in Mitosis and Cytokinesis

As explained in ► Sect. 3.12, microtubules are one component of the cell's cytoskeleton. Microfilaments are the other. Microtubules are polymers of the protein tubulin and can form (polymerize) and dissolve (depolymerize) in response to the needs of the cell. Upon depolymerization, the individual tubulin monomers persist and are recycled into new microtubules via polymerization.

Microtubules are key players in the cell cycle. ◘ Figure 4.5 shows some of the multiple roles they play. Referring to the figure:

(a) *Interphase*: Cortical microtubules are aligned within the inside of the cell wall. The microtubules perform many functions, chief among them being to direct the synthesis of cell wall cellulose microfibrils (refer to ► Chap. 5).

(b) *Pre-prophase band*: Microtubules form a band around the equatorial region of the cell marking the plane of future cytokinesis.

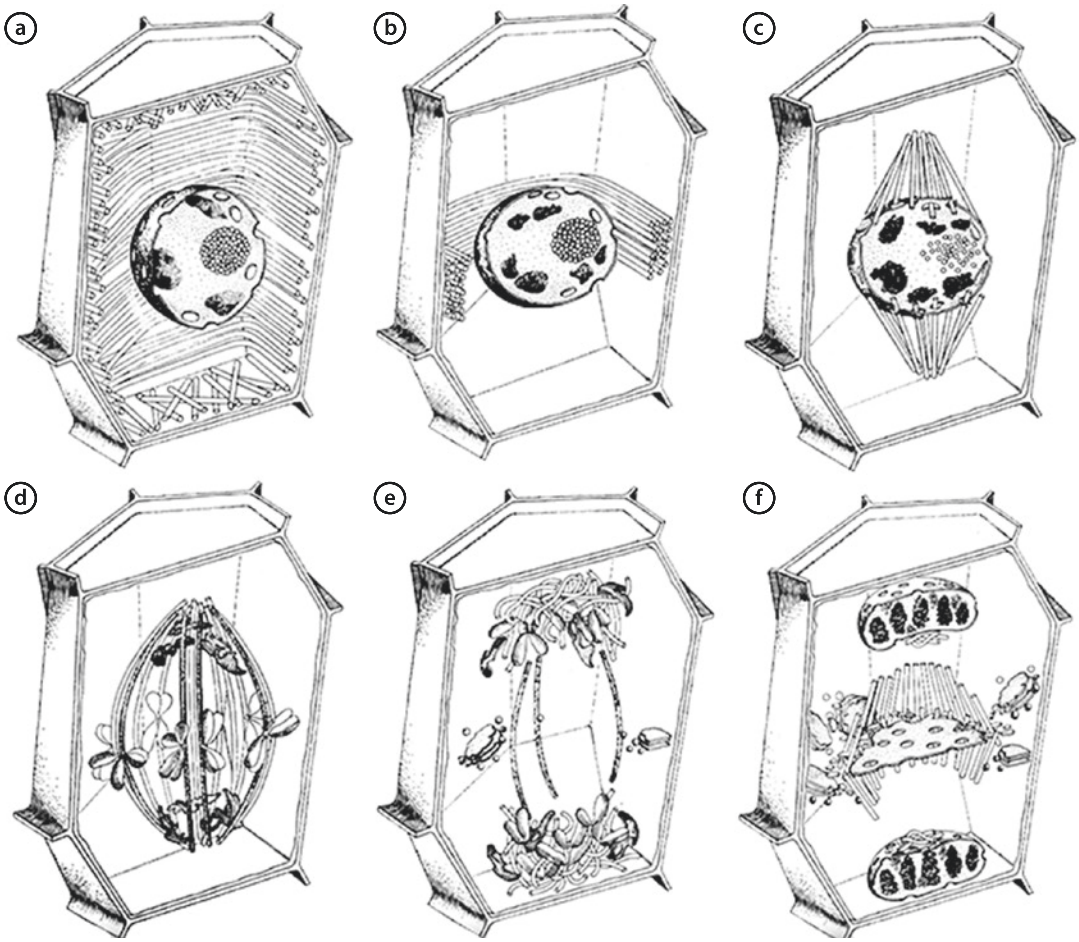


Fig. 4.5 The multiple roles of microtubules throughout the cell cycle. See text for explanation. (Drawing from Ledbetter and Porter (1970), with permission)

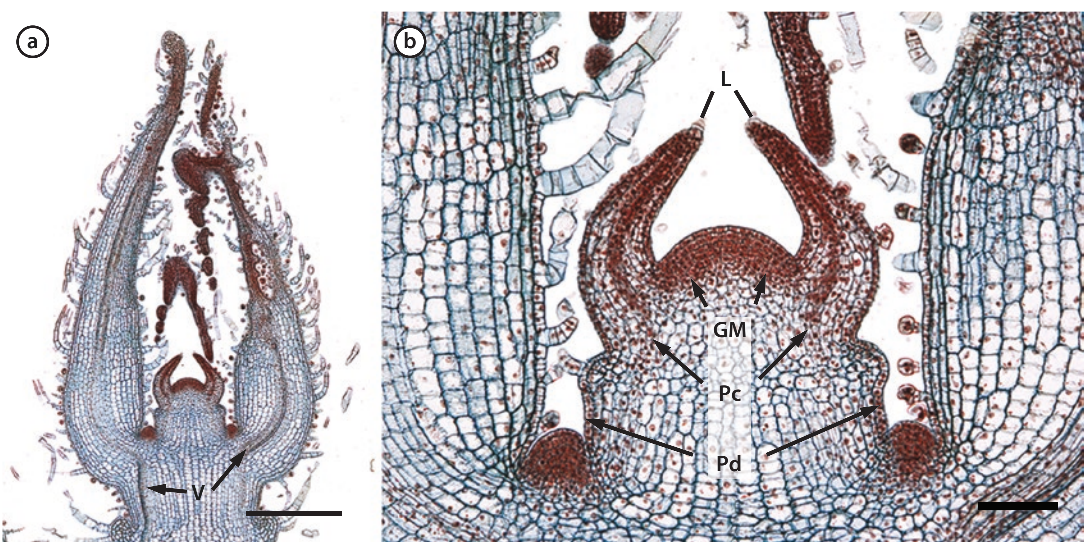
(c) *Prophase*: Cytoplasmic microtubules disappear and a mitotic spindle of microtubules is formed.
(d) *Metaphase*: Chromosomes are aligned on an equatorial plate of the spindle.
(e) *Anaphase*: Interzonal fibers extend from one pole to the other. Chromatids are moved to opposite poles of the spindle. Dictyosomes (two are shown) begin to produce vesicles, which will fuse laterally initiating the cell plate.
(f) *Telophase*: The spindle microtubules disappear, and a phragmoplast is formed whose component microtubules are concentrated at the periphery of the cell plate, and which grows centrifugally toward the parent cell wall. The phragmoplast microtubules remain at the edge of the cell plate until they reach the parent cell wall. They then depolymerize and disappear.

4

4.6 Apical Meristems Are the Sites of Primary Growth

Mitosis occurs in terminal zones of cells called the meristem, of which there are two types—apical meristems, discussed here, and lateral meristems which will be discussed briefly in ► Sect. 4.15 and in more detail in ► Chap. 14 (Vascular Cambium) and ► Chap. 16 (Periderm). Apical meristems originate during embryogenesis at the two poles of the embryo axis as shoot and root apical meristems (refer to ► Chap. 18, Female Reproductive Structures). The shoot apical meristem (SAM) gives rise to all aboveground organs of the plant such as the stem, leaves, and reproductive organs (flower parts, fruits, and seeds). In addition, many belowground organs such as tubers, bulbs, and rhizomes are actually underground stems and are thus derivatives of a shoot apical meristem. The root apical meristem (RAM) will be discussed below in ► Sect. 4.11.

The shoot apical meristem (◘ Fig. 4.6) gives rise to three tissues, which are also called meristems: the protoderm, the procambium, and the ground meristem. The difference between the SAM and the other three meristems has to do with the potential fates of the resulting daughter cells. SAM (and RAM) cells are **totipotent**, meaning that they have the plasticity to differentiate into any other cell type (toti = *all*). Thus, they produce the other meristems. However, the cells generated by the protoderm, procambium, and ground meristem are only **pluripotent** (pluri = *many*). While they can produce a variety of cell types, they are more restricted in how many cell types they can produce, as each of these three meristems has a specific tissue to produce.



◘ **Fig. 4.6** Longitudinal sections of a coleus (*Plectranthus* sp.) shoot tip. **a** Low magnification view showing the position of the shoot apical meristem (*) and mature vascular strands (V). **b** Higher magnification view showing emerging leaves (L), ground meristem (GM), procambium (Pc), and the protoderm (Pd). The developing leaves are covered with trichomes, which are maturing from the protoderm cells. Scale bars = 0.5 mm in **a** and 0.1 mm in **b** (**a**, **b** RR Wise)

The protoderm is the outer layer of cells that covers the young expanding leaves that arise from the apex (◘ Fig. 4.6a) as well as the apex itself (◘ Fig. 4.6b). Their plane of division is perpendicular (**anticlinal**) to the surface of the apex, so as mitosis proceeds, the daughter cells are pushed to either side along the surface in order to cover the expanding shoot tip. Cells are considered to be part of the protoderm as long as they continue to divide via mitosis. Eventually, mitosis will cease, and the epidermal cells produced by the protoderm will mature into epidermal pavement cells (nonspecialized irregular-shaped protective epidermal cells), guard cells, trichomes, and root hairs, in the case of roots.

The procambium (◘ Fig. 4.6b) produces the cells that will develop into the xylem and phloem tissues of the primary vascular strands. As for the protoderm, active mitosis defines the procambium. Keep in mind that the SAM and RAM are engaged in primary growth. Secondary growth is driven by subsequent divisions of the lateral meristems and will add additional vasculature later on.

The ground meristem gives rise to the cortex and pith in stems, cortex in roots, and to mesophyll in leaves. It is indicated in ◘ Fig. 4.6b. Each cell in the ground meristem undergoes multiple rounds of mitosis but stays in the same relative position in the stem. Therefore, the daughter cells appear as ordered columns of cells well down the length of the stem.

4.7 The Shoot Apical Meristem Is the Site of Lateral Organ Initiation

The shoot apical meristem not only produces the meristems that will fuel primary growth of the **epidermis** (protoderm), pith (ground meristem), and vasculature (procambium); it is also responsible for the initiation of lateral organs, such as leaves, axillary buds, flowers, and lateral branches (◘ Fig. 4.7a) (Ha et al. 2010). This external initiation of organs is termed an exogenous origin because the lateral organs arise from the surface (exo- or outside) of the tip.

◘ Figure 4.7b shows the surface of a waterweed shoot tip as viewed in the scanning electron microscope. The SAM is inside the narrow tip region, and a series of ridges, which broaden out, are the emerging leaf primordia. These ridges, also called **leaf buttresses**, alternate in a precise, genetically determined pattern that will determine the phyllotaxy (a.k.a. leaf arrangement). Because leaves and lateral branches are formed exogenously, they are evident from the exterior of the organ as soon as initiated. In contrast, lateral roots are formed endogenously and are not evident until they break through the root rhizodermis. Refer to ► Sect. 4.12.

Leaf initiation from the SAM of eudicots is shown in ◘ Fig. 4.7c. The cotyledons emerge first and, in the case of *Arabidopsis lyrata*, expand and turn green. The SAM is found between the two cotyledons and is the site of leaf initiation, which can be seen in ◘ Fig. 4.7d.

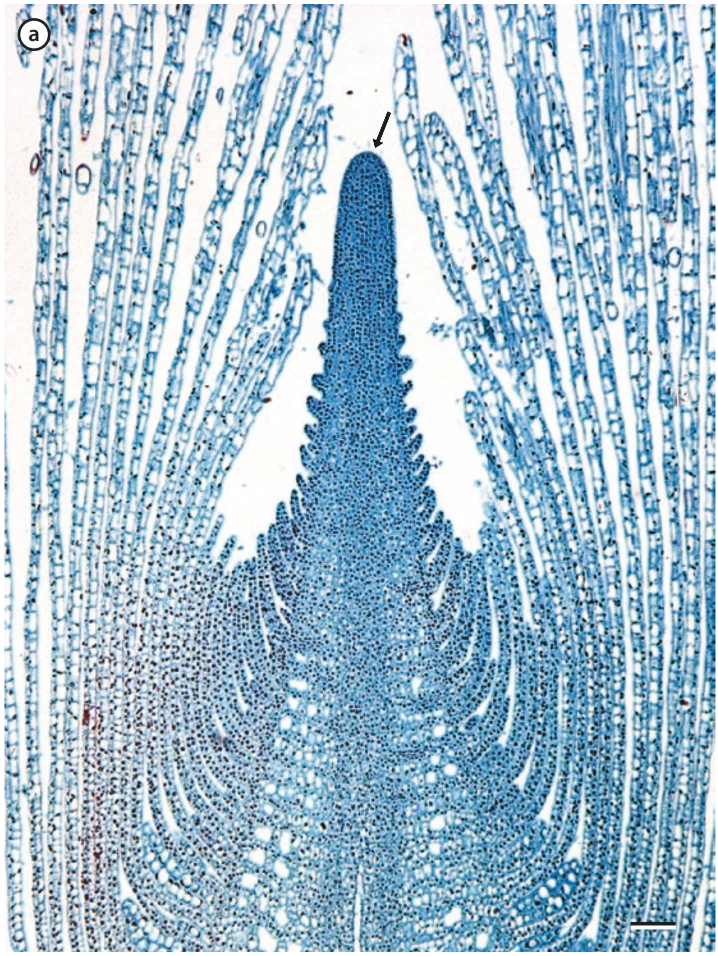
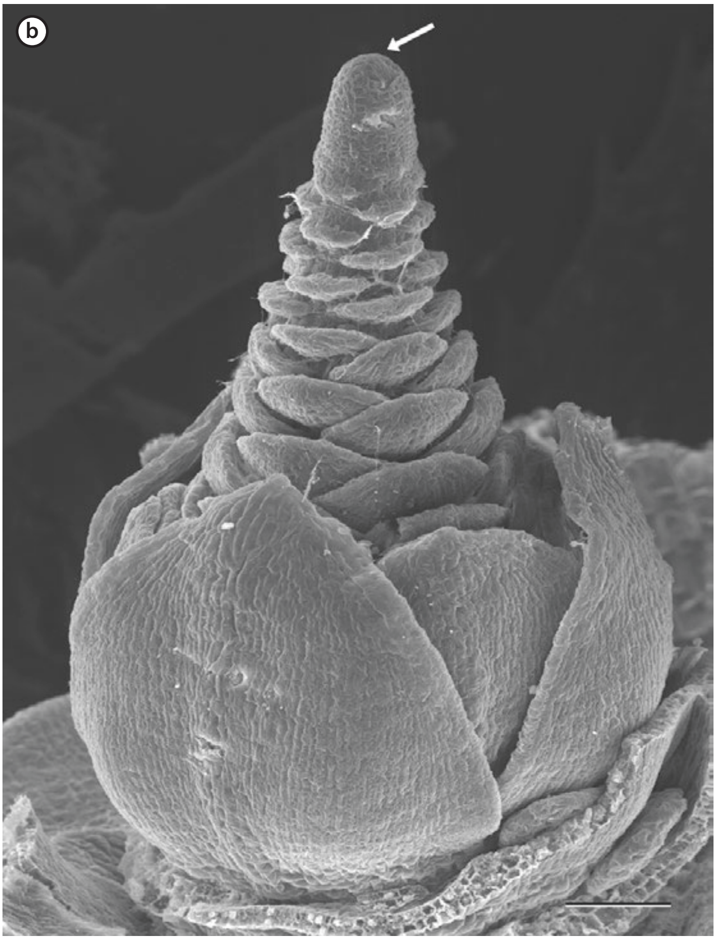


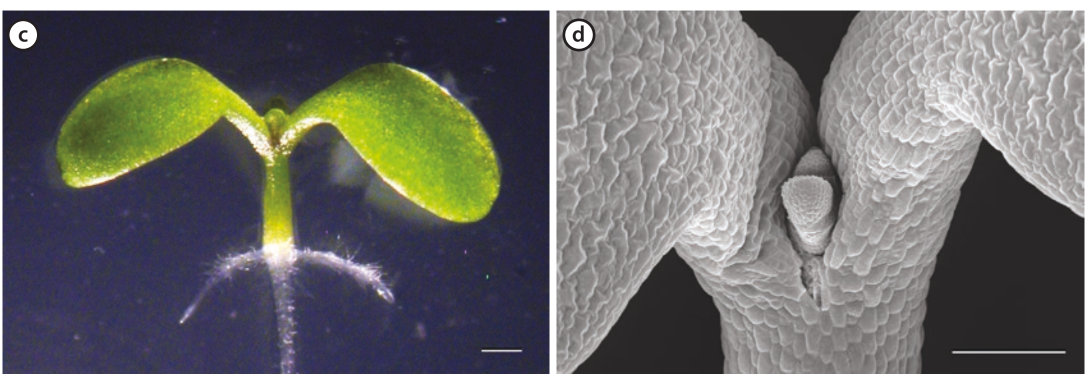
Fig. 4.7 **a** A median longitudinal section of waterweed (*Elodea* sp., an aquatic monocot) shoot apex, showing numerous leaf primordia ranging from small (close to the shoot apical meristem or stem tip) to large (further away from the SAM). Scale bar = 100 µm (RR Wise)

4.8 Axillary Buds Arise De Novo in the Developing Leaf Axis

The **leaf axis** is the upper (and usually smaller) angle between a stem and the petiole of a leaf. Thus, the leaf axis is a location or region, and not a physical tissue or structure, and is the site of lateral buds that are the source of additional leaves, flowers, or branches. **Axillary buds** arise from an **axillary meristem** and begin to form soon after leaf initiation, as can be seen in Fig. 4.8 (single arrows). Within a short period of time, the axillary buds may develop their own SAM, protoderm, ground meristem, procambium, and leaf primordia (double arrows). Actively growing regions, such as SAMs, produce the plant growth regulator indole acetic acid (IAA, Ha et al. 2010), which diffuses down the stem and inhibits the development of axillary buds. This is a phenomenon known



◘ **Fig. 4.7** **b** Scanning electron micrograph of a waterweed (*Elodea* sp.) shoot tip. The shoot tip would normally be enclosed by numerous mature and developing leaves, which were removed from the shoot tip. The SAM is indicated by the arrow. Scale bar = 100 µm (RR Wise)



◘ **Fig. 4.7** Seedlings of the lyre-leaved sand cress (*Arabidopsis lyrata*) showing the emergence of the first true set of leaves from the shoot apex. Large, green cotyledons are visible in the macro image in **c**, while the first two emerging leaves (*arrows*) can be seen in the SEM image in **d**. The shoot meristem is between the two emerging leaves and is not visible in these images. Scale bars = 500 µm in **c** and 200 µm in **d** (**c**, **d** RR Wise)

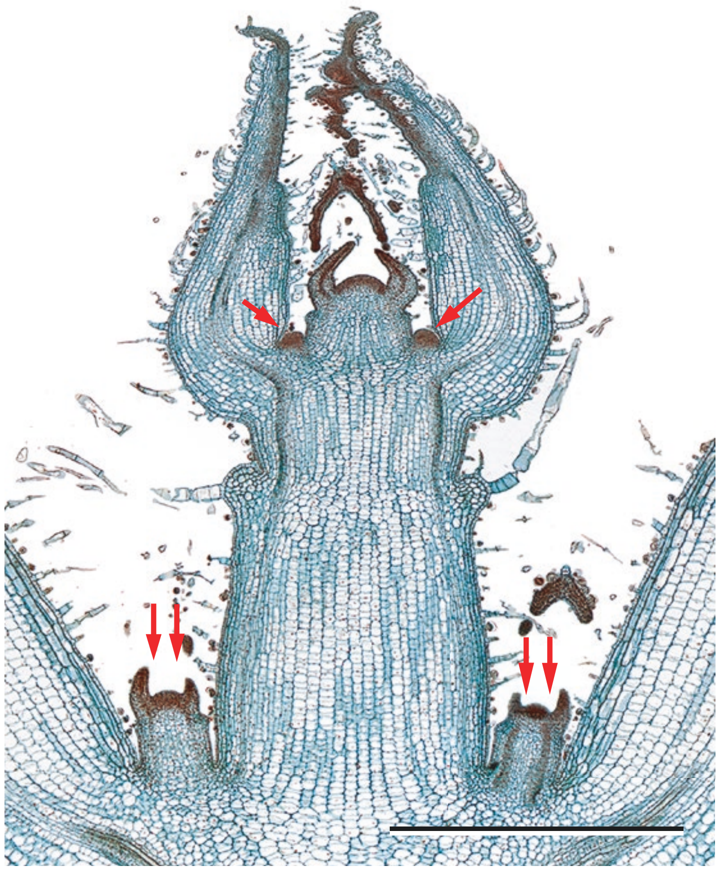
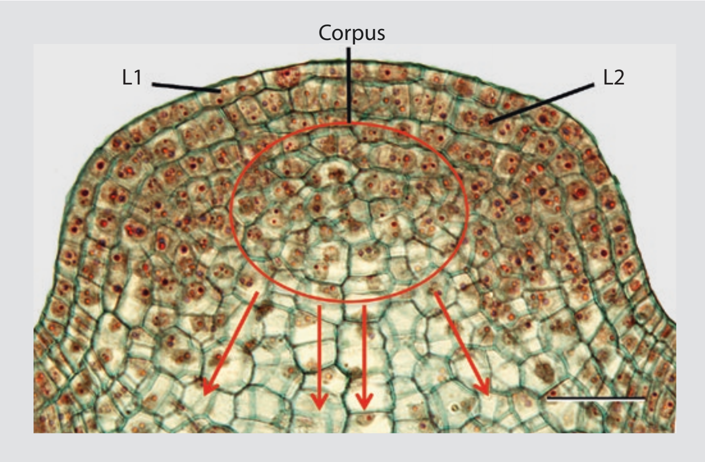


Fig. 4.8 Median longitudinal section of the shoot tip of coleus (*Plectranthus* sp.) showing newly formed buds (*single arrows*) and older (*double arrows*) buds developing in the leaf axis. Scale bar = 1 mm (RR Wise)

as **apical dominance**. Many eudicots can be induced to produce more lateral leaves and stems by removing apical meristems and thus releasing the growth of the axillary meristems. Horticulturists call this "pinching back" and use the technique to produce bushier plants with more flowers.

Box 4.2 Deep Buds Explain Adaptation to Fire in Cork Oak, *Quercus suber*

While many plant species have adapted to fire by remaining below ground as dormant seeds within soil seed bank or as rhizomes that resprout after fire, most plants don't resprout from buds located on stems as either the buds and/or vascular cambium are damaged. There is a least one exception, *Quercus suber*, the cork oak that has a thick, rapid-growing bark. Cork oak is an economically important plant as its phellem is most notably used to cork wine bottles, but the cork is also used as in flooring, shoes, and bulletin boards.



■ **Fig. 4.9** Median longitudinal section of the dome-shaped shoot apical meristem in coleus (*Plectranthus* sp.) showing a tunica-corpus organization in this angiosperm. The red arrows indicate the fate of corpus derivatives. Scale bar = 50 μm (RR Wise)

While cork has isolative properties and doesn't burn readily, little has been known about the physical structures that allow for regrowth from epicormic buds, buds that form beneath the bark of a trunk or stem. Burrows and Chisnall (2016) studied the anatomy and morphology of the thick phellem and epicormic buds (arising from dormant tree buds) of cork oak. Among other findings, they observed that many overlapping bud scales covered the buds. More importantly, they noted that the buds were surrounded by a thick layer of phellem that would provide protection from intense fire. Interestingly, they observed longitudinal sections of buds that were not completely covered by the phellem because a tube formed around the buds allowing for unobstructed growth of the meristem toward the surface. These anatomical and morphological observations help explain why epicormic buds resprout following high-intensity fires in cork oak.
Reference: Burrows and Chisnall (2016)

4.9 Tunica-Corpus Organization Describes Shoot Apical Meristem Growth in Many Eudicots

Most eudicotyledon SAMs have a **tunica-corpus** arrangement (Reeve 1949). The **tunica** comprises two outer layers of the dome in this apex, which are designated L1 and L2 (■ Fig. 4.9). Its cells divide only anticlinally (i.e., in a plane perpendicular to the surface). The cells of the corpus divide in various planes (periclinally [parallel to surface] and anticlinally [perpendicular to surface]). The outer cell layer of the tunica (L1) gives rise to protoderm, which

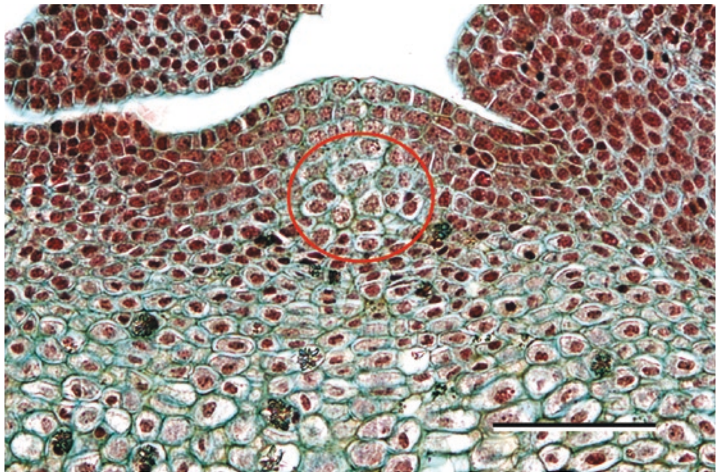


Fig. 4.10 Shoot apical meristem of ginkgo (*Ginkgo biloba*). The zone of central mother cells is indicated within the red circle. Scale bar = 50 µm (RR Wise)

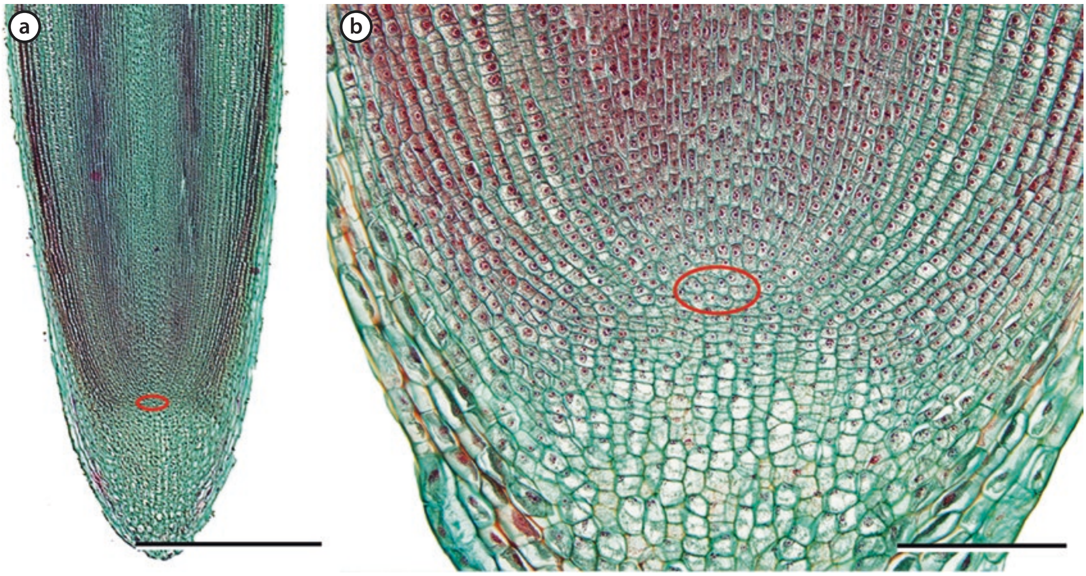
in turn will form the epidermis of the shoot. The second tunica layer (L2) provides cells that add volume to the growing shoot tip. The **corpus** generates cells that will become the ground meristem and procambium, and thus the resulting pith and vasculature.

4.10 Gymnosperms Do Not Possess a Tunica-Corpus

Gymnosperms do not usually show a tunica-corpus type of organization in their shoot apical meristem (Foster 1938). The outer cells of the apical dome divide both anticlinally (i.e., perpendicular to the surface) and periclinally (parallel to the surface), thus contributing cells to the interior of the promeristem. The more striking feature of gymnosperms is the presence of a distinct zone of **central mother cells** in a median position below the surface layer (Fig. 4.10). The central mother cells are irregularly arranged and, for most of the growing season, are relatively large and thick-walled. Note the lack of regular columns of cells in the interior of the ginkgo stem in Fig. 4.10 that would result if ginkgo had a ground meristem proper.

4.11 The Root Apical Meristem Provides the Primary Growth of Roots

The growth of the roots in length (i.e., primary growth), as is the growth of the shoots, is provided by the apical meristems where mitotic cell divisions occur. However, in roots, a small group of cells at the extreme apex, called the **quiescent center** (Fig. 4.11a, b), divide very infrequently, and the highest rate of cell divisions is observed in adjacent tissues of the root tip. Feeding radioactive DNA nucleotides to growing root tips originally identified the quiescent



◘ **Fig. 4.11** **a**, **b** Longitudinal section of a pea (*Pisum sativum*) root tip. The quiescent center (*red circle*) may be distinguished as a zone of convergence of cell tiers. Scale bars = 500 µm in **a** and 100 µm in **b** (**a**, **b** RR Wise)

center. Autoradiography then revealed that a small group of cells at the root tip was unlabeled, because they rarely undergo mitosis. The surrounding cells, however, took up large amounts of the radioactive compounds. Thus, the quiescent center concept was born (Clowes 1956). However, standard light microscopy of stained sections, such as that seen in ◘ Fig. 4.11a, b, cannot reveal which cells are truly quiescent and which are not. Identification of the quiescent center, therefore, is typically based on location, not appearance.

The cells surrounding the quiescent center are mitotically active and produce the protoderm, ground meristem, and procambium, which are active in the so-called zone of division. The overall structure of the root—i.e., the zones of division, elongation, and maturation—will be discussed in more detail in ► Chap. 10, Roots.

The RAM is different from the SAM in two important ways. First, as mentioned previously, it does not produce lateral roots, whereas the SAM does produce leaves. Second, the RAM generates the root cap, and there are two basic types of root cap formation. A "closed" root apical meristem has discrete portions that generate separate regions of the root and root cap. The central core of the root cap (columella) is produced by a discrete cell type in the RAM (called the calyptrogen or the columella mother cells), while the outer cells of the root cap are generated by the same RAM initials that produce the root epidermis. The root cap can be thought of as being exterior to and separate from the developing protoderm (the outermost tissue of the root tip proper), and atypically a boundary may be seen between the two (◘ Fig. 4.11c). The root tip, immediately behind the root cap, develops from a separate region of the RAM, and in much the same manner as the shoot, apical meristem develops. This arrangement is found in some eudicots and many monocots. An "open" RAM lacks the distinctly separate origins of

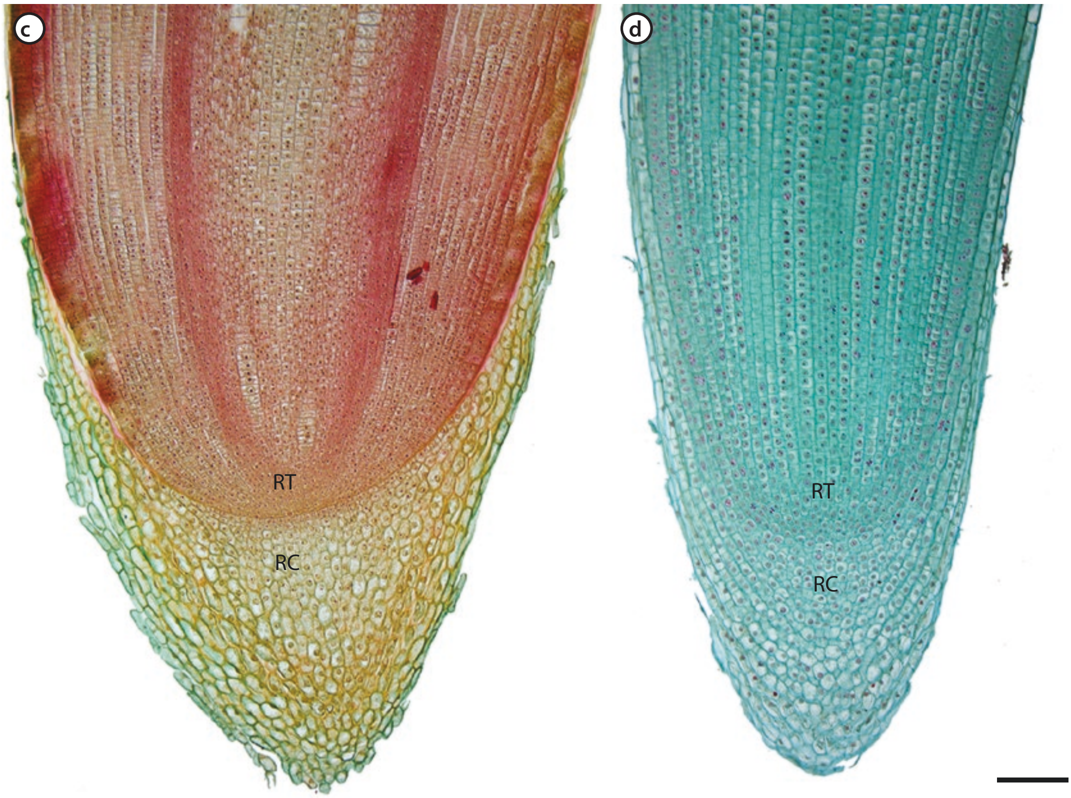


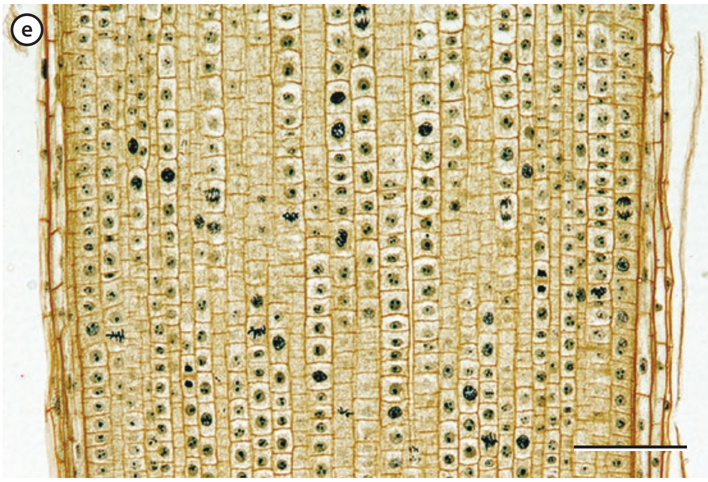
Fig. 4.11 **c**, **d** The closed root apical meristem of maize (*Zea mays*) shows a clear distinction between the root cap (RC) and root tip (RT). The boundary between root tip and root cap is not as apparent in the open root apical meristem of onion (*Allium* sp.) Scale bar = 100 µm (RR Wise)

root tip and root cap (columella). Meristematic initials may at different times produce cells of the columella, cortex, or protoderm, and there is not an apparent boundary between the root tip and root cap (Fig. 4.11c).

The planes of cell division in the root meristem are strictly ordered and are primarily transverse (anticlinal to root surface) divisions that provide growth of the root in length. As the result of such ordered divisions, characteristic cell tiers are formed in the cortex (Fig. 4.11e).

4.12 Lateral Roots Originate from Inside the Pericycle, Not from the Root Apical Meristem

In contrast to shoots, which can produce lateral leaves, shoots, and flowers, roots only produce one type of lateral organ, namely, more roots. In addition, initiation of lateral organs does not occur in the apical meristem at the root tip. Lateral roots arise internally some distance back from the root tip. They thus arise endogenously, unlike lateral branches in the shoot, which arise exogenously.



◘ **Fig. 4.11** **e** Longitudinal section of an onion (*Allium cepa*) root showing ordered tiers of cells produced by the ground meristem, some of which are undergoing stages of mitosis and cell division. Scale bar = 100 µm (RR Wise)

◘ **Fig. 4.12** Lateral root initiation from the pericycle (*arrow*) in a buttercup (*Ranunculus* sp.) root. Scale bar = 0.5 mm (RR Wise)

The vasculature in a root is contained within a central solid core called the vascular **stele** (refer to ► Chap. 10). Lateral roots are initiated by mitotic activity from cells at the outer edge of the stele, and the developing root tip forces its way through the cortex and epidermis (◘ Fig. 4.12). Parenchyma cells of the developing root differentiate into xylem and phloem tissues, which in turn connect to existing vasculature in the stele. A root cap develops and continues primary growth just as in the main root.

4.13 Intercalary Meristems Contribute to Stem and Leaf Growth in Monocots

Monocot roots develop from a root apical meristem, much like those of eudicots. However, monocot shoots typically do not show tip growth or have a shoot apical meristem. Instead, stem and leaf growth are driven by mitosis in a loose arrangement of meristematic cells that are scattered throughout a zone called an **intercalary meristem**. Intercalary meristems have a complicated anatomy that is difficult to image in a single section. They are found between the nodes or at the base of leaves. Stem elongation in bamboo, a large monocot, is driven by multiple intercalary meristems at each stem node (◘ Fig. 4.13a). Turf and lawn grasses have an intercalary meristem at the base of each leaf. It is for this reason one can mow a lawn and not kill the grass. Only the leaf tips are removed and the lower, actively growing region produces more leaf tissue (◘ Fig. 4.13b). Such morphology is an evolutionary adaptation to the frequent fires that strike grasslands. The leaves burn off, but the meristems at the base survive.

◘ **Fig. 4.13** **a** Stem of bamboo (*Bambusa* sp.). The internode (In) is the portion of the stem between the nodes (N). Intercalary meristems lie in the internode, close to the nodes. Scale bar = 10 cm (NE Wise)

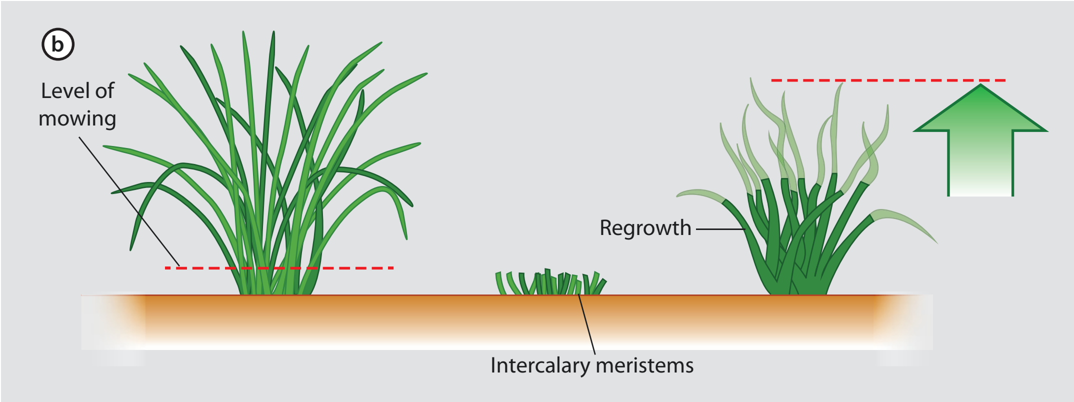


Fig. 4.13 **b** Diagram showing location of intercalary meristems in turf and lawn grasses (Redrawn from Crang and Vassilyev 2003)

Fig. 4.14 **a** Initial cell in the shoot apex of *Equisetum* sp. Scale bar = 50 µm (RR Wise)

4.14 Many Lower Vascular Plants Have a Single Initial Cell in the Shoot and Root Apical Meristems

Apical meristem structure in ferns, horsetails, and related plants is much simpler than that of angiosperms. Typically, a single pyramidal shaped cell—called the **initial cell** (or **apical cell**)—is the source of all shoot (Fig. 4.14a) and root tissues (Fig. 4.14b). The initial cell repeatedly divides by cleaving off daughter cells to either side. Those cells will develop into simple meristematic tissues called **histogens** that will eventually produce the epidermis, ground tissues, and vasculature.

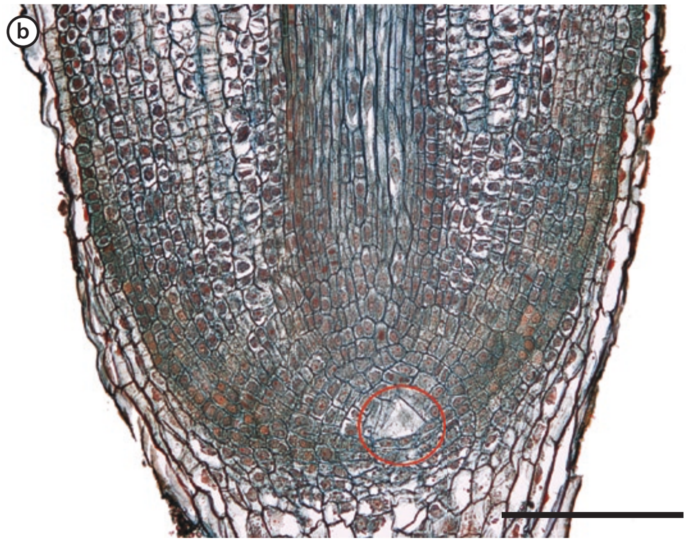


Fig. 4.14 **b** Longitudinal section of a moonwort fern (*Botrychium* sp.) root tip with the initial cell encircled. Scale bar = 200 µm (RR Wise)

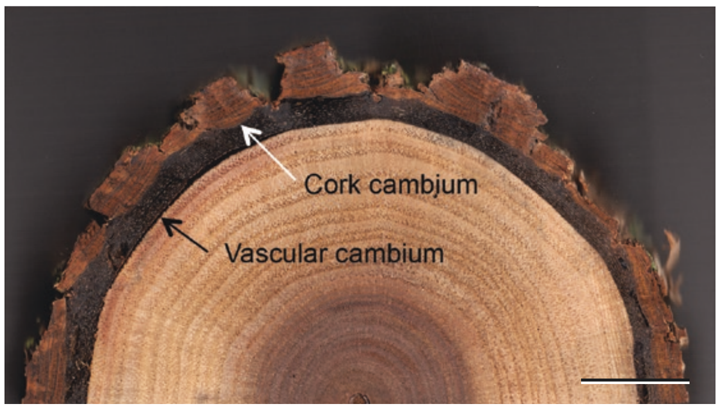


Fig. 4.15 A eudicot stem cross-section showing heartwood, sapwood with annular rings, the vascular cambium, and the nonliving cork cambium to the outside. Scale bar = 2 cm (RR Wise)

4.15 Lateral Meristems Are the Site of Secondary Growth in Eudicots

This chapter has dealt with the meristems involved in primary growth, i.e., growth in length. Such is the province of the shoot and root apical meristems and their derivative meristems. Other meristems, which will be discussed in detail in subsequent chapters, are responsible for secondary growth, or an increase in shoot or root girth (Fig. 4.15). The **interfascicular cambium** and **vascular cambium** (► Chap. 14) generate xylem and phloem (► Chaps. 7 and 8), and the **cork cambium** generates the periderm (► Chap. 16). Monocots lack lateral meristems and true secondary growth. They cannot make wood. However, the intercalary meristem (above), primary thickening meristem, secondary thickening meristem, and heavy sclerification of vascular bundles allow some monocots to develop large, strong stems (▶ Chap. 11).

4.16 Chapter Review

Concept Review

4.1 *The plant cell cycle includes interphase, mitosis, and cytokinesis*. The plant cell cycle includes all the stages in the division of a single cell to two daughter cells. The cell cycle has multiple, well-defined stages. Mitosis is division of the nucleus to produce two nuclei; cytokinesis is division of the cytoplasm to produce two daughter cells.

4.2 *A pre-prophase microtubule band precedes mitosis and defines the plane of cell division*. Cortical microtubules cluster at the cell equator prior to mitosis. This pre-prophase band directs where the new cell wall will be synthesized, and its placement may result in a symmetric division or an asymmetric division.

4.3 *Mitosis is divided into four distinct, but continuous, stages*. Mitosis is nuclear division (not cellular division). As nuclear division proceeds, four distinct stages of chromosome movement are visible—prophase, metaphase, anaphase, and telophase. *Interphase*: DNA is replicated prior to the start of prophase. *Pre-prophase*: the pre-prophase band (PPB) forms. *Prophase*: chromosomes condense and the nuclear envelope dissolves. Mitotic spindle formation initiates. *Metaphase*: the mitotic spindle directs the duplicated, condensed chromosomes to the plane of division (as defined by the PPB). *Anaphase*: duplicated chromosomes separate, and a copy of each is directed to the opposite cell poles. *Telophase*: chromosomes are fully separated, and two nuclear envelopes form. Cytokinesis begins.

4.4 *Cytokinesis begins with initiation of the cell plate and grows by the deposition of callose*. Cytokinesis is cellular division and usually follows mitosis (nuclear division). It starts with the formation of a cell plate containing callose and develops into the primary cell wall containing cellulose that will separate the two new daughter cells.

4.5 Microtubules play a critical role in mitosis and cytokinesis. Microtubules continuously form, dissolve, and reform during the cell cycle. They make up the pre-prophase band and the mitotic spindle. The considerable movement of chromosomes (in mitosis) and cell wall materials (in cytokinesis) is directed by microtubules.

4.6 *Apical meristems are the sites of primary growth*. Apical meristems are zones of active cell division at the tips of shoots and roots. Their growth (fueled by mitosis and subsequent cell enlargement) causes an increase in the length of the organ, which is called primary growth.

4.7 *The shoot apical meristem is the site of lateral organ initiation*. Lateral organs of the shoot (i.e., leaves, axillary buds, flowers, and branches) are formed by budding off at the shoot apical meristem. This is called exogenous organ initiation and contrasts to root development, which occurs endogenously.

4.8 *Axillary buds arise de novo in the developing leaf axis*. The leaf axis is where the leaf attaches to the stem and is the site of axillary buds. By initiating at this site, axillary buds have access to the vascular system of the shoot. Axillary buds may develop into stems, leaves, or flowers—any of the stem lateral organs.

4.9 *Tunica-corpus organization describes shoot apical meristem growth in many eudicots*. The eudicot shoot apical meristem has a definitive structure consisting of an outer layer called the tunica and an inner zone called the corpus. Cells in the tunica divide anticlinally, which provides new cells for the surface of the shoot. Cells in the corpus divide periclinally, which provides new cells for the stem interior.

4.10 *Gymnosperms do not possess a tunica-corpus*. The gymnosperm shoot apex lacks an organized tunica and has a zone in the middle called central mother cells, which contributes to the developing shoot tip.

4.11 *The root apical meristem provides the primary growth of roots*. The root apical meristem (RAM) has at its core a zone of quiescent cells that divide only rarely. The few cells produced subsequently divide multiple times to provide the bulk of the root tissue. The RAM also produces the root cap.

4.12 *Lateral roots originate from the pericycle, not from the root apical meristem*. In contrast to exogenous formation of lateral organs at the shoot apical meristem, lateral roots do not originate from the root tip. They arise from within the stele, proximal to the root tip proper in a process that does not initiate until root elongation has ceased.

4.13 *Intercalary meristems contribute to stem and leaf growth in monocots*. Intercalary meristems are not organized zones of cell division like the shoot and root apical meristems. Rather, they are composed of meristematic cells scattered throughout an area of active growth, such as the crown of a grass plant. This allows for the basal initiation of new leaves and shoots and evolved as a response to fires.

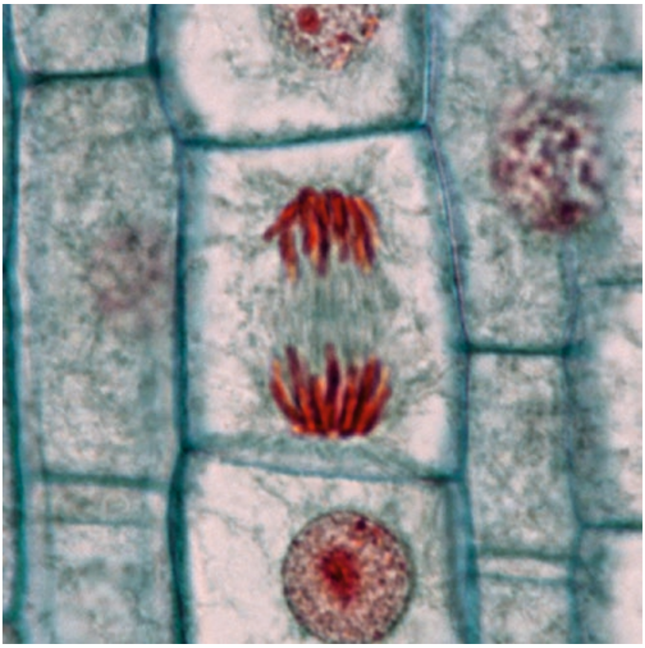
4.14 *Many ancestral vascular plants have a single initial cell in the shoot and root apical meristems*. In contrast to the more complex angiosperm and gymnosperm root and shoot apical meristems, ferns and their relatives have simpler apical meristems consisting of a single apical cell that provides all the cells of the growing shoot or root tip.

4.15 *Lateral meristems are the site of secondary growth in eudicots*. Meristems arranged along the length of the shoot and root contribute to the increase in girth of these organs. This is called secondary growth, because it can only be possible if primary growth has generated the shoot or root initially. Monocots lack lateral meristems and therefore lack true secondary growth. Stem strengthening in monocots is due to primary and secondary thickening meristems and the enhanced development of fibers around each vascular bundle.

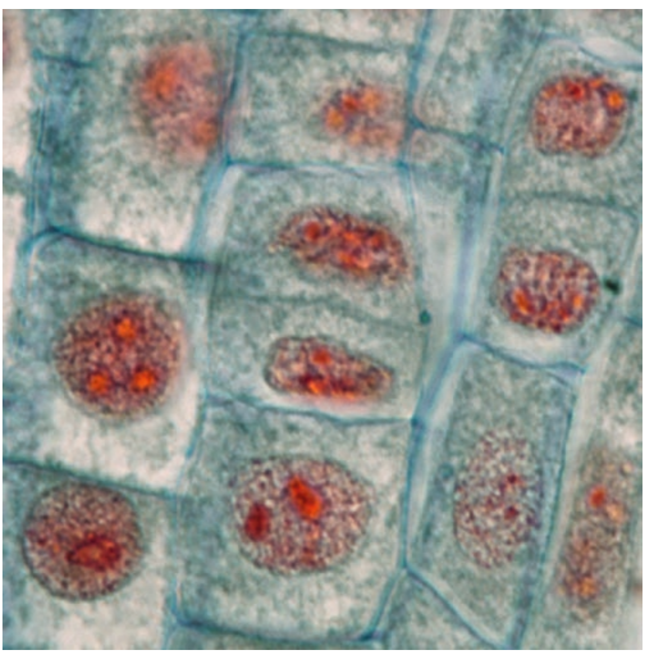
Concept Connections

1. Identify each of the stages of the cell cycle shown in the following images and arrange them in the proper order.

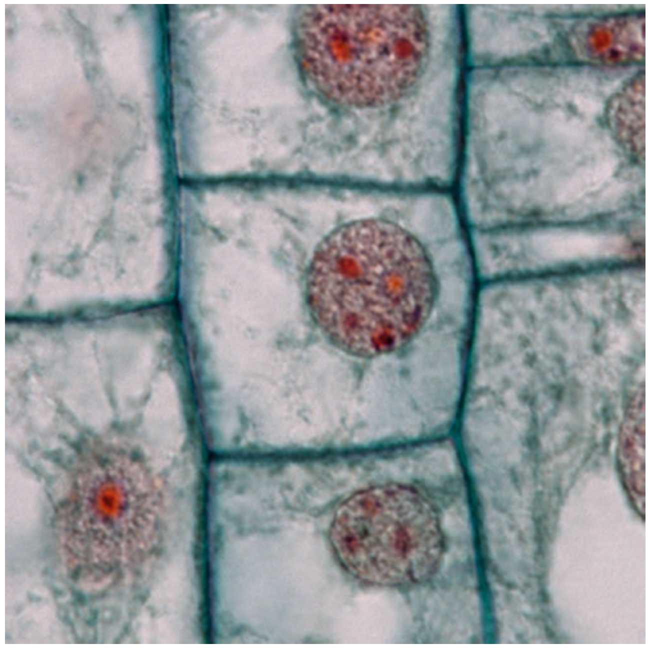
a.



b.



c.



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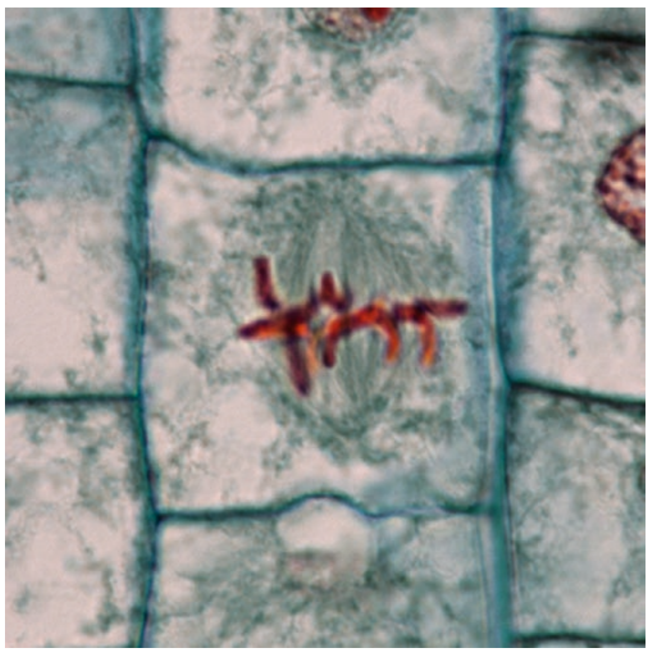
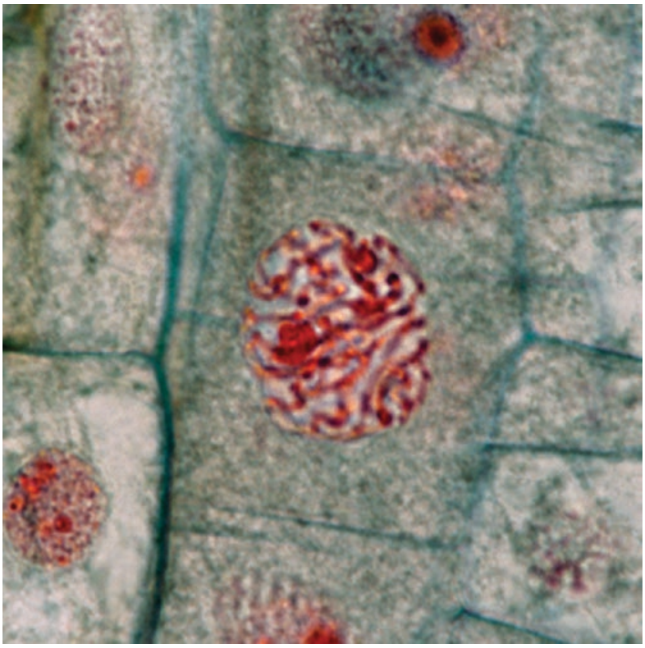
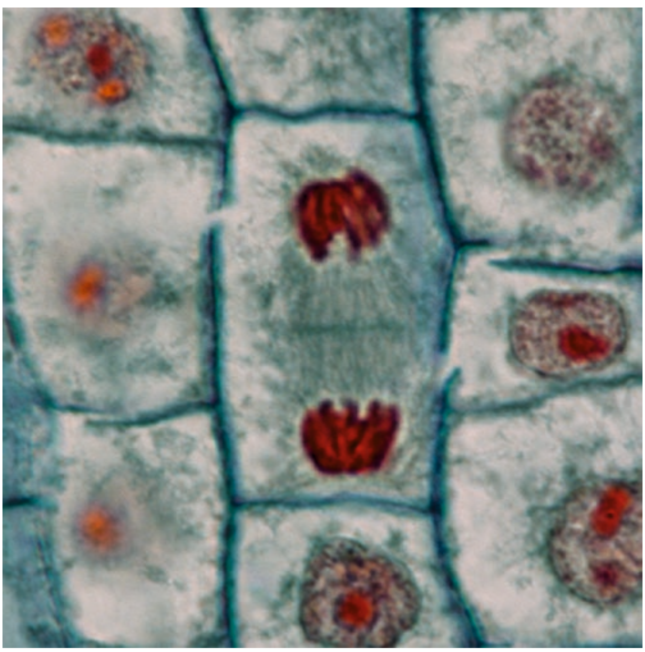


e.



f.



Concept Assessment

2. Which is a correct sequence for stages of the cell cycle and mitosis?
   a. interphase, prophase, metaphase, anaphase, telophase.
   b. interphase, telophase, metaphase, anaphase, prophase.
   c. metaphase, anaphase, telophase, interphase, prophase.
   d. anaphase, prophase, telophase, metaphase, interphase.
   e. telophase, anaphase, prophase, metaphase, interphase.

3. Where is the quiescent center located?
   a. in front of the root apical meristem (distal).
   b. behind the root apical meristem (proximal).
   c. in the root cap.
   d. in the center of the corpus.
   e. the central region of the tunica.

4. During the cell cycle, microtubules
   a. direct the movement of chromosomes during mitosis.
   b. polymerize and depolymerize continuously throughout the cell cycle.
   c. form the pre-prophase band prior to prophase.
   d. transport vesicles from the Golgi apparatus to the developing cell plate.
   e. all of the above.

5. Division of the tunica occurs in which plane(s)?
   a. anticlinal.
   b. periclinal.
   c. metaclinal.
   d. various planes.
   e. none; division does not occur in the tunica.

6. In plant cells, the first visible sign of mitosis is:
   a. thickening of chromosomes.
   b. formation of a spindle apparatus.
   c. development of a cell plate.
   d. appearance of a pre-prophase band of microtubules.
   e. initiation of cytokinesis.

7. What is the derivative of procambium?
   a. root cap.
   b. vascular tissues.
   c. pith and cortex.
   d. epidermis.
   e. apical meristem.

8. Vesicles giving rise to the cell plate originate from
   a. dictyosomes.
   b. the endoplasmic reticulum.
   c. microbodies.
   d. invaginations of the cell membrane.
   e. microtubules.

9. Shoots and roots generate primary growth and lateral organs in different manners. A main difference between shoot primary growth and root primary growth is that
   a. the shoot apical meristem does not generate primary growth.
   b. the root apical meristem produces lateral organs from the root cap.
   c. the shoot apical meristem can produce different organs; the root apical meristem only generates primary growth.
   d. root lateral organs are initiated from within the stele, not at the root apex.
   e. c and d.

10. Intercalary meristems are different than apical meristems in that
   a. intercalary meristems are more organized than apical meristems.
   b. apical meristems produce tip growth, while intercalary meristems produce basal growth.
   c. intercalary meristems are only found in gymnosperms; apical meristems are only found in bryophytes.
   d. apical meristems are found in the crown of a grass plant; intercalary meristems are found at the gymnosperm root tip.
   e. intercalary meristems rarely divide; apical meristems divide often.

11. Lateral meristems contribute to
   a. primary growth.
   b. secondary growth.
   c. increase in stem and root length.
   d. increase in stem and root girth.
   e. b and d.

Concept Applications

12. Explain how root cells sense the direction of gravity.

13. Why can shoot lateral organs originate exogenously, whereas subsequent root organs must originate endogenously?

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Cell Walls

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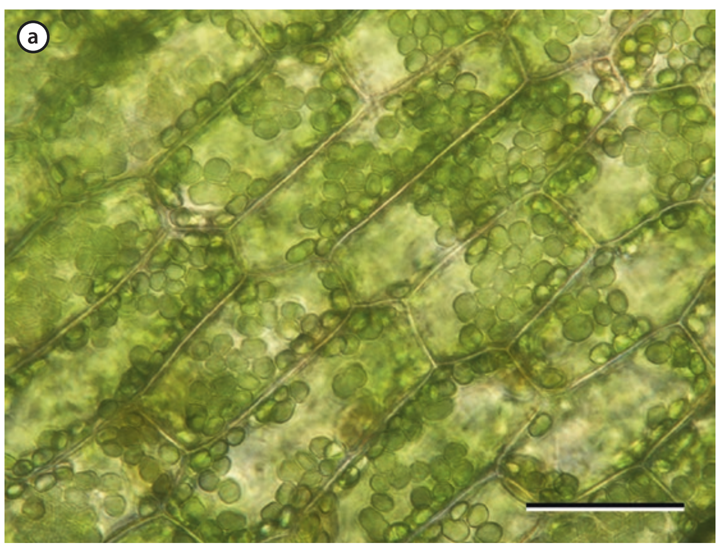
5

Introduction

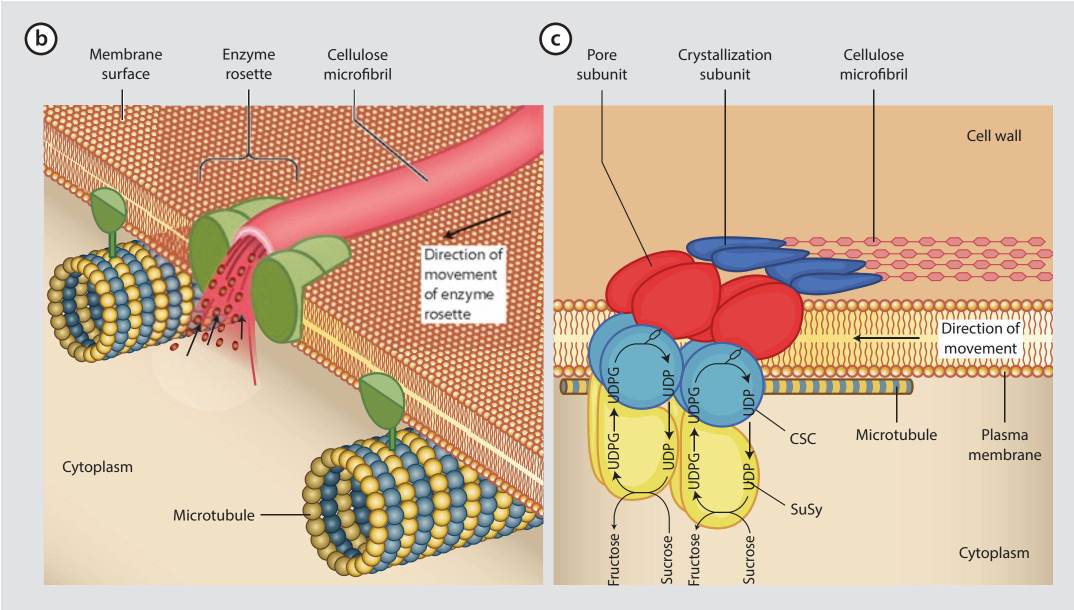
The cell wall is unique to higher plant cells. Due to their reliance on hydraulics for growth, expansion, and transport, plant cells develop tremendous internal pressures. Without walls, they would rupture due to the high osmotic pressures from within. There are two basic types of cell walls. Primary cell walls surround living cells and are made of a loose, and "loosenable," matrix of cellulose, **cross-linking glycans**, and structural proteins and contain enzymes capable of loosening and strengthening the wall. The primary wall offers physical support during the time of growth and in herbaceous tissues. Secondary cell walls are greatly stiffened by the deposition of lignin, are rigid, and are found in tissues or organs that require great strength and support, such as tracheary elements and wood. Typically, those cells are dead at maturity. Cell-to-cell communication and transport, which are of vital importance, occur via plasmodesmata in the primary cell wall or pits in the secondary cell wall.

5.1 Transparent Plant Cell Walls Contain Cellulose and Are Synthesized to the Exterior of the Protoplast

Although most plant cells are highly colored (▶ Chap. 1), **cell walls**, the main structural component of plants, rarely contain pigments. Light needs to penetrate many plant tissues; therefore, most cell walls, especially primary walls, are typically transparent or translucent (◘ Fig. 5.1a).



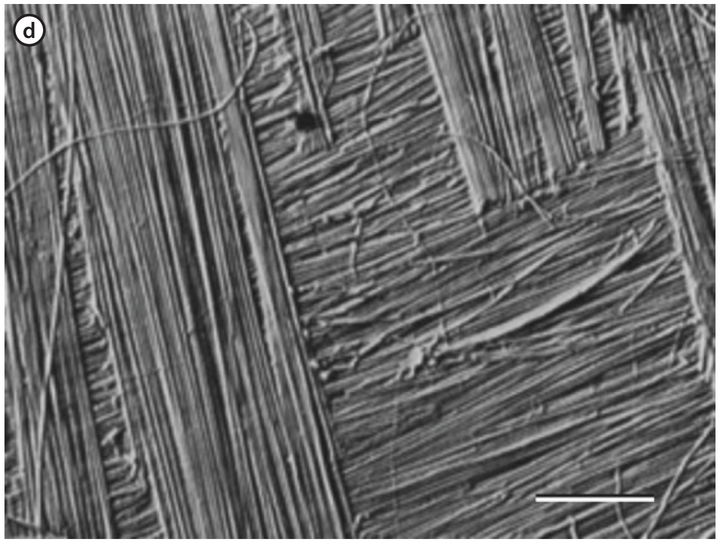
◘ **Fig. 5.1** **a** Chloroplast-containing elodea (*Elodea canadensis*) leaf cells separated by translucent primary cell walls. Scale bar = 50 µm (RR Wise)



◼ **Fig. 5.1** **b**, **c** Diagrammatic representation of portion of a plasma membrane with islands of cellulose synthase complexes (aka rosettes). These enzyme complexes generate the cellulose microfilaments on the outer surface of the membrane but are oriented by the positioning of cytoplasmic microtubules on the inner surface of the membrane. They are mobile and can move throughout the membrane. *CSC* cellulose synthase complexes, *PM* plasma membrane, *CSI1 CSC* associated proteins, *MT* microtubule. (Figure redrawn from John Tiftickjian (Delta State University)) (**b**, **c** RR Wise)

All plant cell walls contain the polysaccharide cellulose, a polymer of ß-glucose units, arranged in crystalline structures only a few nanometers in diameter called microfibrils. Cellulose microfibrils are synthesized to the cell surface by large enzyme **cellulose synthase complexes** having hexagonal symmetry, sometimes called "rosettes" (Lei et al. 2012). Underlying microtubules in the cytoplasm guide the direction of the rosettes as they circle the cell by means of the action of motor proteins (◼ Fig. 5.1b, c, Wightman and Turner 2010). This results in the cell becoming wrapped in layers of cellulose **microfibrils**, which become the early primary cell wall (◼ Fig. 5.1d). Different layers of the cell wall may have different patterns since microtubules can depolymerize and re-polymerize in multiple orientations. The assembly and orientation of cellulose are connected, as several cellulose synthase mutants have phenotypes defective in cellulose orientation and plant structure as well as being depleted in cellulose content.

Not only cellulosic microfibrils but other polysaccharides are exported to the cell wall region either as a part of a permanent wall or as part of temporary secretions that play a significant role in lubricating for the growth of root structures through soil particles, harboring symbiotic and mutualistic microorganisms, and enveloping enzymes for extracellular degradation and transport. Within the cytoplasm, numerous Golgi bodies secrete vesicles that deliver components to the external cell wall either directly or through the endoplasmic reticulum (◼ Fig. 5.1e).



◘ **Fig. 5.1** **d** Orientation of numerous cellulosic microfibrils as shown by scanning electron microscopy that are enveloping the protoplasmic cell surface of a plant. The microfibrils shown here are firmly held to the adjacent fibrils by hydrogen bonds between their –OH groups. Scale bar = 1 µm (Crang and Vassilyev 2003)

5.2 Primary Cell Walls Are a Structural Matrix of Cellulose and Several Other Components

The wall of a dividing and growing cell is called the **primary cell wall** (◘ Fig. 5.2a, Cosgrove 2005). This early wall is composed of multiple compounds formed in complex assemblages from within the cytoplasm of the cell, and transported across the cell (plasma) membrane (a.k.a. plasma lemma), which is a semifluid barrier of the early living cell (refer to ► Sect. 3.3). In addition to the carbohydrate cellulose (◘ Fig. 5.2b), the main component of most cell walls, the primary cell walls also contain a matrix of polysaccharides in the form of amorphous substances (e.g., pectic and cross-linking glycans; ◘ Fig. 5.2c, d). Pectic substances are composed of polymers of galacturonic acid in which some of the carboxyl groups are esterified with methanol. **Pectins** act as a glue to hold adjacent cells together and are a main component of the **middle lamella** (see below). The pectic substances that are extracted from plants are commonly called pectins, and their sticky nature makes them an ideal choice for making jams and jellies. Cross-linking glycans (which used to be called hemicelluloses) bind to cellulose molecules to provide a strong but flexible web-like complex. They are composed of several different sugar monomers including glucose, arabinose, galactose, rhamnose, mannose, and xylose. The next most abundant component usually is water that is followed by a wide variety of compounds such as lignin, proteins, and mineral ions. Cell walls of some cell types may also contain polymeric lipids such as **waxes**, **cutins**, and **suberins** (◘ Fig. 5.2e) which form hydrophobic deposits on hydrophilic walls, particularly conspicuous on the surface of the epidermis, in the Casparian strip of the endodermis and in the walls of **cork**.

Fig. 5.1 **e** A portion of a developing root cell from maize (*Zea mays*) showing many dictyosomes with swollen trans vesicles containing polysaccharides that are emptying their contents at the site of the cell wall (CW). Scale bar = 1 µm. (Micrograph courtesy of Hilton H. Mollenhauer; HH Mollenhauer, Texas A&M University)

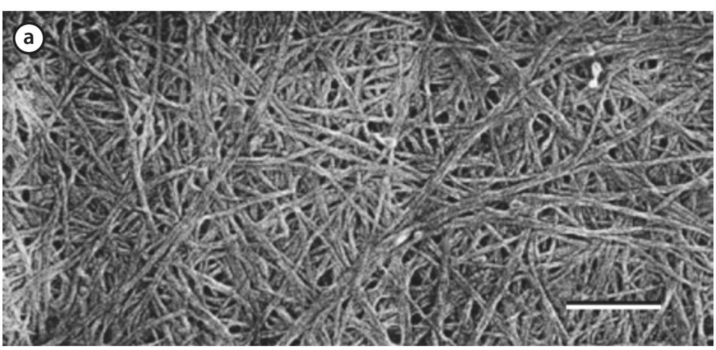


Fig. 5.2 **a** This transmission electron micrograph shows the primary cell wall of an onion (*Allium cepa*) parenchyma cell from a bulb after the extraction of noncellulosic polysaccharides. Although the extraction process enhances the cellulose microfibrils, it has altered their parallel orientation from that in the intact cell wall. Scale bar = 0.2 µm (Crang and Vassilyev 2003)

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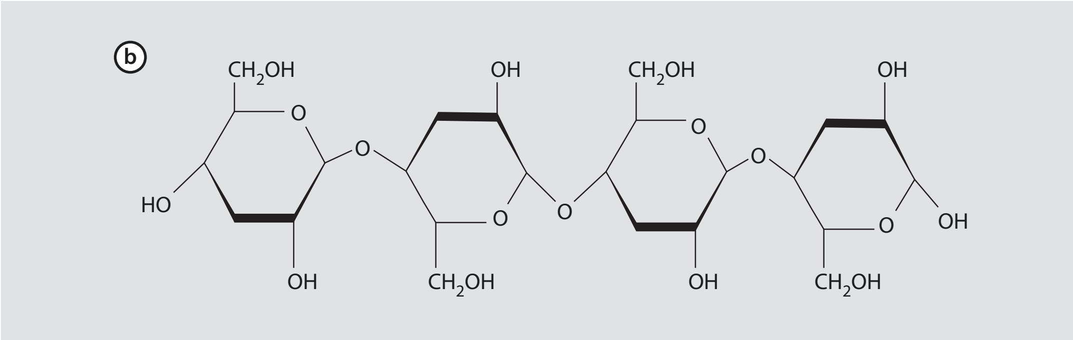


Fig. 5.2 **b** The basic structure of cellulose, a linear polysaccharide with glucose units connected by a beta-acetyl linkage (Redrawn from Wikipedia)

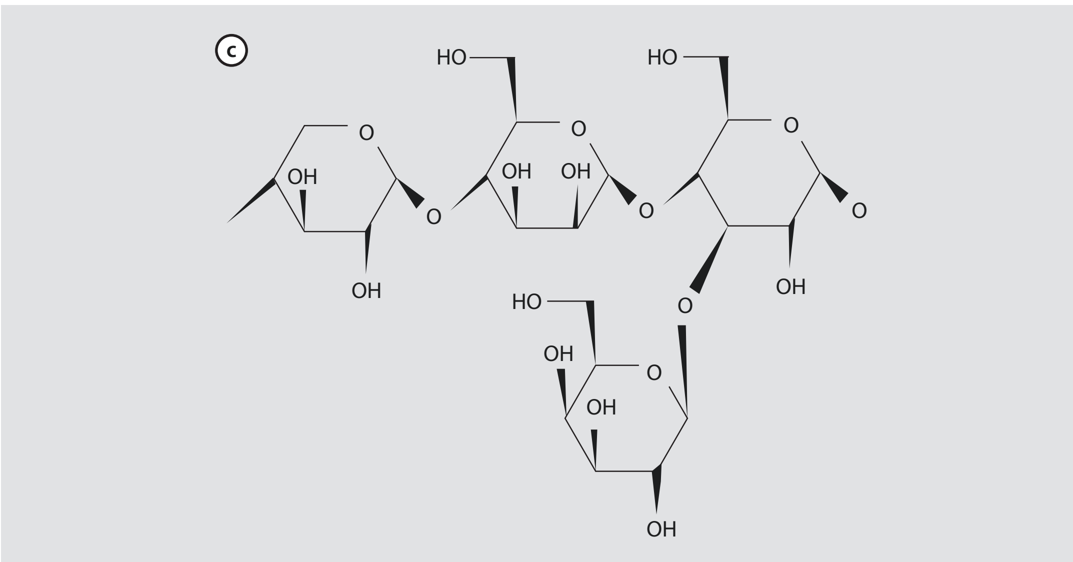


Fig. 5.2 **c** A common molecular orientation of a cross-linking glycan that contains several sugars including glucose, galactose, mannose and xylose (Redrawn from Wikipedia)

Each plant cell develops its own cell wall, and neighboring cells in the plant body are held together by the middle lamella (Zamil and Geitmann 2017), which originates as a pectic cell plate formed at telophase. The middle lamella is very thin and often indistinguishable from the developing primary cell wall (Fig. 5.2f). When two adjacent primary walls are cemented together with a middle lamella, the combination is designated as a **compound middle lamella** (Fig. 5.2g).

If chemical agents or enzymes are used to dissolve the middle lamella, the cell walls become separated from each other. Such an artificial process of cell separation is called **maceration** and is achieved in the laboratory by treatment with enzymes, acid, and/or alkaline solutions. However, a more common event is natural maceration when pectins of the middle lamella are enzymatically dissolved as during the process of leaf loss (e.g., **abscission**). Very often, partial maceration occurs when the middle lamella is solubilized only at certain sites, primarily at the cell corners. Cells round off due to turgor pressure,

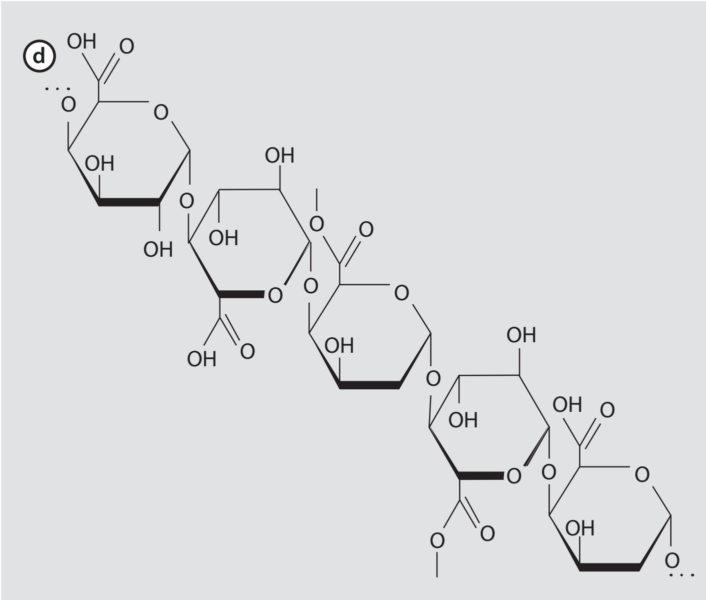


Fig. 5.2 **d** Chemical structure of a pectin which may contain a variety of sugars as well as being rich in galacturonic acid (Redrawn from Wikipedia)

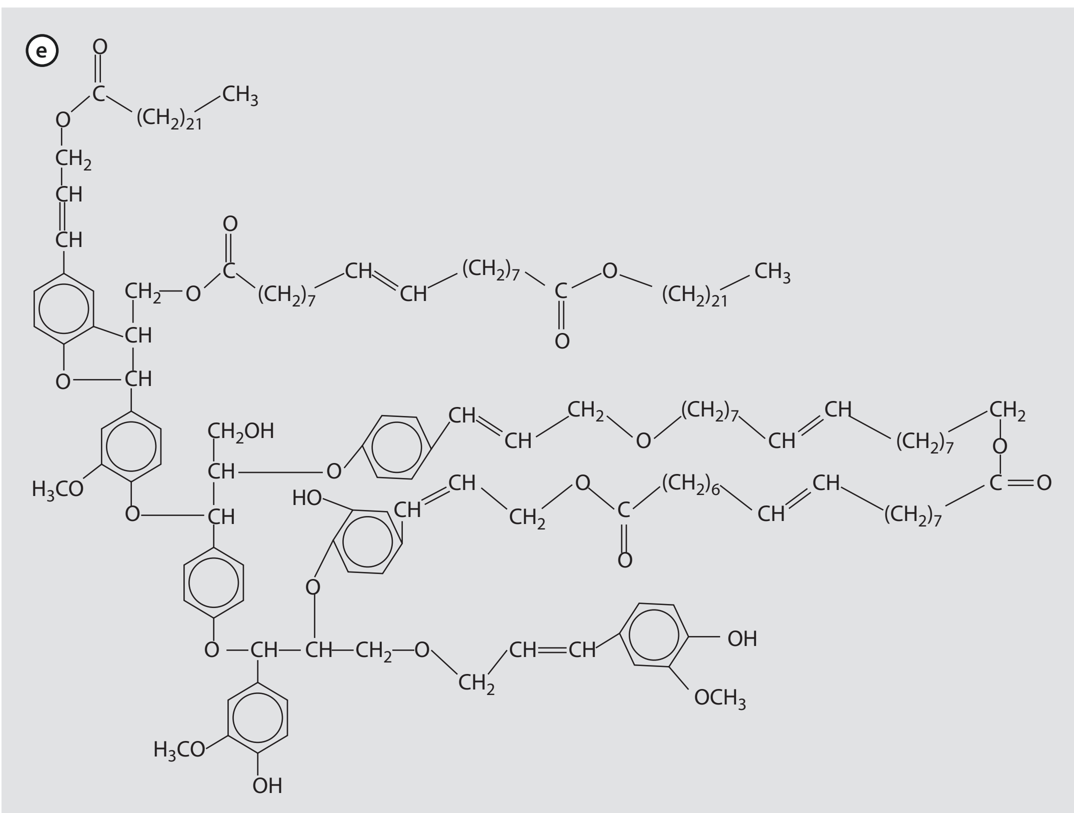


Fig. 5.2 **e** A hypothetical structure of a suberin polymer. Such glycerolipid polymers are specific to plants. Cutin is responsible for the composition of the cuticle on the aerial epidermis. Suberin is mostly present in the bark and underground organs of plants (Redrawn from Wikipedia)

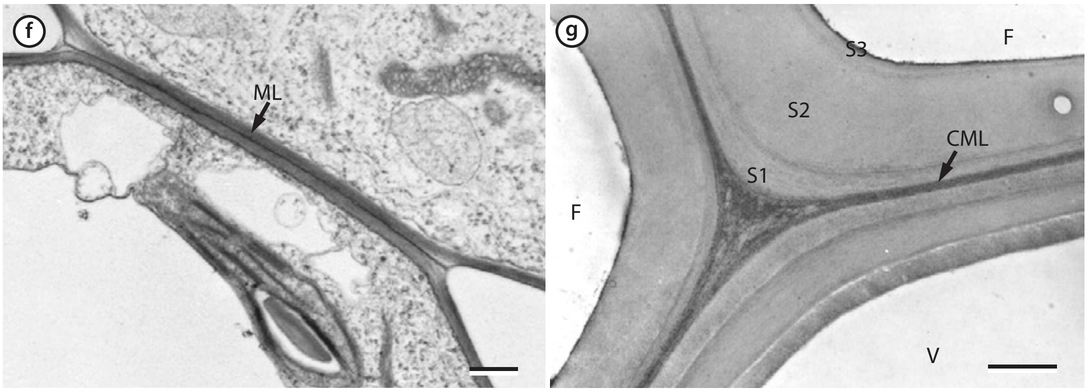


Fig. 5.2 **f** Middle lamella (ML) between adjacent cells in water lettuce (*Pistia stratiotes*). (GM Volk and VR Franceschi, Washington State University). **g** Compound middle lamella between three adjacent cells in developing poplar (*Populus* sp.) wood, two fibers (F) and one vessel element (V). The middle lamella and the two primary walls in **apposition** have fused to form the compound middle lamella (CML), and three layers of secondary wall have developed (S1, S2, and S3). (K Ruel, CNRS, France). Scale bars = 5 µm in **f** and 1 µm in **g**

and intercellular air spaces appear at these sites. These spaces enlarge and fuse with each other as cells grow, and a single-branched system may appear which is filled with gases and water vapor. Therefore, intercellular spaces facilitate exchange into and out of plant cells for gases such as oxygen, water vapor, and carbon dioxide.

Box 5.1 Using Plant Cells for the Oral Delivery of Protein Drugs

Protein drugs include compounds such as hormones, vaccines, and enzymes. They are expensive to manufacture and require cold storage. Because these drugs can be degraded by proteases and acids if ingested and have difficulty crossing intestinal barriers, they are typically administered by injection, often by medical professionals that further increases costs.

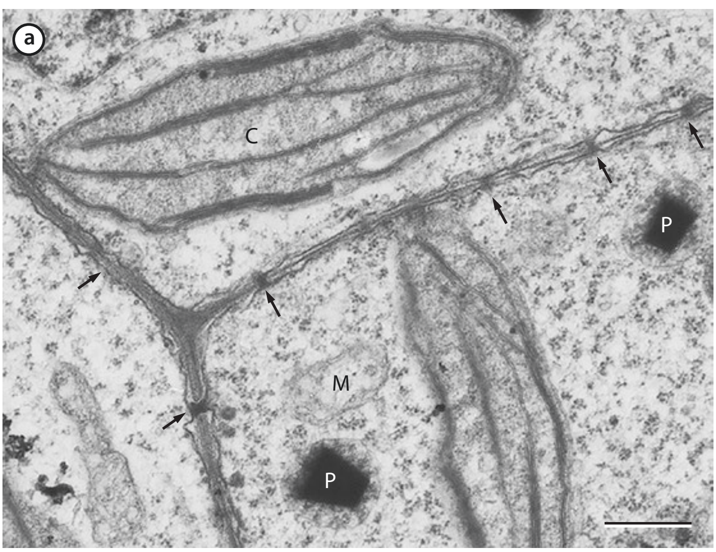
The use of plant cells to manufacture and store protein drugs could provide both convenience of oral delivery and economic relief for patients. Here is the basic concept of drug production and delivery using plant cells: drug companies engineer chloroplasts to express genes of medicinal interest. The plant leaves are harvested, freeze-dried, and placed in a capsule. Envision a patient orally ingesting the capsule containing a gene product, such as insulin, instead of administering the hormone via self-injection. Since the human body does not produce cellulases, enzymes that break down plant cell walls, the drug would not be dispensed until encountering gut bacteria in the intestines can denature the walls, releasing the drug. Within the intestines, the drug can be integrated into the body. Freeze-drying allows these protein drugs to remain stable at room temperature, keeping storage costs down. Since these drugs may not require purification or professional administration, costs to patients would be reduced. This research of drug bioencapsulation within plant cell walls may lead to increased efficiency in treating metabolic disorders and diseases such as diabetes, hypertension, and Alzheimer's. While oral delivery of drugs is still in its experimental stages, it shows much promise.

Reference: Xiao et al. 2016

5.3 Plasmodesmata Connect Adjacent Cells Via Holes in the Primary Cell Wall

Plasmodesmata are tiny (30–60 nm), intercellular, cytoplasmic extensions between adjacent cells and are lined with the plasma membrane of the two adjacent cells (◘ Fig. 5.3a). They are dynamic structures that control the passage of large molecules between cells and also in cell-to-cell communication (Overall and Blackman 1996; Maule 2008).

Practically all living cells of the plant body are interconnected by plasmodesmata. An exception is the subsidiary cells surrounding guard cells found in epidermal layers (refer to ► Sect. 9.3). There are numerous plasmodesmatal connections between the subsidiary cells and guard cells but none between the subsidiary cells and adjacent pavement cells of the epidermis. With that exception, plasmodesmatal connections between adjacent cells link the cytoplasm of practically every cell in the plant into a **symplastic** whole. Due to the presence of multiple plasmodesmata, plant cells can be considered to form a **syncytium** or multinucleate mass with cytoplasmic



◘ **Fig. 5.3** **a** Newly formed cell walls in water lettuce (*Pistia stratiotes*) containing numerous plasmodesmata (arrows). Note also the chloroplasts (C), mitochondrion (M), and two peroxisomes (P) containing darkly stained catalase crystals. Scale bar = 0.5 µm. (Image courtesy of Gayle Volk and Vincent Franceschi; Washington State University) continuity (in contrast to a **coenocyte** which can result from multiple nuclear divisions without accompanying cytokinesis). Accordingly, the tiny channels have caused a significant amount of debate among scientists regarding cell theory, some suggesting that the cells of higher plants are not cells at all since they are not physically separated or structurally independent from one another.

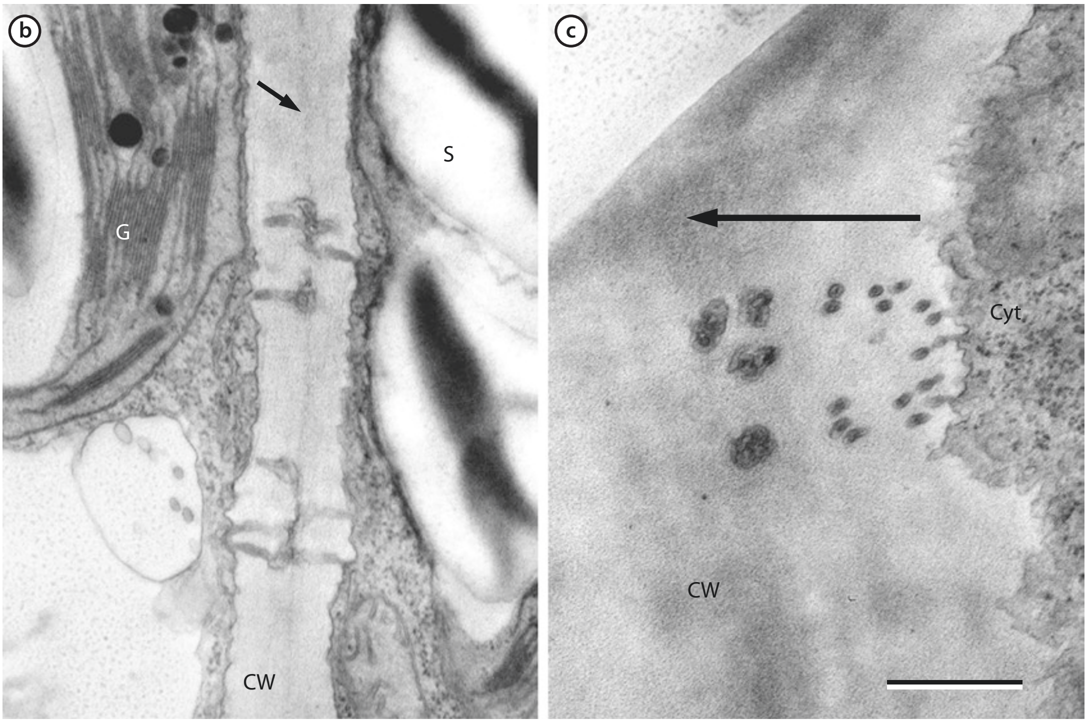
There are two forms of plasmodesmata: primary and secondary (Ehlers and Kollmann 2001). Primary are formed from the sites where strands of endoplasmic reticulum were trapped in the developing cell plate during cytokinesis. Secondary plasmodesmata are formed by insertion into existing cell walls between nondividing cells. Secondary plasmodesmata are a much less common occurrence than primary plasmodesmata.

Areas in the primary cell wall that have a concentration of plasmodesmata are called **primary pit fields**, and in cells that form a secondary wall, the primary wall's pit fields are left exposed. This creates large perforations in the secondary wall called **pits** (refer to ► Sect. 5.5, below). Secondary cell wall pits of adjacent cells are usually aligned with each other so that the two primary cell walls and middle lamella form a selectively permeable pit membrane, pierced by multiple plasmodesmata. Going from one cell to the adjacent one, the sequence of structures is as follows: pit-primary wall-middle lamella-primary wall-pit. Such a secondary wall pit pair can transmit water, nutrients, plant growth regulators (hormones), etc. between adjacent cells.

Plasmodesmata may be straight or branched, and plasmodesmatal diameter varies across the length (◘ Fig. 5.3b, c). They are 30–40 nm at the wall surface and approximately 50–60 nm in diameter at the midpoint. Note the plasmodesmata in ◘ Fig. 5.3c that are closer to the cytoplasmic surface of the cell wall are smaller than the plasmodesmata further from the cytoplasm and thus deeper in the wall.

Plasmodesmatal internal structure is delimited by a plasma membrane encircling a solid-looking core (or **desmotubule**) and an intervening layer known as the **cytoplasmic annulus** (◘ Fig. 5.3d). The cytoplasmic annulus is the space between the desmotubule and the plasma membrane. Around the desmotubule and the plasma membrane, areas of an electron-dense material have been observed with the aid of the transmission electron microscope and often joined together by spoke-like structures that seem to split the plasmodesmata into smaller channels. In this case, these proteins may be used in the selective transport of relatively large molecules between adjacent cells. It has been found that a typical plant cell may have between 10^3 and 10^5 plasmodesmata connecting adjacent cells, which may equate to between 1 and 10 per μm^2.

Plasmodesmata are more than merely passive holes connecting adjacent cells (Ehlers and Kollmann 2001). Plants may regulate plasmodesmatal transport by the accumulation of callose around the end regions of plasmodesmata to form a restriction, which may reduce the diameter of the plasmodesmata at those sites and thereby control the passage of substances through the plasmodesmata. Through the action of ATP, proteins associated with the desmotubule can expand the radius of the plasmodesmata, allowing larger unfolded proteins to pass through from one cell to the next. Also,



◘ **Fig. 5.3** **b** Branched plasmodesmata seen in cross-section traversing the two primary cell walls (CW) separating two leaf cells. The middle lamella is indicated with an arrow. Chloroplasts with grana (G) and starch (S) are also indicated. **c** Plasmodesmata seen in face view in an oblique section of a primary cell wall (CW). Cytoplasm (Cyt) is to the right in the image, and the arrow indicates increasing depth into the cell wall. Both images are from the leaf of the lyre-leaved sand cress (*Arabidopsis lyrata*). Scale bar = 0.1 µm for both panels (**b**, **c** RR Wise)

cells can utilize both passive and active transport to move molecules and ions through the plasmodesmata.

Numerous large molecules have been shown to traffic from cell to cell via plasmodesmata. Studies have tracked cell-to-cell movement of proteins, transcription factors, messenger RNA, and even entire viral genomes. The latter is mediated by proteins encoded by the virus called "movement proteins." The ability of a virus to make movement proteins is key to its virulence because it allows the virus to spread throughout the plant (Heinlein 2015). Tobacco mosaic virus encodes MP-30, a 30 kDa movement protein that binds to and traffics the entire viral genome through the plasmodesmata, thus spreading the infection.

Finally, the plant cell membrane typically has a rather large electrical potential, in the range of −150 mV (negative on the inside) as compared to the −40 to −60 mV potentials found in most animal cells (Flickinger et al. 2010). Because plasmodesmata allow for ion (electrolyte) transport between cells, uniform membrane potentials across a plant organ can be maintained.

Persimmon fruit contains cells with extremely thick primary cell walls (◘ Fig. 5.3e) and is a common specimen for classroom study of bundles of plasmodesmata as the long channels are easily seen with the light microscope. This allowed early microscopists to visualize plasmodesmata long before the development of the transmission electron microscope permitted high-resolution studies, ones that continue to this day.

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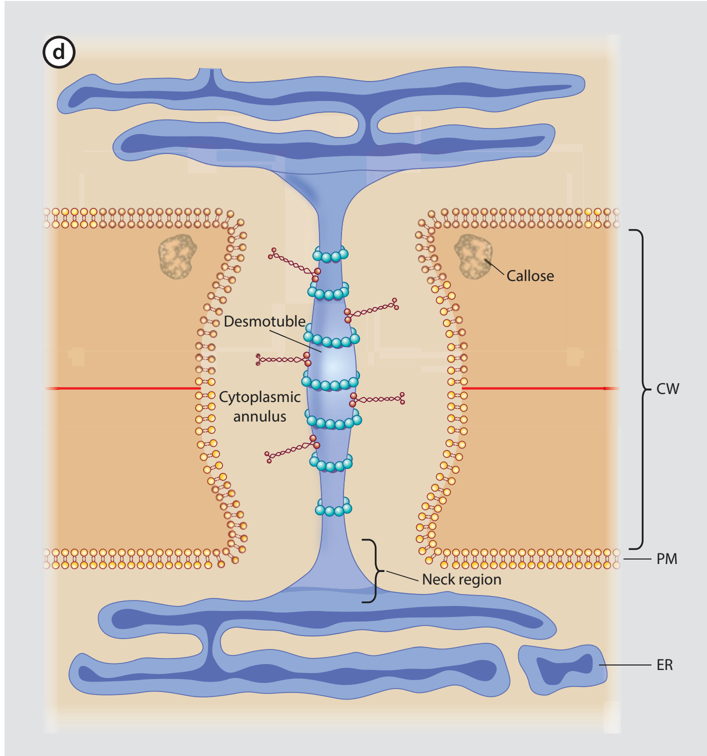


Fig. 5.3 **d** The structure of an unbranched plasmodesmata. Light green area cytoplasmic sleeve; *CW* cell wall, *CA* callose, *PM* plasma membrane, *ER* endoplasmic reticulum, *DM* desmotubule, purple circles and spokes – other agents such as ATP and proteins within the cytoplasmic sleeve that may include myosin. The combination of actin and myosin may be in the selective transport of large molecules between two cells through the plasmodesmata and along the desmotubule. (Figure modified from Sevilem et al. (2015))

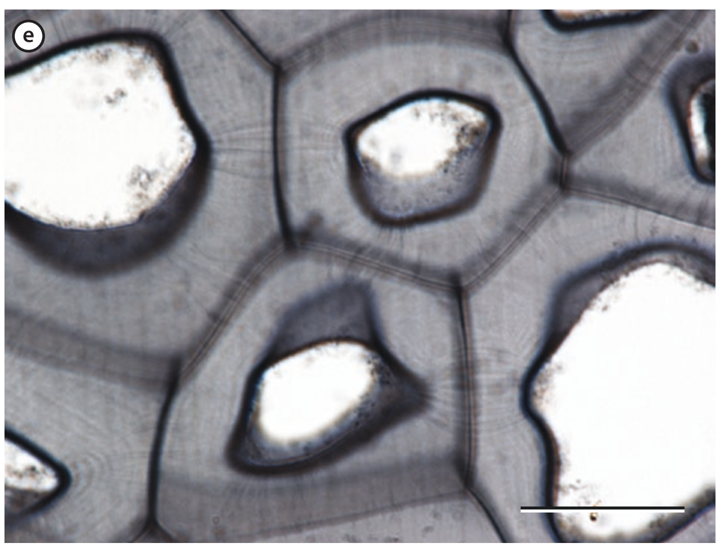
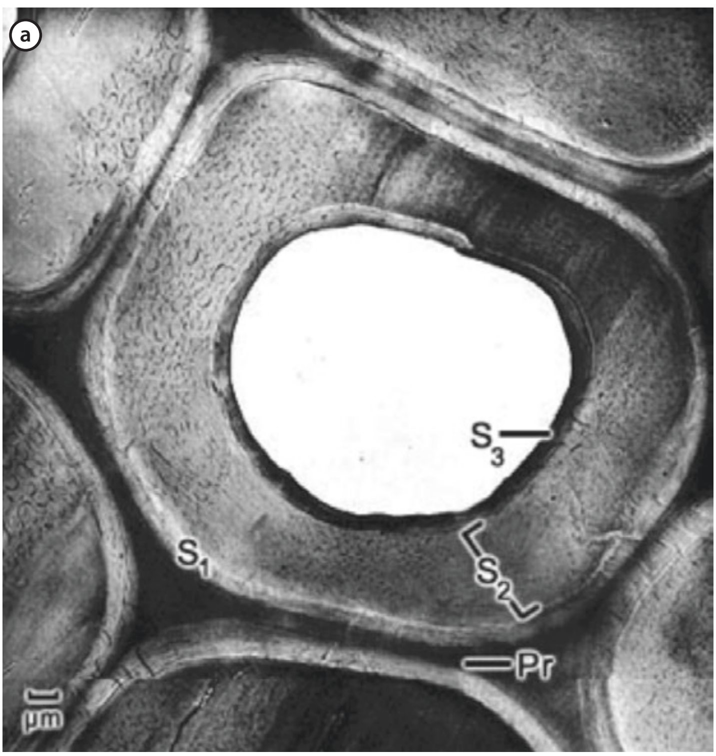


Fig. 5.3 **e** Cell walls of persimmon (*Diospyros* sp.) in cross-section showing fine bundles of plasmodesmata traversing the walls, through the middle lamella, and interconnecting every cell in the field of view. Scale bar = 25 µm (RR Wise)

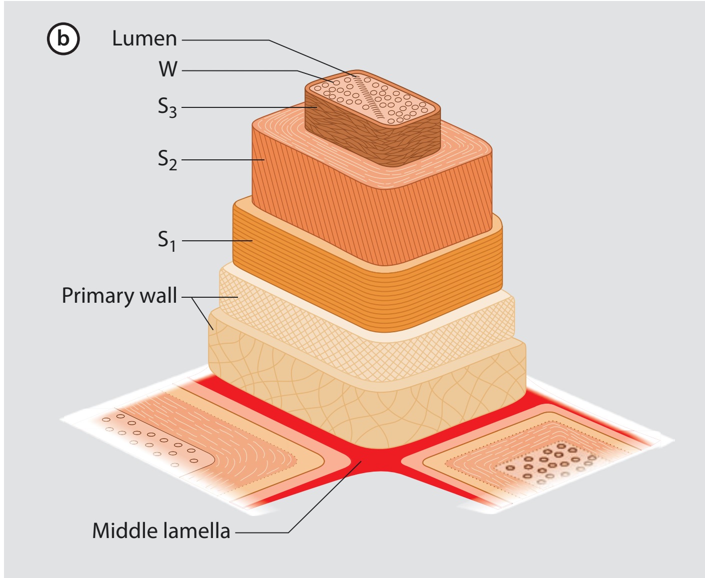
5.4 Secondary Cell Walls Are Rigid, Thick, and Lignified

For many cell types, wall formation ends with the cessation of cell growth. Such cells remain surrounded by a thin primary wall during their whole life. But in other cell types, the deposition of wall material continues. The wall layers deposited after cell enlargement ceases are collectively termed the **secondary cell wall**. Because of secondary wall growth, the thickness of the wall increases, at the expense of the volume of the living cell cavity (◘ Fig. 5.4a).

Primary cell walls of different tissues and plant species will vary in their composition and function. Likewise, secondary walls will also vary in that regard for the different layers that can be established. For some cell types, such as tracheids, vessel members, cork cells, and some sclereids and fibers, the formation of the secondary wall is the main function of their **protoplasts**, and the cells eventually die because of fulfilling that principal function. In such a case, the secondary wall mainly provides mechanical support and is responsible for the specific structural features of wood, textile fiber, and paper.



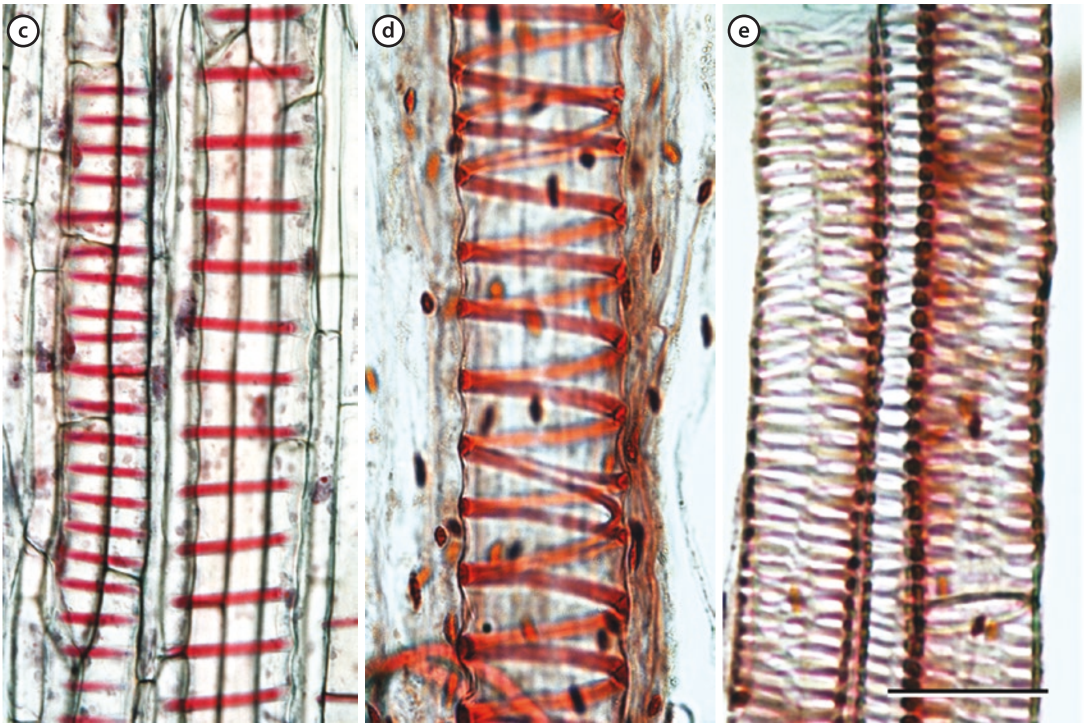
◘ **Fig. 5.4** **a** Cross-section of late-wood tracheids of longleaf pine (*Pinus palustris*) showing the layers of the secondary wall (S_1, S_2, and S_3), the thin primary wall (Pr), and the true middle lamella, which is markedly thickened at the cell corners. The combination of the primary cell walls and the middle lamella is often termed a compound middle lamella. Scale bar = 1 µm (Crang and Vassilyev 2003)



◘ **Fig. 5.4** **b** This diagram shows the order of wall layers for a cell with secondary wall development. The middle lamella is amorphous in organization. The primary wall typically shows a nonlinear pattern of cellulose microfibril deposition. The orientation of fibrils may determine the direction of cell elongation. Fibril patterns that are nonlinear cause the walls to undergo minimal expansion. Note, however, that the three layers of secondary wall material (labeled, S_1, S_2, and S_3) have distinct orientations of the cellulose microfibrils. A "warty" layer (possibly representing the remaining nonliving cell contents) may also be found as a lining to the S_3 layer. Not all cells that form secondary wall material will result in all the layers. (Figure modified from Esau (1977))

In cells with well-developed secondary walls (S), up to three concentric wall layers may be distinguished: an outer narrow S_1 layer adjacent to the primary wall, a thicker middle S_2 layer, and a thin inner layer bordering on the cell cavity (S_3, ◘ Fig. 5.4b). The layers differ not only in thickness but also in chemical composition and in the angle of cellulose microfibril orientation in relation to the cell axis (Richter et al. 2011). The three-layered structure of secondary walls is characteristic of wood elements of conifers and some angiosperms, but in some cells the S_3 is lacking. The S_2 layer is the richest in cellulose and is responsible for most of the properties of secondary walls. **Lignification** results in the substantial modification of cell wall properties, e.g., the loss of elasticity, a drastic increase in hardness and tensile compression, and a decrease in the permeability of water as the lignin polymerizes within the cell walls. Lignin is found in many or all the secondary wall layers.

In some specialized cells (mainly those engaged in water conduction, called xylem tracheary elements), the secondary wall is not deposited over the entire inner surface of primary wall but appears as individual rings, continuous helices, or net-like arrangements (◘ Fig. 5.4c). Xylem tracheary element structure will be covered in more detail in ► Chap. 7.



◘ **Fig. 5.4** Variations in secondary cell wall thickening patterns in protoxylem tracheary elements from celery (*Apium* sp.) petiole. **c** Annular thickenings, **d** helical thickenings, **e** reticulate thickenings. Scale bar in e = 50 μm for all three panels (**c**–**e** RR Wise)

The different compositions of cell walls in plants allow for a variety of economic and practical uses of the materials. For example, an obvious and vastly important product is lumber, used as a building product. Also, other products that derive value from the cell wall include the following: paper products, fibers for weaving and as dietary supplements, extracts for textiles, ink products, food thickening and flavor products, oils, as well as cellulosic materials for hydrolysis and fermentation into biofuels.

5.5 Pits Are Holes in the Secondary Cell Wall

In secondary walls of all types of cells, areas remain where secondary wall material is not deposited. Such interruptions in the secondary wall (◘ Fig. 5.5a) are called pits due to their appearance in the light microscope. Three main types of pits are recognized: **simple pits** (◘ Fig. 5.5b, c), **bordered pits** (◘ Fig. 5.5d, e), and **half-bordered pits**. In simple pits, the canal typically has a cylindrical form, whereas in bordered pits, the canal becomes much narrower in the process of secondary wall deposition and consequently, the diameter of the **pit aperture** facing the cell cavity is significantly less than the diameter of the so-called pit membrane. In adjacent cells, pits arise opposite

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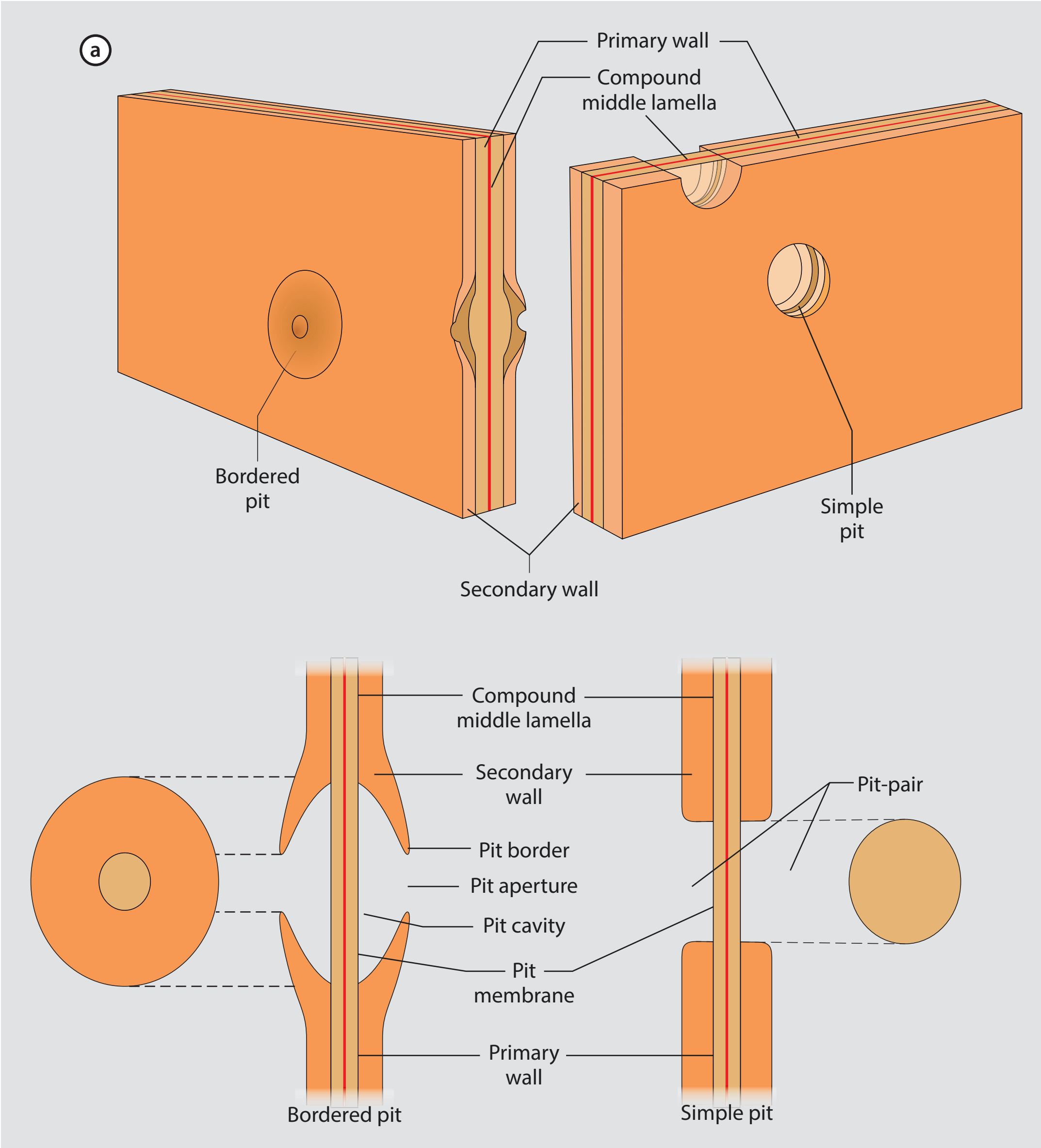
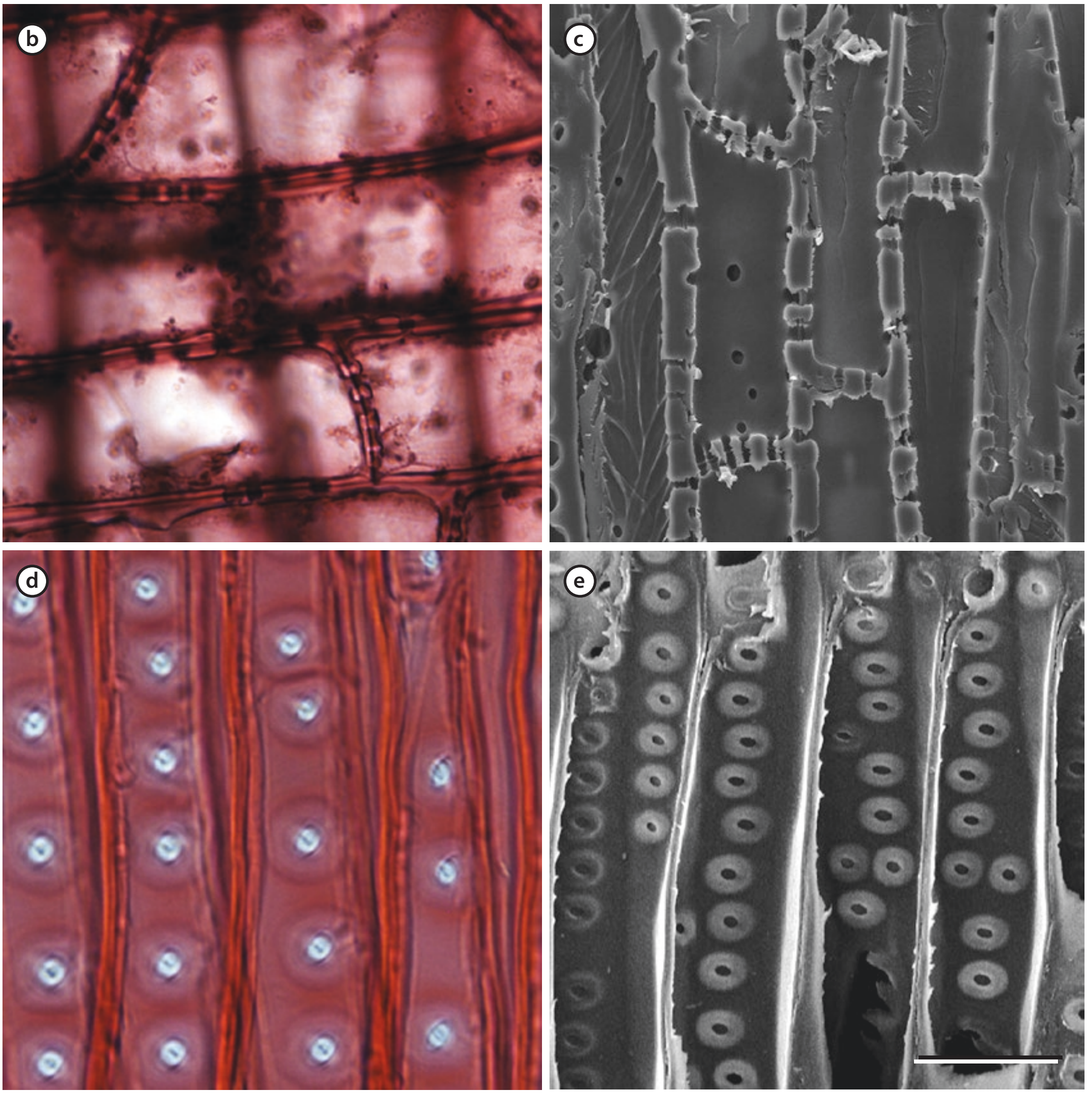


Fig. 5.5 **a** A diagrammatic representation of two segments of cell walls, with the orientation of middle lamella, primary and secondary layers shown. Each represents a model of adjacent cell walls appressed to each other. On the left are shown bordered pits in which the secondary wall material forms an overlaying circular rim over the compound middle lamella. On the right, the simple pits have only the compound middle lamella extending across the pit opening, and the primary and secondary layers of the cell wall are of common dimension (Redrawn from Crang and Vassilyev 2003)

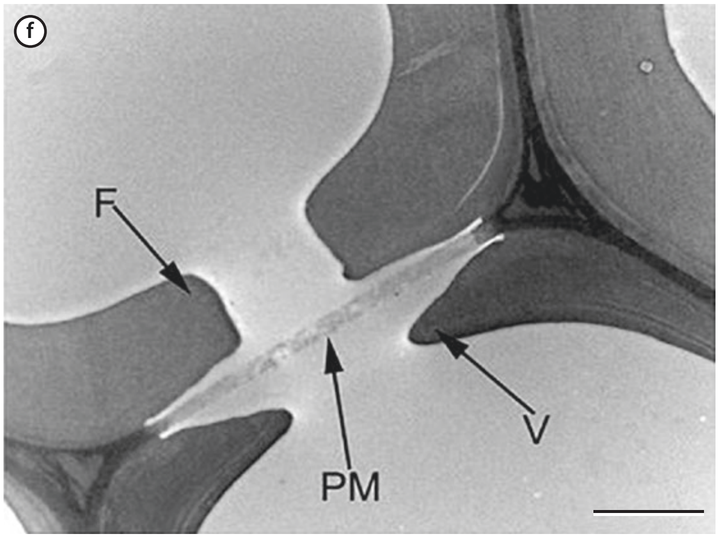
each other and have a common pit membrane. Such a configuration is said to be a **pit pair**. While the two pits of a pit pair are usually of the same type – i.e., simple or bordered – half-bordered pits are a combination of a simple pit and a bordered pit. Simple pits are found in cell walls of living cells such as cells of parenchyma and some fibers. Bordered pits are characteristic of water-conducting cells of wood, which are dead at maturity (tracheids and vessel members). Pits facilitate the intercellular transport of water and solutes.



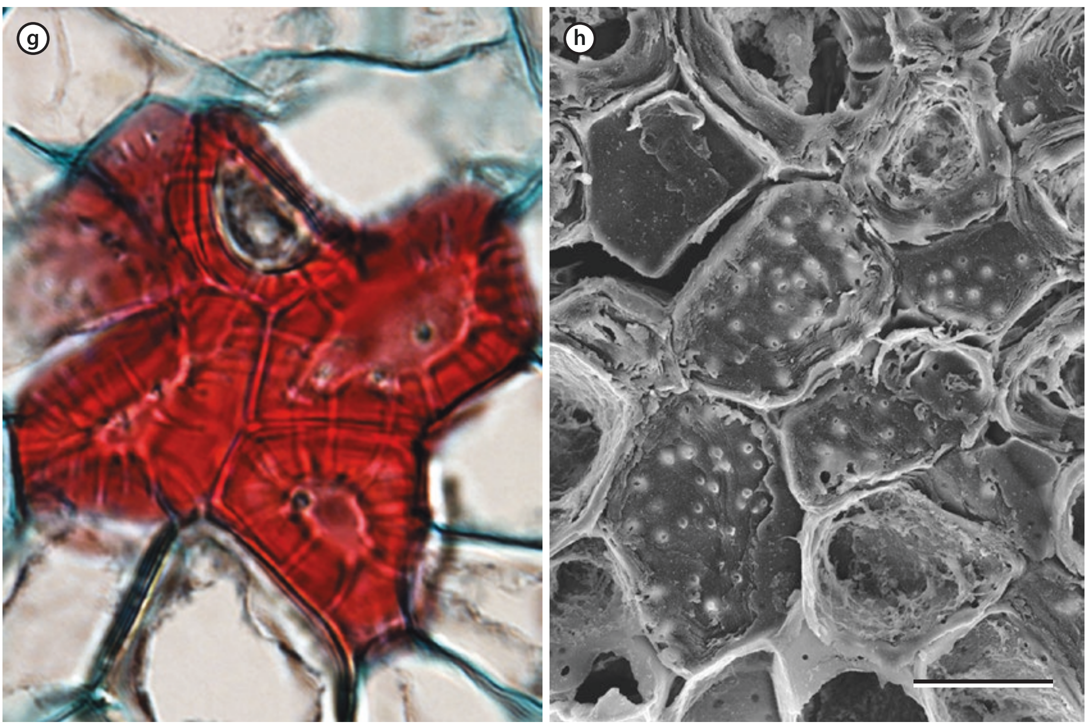
■ **Fig. 5.5** **b** Simple pits seen in cross-section from radial parenchyma in catalpa (*Catalpa speciosa* and **c** honey locust (*Gleditsia triacanthos*) wood. **d** Bordered pits seen face-on in **d** tracheids of white cedar (*Thuja occidentalis*) and **e** pine (*Pinus* sp.). Scale bar in **e** = 20 µm and applies to all panels (**b**–**e** RR Wise)

The portion of the primary cell walls and middle lamella that traverses the pit is called the **pit membrane** (■ Fig. 5.5f). Despite its name, there is no living membrane present, the "membrane" being the original primary cell wall. The primary cell wall is modified from that of a living cell to increase its permeability for water transport.

In cells with very thick secondary walls, pits can be very long indeed. For instance, in brachysclereids of pear fruit (e.g., stone cells; refer to ► Sect. 6.7), pits appear in sectional view as long radial canals through the secondary cell wall, extending from one cell to another (■ Fig. 5.5g). The scanning electron microscope allows visualization of the inner cytoplasmic surface of secondary cell wall and shows the density of pits (■ Fig. 5.5h).



◘ **Fig. 5.5** **f** A pit membrane (PM) between a fiber (F) and a vessel (V) in Tatarian dogwood (*Cornus alba*). Note that the fiber has a simple pit, while the vessel has a bordered pit. Scale bar = 1.0 µm. (Image courtesy of Feng Xu; Beijing Forestry University)



◘ **Fig. 5.5** Simple pits in the brachysclereids of pear (*Pyrus communis*) fruit. **g** Pits are shown in cross-sectional view in the light microscope. The thick secondary cell walls are stained red. **h** Pits are shown in face view in the scanning electron microscope. Scale bar in **h** = 20 µm for both panels (**g**, **h** RR Wise)

5.6 Transfer Cells Have Elaborated Primary Cell Walls for High Rates of Transport

Transfer cells are characterized by extensive ingrowths of the primary cell wall (Gunning and Pate 1969). Such ingrowths function by greatly enlarging the surface area of the plasma membrane, thereby facilitating the absorption or secretion of ions, products, metabolites, etc. They are usually confined to only one area of a cell, and are often found in tissues, which sustain large amounts of metabolite transport such as the "stem" (pedicel and/or suspensor) that attaches a developing fruit to the parent plant (McCurdy and Hueros 2014).

Mangrove is also a unique example in that it is a viviparous plant, meaning that seeds germinate while still in the fruit and the seedling remains attached to the mother plant for the first several weeks of development (◘ Fig. 5.6a). The entire surface of the developing seedling that remains in contact with the fruit develops into transfer cells (◘ Fig. 5.6b, c, Wise and Juncosa 1989). Some recent evidence suggests that a small amount of secondary wall deposition may be present in certain plant species.

◘ **Fig. 5.6** **a** Developing seedling (S) of red mangrove (*Rhizophora mangle*) emerging from the fruit (F). The top end of the seedling and the zone of transfer cells are indicated by the dashed line. Scale bar = 5 cm (RR Wise)

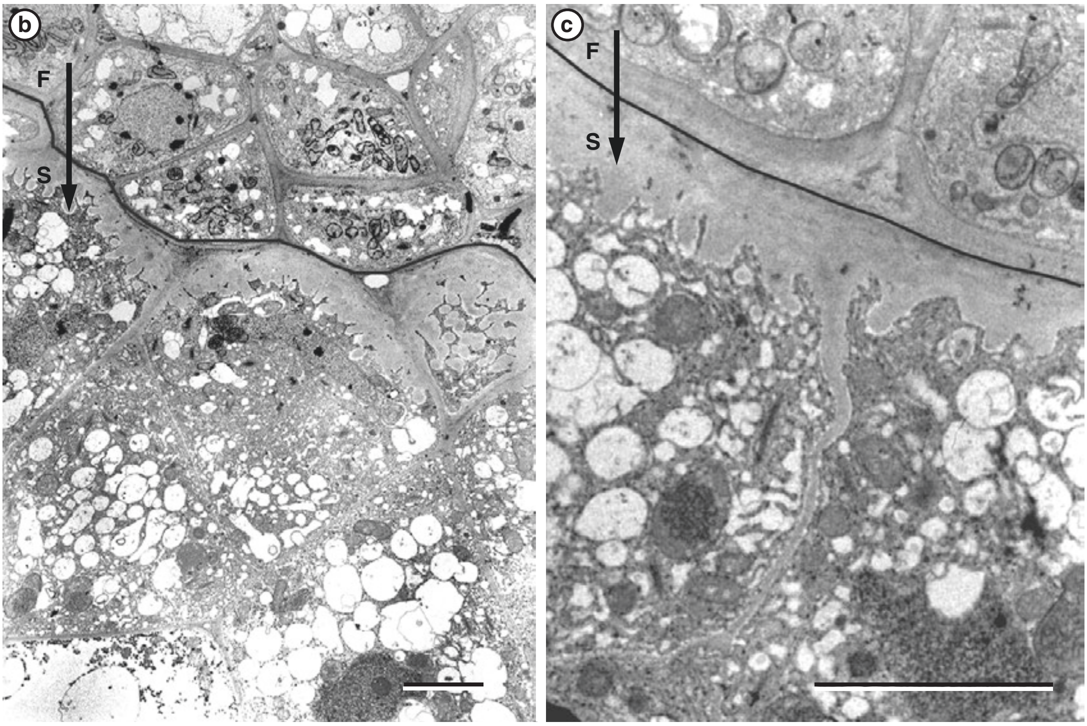


Fig. 5.6 Two views of transfer cells in a mangrove (*Rhizophora mangle*) embryo. **b** Note the substantial protrusions of the primary cell wall that increases the surface area for molecular exchange. Mangrove seeds germinate while still in the fruit (F, above the black lines in both panels), and the seedling (S, below the black lines) stays attached to the mother plant for the first several weeks of development. **c** All water and nutrients are transported from the fruit to the seedling across the transfer cell zone in the direction indicated by the arrows. Scale bars = 10 μm in both panels (**b**, **c** RR Wise)

Box 5.2 Understanding Gene Control of Transfer Cell Development and Function May Lead to Increases in Crop Yield

The elaborate and characteristic cell wall ingrowths of transfer cells, and their location at critical plant exchange surfaces, have confirmed their roles in nutrient and solute transport. They play a role in phloem loading/unloading, providing nutrition to the developing embryo in viviparous plants, and for the transfer of nutrients into the endosperm during seed development. In the latter two cases, the transfer process is between different generations and genetically distinct individuals, thus requiring coordinated communication between the individuals during transfer cell development and functioning. Lopata et al. (2014) reviewed the recent literature on the expression of genes during endosperm transfer cell (ETC) development of cereal crops. ETC-specific genes were placed in five categories: (1) Signal reception and transduction proteins that form the basis of a two-component signaling system between maternal tissue and developing grain (this communication is important for ETC differentiation and development), (2) transcriptional regulators and cofactors which also play a role in ETC differentiation, (3) genes responsible for sugar conversion and transport from the maternal vascular system into the developing endosperm, (4) genes that code for lipid transfer proteins found in the cell membrane, and (5) a group of genes with unknown functions. The authors make particular note of the potential application of this knowledge to the manipulation of seed filling rates, and increased plant yield, which has been a goal of agronomists for roughly the past 10,000 years.

Reference: Lopata et al. (2014)

5.7 Chapter Review

Concept Review

5.1 *Transparent plant cell walls contain cellulose and are synthesized to the exterior of the protoplast*. The plant cell wall is a major structural component of the plant body. Cell walls are mostly transparent; therefore light can penetrate the plant body and be absorbed by a variety of plant pigments. The building blocks of the primary wall are synthesized in the cell cytoplasm but exported to the exterior where they are assembled into the structural components in the wall.

5.2 *Primary cell walls are a structural matrix of cellulose and several other components*. The primary cell wall is composed of several complex carbohydrate molecules such as cellulose, cross-linking glycans, and pectic substances in addition to numerous proteins and ions. Individual cells secrete a cell wall to the exterior of the plasma membrane. The middle lamella glues the cell to the wall of the adjacent cell.

5.3 *Plasmodesmata connect adjacent cells via holes in the primary cell wall*. Plasmodesmata are membrane-lined passages linking adjoining living cells. Primary plasmodesmata develop during cytokinesis to connect daughter cells and secondary plasmodesmata form between existing cells. Plasmodesmata are a tube of a plasma membrane containing a cytoplasmic sleeve and a desmotubule. Proteins, mRNA, and viral genomes are known to be passed through plasmodesmata.

5.4 *Secondary cell walls are rigid, thick, and lignified*. Secondary cell walls are laid down between the plasma membrane and the existing primary cell wall. Thus, they push inward against the cytoplasm and reduce protoplasmic volume. The secondary cell wall may cover the entire cell surface or be deposited in a helical or spiral fashion depending on cell function. The secondary cell wall has multiple layers of different orientation and chemical composition. The deposition of lignin provides significant strength.

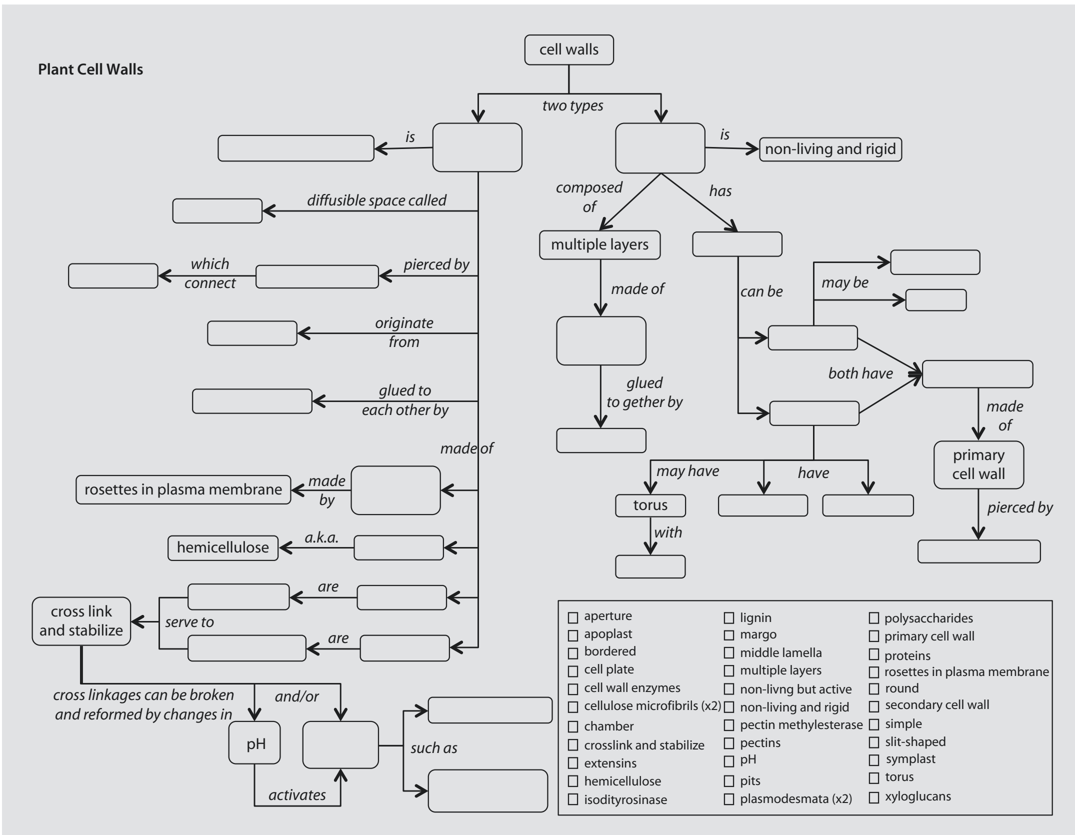
5.5 Pits are holes in the secondary wall. Pits represent a secondary cell wall gap in adjacent cells that allows for the high rate of water movement from cell to cell. Both simple and bordered pits exist in pit pairs—one pit for each of the two adjacent cells.

5.6. *Transfer cells have elaborated primary cell walls for high rates of transport*. The highly folded cell walls of transfer cells increase the surface area available for membrane transport. Accordingly, transfer cells are found in tissues that engage in higher than normal rates of metabolite transport. While normally having primary cell walls, some plants may also possess secondary thickenings to their infolded walls.

5

■ Concept Connections

1. Fill in the concept map below.



■ Concept Assessment

2. The primary function of intercellular spaces in most plant tissues is to
   a. allow for the movement of organic compounds.
   b. provide space for the addition of secondary wall materials to cells.
   c. facilitate gaseous exchange of cells.
   d. maintain turgor pressure.
   e. provide a site of extracellular storage.

3. Where may lignin be found?
   a. secondary walls only.
   b. compound middle lamella.
   c. s_3 layer only.
   d. primary walls only.
   e. all cell wall layers.

4. The S_2 layer of a cell wall is found
   a. adjacent to the cell membrane.
   b. inside of the S_3 layer.
   c. adjacent to vacuolar membrane (tonoplast).
   d. outside of the S_1 layer.
   e. inside of the S_1 layer.

5. Pectic substances are polymers of
   a. galacturonic acid.
   b. lipids.
   c. glucose residues.
   d. amino acids.
   e. calloses.

6. Cellulose is a polymer of
   a. galactose.
   b. glucose.
   c. mannose.
   d. rhamnose.
   e. xylose.

7. The role of pectin in the primary cell **wall is to**
   a. reinforce the cellulose in the wall.
   b. make the wall transparent.
   c. transport precursors to the developing cell wall.
   d. glue adjacent cells together.
   e. cross link the cross-linking glycans.

8. Viruses can spread throughout the cell via
   a. the vacuole.
   b. the cell wall.
   c. secondary cell wall.
   d. pits.
   e. plasmodesmata.

9. Compared to primary cell walls, secondary cell walls are typically
   a. thicker.
   b. stronger.
   c. less active.
   d. more lignified.
   e. all of the above.

10. The elaborate cell walls of transfer cells allow for
    a. the movement of viruses from one cell to the next.
    b. the formation of pits and pit membranes.
    c. the deposition of multiple secondary cell wall layers.
    d. high rates of metabolite transport.
    e. both straight and branched plasmodesmata.

11. Plant cell walls are the basis of which of the following industries?
    a. paper, fiber, and pulp.
    b. lumber, timber, resins, and tars.
    c. textiles, inks, and biofuels.
    d. food thickening and flavor products.
    e. all of the above.

Concept Applications

12. Global climate change is being driven largely by an increase in atmospheric CO_2 levels. Plants take CO_2 out of the atmosphere via photosynthesis and use it to make, among other things, cell walls. Herbaceous plants contain mostly primary cell walls, while woody plants contain mostly secondary cell walls. If you were to plant a garden of plants to sequester CO_2 from the atmosphere, would you use herbaceous or woody plants, and why?

13. A class of enzymes called pectin methyl esterases (PMEs) degrade pectin molecules (by breaking methyl ester bridges between pectin molecules). Why would PMEs be most active in ripening fruit?

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Parenchyma, Collenchyma, and Sclerenchyma

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Introduction

Regardless of the organ or tissue, all plant cells belong to one of three cell types: parenchyma, collenchyma, or sclerenchyma. Unlike animals, in which an organ, tissue, and cell type may have all the same name, the nomenclature of plant structures is more specific and detailed. For instance, we may speak of an organ called the liver, which is made of both liver tissue and liver cells. In this instance, the organ, tissue, and cell type all have the same name.

Plants are arranged differently. The plant body has four basic organs: roots, stems, leaves, and flowers/fruit (► Sect. 1.11), which in turn, are composed of tissues. Tissues are cell complexes, which are similar in origin and structure, and are designed to carry out specific functions. Tissues may be simple (consisting of one cell type only), as in the case of **aerenchyma** or **chlorenchyma**, or complex (consisting of two or more cell types) as in the case of xylem (► Chap. 7) or phloem (► Chap. 8). Thus, an organ such as a leaf is made of three different tissues (epidermis, mesophyll/chlorenchyma, and vasculature), with each tissue composed of up to three general cell types (parenchyma, sclerenchyma, or collenchyma). The three general cell types may be further divided based on function.

6.1 Parenchyma Cells Are the Most Common Plant Cell Type

◘ Table 6.1 give examples of different forms and functions of the three basic plant cell types — parenchyma, collenchyma and sclerenchyma. **Parenchyma** cells are simple cells—alive, metabolically active, capable of dividing, and bounded by a primary cell wall. Altogether, parenchyma represents about 90% of the cells found in a typical herbaceous seed plant. Some of the most important activities of the plant, such as photosynthesis, nutrient assimilation, respiration, storage, and secretion are primarily based in parenchymatous tissues. While many parenchyma cells may be simple or unspecialized, they also possess the highest degree of developmental plasticity. This enables them in specialized circumstances to become transformed into all other cell types, a feature important for wound repair and a key characteristic of meristematic tissues (► Chap. 4). It is also noteworthy to point out that more primitive multicellular non-tracheophytes (► Sect. 1.14) tend to consist of parenchyma only. Lacking the support and water conduction made possible by collenchyma and sclerenchyma, bryophytes are mostly of small stature and typically only occupy moist habitats.

Parenchyma cells are found in ground tissues. Examples of such tissues are the pith of stems (◘ Fig. 6.1a, b) and the cortex of stems and roots (◘ Fig. 6.1c, d). Here, the cells serve primarily as basic filler tissue but may also be involved in apoplastic and symplastic transport and/or storage. Parenchyma cells may be highly specialized when they are parts of a complex tissue like the

Table 6.1 Characteristics, functions, and examples of parenchyma, collenchyma, and sclerenchyma cells (RR Wise)

	Parenchyma	Collenchyma	Sclerenchyma
Characteristics	1° cell wall only* connected via plasmodesmata living at maturity may be toti-/pleuropotent	1° cell wall only unevenly thickened cell walls connected via plasmodesmata living at maturity	mostly 2° cell wall various patterns of wall thickenings if connected, by pits usually dead at maturity*
Functions	serve as ground tissues photosynthesis (chloroenchyma) protection (epidermis) storage meristematic conduction (translocation, via phloem) secretion wound repair	support of annual or young stems and leaves	protection support conduction (transpiration, via xylem)
Examples	pith parenchyma cortical parenchyma leaf mesophyll (chloroenchyma) epidermis pavement cells subsidiary cells guard cells trichomes glandular/nonglandular uniseriate/multiseriate 1° meristems protoderm procambium ground meristem calyptrogen 2° meristems fasicular interfascicular lateral phelloderm pericycle phloem sieve tube elements (angiosperms) sieve cells (gymnosperms) companion cells (angiosperms) albuminous cells (gymnosperms) phloem parenchyma sclerified xylem parenchyma* secretion idioblasts hydathodes resin duct epithelia lithocysts glandular trichomes nectaries collaters	angular collenchyma annular collenchyma lamellar collenchyma lacunar collenchyma	xylem and phloem fibers sclereids* brachysclerids astrosclerids macrosclerids osteosclereids xylem tracheary elements imperforate (andiosperms and gymnosperms) perforate (angiosperms)

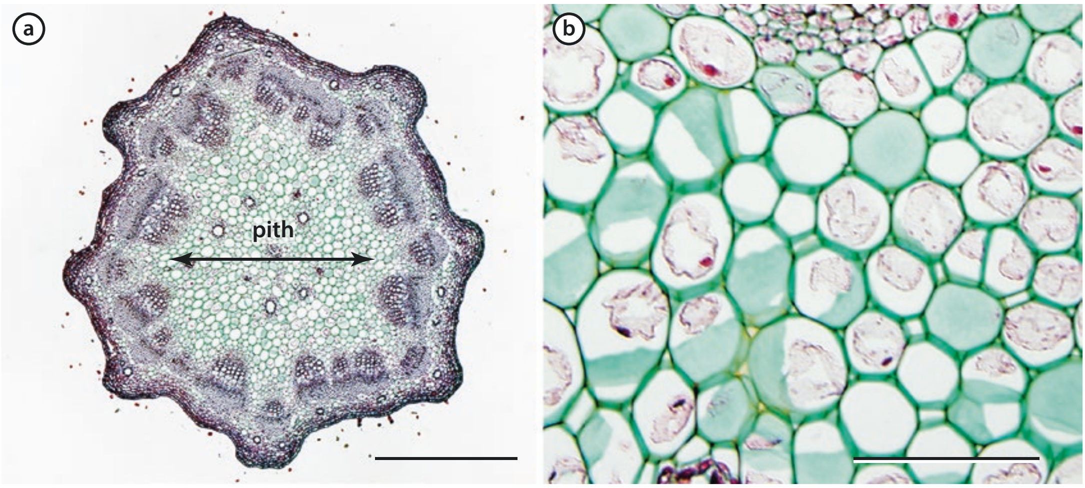
"enchyma" is from the Greek έγ (in) and χεῖν (to pour) and means to "pour in", "fill" or "occupy". Originally, the term was used to describe the primitive formative juice of animal and plant bodies. That "juice" was later found to be made of individual cells, but the root word persists.

"par(e)" is from the Greek παρα (para) meaning "beside"

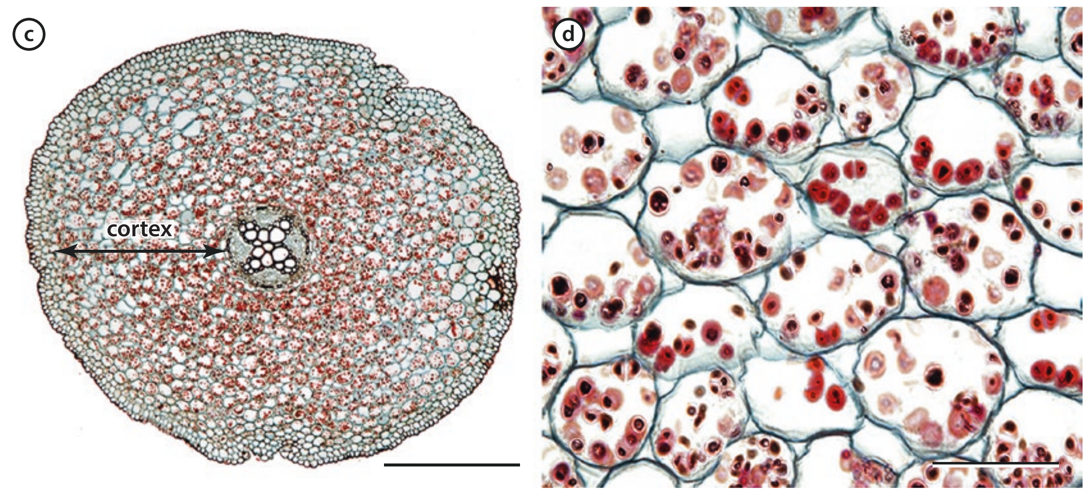
"scler" is from the Greek σκληρός (scleros), meaning "hard"

"coll" is from the Greek κολλα (kolla), meaning "glue", which refers to the thick, glistening appearance of the walls in fresh tissues

**Some sclerids maintain a living protoplasm at maturity, but they are metabolically very quiet.*



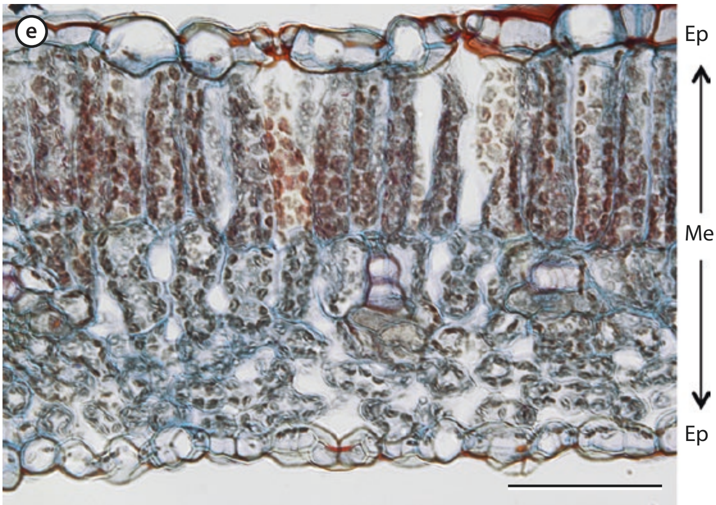
■ **Fig. 6.1** **a** Pith parenchyma in a mugwort (*Artemisia* sp.) stem. **b** The pith tissue is composed of tightly packed parenchyma cells. Scale bars = 500 µm in **a**, and 50 µm in **b**. (**a**, **b** RR Wise)



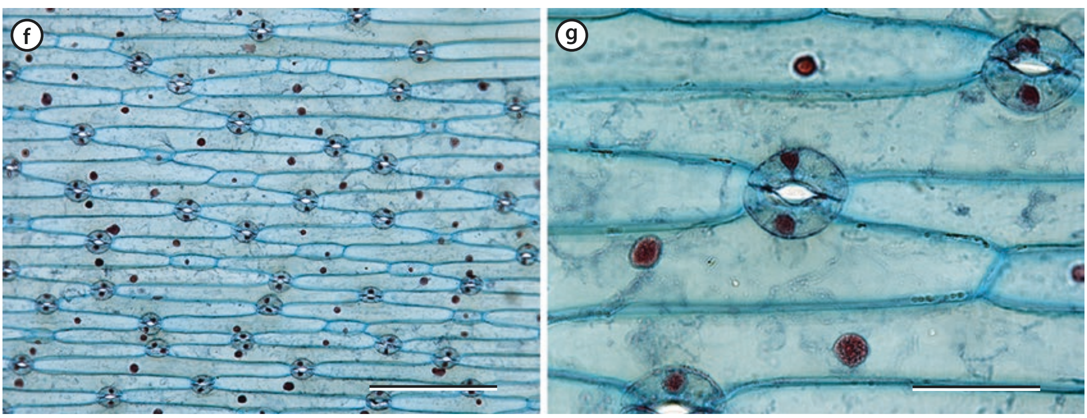
■ **Fig. 6.1** **d** Cortical parenchyma in a buttercup (*Ranunculus* sp.) root. The vascular system is in the center of the root, and the epidermis lies to the outside. **d** Note the presence of numerous starch grains (stained as red dots); thus, this cortical parenchyma is also storage parenchyma. Scale bars = 500 µm in **c**, and 50 µm in **d**. (**c**, **d** RR Wise)

chlorenchyma (chloroplast-containing parenchyma) of leaves that carry on abundant photosynthesis (■ Fig. 6.1e). Parenchyma cells are well suited for photosynthetic activity because their thin primary cell walls allow more efficient diffusion of light, water, gases, and metabolites.

The plant epidermis is made of parenchyma cells and may include **pavement cells** (a.k.a. **ground epidermis**), guard cells of the stomata (■ Fig. 6.1f, g), and glandular or non-glandular trichomes (► Chap. 9). Guard cells are the only epidermal cells to contain chloroplasts, which play a key role in stomatal opening and closing.



◘ **Fig. 6.1** **e** Cross-section of a cucumber (*Cucumis sativus*) leaf showing chlorenchyma (with red-stained chloroplasts) in the center of the leaf (mesophyll, Me) with epidermal parenchyma (Ep) on the top (**adaxial**) and bottom (**abaxial**) surfaces. Scale bar = 50 µm. (RR Wise)



◘ **Fig. 6.1** **f** Epidermal parenchyma on the surface of an onion (*Allium* sp.) leaf. Multiple pairs of guard cells can be seen. All other cells in the images are subsidiary (or pavement) cells. Trichomes (not shown here) are also parenchyma cells. **g** The dark red dots are nuclei. Scale bars = 100 µm in **f**, and 25 µm in **g**. (**f**, **g** RR Wise)

Aerenchyma tissue is composed of parenchyma cells and is quite common in the leaves, stems, and roots of aquatic plants (◘ Figs. 6.1h–j) (Takahashi et al. 2014). In these plants, the air in the spaces serves not only for aeration, but (when they occur in floating leaves or stems) also to give the plants buoyancy and support. The air spaces form an elaborate system that is continuous from the leaf to the root, thereby allowing oxygen to diffuse from its point of highest concentration in the leaves, to places of scarcity in the tissues that are lacking chlorophyll. The buoyancy of many water plants further enables them to capture light at the surface of the water for effective photosynthesis.

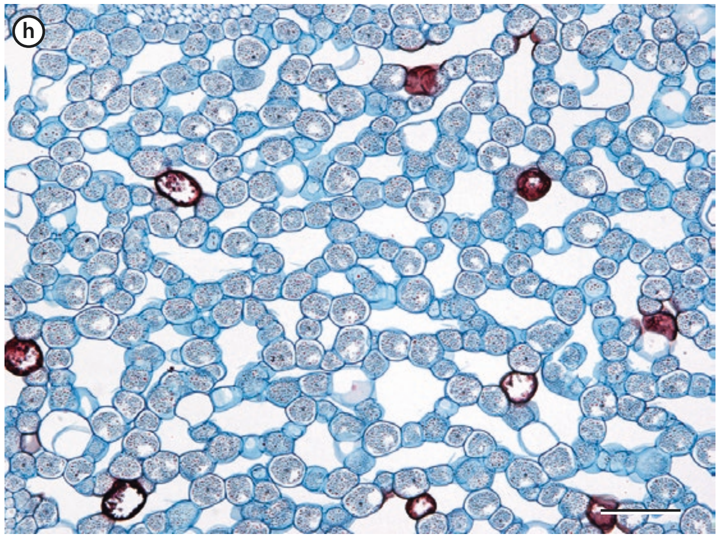


Fig. 6.1 **h** A section through the underground stem of sweet flag (*Acorus* sp.) showing large separation of the parenchyma tissues along the middle lamella. The intercellular spaces enable the movement of large amounts of water, dissolved gasses, and minerals to travel throughout much of the plant. The red cells are sclerified and serve as support tissue. Scale bar = 100 µm. (RR Wise)

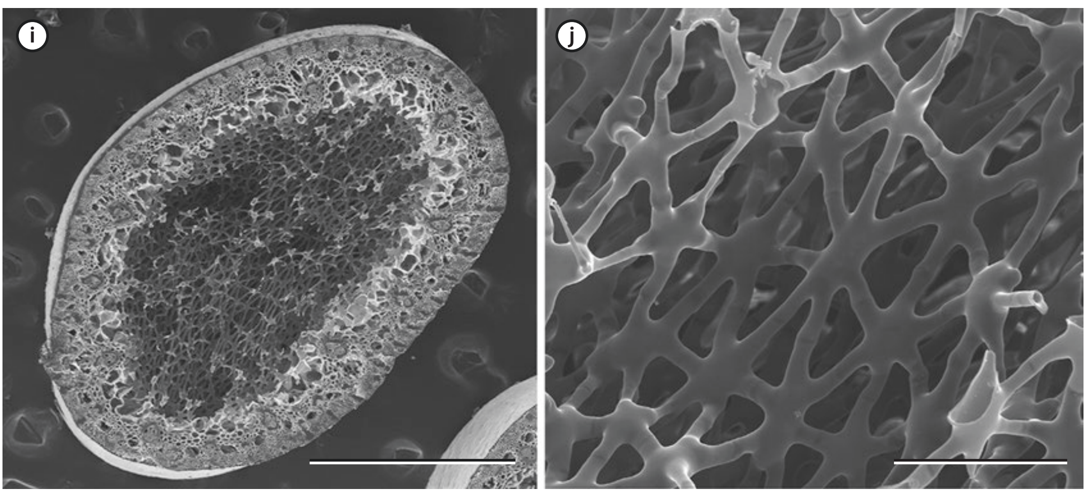


Fig. 6.1 **i** Aerenchyma tissue occupying the center of a bullrush (*Juncus* sp.) stem. **j** The individual parenchyma cells form a network of aerenchyma tissue. Scale bars = 1 µm in **i** and 100 µm in **j**. (**i**, **j** RR Wise)

Storage parenchyma of seeds and tubers contains large quantities of carbohydrates, mostly in the form of starch, or oils (Fig. 6.1k, l). In seeds such as *Asparagus*, *Coffea*, *Diospyros*, and *Iris*, the carbohydrates may be in the form of thickened walls and are represented by hemicelluloses. Oils are typically in the form of triglycerides in seeds, but in tubers and roots, there are many complex oils that vary by species as well as climatic and environmental conditions.

While parenchyma cells are generally thought of as being thin-walled, they sometimes have very thick primary walls as in the case of seed endosperm cells of lily (*Lilium* sp., Fig. 6.1m), date palm

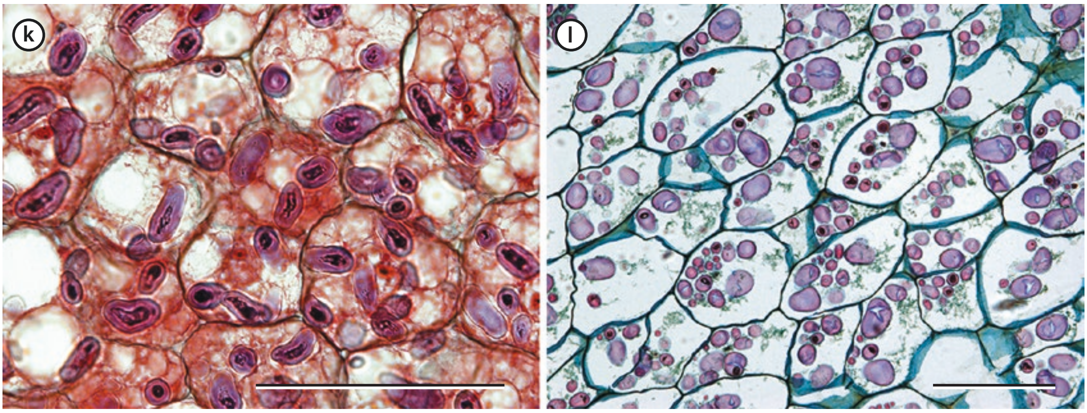


Fig. 6.1 **k** Storage parenchyma of bean seed (*Phaseolus vulgaris*) and **l** potato tuber (*Solanum tuberosum*, right). Both tissues were stained with I_2KI to enhance internal starch deposits, which appear as purple grains. The cells are compressed into a multifaceted form by contact pressure, with little intercellular air space in these storage tissues. Scale bars = 50 µm in both panels. (**k**, **l** RR Wise)

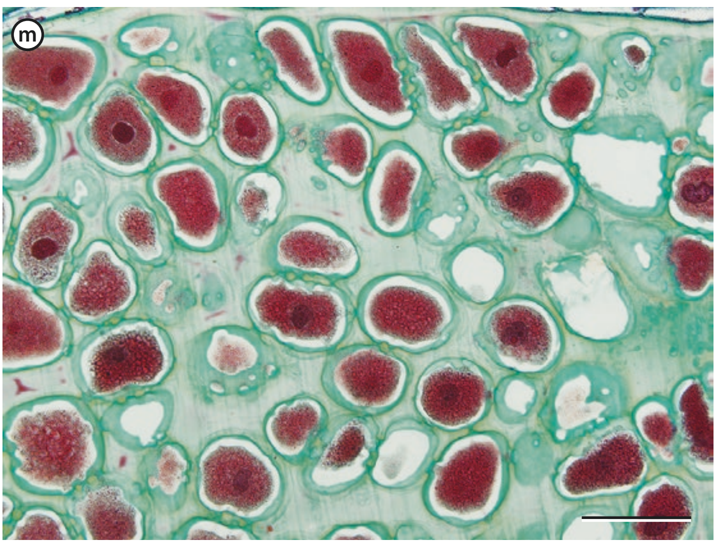


Fig. 6.1 **m** Lily (*Lilium* sp.) seed endosperm showing thick primary walls, stained green. The cell protoplasm has stained red, with the nucleus slightly darker. Scale bar = 100 µm. (RR Wise)

(*Phoenix dactylifera*), asparagus (*Asparagus* sp.), and coffee (*Coffea arabica*). This is often due to the large deposition of hemicelluloses.

The three-dimensional shape of parenchyma cells has been a matter of considerable study (Fig. 6.1n). A number of studies have shown that parenchyma cells consist of a variety of three-dimensional polyhedra that have an average of 14 faces. A geometrically perfect, 14-sided polyhedron with 8 hexagonal and 6 quadrilateral faces has been named an **orthic tetrakaidecahedron**. This ideal figure is compromised in plants that may have a range of facets, but usually averaging 14. Pressure and surface tension both appear to play a major role in determining the number of facets for a particular parenchyma cell.

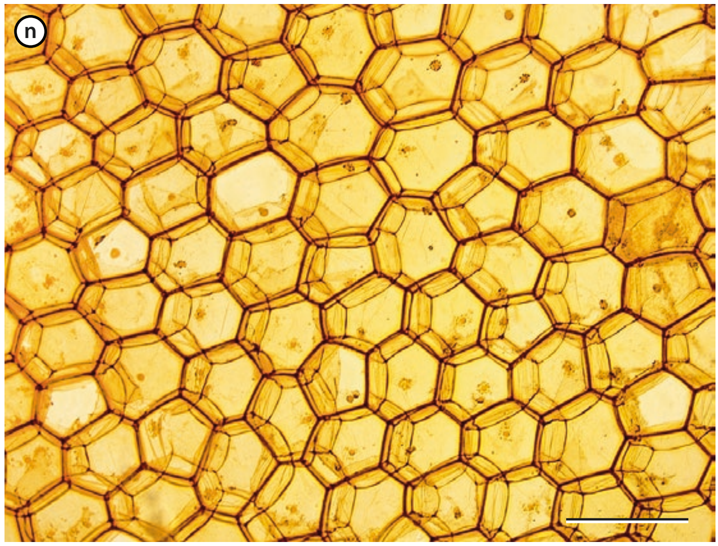


Fig. 6.1 **n** LM of Wandering Jew (*Tradescantia zebrina*) adaxial epidermis showing its angular appearance. Scale bar = 100 µm. (RR Wise)

6.2 Parenchyma Cells May Exhibit Totipotency

Parenchyma is the only one of the three cell types that can engage in mitotic divisions, and they can retain that ability for years. In animals, only stem cells, which are quite rare, retain the ability to carry out mitosis. Consequently, parenchyma cells are the types found in primary and secondary meristems (refer to ► Chap. 4) and the cells that are used for wound repair. The retention of the ability to divide and then continue to differentiate into any of the other cell types is called totipotency, and it enables some parenchyma cells (under the right environmental conditions) to develop into other specialized tissues, including an entirely new viable plant (White 1939).

Figure 6.2 shows plantlets derived from plant tissue culture techniques. As an example, carrot tissue is easily cultured with the following procedure. A carrot root can be sliced into several sections, and the parenchyma storage tissue (cortex) is pulverized with a blender that separates individual cells. Some of these may be cultured in a nutrient medium and will undergo mitosis. Placing these young developing cells into a semisolid nutrient medium will allow them to start growing into new young plantlets due to their totipotency (ability to differentiate into any number of cell types). These, in turn, can be transferred to an enriched soil where full development occurs into a mature carrot plant. Plant tissue culture has many uses in horticulture, plant propagation, and biotechnology.

■ **Fig. 6.2** Plant tissue cultures being grown at a USDA facility (USDA, public domain)

6.3 Collenchyma Cells Are Used for Support and Are the Least Common Cell Type

Collenchyma, together with sclerenchyma, belongs to a group of plant tissues often designated as supporting or mechanical and is primarily found in angiosperms. They essentially have only primary walls (■ Fig. 6.3a), but in some cases, it is believed that secondary deposition may occur resulting in a gradient of development (Leroux 2012). The designation, collenchyma, is derived from the Greek word, κόλλα, meaning glue, which is a reference to the thick, glistening appearance of unstained collenchyma cell walls (refer to Leroux 2012 for the etymology). Of the three types of fundamental tissue found in plants, only about 1% can be considered to be collenchyma.

Given the lack of a secondary cell wall, collenchyma cells can be thought of as being relatively "inexpensive" to produce and reasonably stretchable. Therefore, they are typically in one of two places in herbaceous plant organs. First, collenchyma cells are found in short-lived and rapidly expanding tissues such as large leaf petioles where there is not the time or need to invest in sclerenchyma for support. Second, they may be found in elongating stems, which could not continue to expand in the presence of rigid sclerenchyma. While there have been a few cases in which collenchyma tissues have appeared in roots, most of those have been aerial roots. In leaves, collenchyma appears as axially elongated strands, often located above and below major veins, as well as in petioles and sometimes

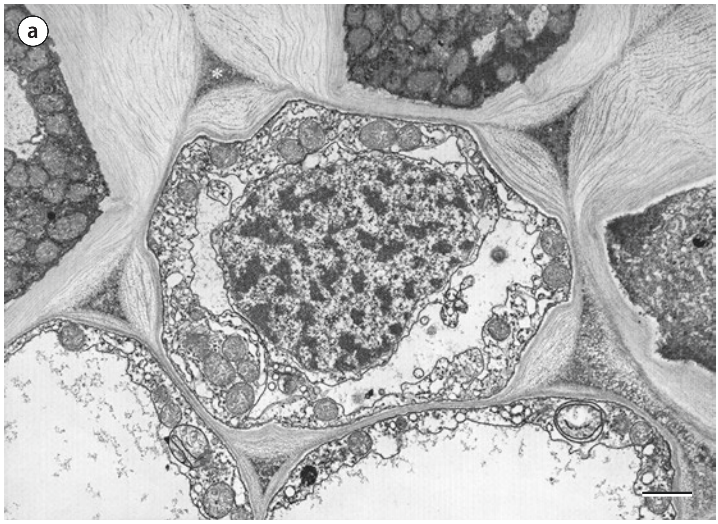


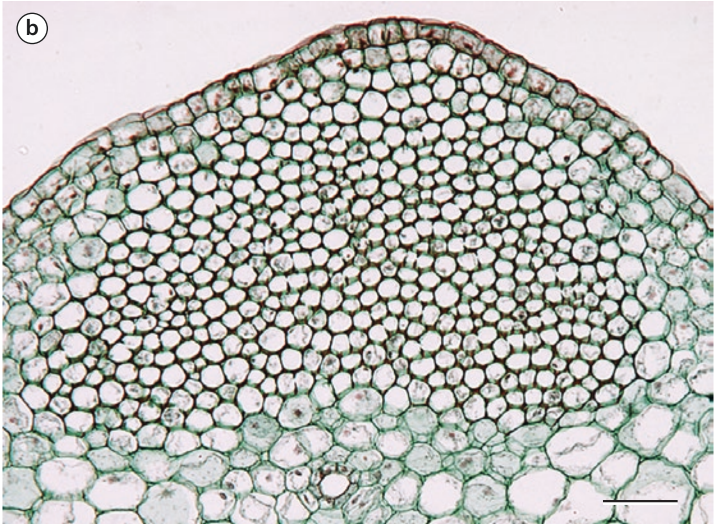
Fig. 6.3 **a** A transmission electron micrograph of angular collenchyma from the petiole of celery (*Apium* sp.) revealing detail of walls and cytoplasmic structure. Note the irregular primary cell wall thickenings in the corners of the cell. Scale bar = 1 µm. (Image from: Ledbetter and Porter 1970, Introduction to the Fine Structure of Plant Cells, Springer-Verlag, with permission)

leaf blade margins. In stems, it appears as a hollow cylinder around vascular tissues,or as peripheral longitudinal strands even though the cells have various amounts of living protoplasm. Chloroplasts are rarely found.

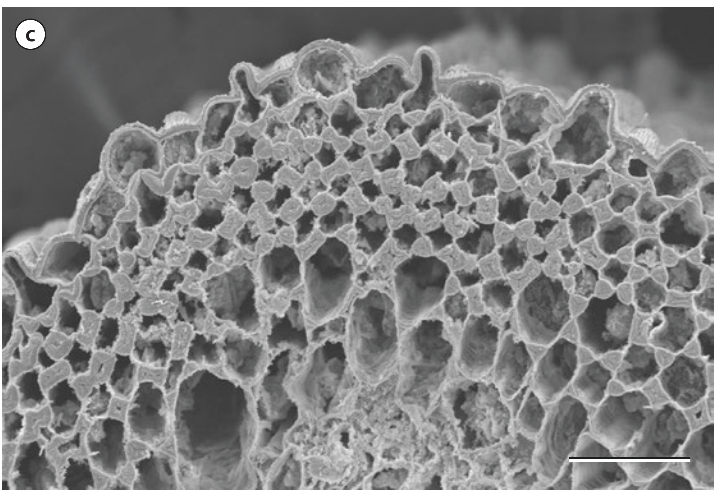
The walls of collenchyma are largely hydrated cellulose, but small amounts of hemicelluloses and pectins have also been reported (Leroux 2012). Lignin does not appear to be a normal component of collenchyma cell walls. Collenchyma cells have unequally thickened primary walls, especially when observed in cross-sectional view. The different thickness patterns of the wall are a characteristic feature formed during elongation. There are four primary types of collenchyma based on the arrangement of the wall thickenings: **angular** (Fig. 6.3b, c), **lamellar** (or plate, Fig. 6.3d), **lacunar** (Fig. 6.3e), and **annular** (Fig. 6.3f).

Collenchyma is a living tissue composed of elongated cells with thick non-lignified primary walls. Such cells are most closely aligned physiologically with parenchyma cells. Where collenchyma and parenchyma cells are found adjacent to each other, they frequently intergrade through transitional cells. The resemblance to parenchyma is further stressed by the ability of this tissue to undergo reversible changes in wall thickness and to engage in meristematic activities. Thus, it is entirely appropriate to consider these two cell types in the same chapter of study.

The thickened walls of collenchyma cells consist mainly of cellulose and hemicelluloses and contain considerable water (as much as 67% based on fresh weight). Thickening of the walls occurs during elongation growth of the cells, with successive layers of wall material



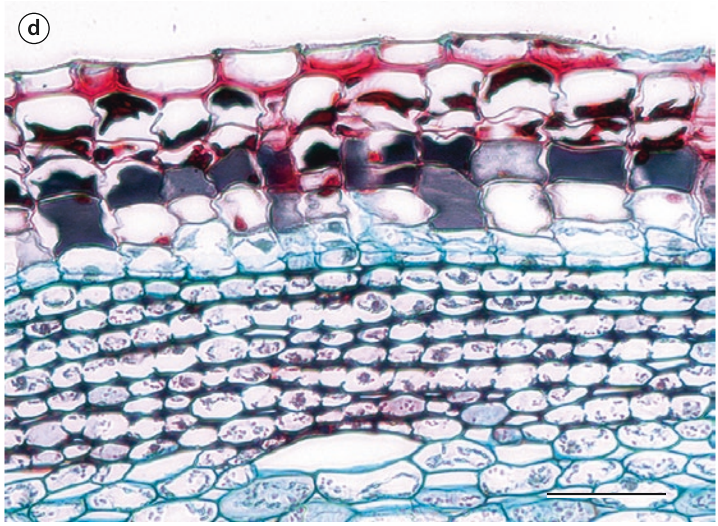
◘ **Fig. 6.3** **b** Angular collenchyma from celery (*Apium* sp.) petiole. Angular collenchyma has greatest wall thickenings where cells meet in corners. The thickened portion of cell walls in contiguous collenchyma cells merges, forming three to four angles. Scale bar = 100 µm. (RR Wise)



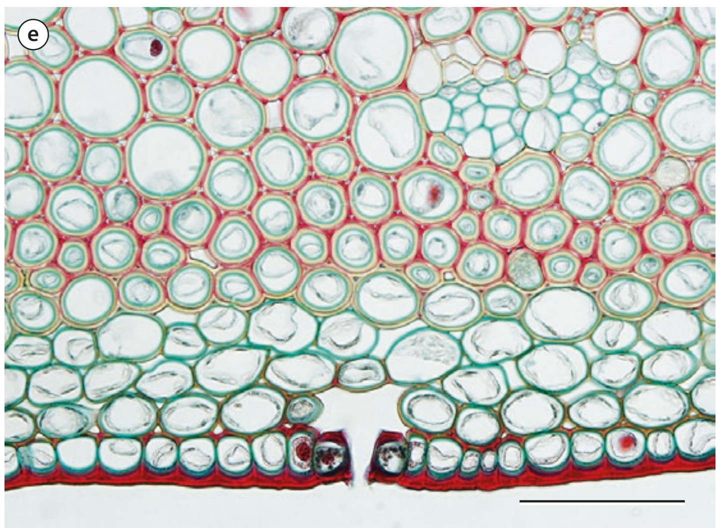
◘ **Fig. 6.3** **c** Angular collenchyma from rhubarb (*Rheum rhabarbarum*) leaf petiole showing the extensive amount of angular collenchyma, as viewed with scanning electron microscopy. Scale bar = 100 µm. (RR Wise)

formed around the entire cell, but they are wider in the places of thickenings. Cellulose microfibrils have a helicoidal texture in collenchyma cell walls that largely sets them apart from parenchyma cells (◘ Fig. 6.3g).

In some cases, it has been reported that the degree of wall thickening in collenchyma is increased if, during development, the plants are exposed to motion by wind or other mechanical forces. On the other hand, wall thickenings may be removed in response

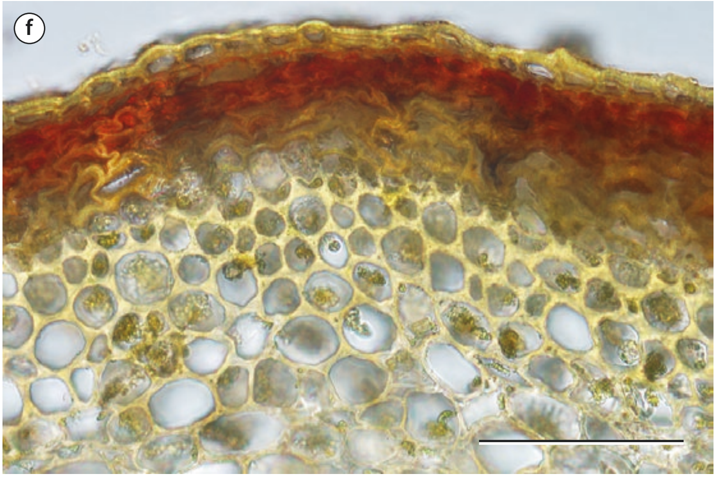


■ **Fig. 6.3** **d** Lamellar (a.k.a. plate) collenchyma from a black elderberry (*Sambucus canadensis*) stem is characterized by thickened portions of cell walls that are present only on tangential cell walls, i.e., those parallel to the surface. There are no substantial thickenings on the radial cell walls, and thus they often tear during sectioning. Scale bar = 100 µm. (RR Wise)



■ **Fig. 6.3** **e** Lacunar collenchyma in the outer cortex of a young stem of lily (*Lilium* sp.). The presence of intercellular spaces is a characteristic feature of a less common type of collenchyma called lacunar. It is somewhat similar to angular collenchyma but contains an intercellular space in the center of "angles." Note the guard cell pair and thick wax coating of the stem epidermis. Scale bar = 50 µm. (RR Wise)

to injuries and wound-healing reactions. Collenchyma that differentiates early in a given organ becomes more highly specialized, whereas that which is formed later is often more like parenchyma (Leroux 2012).



◘ **Fig. 6.3** **f** Annular collenchyma in the stem of paper flower (*Bougainvillea glabra*) is the least common type of collenchyma. It is characterized by evenly deposited primary wall thickenings and little or no intercellular spaces. The cell lumen acquires a rounded outline in cross-section, and the cells become similar to fibers, but with unlignified walls. Fresh section and stained with phloroglucinol. Scale bar = 50 µm. (RR Wise)

6.4 Birefringence Is a Common Phenomenon in Collenchyma Walls

A phenomenon called **birefringence** occurs when crystalline materials or specimens with highly ordered molecules are being observed with the polarized light. When a polarizing filter is used to order light into a single plane through the specimen, some of the light is retarded and rotated by the specimen so that when the light encounters a second polarizing filter above the objective lens of the light microscope, some light has rotated to a new plane and may have experienced interference to produce new colors. Light leaving the filter is said to be plane polarized and consists of light waves essentially in a single plane (all parallel to one another). That light not changed by the specimen will be blocked and will not appear. The birefringence seen in collenchyma cell walls (◘ Fig. 6.4a, b) is a direct consequence of their layered structure.

Box 6.1 Chemical Composition of Collenchyma Cell Walls (Finally) Revealed

Collenchyma, as a distinct cell type, has been described for over 100 years. Collenchyma cell shape, location, mechanical properties, and wall appearance are very well known. Surprisingly, however, the chemical composition of the collenchyma cell wall was only recently revealed. Chen et al. (2017) reported the first detailed investigation of the cell wall composition of collenchyma from any plant. The authors isolated collenchyma strands from celery petioles, a classic study system for collenchyma. Using a vast array of modern

Fig. 6.3 **g** Transmission electron micrograph of angular collenchyma from burdock (*Arctium* sp.) petiole. The thickenings of the collenchyma cell wall have a helicoidal arrangement of the cellulose microfibrils that may make the walls more flexible. In cross-section, the wall appears to be multilayered because the microfibrils gradually change their orientation from longitudinal to transverse and back again to longitudinal during cell elongation. In the thin layers of the wall, the microfibrils are cut longitudinally, and in the thicker regions, there are many layers of microfibrils. Note the very thin layer of cytoplasm at the inner surface of the wall (arrow). Scale bar = 100 nm. (Crang and Vassilyev 2003)

chemical analytical techniques, they determined that the collenchyma cell wall contained many of the same polysaccharide components as found in the extensively studied parenchyma cell wall. However, the proportions and chemical species were distinctly different. Pectin is the major polysaccharide in the *Apium* collenchyma cell wall, followed by cellulose, xyloglucans, heteroxylans, and heteromannans. This long overdue study on collenchyma will serve as a good comparison to the large amount of data available for the structure and chemical composition of cell walls of parenchyma tissues.

Reference: Chen et al. (2017).

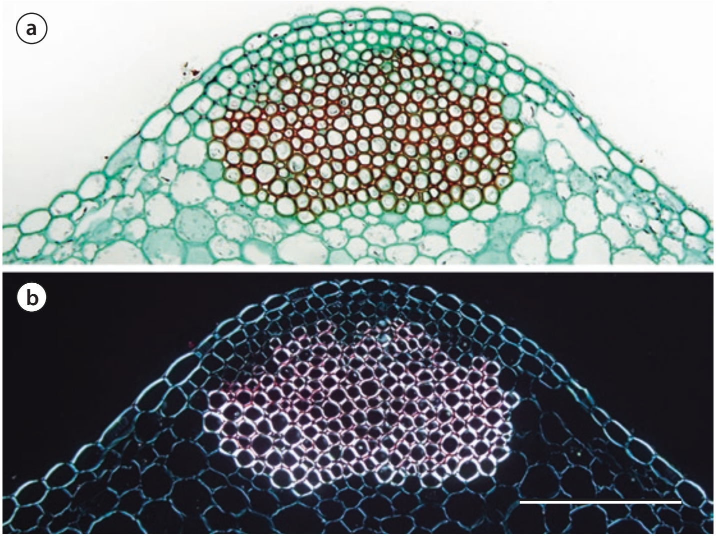


Fig. 6.4 **a**, **b** Collenchyma in a carrot (*Daucus carota*) petiole. **a** Brightfield microscopy. **b** Polarized light microscopy. Scale bar = 100 µm. (**a**, **b** RR Wise)

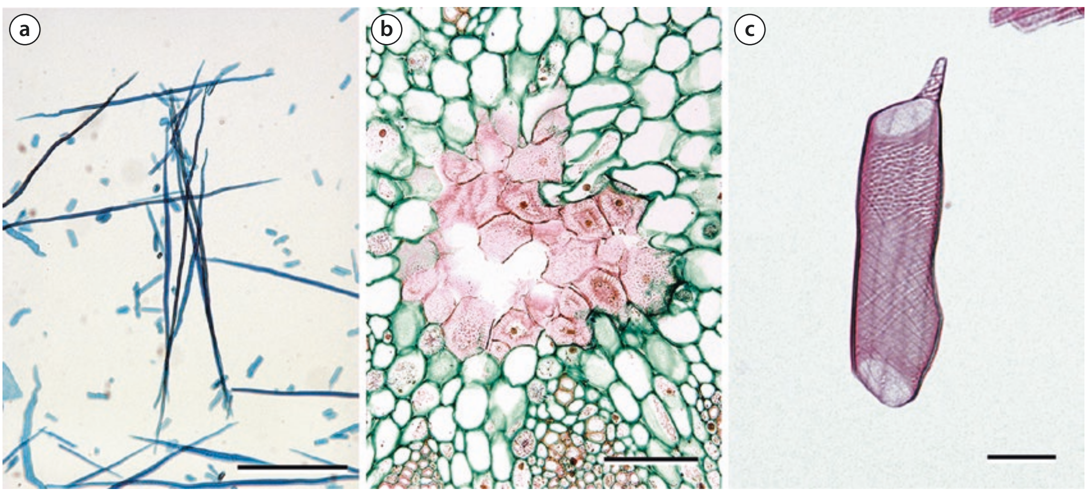


Fig. 6.5 **a**–**c** Three basic sclerenchyma cell types. **a** Fibers from macerated red oak (*Quercus rubra*) wood. Scale bar = 500 µm. **b** Sclereids in the central pith of a mistletoe (*Viscum* sp.) stem. Scale bar = 100 µm. **c** A water-conducting xylem vessel element from macerated basswood (*Tilia americana*) wood. Scale bar = 50 µm. (**a**–**c** RR Wise)

6.5 Sclerenchyma Cells Provide Support, Protection, and Long-Distance Water Transport

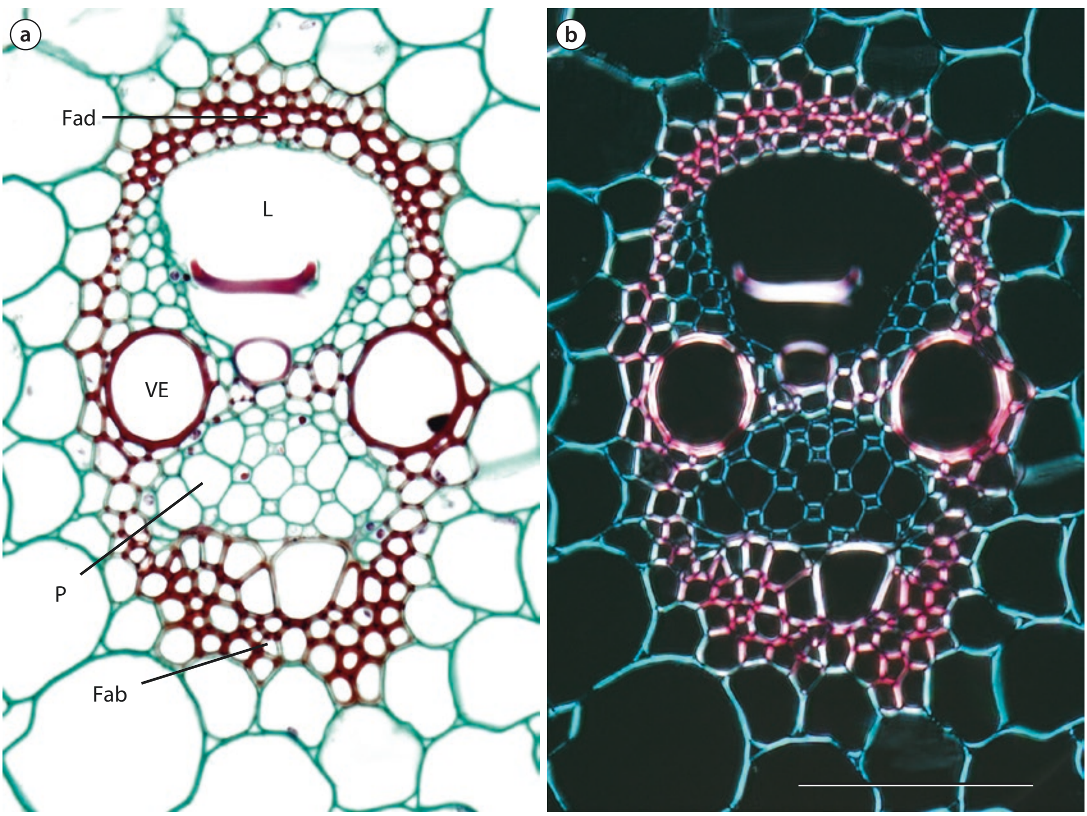
Sclerenchyma cells vary greatly in regard to their origin, distribution, shape, and structure. However, they may be classified into three categories, namely, fibers, sclereids, and water-conducting sclerenchyma (Fig. 6.5a–c). Along with parenchyma and collenchyma, they constitute the third group of fundamental tissues but in total represent only less than 10% of all the cells in living (i.e., non-woody) tissues. Sclerenchymas are structural support cells that do not depend on turgor to remain rigid, but rather on the presence of a rigid secondary wall, and are usually dead at maturity.

Water-conducting sclerenchymas, such as vessel elements, are a major cell type in xylem tissue and will be presented in detail in ► Chap. 7. Fibers and sclereids will be discussed below in ► Sects. 6.6, 6.7, and 6.8.

6.6 Fibers Impart Support and Protection

Fibers are long (up to 2 mm), narrow (typically 20 μm), thick-walled cells that are dead at maturity. Generally, fibers are not associated with water conduction, although one type of fiber—the fiber tracheid—has sidewall pits (► Chap. 7). Fibers are found in various parts of plants, often in association with vascular tissues, particularly phloem in primary growth (◘ Fig. 6.6a, b) and secondary xylem/wood (► Chap. 15). Fibers differentiate early into elongated cells with few simple pits in their cell walls and always appear in clusters.

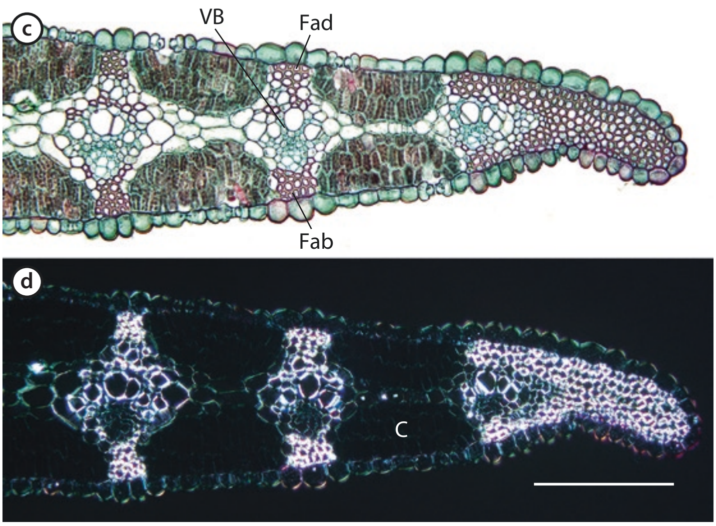
◘ Figure 6.6a shows fibers to the adaxial (at the top in the figure) and abaxial (at the bottom) sides of a vascular bundle in a maize stem. In young maize stems, the fibers serve primarily to protect the fragile



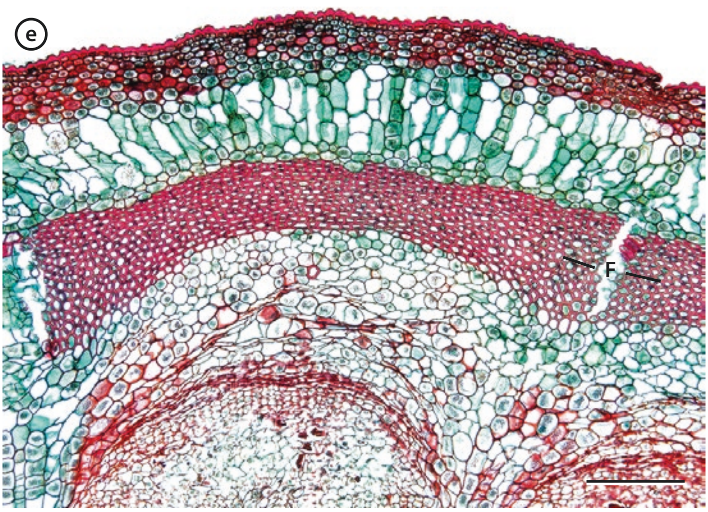
◘ **Fig. 6.6** **a** Caps of fibers adaxial (Fad) and abaxial (Fab) to a vascular bundle in a young maize (*Zea mays*) stem. The two large cells to either side are xylem vessel elements (VE), and a patch of phloem (P) is visible in the center. The empty space in the top-middle is a lacuna (L), or hole, caused by tearing of the tissue during growth. **b** Same specimen viewed in polarized light to show lignification of fibers and vessel elements. Scale bar = 50 μm. (**a**, **b** RR Wise) phloem tissues with structural support being a secondary function. The lignified cell walls of the fibers and the two large vessel elements show red birefringence when viewed in polarized light (◘ Fig. 6.6b).

In leaves such as those found in cattail (◘ Fig. 6.6c, d), fibers provide most of the leaf support, in addition to protecting the phloem. Large bundles of fibers to either side of the vascular bundles and at the leaf margin make for a stiff leaf that will support itself and be resistant to tearing in the wind.

Fibers may be commonly found in the cortex of developing or older stems. ◘ Figure 6.6e shows a large patch of fibers in a



◘ **Fig. 6.6** **c** Brightfield and **d** polarized images of fiber bundles (F) in a cattail (*Typha latifolia*) leaf. Fibers are adaxial and abaxial (Fad and Fab) to the three vascular bundles (VB) and strengthen the leaf margin (far right). Note the large patches of chlorenchyma (C) in the leaf mesophyll. Scale bar = 100 µm. (**c** MC Ledbetter and KR Porter (1970); **d** RR Wise)



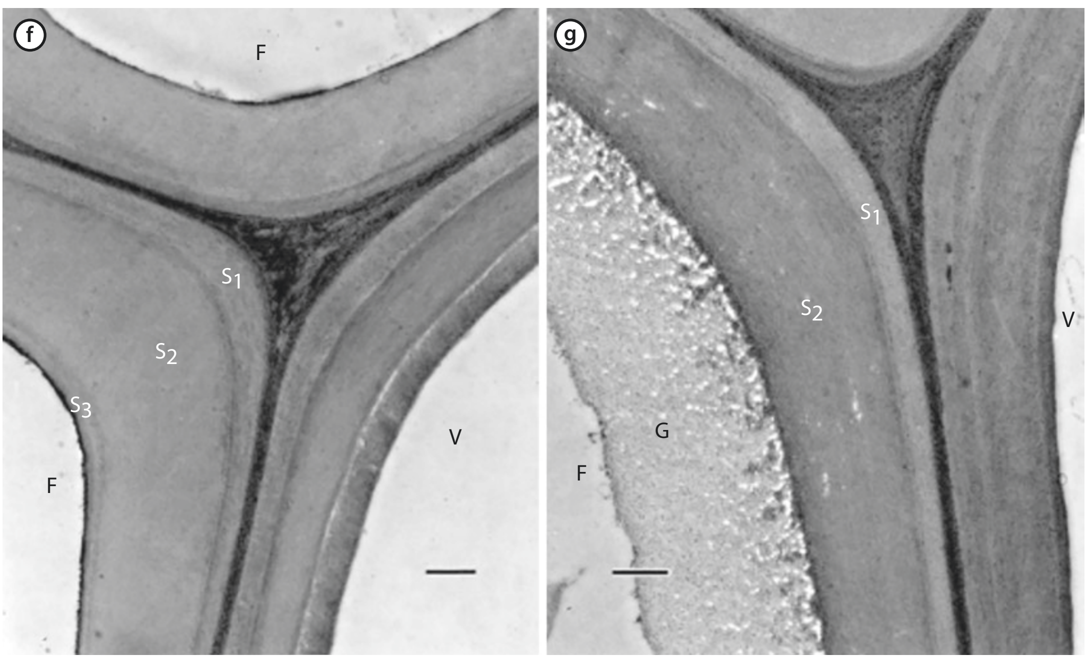
◘ **Fig. 6.6** **e** Large area of fibers (F) in a 2-year-old Dutchman's pipe (*Aristolochia* sp.) stem. Scale bar = 100 µm. (RR Wise)

2-year-old *Aristolochia* stem. Because perennial stems grow for multiple years, large areas of fibers can accumulate. The fiber cells are initiated as cortical parenchyma, which subsequently differentiate into sclerenchyma and develop thick secondary walls.

Bundles of fibers are often found in the leaves of monocots where they provide support, particularly in large leaves of tropical plants. These heavily lignified bundles are often referred to as "hard" fibers. On the other hand, "soft" fibers may or may not be lignified and are usually quite flexible. The terms "soft" and "hard" are commercial designations referring to the texture of the raw materials used in making products and are not strict anatomical terms.

The walls of fibers are rather elastic, a feature which allows them to return to their original shape after bending or stretching, although the cells themselves are usually rigid. **Gelatinous fibers** are found in the tension wood (a type of reaction wood of dicots that shrink and pull, ► Chap. 15), and have a non-lignified cell wall, which is deposited over one or more layers of the secondary walls (◘ Fig. 6.6f, g).

Sclerenchyma fibers are subdivided according to their localization into xylary (or woody) fibers or extraxylary fibers. **Libriform**



◘ **Fig. 6.6** **f**, **g** Transmission electron micrograph of thin sections through *Populus deltoides* wood. Periodic acid-thiocarbohydrazide-silver proteinate (PATAg) staining. **g** Tension wood fiber has developed a gelatinous layer (G-layer) against an S_2 layer that is thinner than in **g** normal wood fiber. F = fiber; V = vessel; S_1, S_2, and S_3 = secondary wall sub-layers; G = gelatinous layer. Scale bars = 0.5 µm. (TA Tabet and FA Aziz, National University of Malaysia, CC BY 3.0)

fibers and **fiber tracheids** are part of the vascular bundle and are considered to be xylary fibers. They will be discussed further in ► Chap. 7—Xylem. Extraxylary fibers, on the other hand, are not located within a vascular bundle or xylem tissue meaning they may be mitotically derived from the phloem (phloem fibers), from cells immediately external to the phloem (perivascular fibers) or in the cortex (cortical fibers). All of the fibers discussed in this section have been extraxylary fibers. Wood fibers are discussed in ► Chap. 15.

Bast is a term used for over 150 years to refer to several different extraxylary fibers or tissues that could be stripped from a plant stem and used to tie or bind. As knowledge of plant anatomy developed, bast was first used to refer to phloem tissue (known then as the "inner bark" or "skin"), before the true nature of that tissue was known (► Chap. 8). Now, the term is used in a generic sense to refer to a variety of fibers of commercial importance, and its value as an anatomical term has diminished. The cell walls of most bast fibers, although thick and strong, are often not lignified and are therefore considered to be soft fibers. Some well-known examples of bast fibers are hemp for cordage (◘ Fig. 6.6h, i), jute for cordage and coarse textiles (◘ Fig. 6.6j), and flax for linen thread, textiles and fine papers, and ramie, which is used

◘ **Fig. 6.6** **h** A hemp (*Cannabis* sp.) field in Brittany, France. (SA 3.0). **i** Cross-section of a hemp (*Cannabis sativus*) stem showing green, thick-walled, non-lignified bast fibers in the stem cortex. Scale bar = 100 µm. (**h, i** RR Wise)

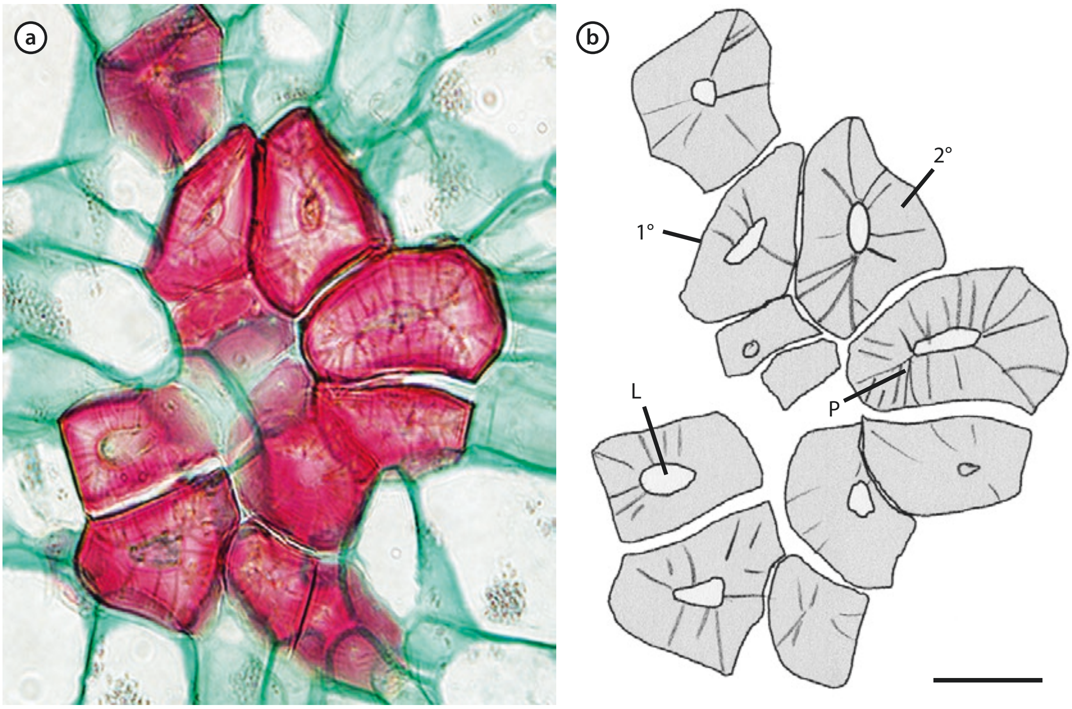
Fig. 6.6 **j** Jute (from *Corchorus* sp.) being placed out to dry. The hanging fibers are used for making textiles. (Image by La Roche Jagu-Chanvre, attribution ShareAlike 3.0)

for various textiles (Pari et al. 2015). Refer to ► Sect. 8.6 for more on phloem fibers. Leaves are also a good source of fibers, such as those found in New Zealand flax (*Phormium tenax*, Carr et al. 2005) and sisal (*Agave sisalana*).

6.7 Sclereids Are Reduced Sclerenchyma Cells That Occur Singly or in Clumps

Unlike the elongated fibers (► Sect. 6.6) and water-conducting sclerenchyma (► Chap. 7), **sclereids** are smaller in size and more varied in shape. Fibers and water-conducting sclerenchyma are characteristics of vascular tissues and may extend, in an overlapping fashion, the entire length of the root or shoot. Sclereids, on the other hand, occur singly or in clusters in various locations in the plant body such as stems, seed coats, fruit pulp, and leaves (especially in the mesophyll). They have thick secondary walls that are heavily lignified. Development of sclereids appears to be dependent, at least in part, on plant hormonal (auxin) levels. Elevated levels of auxin (as may occur in wounding) may elicit the development of greater numbers of sclereids. Sclereids are classified as brachysclereids, astrosclereids, osteosclereids, or macrosclereids. Examples of each type are discussed below.

Brachysclereids (also termed **stone cells**) are the smallest form of sclereids (■ Fig. 6.7a, b). Brachysclereids are complex cells that lend



◘ **Fig. 6.7** **a**, **b** Fresh brachysclereids are naturally yellow in pear (*Pyrus communis*), but in **a** are stained with phloroglucinol that gives them a reddish appearance due to the presence of lignin. They give support to the soft tissues of the fruit. **b** Interpretation of the pit details. Due to concentric cell divisions, clusters of sclereids typically develop as shown here. 1° = primary wall, 2° = secondary wall, P = ramified pit, L = cell lumen. Scale bar = 50 µm. (**a**, **b** RR Wise)

strength and support to tissues such as the **peduncle**, the stem by which an apple is attached to the tree (Horbens et al. 2015). They occur in many species and organs but are probably the most easily seen in the flesh of pear fruit, where they impart the gritty texture found when eating fresh pears. Brachysclereids occur in clumps of 10–50 cells, are **isodiametric**, and possess very thick lignified cell walls with numerous pits, many of which may be branched (thus are said to be **ramiform** in organization). Such ramiform pits develop by fusion of simple pits during the increase in thickness of the secondary wall.

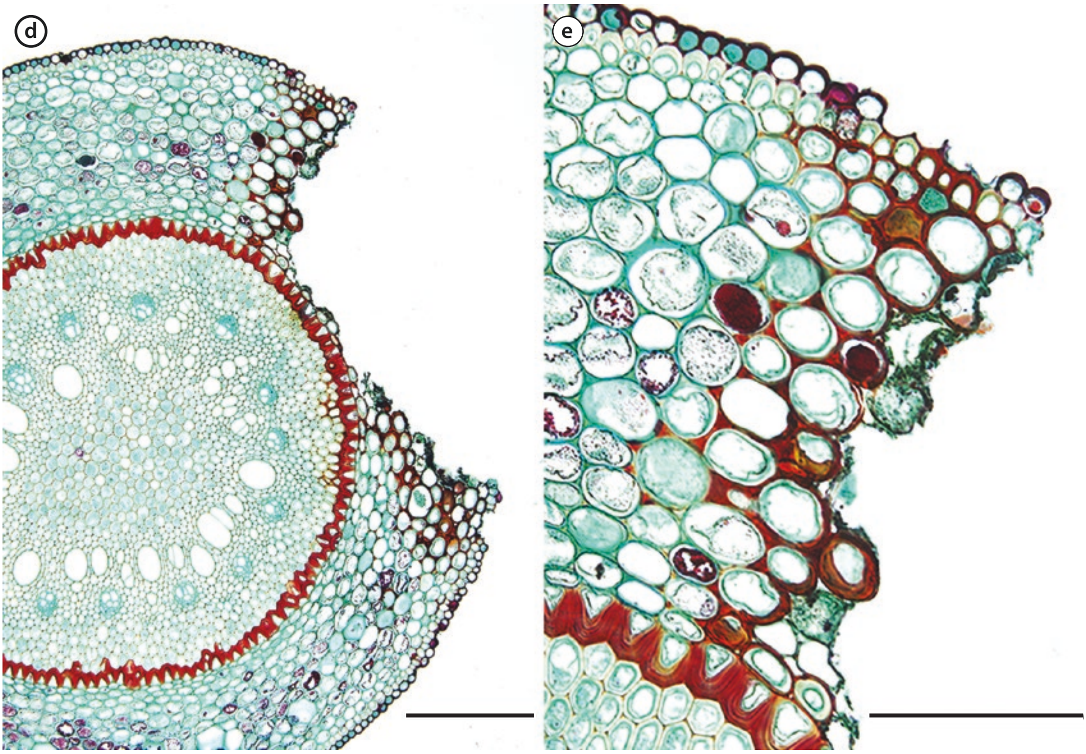
The brachysclereid secondary wall consists of many thin concentric layers, which are laid down to the interior of the cell. As a consequence, the living protoplasm of the cell continually shrinks as the cell wall thickens. ◘ Figure 6.7c shows how the cytoplasm has been reduced to less than 10% of the cell volume. Pits traverse the secondary wall and connect adjacent cells with living cytoplasm (◘ Fig. 6.7c, insert).

Plants respond to wounding caused by insect or other damage by sealing off the damaged area. Sclerification, which is the rapid production of a thick secondary cell wall, forms an effective seal,

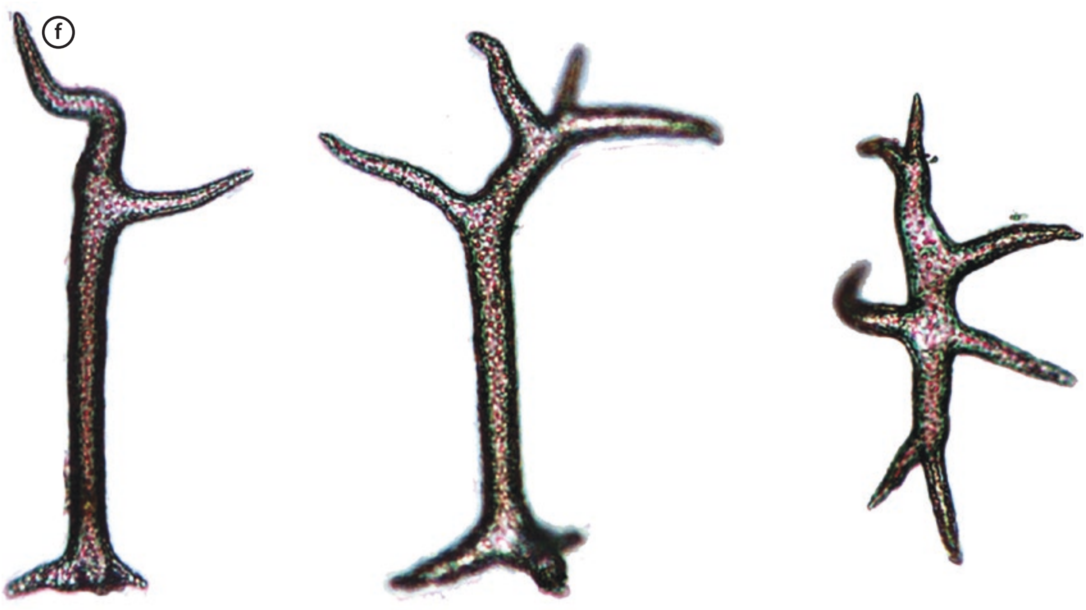
◘ **Fig. 6.7** **c** Transmission electron micrograph of a single pear (*Pyrus communis*) brachysclereid. Note the dark primary cell wall (CW_1) and the extremely thick secondary cell wall (CW_2). Inset: two simple pits appear with plasmodesma (Pd) in the pit membrane. Scale bar = 1 µm. (Image from: Ledbetter and Porter 1970, Introduction to the Fine Structure of Plant Cells, Springer-Verlag, with permission)

and can convert living parenchyma cells into brachysclereids at the site of the wound (◘ Fig. 6.7d, e). The parenchyma cells at the site of the injury are mostly isodiametric; therefore, they differentiate into similarly shaped brachysclereids upon the deposition of a thick secondary cell wall.

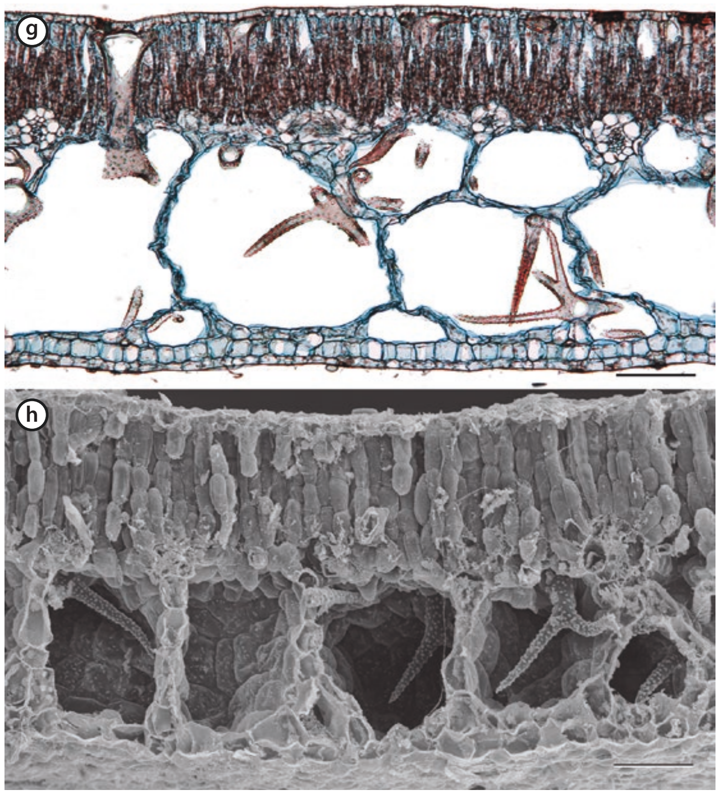
Astrosclereids (star-shaped sclereids) appear as radiantly branched structures with numerous processes (◘ Fig. 6.7f) and are found in such disparate tissues as needles of the Douglas fir (*Pseudotsuga menziesii*), leaves and petioles of water lily (*Nymphaea odorata*, ◘ Fig. 6.7g, h), and the leaves of monstera (*Monstera deliciosa*), a common houseplant. Their function is assumed to be one of support, although little experimental evidence supports this notion. Astrosclereids are often covered with calcium oxalate crystals, which are easily identified by their birefringence under polarized light (◘ Fig. 6.7i–k). Astrosclereids are



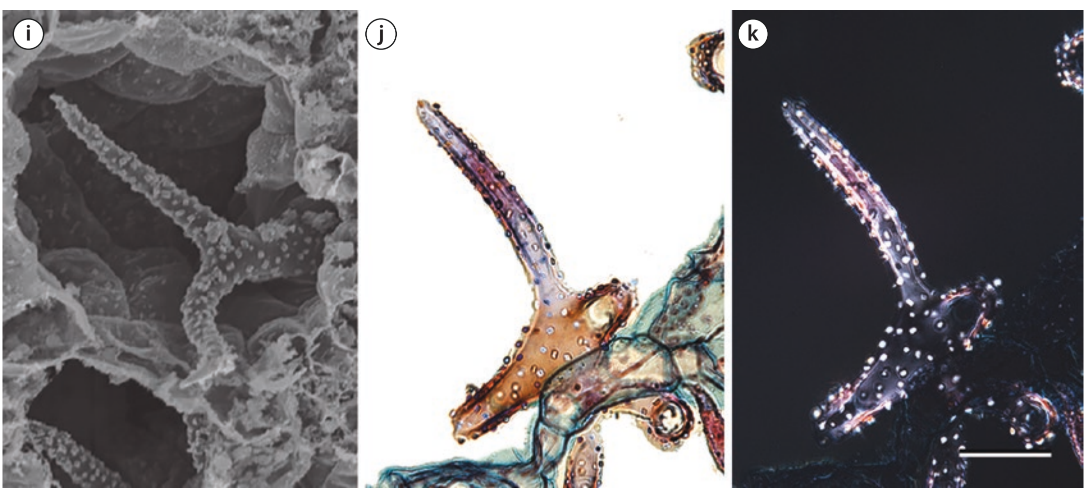
◘ **Fig. 6.7** **d** A large wound in a greenbrier (*Smilax* sp.) root. **e** Sclereids showing lignification have developed at the site of the damage. Scale bars = 200 µm in **d** and 100 µm in **e**. (**d**, **e** RR Wise)



◘ **Fig. 6.7** **f** Representative astrosclereids isolated from an American white water lily (*Nymphaea odorata*) leaf. Scale bar = 50 µm. (RR Wise)



◘ **Fig. 6.7** **g**, **h** Cross-sectional views of a leaf blade of a water lily (*Nymphaea odorata*) with portions of several astrosclereids observed via light microscopy of **g** a stained section and **h** an SEM of a fresh section. Scale bars = 100 µm in both panels. (**g**, **h** RR Wise)



◘ **Fig. 6.7** **i**–**k** Astrosclereids of water lily (*Nymphaea odorata*) leaf covered with numerous calcium oxalate crystals. **i** Viewed with SEM, **j** brightfield light microscopy, and **k** polarized light showing birefringence of the CaOx crystals. Scale bar in **k** = 50 µm and applies to all three panels. (**i**–**k** RR Wise)

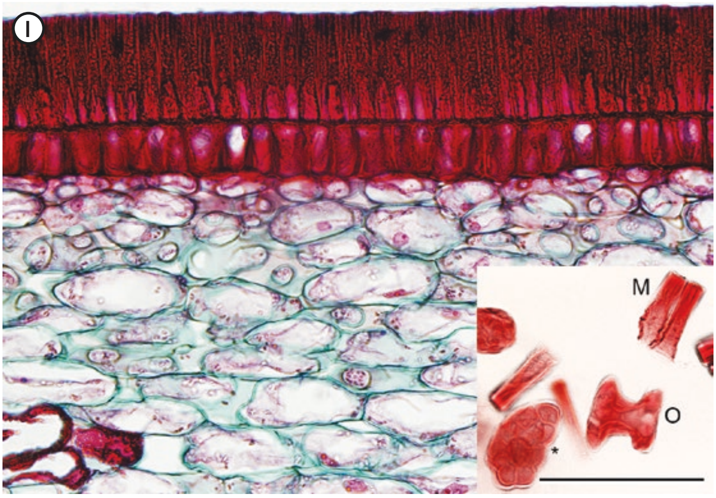


Fig. 6.7 **I** Bean (*Phaseolus vulgaris*) seed coat with an outer layer of macrosclereids and an inner layer of osteosclereids. Starch-containing endosperm is to the bottom of the image. Inset: isolated macrosclereids (M) and ostosclereids (O) from a chemically macerated broad bean (*Vicia faba*). A small bundle of 10 macrosclereids seen end-on is in the lower left corner of the inset. Scale bar = 50 µm for both main image and inset. (RR Wise)

resistant to decay. Those from the yellow water lily (*Nuphar lutea*) can persist in lake sediments for millennia and have proven useful in reconstructing paleoenvironments (Lacourse and Davies 2015).

Osteosclereids and **macrosclereids** (Fig. 6.7I) form the thick, waterproof layer of the **seed coats** of certain legumes. The cells are tightly adhered to each other and prevent desiccation, keep dormancy-promoting hormones from leaching out, and deter herbivory. When isolated (inset to figure), they often appear as "dog bones."

Box 6.2 Anatomical and Biochemical Changes in Legume Pod Wall Were Driven by Crop Domestication

The domestication of crop plants required the selection for many features such as reduced dormancy, reduced seed dispersal (which leads to a preharvest loss of valuable seeds), and increased cooking ability—three traits that are directly influenced by the anatomy of the seed coat. In legumes, domestication favored a thinning of the pod wall which increased the retention of seeds in the pod until they could be harvested (reduced pod shattering) and eased the steps involved in cooking and food preparation. Hradilová et al. (2017) performed an extensive study of seed coats from the wild, dehiscent species *Pisum elatius* (which releases seeds upon pod maturity, the seeds maintain dormancy) and the cultivated, indehiscent *Pisum sativum* (which does not release seeds upon pod maturity, the seeds lack dormancy). The *P. elatius* seed coat was found to have significantly larger macrosclereids and be much more structurally robust than the domesticated *P. sativum*, which would lead to increased shattering and loss of seeds upon harvest. This anatomical trait was also associated with higher amounts of dormancy-promoting chemicals such as proanthocyanidins, quercetin, myricetin rhamnosides, and hydroxylated fatty acids. Loss of dormancy allows for more even and predictable germination upon planting. Genetic analysis showed a downregulation of several genes associated with pod shattering in *P. sativum*, as compared to *P. elatius*. Together, these results show that domestication of the garden pea resulted in the selection of seed coat anatomical and biochemical characteristics that made for more dependable germination, higher yield, and ease of cooking ability.

Reference: Hradilová et al. (2017).

6.8 Xylem Vessel Elements Are Water-Conducting Sclerenchyma

The third type of sclerenchyma, water-conducting sclerenchyma, are also called tracheary elements. They will only be mentioned here to complete the survey of sclerenchyma but will treated more fully in ► Chap. 7, Xylem. In brief, **tracheary elements** provide a conduit for the water of the transpirational stream to flow from the roots to the leaves. There are two basic types (with many variations) of tracheary elements: **tracheids**, which are long and narrow and **vessel elements**, which are shorter and much wider. Gymnosperms only possess tracheids, while angiosperms have both tracheids and vessel elements. Tracheid morphology does not vary significantly, but vessel elements range from relatively long and narrow to extremely wide and short (◘ Fig. 6.8a–d).

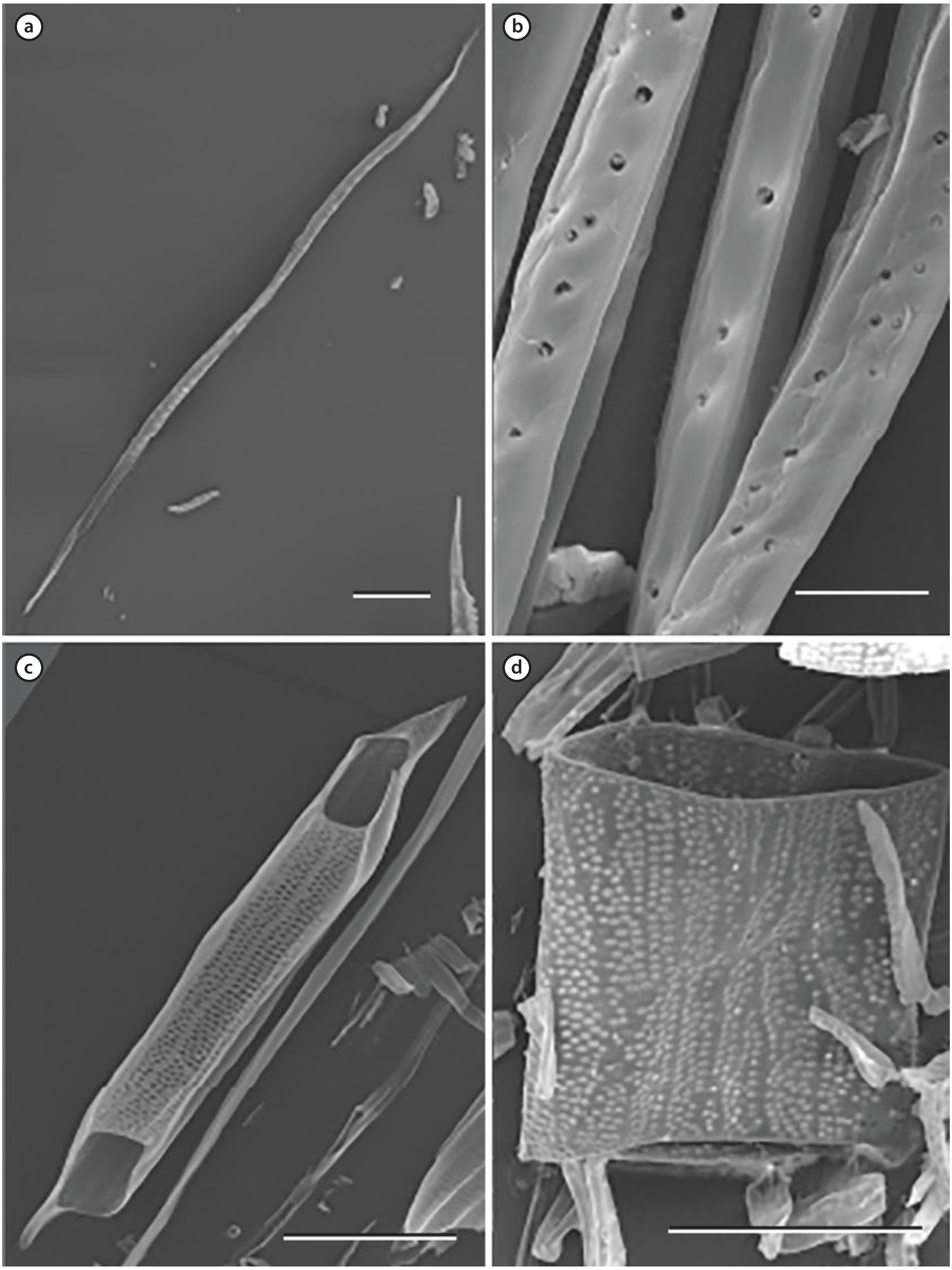


Fig. 6.8 **a**–**d** Examples of tracheids and vessel elements from various woods. **a** Tracheid from grape (*Vitis riparia*) stem. Scale bar = 100 µm. **b** Tracheid from grape (*Vitus riparia*) stem. Scale bar = 20 µm. **c** Vessel element from red maple (*Acer rubrum*) wood. Scale bar = 100 µm. **d** Vessel element from honey locust (*Gleditsia triacanthos*) wood. Scale bars = 100 µm. (**a**–**d** RR Wise)

6.9 Chapter Review

Concept Review

6.1 *Parenchyma cells are the most common plant cell type.* Parenchyma cells are living, thin-walled cells that perform a wide variety of functions in the plant. They are generated at the meristem and are the precursors to all other cell types. Parenchyma cells make up the bulk of the stem pith and root cortex, the epidermis, and the aerenchyma tissue. Storage tissues in seeds and tubers are made of parenchyma cells.

6.2 *Parenchyma cells may exhibit totipotency.* Parenchyma cells are physiologically active and, under many circumstances, are capable of mitosis and differentiation into all other cell types. This is important for wound repair and has been exploited by plant scientists to regenerate entire plants from a single cell.

6.3 *Collenchyma cells are used for support and are the least common cell type.* Collenchymata are living cells with thick, unevenly deposited primary cell walls consisting mostly of cellulose. They are found in short-lived or expanding tissues where sclerenchyma would be too costly or too restrictive. Four types of collenchyma may be identified depending on the pattern and location of cell wall thickenings: angular, annular, lamellar, and lacunar.

6.4 *Birefringence is a common phenomenon in collenchyma walls.* The layered collenchyma cell wall shows birefringence using crossed polarizers for light microscopy due to the orientation of multiple cell wall layers of microfilaments.

6.5 *Sclerenchyma cells provide support, protection, and long-distance water transport.* Sclerenchyma cells have thick secondary walls and are usually dead or have little physiological activity at maturity. There are three general classifications: fibers, sclereids, and water-conducting sclerenchyma.

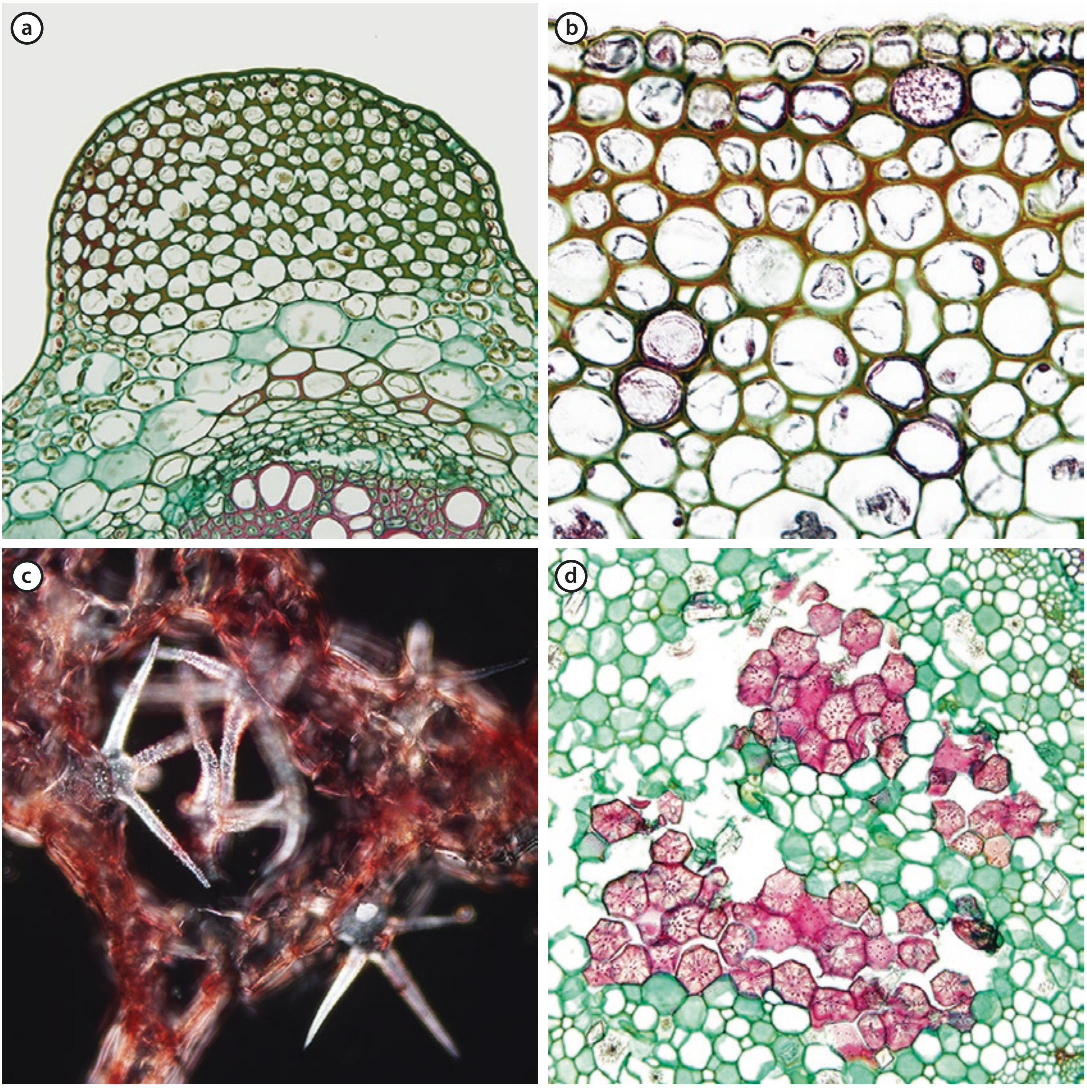
6.6 *Fibers are elongated with tapered ends.* The long, thin sclerenchyma fibers are almost exclusively structural and are found in a variety of tissues and organs, particularly alongside vascular bundles and in the cortex of stems and roots. Fibers are somewhat elastic, with gelatinous fibers being the most flexible. Fibers found in the wood are called xylary fibers (two types: libriform fibers and fiber tracheids), while those not associated with wood are extraxylary (or bast) fibers.

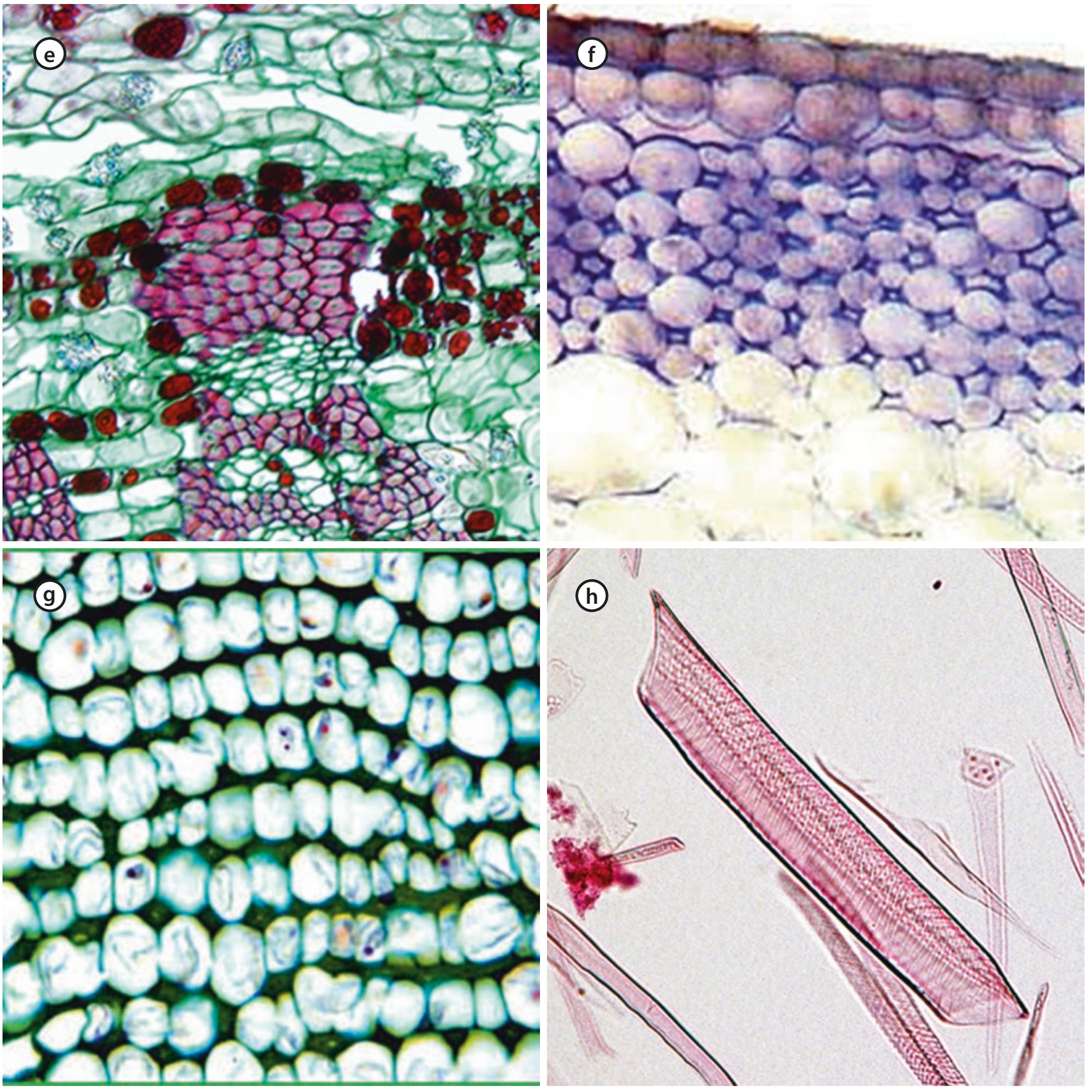
6.7 *Sclereids are compact sclerenchyma cells that occur singly or in clumps.* Sclereids have a variety of shapes (brachysclereids, astrosclereids, macrosclereids, and osteosclereids) and, like fibers, provide structural support and protection to stems, leaves, seeds, and fruit. Many are studded with calcium oxalate crystals.

6.8 *Xylem vessel elements are water-conducting sclerenchyma.* Water-conducting sclerenchyma, also known as xylem tracheary elements, functions in the movement of water from the roots to the leaves during the process of transpiration. Tracheids are long and narrow with tapered ends. Vessel elements are short and wide with various end-wall styles.

Concept Connections

1. Identify each of the cell types shown in the following images.





Concept Assessment

2. Cell walls of collenchyma cells are flexible due to
   a. a high lignin content.
   b. their elastic nature due to contractile proteins.
   c. irregular secondary thickenings.
   d. a helicoidal arrangement of cellulose microfibrils.
   e. layers that slide past one another.

3. Sclereids develop from
   a. fibers.
   b. parenchyma cells.
   c. collenchyma cells.
   d. apical meristems.
   e. cork cambium.

4. Libriform fibers are found in
   a. epidermis.
   b. cortex.
   c. phloem.
   d. xylem.
   e. pith.

5. Most parenchyma cells are capable of
   a. mitosis.
   b. metabolism.
   c. dedifferentiation.
   d. sclerification.
   e. all of the above.

6. Lamellar collenchyma shows thickenings
   a. on the tangential (periclinal) walls.
   b. on the radial (anticlinal) walls.
   c. uniformly around the cell.
   d. adjacent to intercellular spaces.
   e. at the ends of elongated cells.

7. Totipotency is the ability of a cell to
   a. undergo metabolism.
   b. undergo mitosis.
   c. differentiate into any cell type.
   d. die at maturity.
   e. secrete cell wall material.

8. Macrosclereids are most often found in
   a. leaves.
   b. seed coats.
   c. root tips.
   d. vascular bundles.
   e. ground (storage) tissues.

9. The three basic types of sclerenchyma are
   a. collenchyma, parenchyma, and stone cells.
   b. totipotent, monopotent, and dedifferentiated.
   c. astrosclereids, macrosclereids, and osteosclereids.
   d. fibers, sclereids, and water-conducting sclerenchyma.
   e. angular, lacunar, and lamellar.

10. Vascular tissues in herbaceous stems are frequently accompanied by bundles of extraxylary fibers. These fibers serve to
    a. deter herbivory.
    b. provide structural support to the stem.
    c. expand with the expansion of the stem.
    d. conduct water from the roots to the leaves.
    e. protect fragile phloem tissues from damage.

11. Collenchyma cells are most commonly found in
    a. stems that are still growing.
    b. leaves of aquatic plants.
    c. rapidly expanding leaf petioles.
    d. aerial roots.
    e. a and c.

Concept Applications

12. In animals, the word "liver," as an example, is used to describe an organ (liver), a tissue (liver tissue), and a cell type (liver cells). The same is true for the heart, muscle, bone, etc. Most animal organs, tissues, and cell types share a common name. However, in plants, organs (roots, stems, leaves), tissues (dermal, ground, vascular), and cell types (parenchyma, sclerenchyma, collenchyma) do not share common names. Explain this *fundamental* difference in animal versus plant organ/tissue/cell organization.

13. Define totipotency and explain how it differs between animal cells and plant cells.

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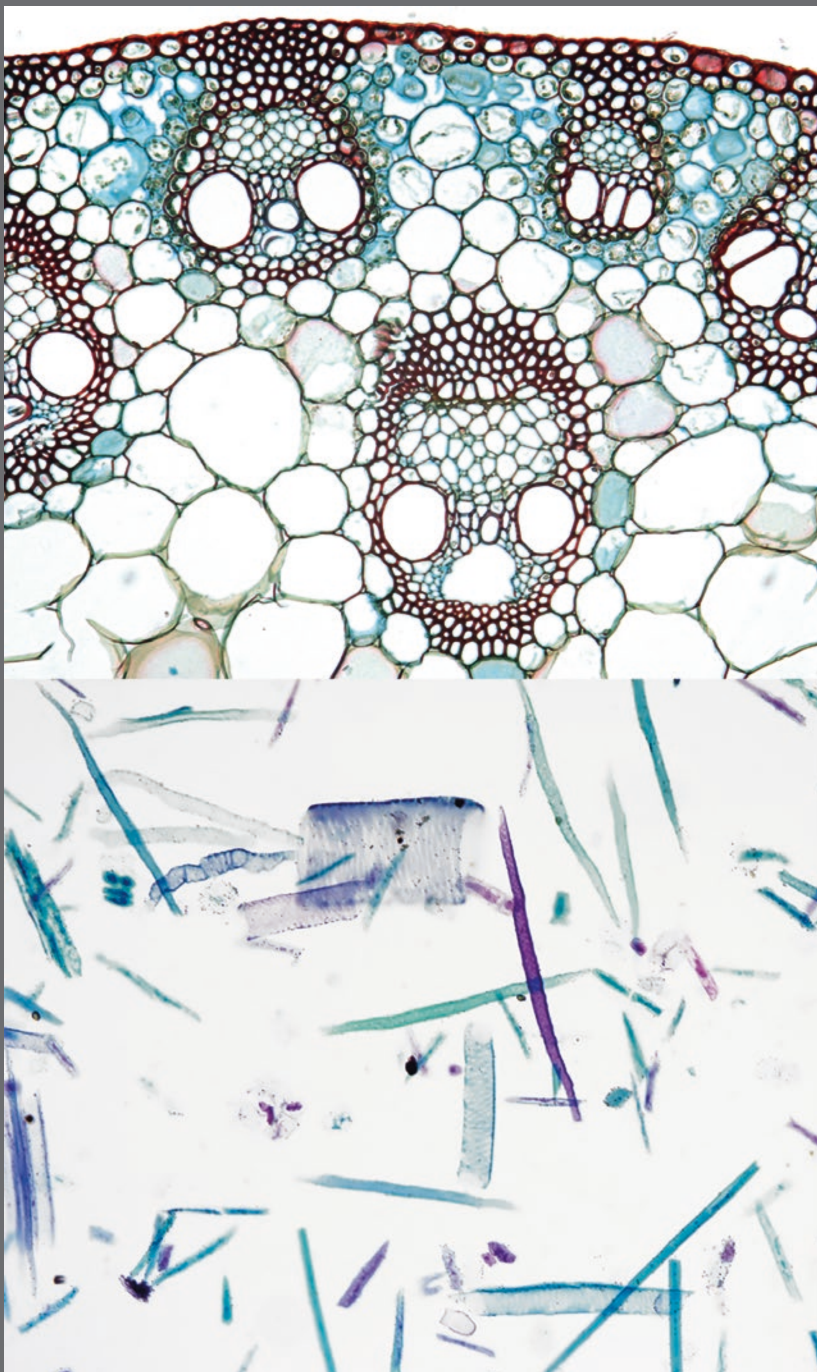
Vascular Tissues



Light micrograph of a maize (*Zea mays*) stem. LM of a Dutchman's pipe (*Aristolochia* sp.) stem maceration. (All images by RR Wise.)

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Introduction

Land plants have two primary conducting systems, designated as xylem and phloem. Xylem is a conductor of water and dissolved substances mostly from the soil through the roots, stems, and leaves. Phloem transports the sugars made by photosynthesis from green tissues where they are manufactured to other parts of the plant, as well as moving a variety of growth regulators. Fossil studies have indicated that water-conducting cells, termed tracheary elements, evolved first in primitive root systems of early land plants, providing both transport of water and support. Subsequent evolutionary development of tracheary elements occurred throughout progressively higher stem and leaf structures. In a similar fashion, phloem elements have developed along with vascular cambium in land plants. Phloem will be covered in ► Chap. 8, and the vascular cambium, which gives rise to both xylem and phloem, is discussed in ► Chap. 14.

7.1 Xylem Is a Complex Tissue Containing Multiple Cell Types, Each with a Specific Structure and Function

Xylem is responsible for the transpiration of water from the soil to the leaves (ascending transport, refer to ► Sect. 7.2), while phloem translocates the products of photosynthesis from leaves to the rest of the plant (ascending and descending transport, refer to ► Sect. 8.2). Both xylem and phloem are complex tissues containing multiple cell types, and being the main highway for transport throughout the plant, they play multiple roles in whole-plant transport, communication, and coordination. The structure and function of xylem will be considered in this chapter. Phloem is discussed in ► Chap. 8.

The evolution of vasculature was a major and necessary advancement for the colonization of land by plants. Indeed, lacking vasculature, bryophytes are limited to short stature and moist environments. As noted above, xylem is a tissue with multiple types of cells. The cell types will be briefly introduced in ► Box 7.1 and ◘ Fig. 7.1a, b and then treated in more detail in ► Sects. 7.3–7.8. It is common in many botany texts to distinguish only two types of tracheary elements—tracheids and vessel elements—and then proceed to state that gymnosperms have tracheids, whereas angiosperms have tracheids and vessel elements. To be more precise, the sclerified xylem cells (which excludes xylem parenchyma, which have primary cell walls) can be divided into two groups—**imperforate** (refer to ► Sect. 7.3) and **perforate** (refer to ► Sect. 7.5). The angiosperm tracheid, fiber tracheid, and libriform fiber are all imperforate xylem cells, meaning they lack perforations in the side walls and end walls. Perforate cells possess perforation plates at both ends of the cell and, in some instances, on the side wall (refer to ► Sect. 7.5). The angiosperm vessel element is the only perforate cell type, although there is considerable variation in length, width, side wall (refer to ► Sect. 7.6), and end-wall (refer to ► Sect. 7.7) design. The distinction between imperforate and perforate sclerified xylem cells is very useful for plant anatomists and is supported by numerous

Box 7.1 Xylem Cell Types

Gymnosperm

1. Tracheid: function in conduction of water and minerals, densely covered with circular bordered pits, lack a perforation plate (therefore, imperforate)
2. Parenchyma: alive at maturity, function in storage/synthesis/cavitation recovery

Angiosperm

1. Imperforate tracheary elements: long, narrow, tapered at ends, lack a perforation plate
    1. Tracheid: function in conduction of water and minerals, densely covered with circular bordered pits, usually found adjacent to vessels.
    2. Fiber-tracheid: function in support, largely non-conductive, fewer and smaller bordered pits than found in tracheids
    3. Libriform fiber: function in support, largely nonconductive, may be alive at maturity, containing a few simple pits, pits often slit-shaped
2. Perforate tracheary elements: possess a perforation plate, short, wide, connected end-to-end to form a vessel
    1. Vessel elements: function in conduction of water and minerals, large diversity in size and shape, side walls thickenings may be annular, helical, reticulate or pitted, perforation plates may be simple or compound
3. Parenchyma: storage/synthesis/cavitation recovery

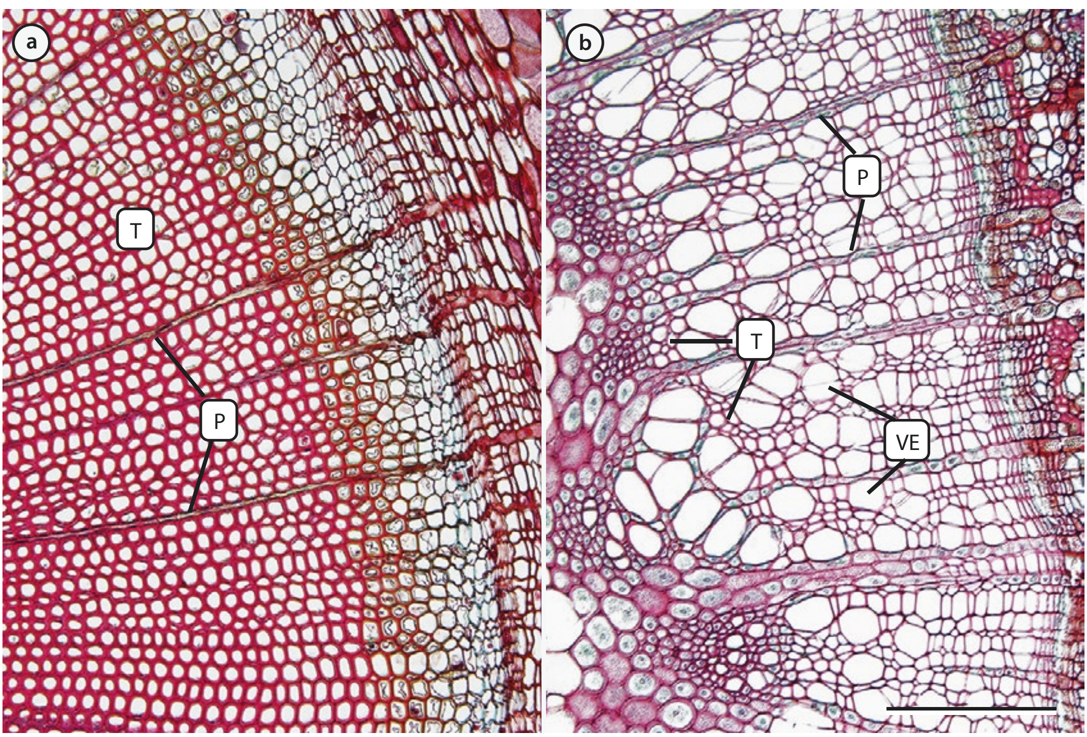


Fig. 7.1 Representative cell types in cross sections of young stems of **a** Canadian yew (*Taxus canadensis*, a gymnosperm) xylem has parenchyma (P) in the xylem rays against a field of axial tracheids (T, imperforate tracheary elements). **b** Tulip tree (*Liriodendron tulipifera*, a woody eudicot) has ray parenchyma and tracheids intermixed with the much larger axial vessel elements (VE, perforate tracheary elements). Both of the images are from one-year-old stems. Scale bar in **b** = 100 µm and applies to both panels. (**a**, **b** RR Wise)

anatomical, physiological, and evolutionary studies. Finally, parenchyma cells are found in the xylem of both gymnosperms and angiosperms (refer to ► Sect. 7.8). They function in storage, synthesis, and recovery from cavitation (the deleterious formation of gas bubbles in the transpiration stream).

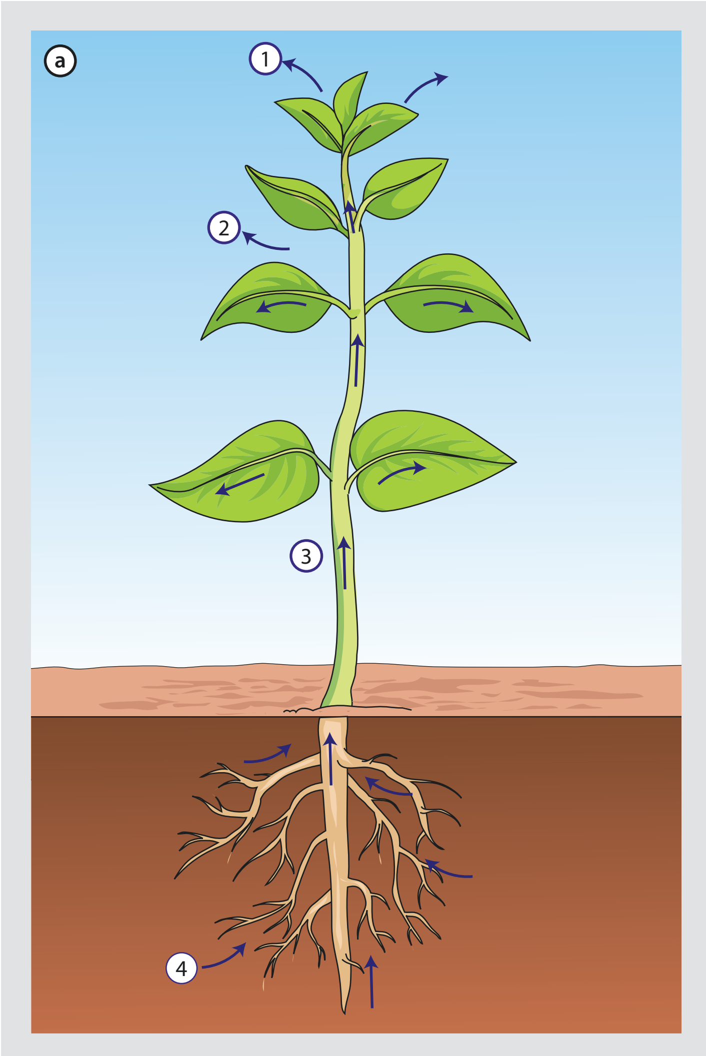
7.2 The Primary Functions of Xylem Are Water Conduction, Mineral Transport, and Support

Transpiration is the movement of water from the soil, through the xylem tracheary elements (vessel elements and/or tracheids), and finally to the atmosphere through the stomata. Like every process that involves movement, there has to be an energy source to drive transpiration; transport moves from an area of high energy to an area of less energy. In the case of transpiration, the driving force is the difference in the free energy of the water at the beginning of the transpirational stream (the H_2O in the soil) and the energy of the water at the end of the stream (the H_2O in the air). With very few exceptions, air water has significantly less energy than soil water, although either can vary tremendously depending on rainfall, soil type, relative humidity, and climate. The energy differential between the water in the soil and the water in the air is sufficient to draw water to the top of a 100 meter tree. Minerals dissolved in the soil water are passively carried with the transpiration stream. They likewise enter the root and are pulled upward with the cohesive transpirational water.

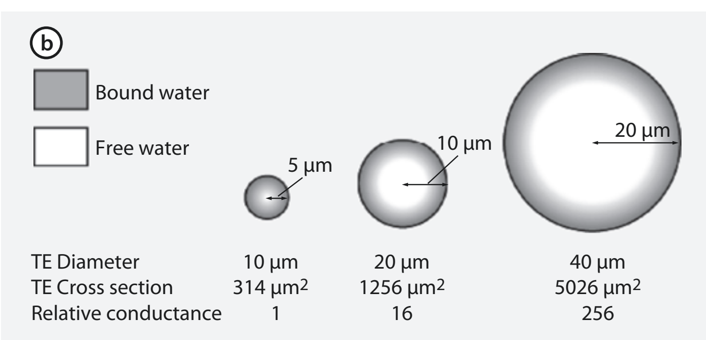
The movement of water is described by the **cohesion-adhesion-tension model**. Water is very polar; it sticks to itself (cohesion) and any other molecule with a polar group (adhesion). Water is drawn through the xylem by its evaporation at the stomatal pore (stomata are discussed in ► Sect. 9.2). The water lost to the atmosphere is replaced, in turn, by water from the leaf mesophyll cells, the leaf xylem, the stem xylem, the root xylem, and ultimately, the soil water (◘ Fig. 7.2a). Being pulled by the atmosphere, transpirational water is always under tension [in contrast, phloem sap is under pressure and is pushed through the sieve tube (► Sect. 8.2)]. At night, when stomata close and water is no longer evaporating to the atmosphere, the water is held in the plant by adhesive and cohesive forces and does not run back down to the roots.

The constant tension applied to the water in the transpiration stream has a direct impact on xylem functioning and architecture. If the water column is pulled too hard because the air (large driving force) or the soil (limited supply) are too dry, the water column will break, or **cavitate**, and produce a bubble of gas in the form of water vapor that blocks any further transpiration in that vessel element or tracheid (Tyree and Sperry 1989). Recovery from cavitation is possible with the adjacent living xylem parenchyma cells providing the water needed to refill the tracheary element (Brodersen et al. 2010).

The relationship between tracheary element diameter and water conductance is illustrated in ◘ Fig. 7.2b. Water is a highly polar molecule with an asymmetric distribution of positive and negative charges. As such, it will stick to itself (cohere) and stick to other



■ **Fig. 7.2** **a** A schematic drawing of the path of transpirational water from the soil to the atmosphere. (**1**) The process starts with the evaporation of water from stomata on the leaf epidermis. (**2**) That water is replaced by water in the leaf, which is supplied by xylem of the leaf vasculature. (**3**) That creates a tension in the water column and draws water through the stem and (**4**) ultimately from the soil. (Redrawn from Crang and Vassilyev 2003)



■ **Fig. 7.2** **b** The relationship between tracheary element (TE) diameter and relative water conductance. (Redrawn from Mauseth (1988), with permission) polar molecules or groups (adhere). The cellulosic plant cell wall has numerous polar groups with which water can adhere; therefore, the water in a tracheary element closest to the cell wall is adhered to the cell wall. This is called bound water. The water that is one H_2O molecule away is cohered to the water bound to the wall; other water molecules are cohered to those and so on with progressive distance from the cell wall. The energy of the water-to-wall adhesion is higher than that of water-to-water cohesion. Therefore, as the distance from the cell wall increases, the water becomes less bound and freer. As the conducting cell diameter increases arithmetically, the cell cross-sectional area and the conductance to water flow increase geometrically.

It can be seen that a larger tracheary element (either tracheid or vessel element) will offer less resistance to water flow because the water is bound with less energy, requiring less energy for transport. However, it also takes less energy for a cavitation event to occur and therein lies the conflict in tracheary element design. When water is freely available, as in the spring, larger diameter tracheary elements allow for a large flux of water at a time when the risk of cavitation is low. Later in the growing season, or higher up in the plant, the transpirational water is under greater tension and the risk of cavitation is higher. Gymnosperms and angiosperms respond to this seasonal variation in water supply and cavitation risk by varying the diameter of tracheids and vessel elements throughout the growing season.

Note that the unit of conduction for gymnosperm tracheids is the tracheid itself. Water, and cavitation events, must pass through pits to move from one tracheid to another. However, the unit of conduction for angiosperm vessel elements is the vessel, which is series of dozens or even hundreds of individual vessel elements connected end-to-end. With large perforations at the end of each cell, water and cavitation events can pass easily through the vessel. This distinction, and the presence, size, and mixture of tracheids and vessel elements between angiosperms and gymnosperms as well as across a growing season, has allowed vascular plants to adapt to a wide variety of ecological niches.

Box 7.2 Phloem to the Rescue: Symplastic Transport of Water

Daily cycles of transpiration and water supply can impose undue tension on the xylem water column and cause cavitation. Pfautsch and colleagues injected a fluorescent dye into the phloem and were able to visualize water movement between the phloem and xylem. They demonstrated that under conditions of high transpiration demand, water moved from the phloem parenchyma cells into the xylem tracheary elements. Thus, it is apparent that phloem tissue can serve as a water reservoir for, and relieve, xylem tension when xylem tissue is at risk for cavitation.

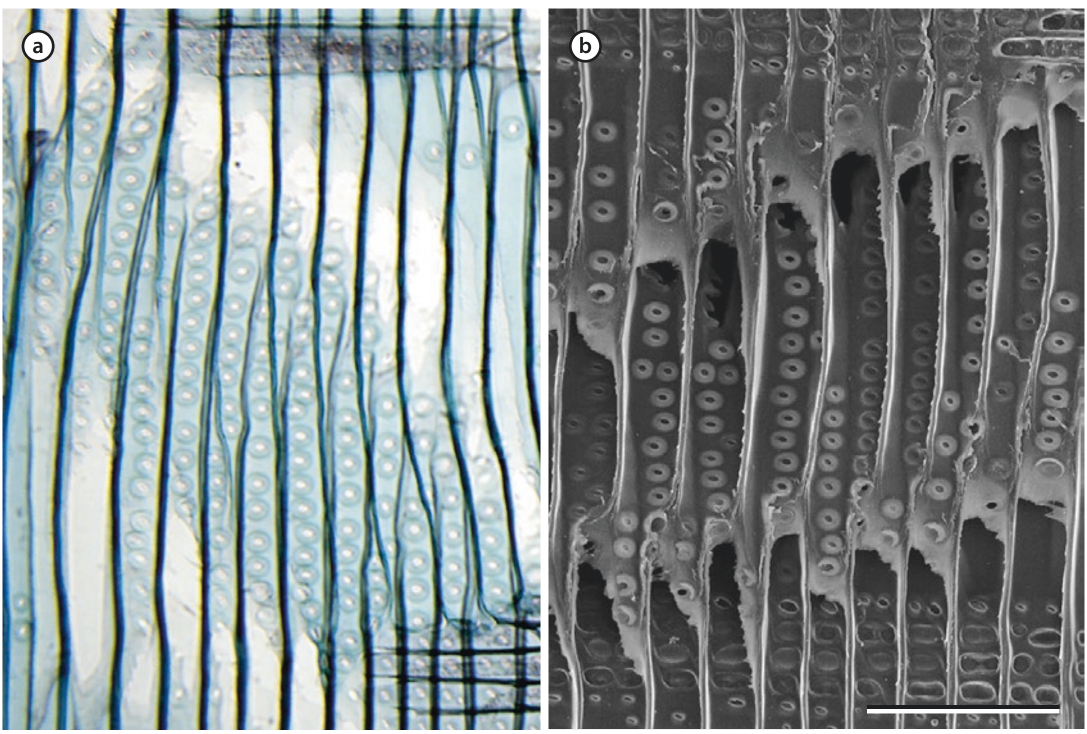
Reference: Pfautsch et al. (2015)

7.3 Tracheids Are Imperforate Tracheary Elements and the Sole Water Conductors in Gymnosperms

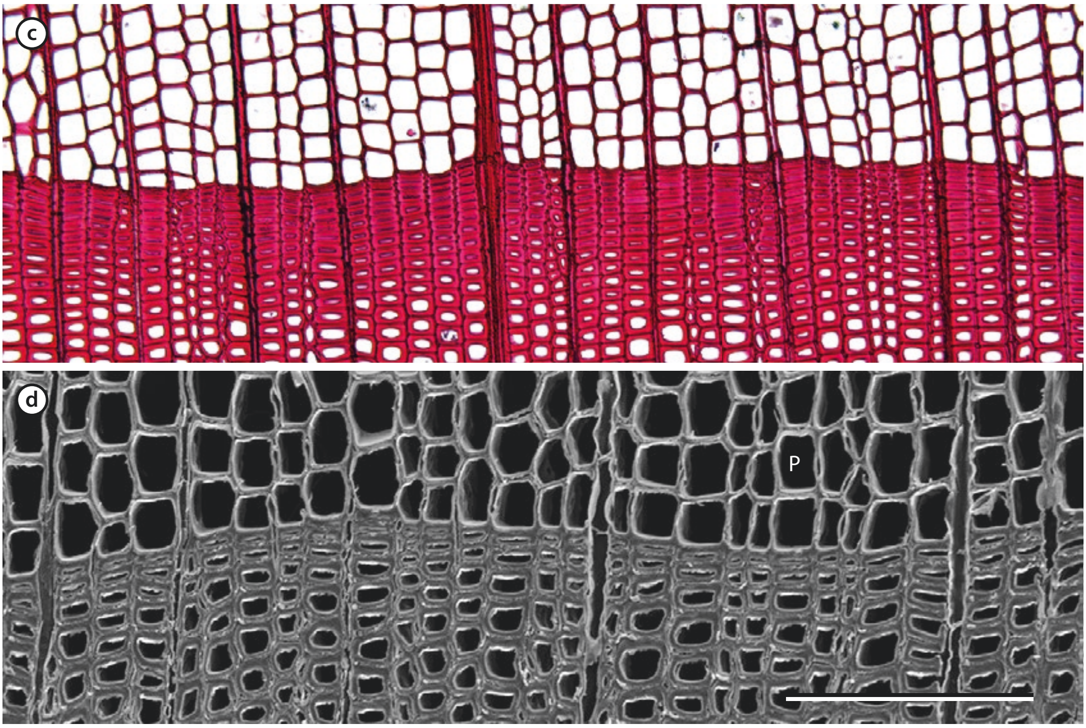
With few exceptions, gymnosperms only have tracheids (imperforate tracheary elements), whereas angiosperms contain both tracheids and vessel elements (perforate tracheary elements) (▶ Box 7.1). The exceptions are the advanced, vessel-containing gymnosperms of the Gnetophyta and the primitive, vessel-less angiosperms in the Winteraceae family. Both of those groups are discussed in more detail in ▶ Chap. 15—Wood.

Gymnosperm tracheids can be quite flexible in both structure and function with the key to the specific function due to the lignified and sculptured cell walls. Tracheids are produced by the vascular cambium. Environmental conditions during development are sensed by the developing cells, in a manner that is not well understood, and result in cell morphologies that are suited to the particular water status at the time of development. Therefore, at maturity, tracheids may differ significantly in their proportion, size, shape, and cell wall thickness. Basic tracheid anatomy is discussed below.

Tracheids are long and narrow, with tapered ends. The tapering is gradual, such that tracheids lack an obvious end wall and terminate in a point (◘ Fig. 7.3a, b); hence, they are imperforate. Water movement from one tracheid to its neighbor is through the numerous pit



◘ **Fig. 7.3** **a**, **b** Tapered ends of tracheids in radial sections of coast redwood (*Sequoia sempervirens*) and pine (*Pinus* sp.). Note the numerous circular bordered pits in the radial walls. Scale bar in **b** = 100 µm and applies to both panels. (**a** RR Wise; **b** JD Mauseth, UT Austin)



■ **Fig. 7.3** **c**, **d** Seasonal growth ring boundaries in **c** Norway spruce (*Picea abies*) and **d** pine (*Pinus* sp.) stems in cross-section. **Early wood** tracheids (toward the top in each panel) have a large diameter and thin walls, while **late wood** tracheids (toward the bottom) are narrow with thick walls. Note several bordered pits surrounding the letter P in **b**. Scale bar in **b** = 200 µm and applies to both panels. (**c**, **d** RR Wise)

7

pairs in the radial walls. Tracheids are packed tightly in the xylem tissue with little to no air space between adjacent cells, giving them an angular, often square cross-section (■ Fig. 7.3c, d). Gymnosperm tracheids range from 100 to 6000 µm in length and 10 to 70 µm in width, with root tracheids being longer and wider than shoot tracheids (data reported in Sperry et al. 2006). While there is significant resistance to water flow from cell-to-cell through the pits and across the pit membrane, resistance within any one tracheid is much less. Thus, tracheids allow for efficient water movement while minimizing the risk of cavitation, and the tight packing of cells provides support.

Tracheids are considered to be more primitive in design and derivation than vessel elements (Friedman and Cook 2000). Lacking vessel elements, gymnosperm tracheids are more varied in size and shape than angiosperm tracheids and vessel elements, as xylem development responds to seasonal changes in water supply and demand. Diameter is larger in the spring and narrower later in the season as soil water is depleted (■ Fig. 7.3c, d). The wood of conifers and angiosperms not only transports water but also provides support for free-standing plants. In the wood of conifers, the tracheid must be strong enough to hold open the water column and hold up the tree at the same time. In angiosperm wood, xylary fibers take on much of the plant support task, reducing this demand on vessel element strength. Thus, any mechanical constraint on conduit size is more limiting for conifer tracheids than individual angiosperm vessel elements.

7.4 Angiosperm Tracheids, Fiber Tracheids, and Libriform Fibers Represent a Continuum of Imperforate Tracheary Element Design and Function

As noted in ► Box 7.1, angiosperm xylem contains three forms of imperforate tracheary elements—the tracheid, the fiber-tracheid, and the libriform fiber (Carlquist 2001). All three share the common features of 1) the presence of a secondary cell wall, 2) the absence of a perforation plate (i.e., all three are imperforate), and 3) all are derived from the vascular cambium. Their general shape is long and narrow with thick, pitted walls and tapered ends. Angiosperms have tracheids, fiber tracheids, and libriform fibers in addition to vessel elements (refer to ► Sects. 7.5, 7.6, and 7.7). Gymnosperm wood is composed almost exclusively of tracheids with fiber tracheids in only a few, advanced groups such as the Gnetales.

The main differences between the three cell types are in the number and shape of pits in the walls. Angiosperm tracheids, like gymnosperm tracheids, are covered with a dense covering of **circular bordered pits** (◘ Fig. 7.4a). Fiber tracheids are similar except they have fewer pits and those pits have lenticular to slit-like pit apertures (◘ Fig. 7.4b). Libriform fibers have the fewest pits and those pits are simple (◘ Fig. 7.4c) (IAWA 1964). The libriform fiber is the most abundant imperforate tracheary element type in most hardwoods. In addition to their anatomical differences, libriform fibers and fiber tracheids may be distinguished by differential staining based on cell wall lignin content, with libriform fibers containing less lignin than fiber tracheids (Vazquez-Cooz and Meyer 2002).

Tracheids, fiber tracheids, and libriform fibers are located in the angiosperm wood and are therefore called **xylary fibers**, due to their location and not necessarily their **ontogenetic** origin. **Extraxylary fibers** (those not found in the wood) include phloem or bast fibers. Intermediate forms exist, making a positive identification difficult in many instances (Carlquist 2001). Nonetheless, the morphologies do have distinct differences. The evolutionary sequence was from tracheids to fiber tracheids, libriform fibers, and ultimately vessel elements. Angiosperm tracheids, especially those found adjacent to a vessel (called vasicentric tracheids), are involved in water transport, whereas fiber tracheids and libriform fibers have lost that function and serve mainly in support (Sano et al. 2011).

Angiosperm imperforate tracheary elements tend to be shorter and make up a smaller proportion of the wood than gymnosperm tracheids, as is to be expected given that gymnosperm wood is almost 100% tracheids, and angiosperm wood has a diversity of cell types. Bailey and Tupper (1918) measured tracheid length in 152 gymnosperm species and 275 angiosperm species. They reported that the average gymnosperm tracheid length was 3530 µm, and that for angiosperms, the value was 1200 µm, with large variation around both means. That comparison is useful in terms of comparative xylem anatomy, and for taxonomic applications, but it is not particularly suitable in comparative xylem phys-

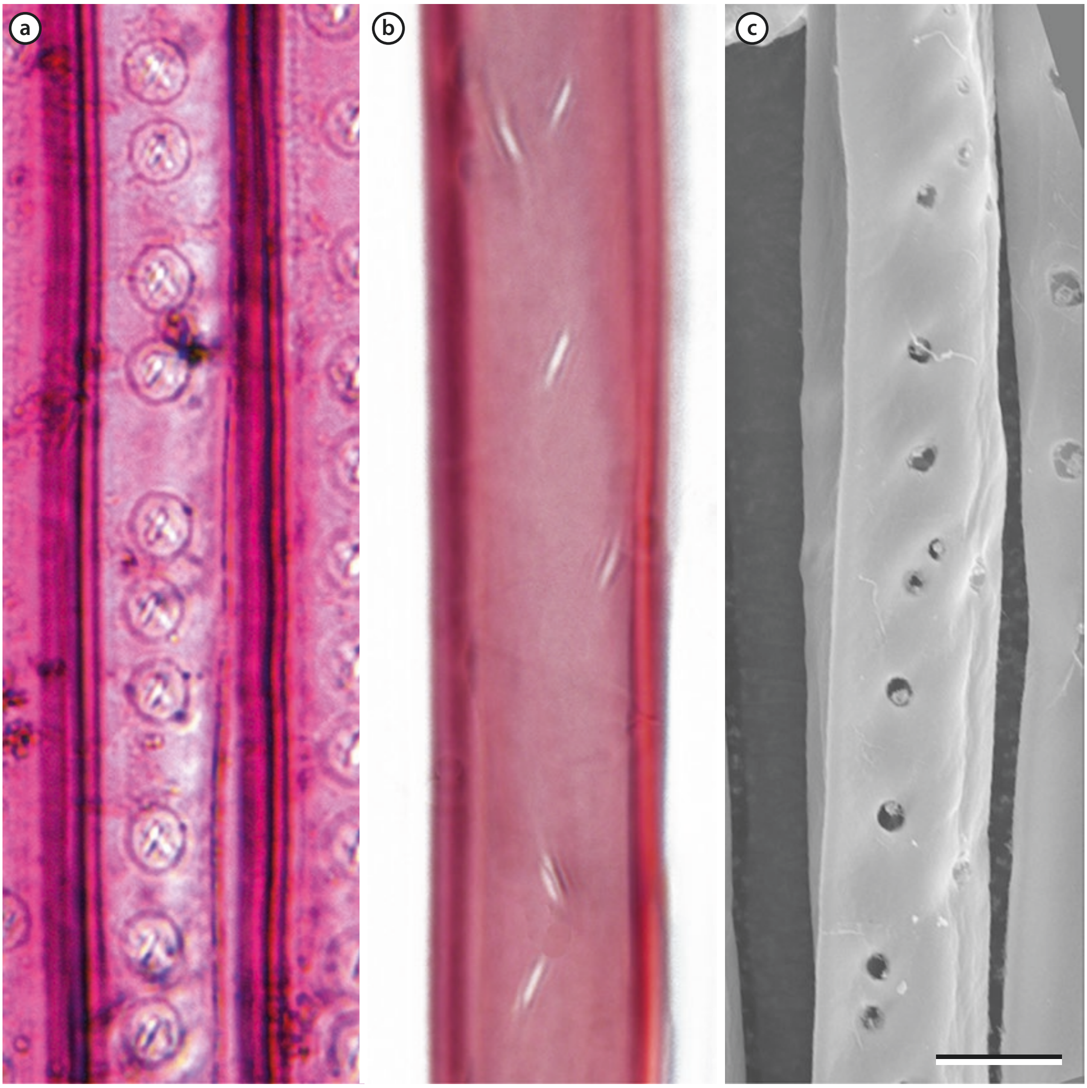
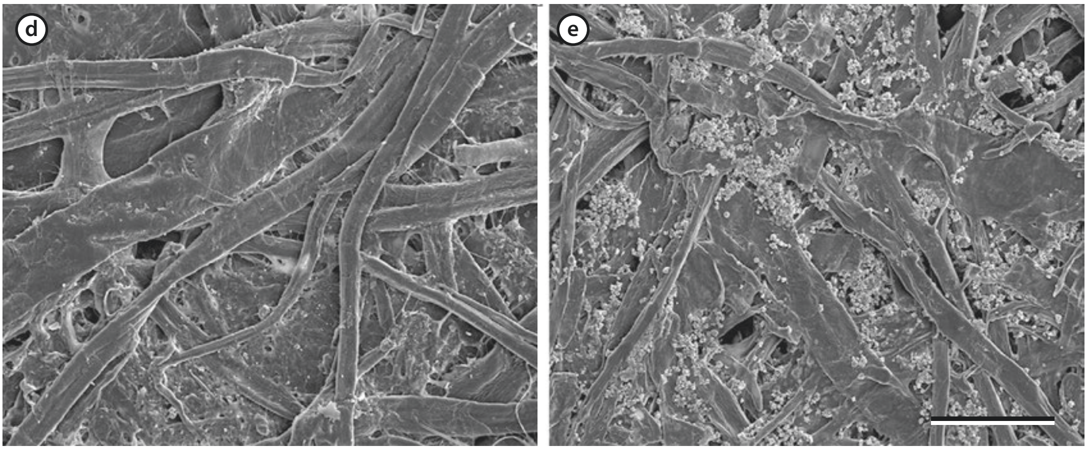


Fig. 7.4 **a**–**c** Pitting patterns of imperforate tracheary element side walls. **a** Tracheids from *Drimys*, a primitive vessel-less angiosperm, have side walls with numerous circular bordered pits. **b** Fiber tracheids from red maple (*Acer rubrum*) have fewer pits, with slit-like apertures. **c** Libriform fibers from grape (*Vitis* sp.) have simple pits. Scale bar in **c** = 10 µm and applies to all panels. (**a**–**c** RR Wise)

iology. As pointed out above, the tracheid is the conducting unit for gymnosperms; however, the vessel, which is composed of may interconnected vessel elements, is the main conducting unit for angiosperms, not the tracheid. That is why studies comparing xylem transport in gymnosperms and angiosperms compare size and function of gymnosperm tracheids to angiosperm vessels (e.g., Sperry et al. 2006).

Paper is manufactured by chipping and then delignifying gymnosperm and angiosperm wood. This process releases the individual imperforate and perforate tracheary elements, which in the paper industry are collectively called "fibers." The fibers are suspended in water, sprayed onto a screen, flattened, and dried into a sheet of paper. Unbleached fibers are brown from residual lignin,



■ **Fig. 7.4** **d**, **e** High-magnification view of **d** a brown paper bag and **e** white copier paper. Note the different size and texture of the fibers that make up each paper. The granular material in the copier paper is clay and other materials added during the paper making process to control the color, sheen, and printing qualities. Scale bar in **e** = 100 μm and applies to both panels. (**d**, **e** RR Wise)

whereas bleaching will remove the color. Softwood (i.e., gymnosperm) fibers are long and coarse, and produce a strong paper with large pores (■ Fig. 7.4d), suitable for paper bags and cardboard, but not for printing. Hardwood (i.e., angiosperm) fibers are shorter and finer, thus capable of producing a paper that interacts well with wet and dry inks (■ Fig. 7.4e). Paper qualities such as strength, thickness, density, color, and porosity are controlled by specifying the types and percentages of wood and fibers used in the paper making process.

7.5 Vessel Elements Are Perforate Cells and the Main Water Conductors in Angiosperms

While gymnosperms are clearly a successful group of plants, the evolution of vessel elements in angiosperms gave them greater flexibility and adaptive capacity (Pitterman 2010). The lineage was from tracheids, to fiber tracheids, to libriform fibers, and to vessel elements. Vessel element evolution had four major stages as shown in ■ Fig. 7.5a, which is an oft-reproduced diagram from Bailey and Tupper's seminal 1918 paper on size variation in tracheary cells: (1) decrease in length and increase in width of the vessel element, (2) decrease in the angle of inclination of the end wall and perforation plate, (3) a transition from scalariform to simple perforation plates, and (4) a transition from scalariform vessel-to-vessel, lateral pits in the side walls to an alternate arrangement of pits in the side walls.

A representative sample of vessel elements is shown in ■ Fig. 7.5b–e. They are characterized by being short and wide. Indeed, with a width of ~380 μm and a height of ~100 μm, the example from honey locust (■ Fig. 7.5c) is more drum-shaped than

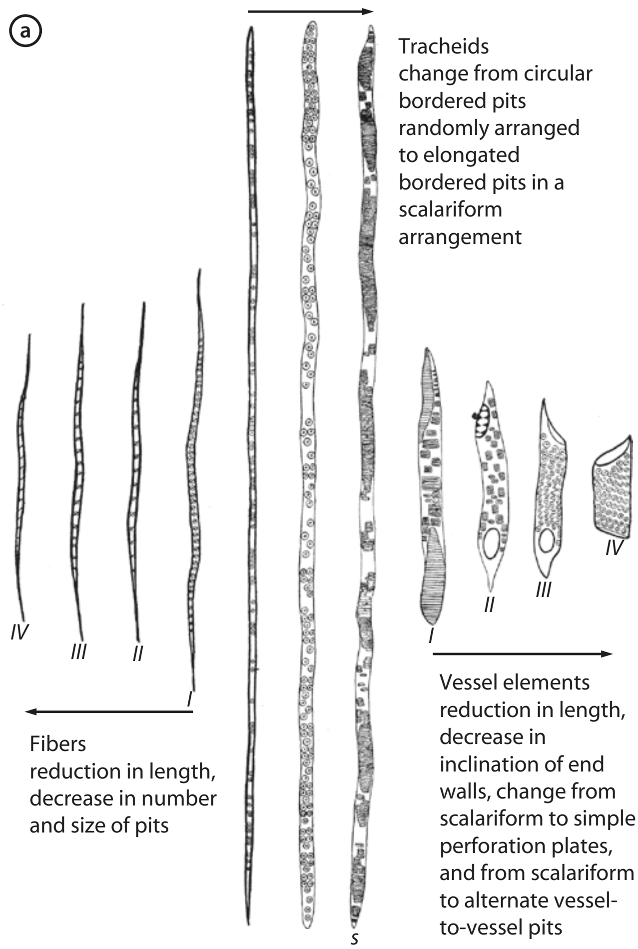


Fig. 7.5 **a** Drawings indicating the evolution of eudicot fibers (left), tracheids (middle), and vessel elements (right). All cells are drawn to scale with the exception of the tracheid labeled with an "S," which is shorter than the others. For the vessel elements, I = scalariform, II = intermediate between scalariform and porous, III and IV = porous. Arrows indicate the direction of the adaptive changes over evolutionary time. (From Bailey and Tupper (1918), public domain)

tubular. Vessel element side walls contain numerous pits that allow for the lateral, vessel-to-vessel exchange of water. A curious feature of vessel elements is the presence of a tail (sometimes called a beak) at either end (Fig. 7.5b), the function of which is unknown.

During development, the cells enlarge and lay down the requisite pattern of secondary cell wall on the sides and at the perforation plate. At maturity, the remaining pit membrane (the original primary cell wall) in the perforation is degraded, opening the perforation to the adjacent vessel element in the vessel. The cell protoplasm is lost and degraded, via a process called programmed cell death (Fukuda 2000), and the resulting mature tracheary element is dead. That does not, however, mean the cell is totally unresponsive to environmental conditions. See the side box on how cations can alter xylem function.

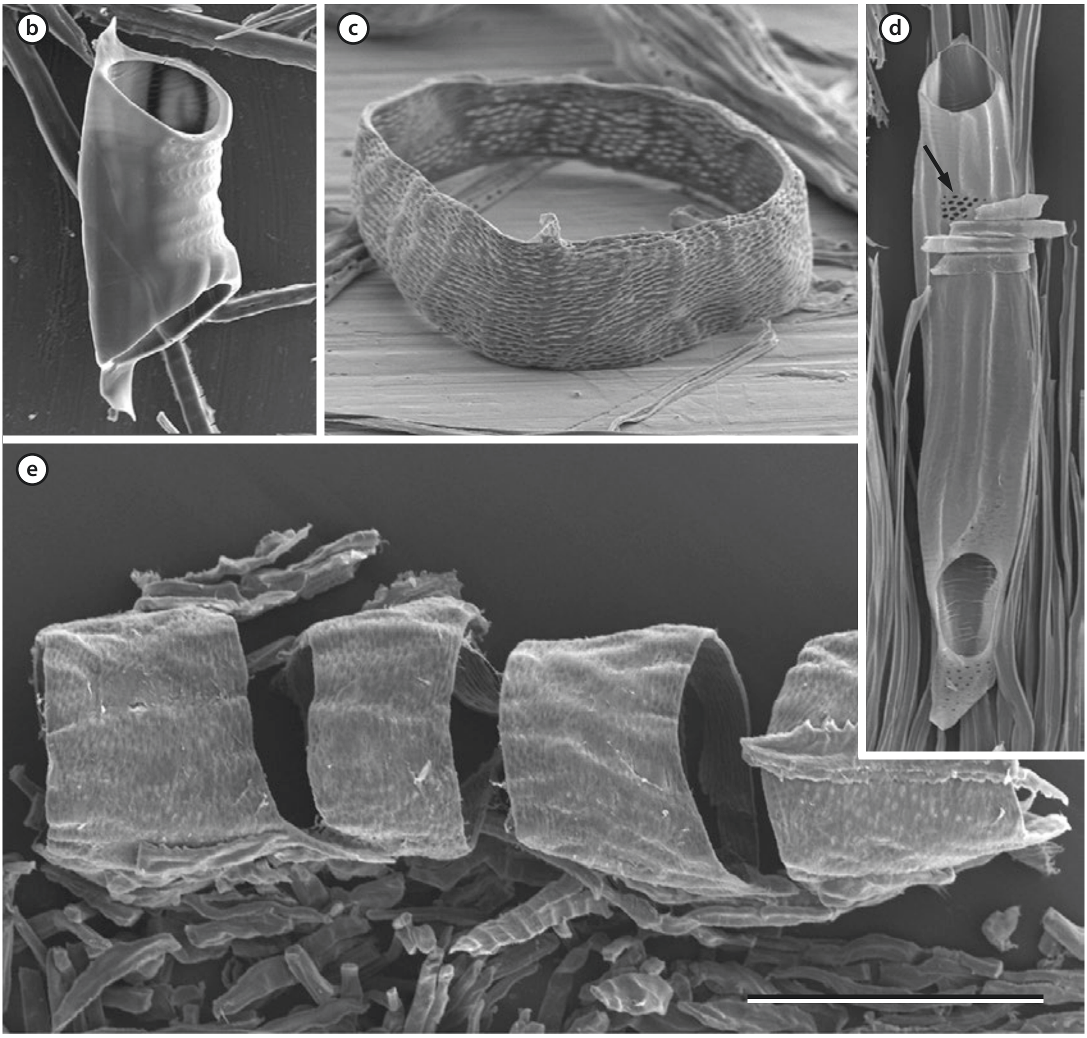


Fig. 7.5 **b**–**e** Representative vessel elements. **b** This vessel element from red oak (*Quercus rubra*) has large, prominent tails at both ends. **c** A honey locust (*Gleditsia triacanthos*) vessel element is larger in diameter than height. A small tail is present in the middle of the figure. The side walls contain numerous scalariform pits. **d** and **e** Red maple (*Acer rubrum*) vessel elements. Note the lateral pit field and associated ray parenchyma at the top of the vessel element in **d** (arrow). The four vessel elements in **e** were once interconnected to form part of a vessel. All of these vessel elements shown here have simple perforation plates. Scale bar in **e** = 200 µm and applies to all panels. (**b**–**e** RR Wise)

Box 7.3 Xylem: More Active than You Thought

The cohesion-adhesion-tension model of transpiration only requires that xylem tracheary elements have a continuous water column from soil to atmosphere. The resistance to flow (or its inverse, conductance) under different conditions, therefore, should remain constant, in the absence of cavitation. However, recent evidence has accumulated indicating that xylem hydraulic conductance varies over the short term as a consequence of the concentrations of cations in the xylem sap. The working hypothesis is that the ions are affecting the hydrogel properties of the pit membrane, allowing more water to flow from element to element when cations are present. The source of the cations may be the adjacent, living phloem, in which case, the phloem is mediating a direct control over xylem hydraulic properties. This would increase xylem-phloem coordination and may be an adaptive advantage under rapidly changing environmental conditions of water and light.

Reference: Nardini et al. (2011)

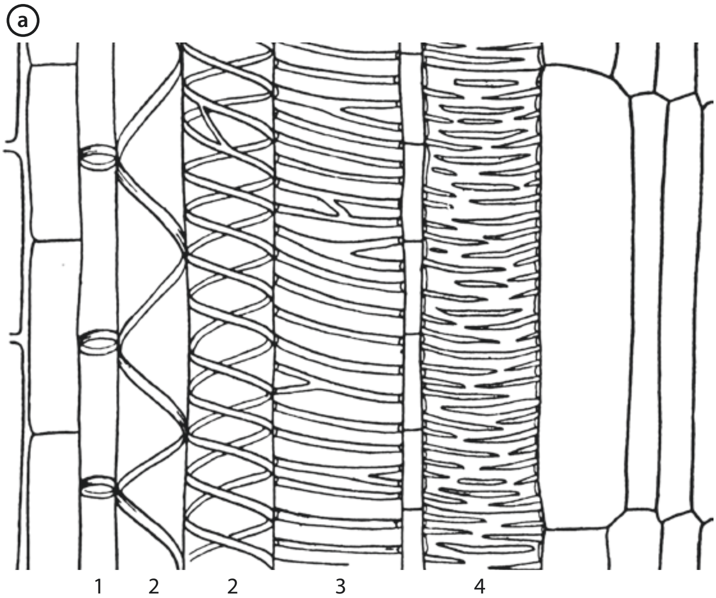
7.6 Vessel Element Side Walls Are Patterned for Strength and Water Movement

Unlike tracheids (which are imperforate), vessel elements have perforations in their end walls and, less commonly, side walls (are perforate). The side walls are optimized for lateral or radial water flow, which tends to be minimal, and strength. Vessel elements must allow for the free movement of water, but not collapse under the negative pressures generated during active transpiration. Vessel element end walls are optimized for axial water flow (the direction of the majority of the water follows). Patterns of side wall secondary wall deposition will be discussed in this section; end wall perforations are covered in ► Sect. 7.7.

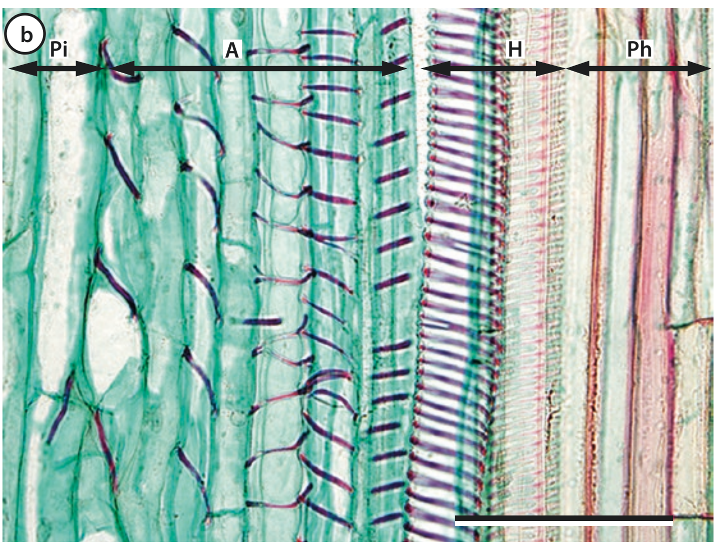
There are five basic patterns of vessel element side wall thickenings, (1) annular, (2) helical or spiral, (3) scalariform, (4) reticulate, and (5) an almost continuous wall pierced by bordered pits (◘ Fig. 7.6a). With few exceptions, this sequence of cell wall patterns, which is arranged in order of complexity, is also ordered in terms of evolutionary advancement (Esau 1953).

A vessel element with **annular** secondary thickenings has individual rings of lignified secondary cell wall. This is the simplest and most economical form of vessel element wall patterning (◘ Fig. 7.6b). The remainder, and majority, of the vessel wall is composed of primary cell wall which, although fairly weak, represents a low resistance of vessel-to-vessel water movement. The primary cell wall is also extensible, allowing the annular vessel element to stretch a certain amount in an axial dimension. With this combination of low cost and extensibility, annular vessel elements are frequently found in young, expanding stems, roots, and leaves and represent a common form found in protoxylem (refer to ► Sect. 11.6 for details of protoxylem development). Ultimately, the weak primary cell walls will be stretched and broken, and the vessel will be replaced by metaxylem.

A **helical** or **spiral** vessel element wall pattern is one in which secondary wall thickenings wrap around the cell (◘ Fig. 7.6a, b). The vast majority of the cell wall is primary, with only the thickened rings made of secondary wall. A vessel element with a helical pattern has the same strength, water flow, and extensibility characteristics as found in annular patterns and would be found in young, expanding tissues.

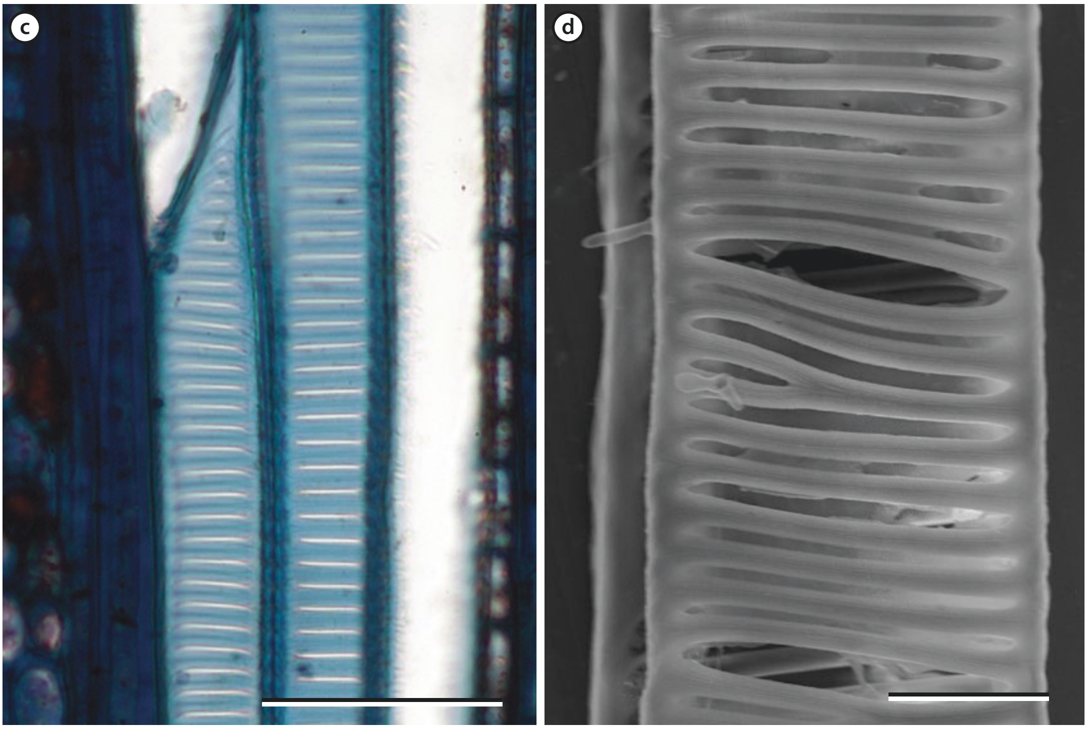


■ **Fig. 7.6** **a** Patterns of secondary cell wall deposition in vessel elements. 1 = annular, 2 = spiral or helical, 3 = scalariform, 4 = reticulate. (From Coulter et al. (1910), public domain)



■ **Fig. 7.6** **b** Annular and helical (or spiral) wall patterns in a single longitudinal section of a hemp (*Cannabis sativa*) stem. The stem shows primary growth of pith (Pi) to the left, five xylem vessels made of vessel elements with annular wall thickenings (A), two with helical thickenings (H), and phloem (Ph) to the right. The vessels to the far left, adjacent to the pith, were laid down first (protoxylem) and have been stretched in an axial direction as the stem elongated. Scale bar = 50 µm. (RR Wise)

Scalariform, thickenings run in a transverse direction, like the rungs of a ladder, and cover large portions of the vessel element side wall (■ Fig. 7.6c, d). Because the ends of the "rungs" are attached to vertical portions of the wall, a scalariform vessel element cannot



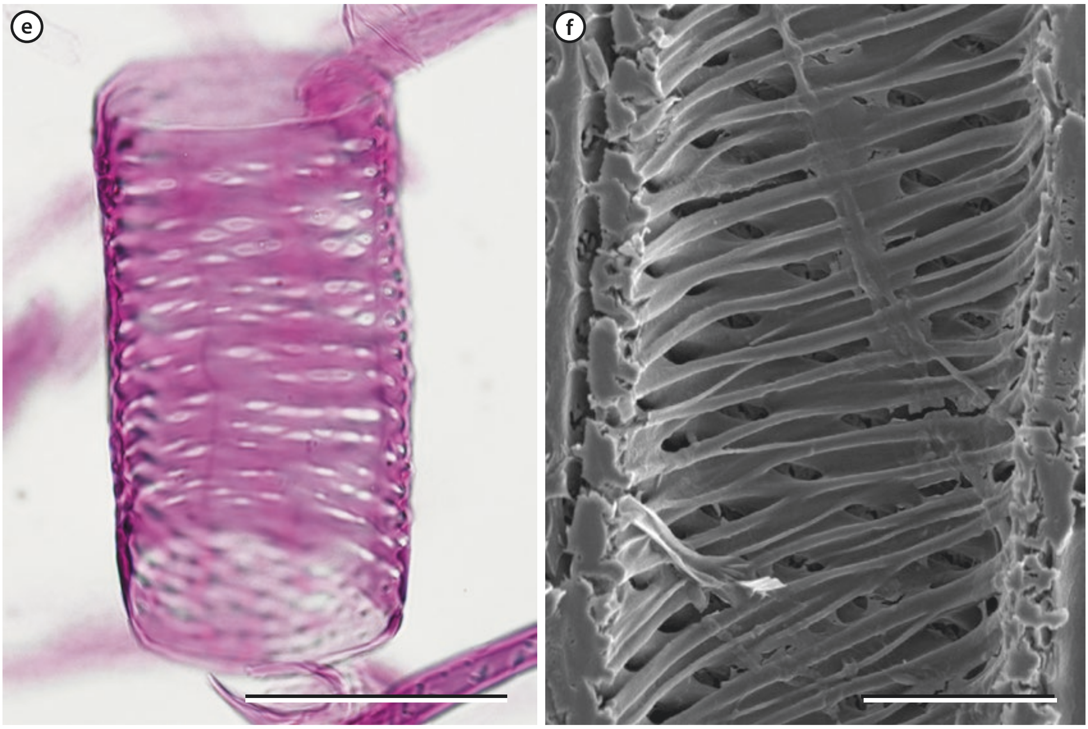
■ **Fig. 7.6** **c**, **d** Scalariform wall patterning as seen in vessel elements from grape (*Vitis* sp.) stem as visualized with **c** light microscopy and **d** scanning electron microscopy. Scale bars = 50 µm in **c**, and 10 µm in **d**. (**c**, **d** RR Wise)

stretch in an axial direction; therefore, scalariform vessel elements are found in tissues that have ceased elongation.

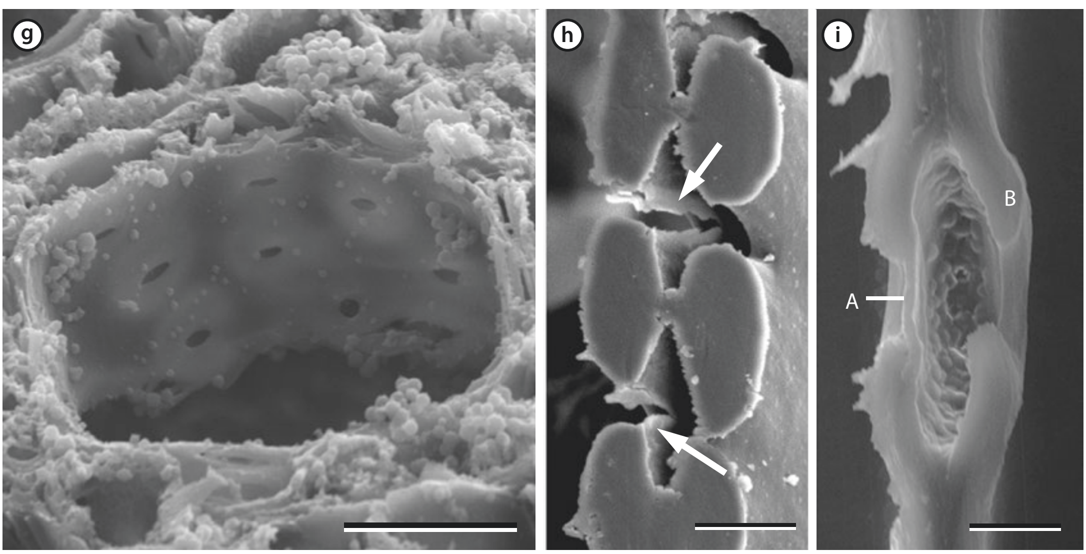
The **reticulate**, vessel element wall pattern is an irregular, net-like combination of different secondary cell layers of slightly different orientations (■ Fig. 7.6e, f). The majority of the cell surface is covered by wall material, leaving less area for vessel-to-vessel water movement but providing for greater strength in both the radial and axial dimensions. Vessel elements with a reticulate wall pattern are not capable of axial extension.

The secondary lateral walls of tracheary elements may be more or less continuous, interrupted only by pits, which were introduced in ► Sect. 5.5. Because pits allow for cell-to-cell water movement, and each cell has a cell wall, pits almost always exist as a pit pair, with the pit in one secondary cell wall aligned with a pit in the secondary cell wall of an adjacent cell. In walls shared between a vessel element and a parenchyma cell (which lacks a secondary wall), **half-bordered** pits are found. Several examples of bordered pit pairs are given in ■ Fig. 7.6g–i. Simple pits are the least common (■ Fig. 7.6j) and composed of a hole in the secondary cell walls of two adjacent cells; the opening is spanned by the pit membrane. The pit membrane is made of the remnants of the primary cell walls of the adjacent tracheary elements. As such, the pit membrane is not lignified and is relatively porous to water, but will block an air embolism. It is, however, weak and can rupture if stretched too far.

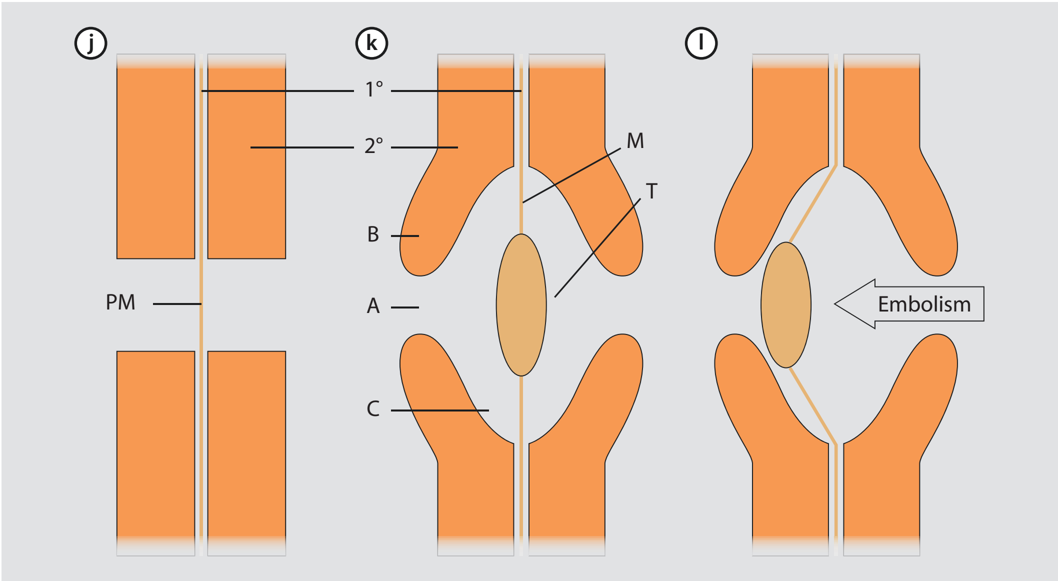
The bordered pit pair is common in gymnosperms, but less so in angiosperms. It represents a means to maximize water flow while



◘ **Fig. 7.6** **e**, **f** Reticulate wall patterning in isolated vessel elements from **e** Dutchman's pipe (*Aristolochia* sp.) and **f** honey locust (*Gleditsia triacanthos*) vessel elements. Note the multiple layers of secondary wall thickenings in the honey locust vessel element as seen in the scanning electron microscope. Scale bars = 50 µm in **e** and 20 µm in **f**. (**e**, **f** RR Wise)



◘ **Fig. 7.6** **g** Oak (*Quercus* sp.) vessel element with circular bordered pits. **h** section of two adjoining vessel element walls from black walnut (*Juglans nigra*) showing pit pairs. Remnants of the broken pit membrane can be seen (arrows). **i** A bordered pit pair from pine (*Pinus* sp.) wood. The pit membrane has been lost during specimen preparation, but the apertures (A) and borders (B) are clearly evident. Scale bars = 10 µm in **g** and 5 µm in **h** and **i**. (**g**–**i** RR Wise)



■ **Fig. 7.6** **j–l** Cross-sectional views of pit pairs. **j** A simple pit is a pair of gaps in the secondary cell walls (2°) of adjacent cells. It has a pit membrane (PM), which is derived from the primary cell walls (1°) and the middle lamella of the two cells. Water movement is across the entire pit membrane, which is somewhat effective at blocking embolisms. **k** In a bordered (B) pit pair, water flows through the pit aperture (A), enters the pit chamber (C), and crosses the permeable margo (M) to the opposite pit chamber. **l** If an embolism forms, it pushes the torus (T) against the pit aperture and blocks water flow and the propagation of the embolism. In this condition, the pit is said to be **aspirated**. (j–l RR Wise)

minimizing the structural weakness caused by having a hole in the wall that supports the cell. It also protects the pit membrane from rupturing. ■ Figure 7.6k shows the structure of a bordered pit pair. The pit apertures are small openings in the secondary cell walls, one each per cell. The areas of the pit apertures are small, but unobstructed, and therefore resistance to water flow is low. The pit apertures open in the pit chamber, a much larger area. The two pit chambers are separated by the pit membrane. The pit membrane of a bordered pit pair has two components, a central, impermeable **torus** and a peripheral, permeable region called the **margo** (■ Fig. 7.6k, l, m). The bordered pit pair, with its margo and torus, are an engineering marvel. Each is a little valve that allows cell-to-cell water flow, but seals shut when an embolism caused by a cavitation event occurs in one of the cells.

Vestured pits are bordered pits containing tiny outgrowths that project into the pit cavity from the secondary wall that surrounds the pit (■ Fig. 7.6n, o). They are found in *Eucalyptus* and related species of the Myrtaceae as well as legumes (Fabaceae), members of the Malpighiaceae, and the gymnosperm order Gentianales. Vestures may also be found in the inner walls of some vessel elements as well as the rim of perforation plates. Vestured pits are more common in tropical plants and may be of an advantage in managing the lateral stresses on the pit membranes caused by repeated or continuous drought conditions (Jansen et al. 2004). In short, they provide even more protection to the delicate pit membrane in those plants that experience repeated cavitation.

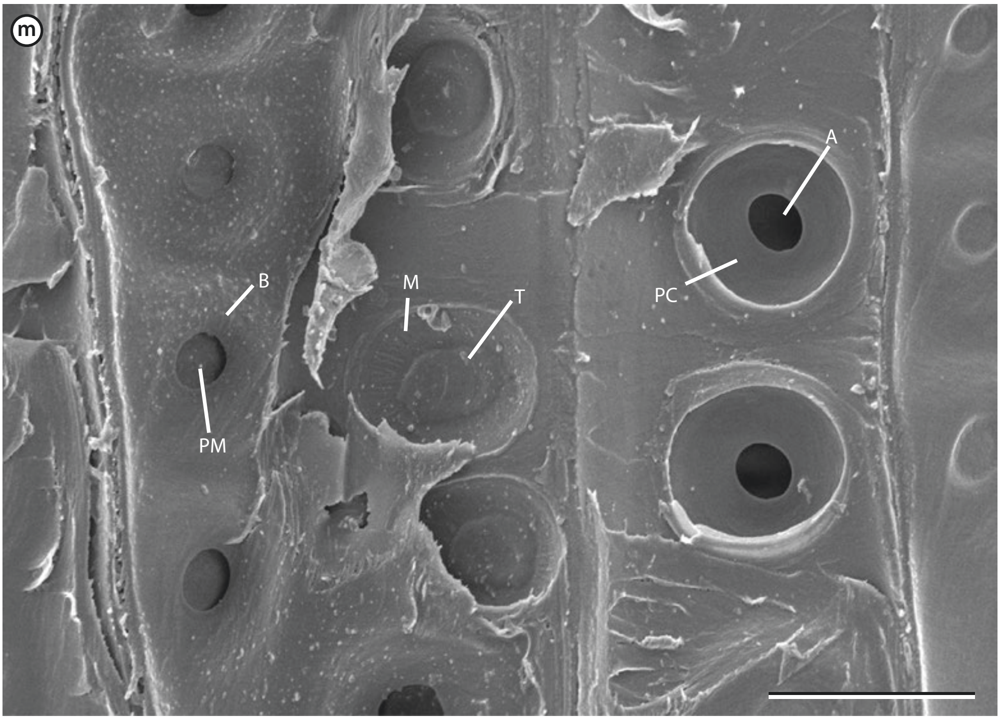
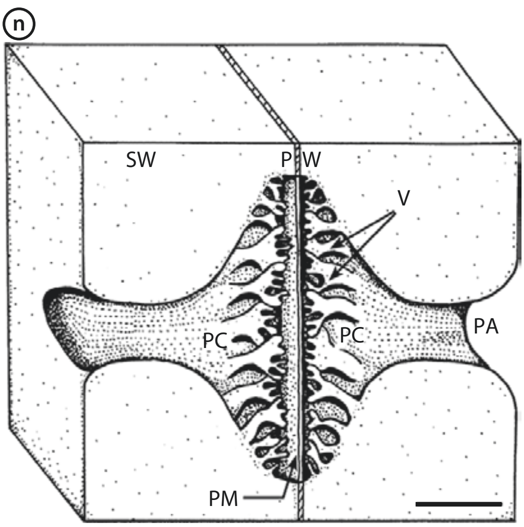


Fig. 7.6 **m** Face view of a fortuitous section through three columns of pit pairs in pine (*Pinus* sp.) wood. The three pits to the left are viewed from the interior of a tracheid and have a prominent pit border (B) and pit membrane (PM) viewed through the pit aperture. The three pits in the middle have been sectioned to show the margo (M) and torus (T) in the center of the pit pair. The two pits to the right have been sectioned to show the pit chamber (PC) and the aperture (A) leading to the adjacent cell. Scale bar = 20 µm. (RR Wise)



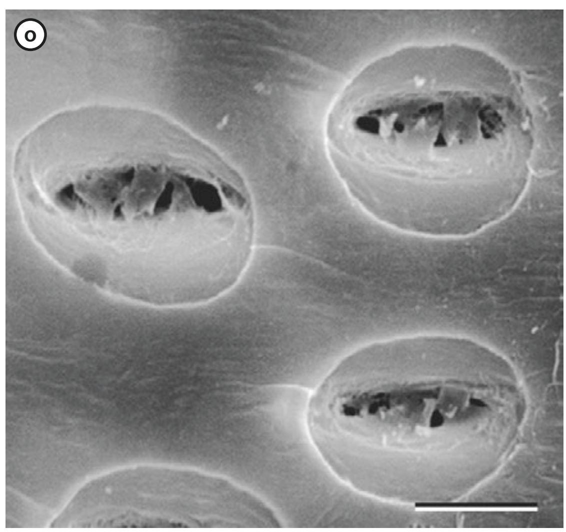
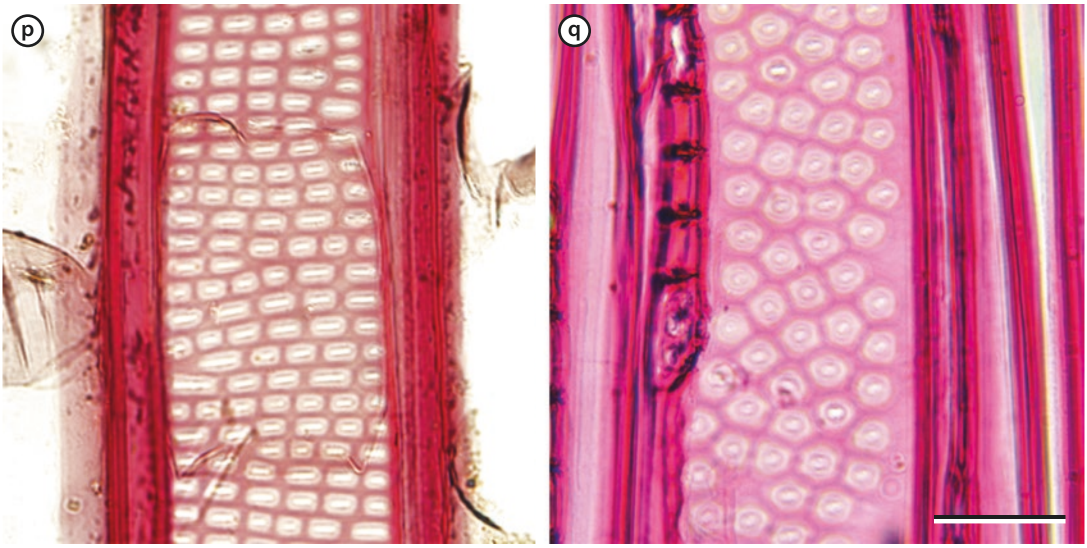


Fig. 7.6 **n** Side view of a vestured pit pair in *Flabellaria paniculata* (no common name, Malpighiaceae) with overarching secondary cell wall (SW), vestures (V), pit chamber (PC), pit aperture (PA), pit membrane (PM), and primary cell wall + middle lamella (PW). Bar = 2µm. From Jansen et al. 2004, with permission. Copyright (2004) National Academy of Sciences, USA **o** Face view of vestured pits from the wood of honey locust (*Gleditsia triacanthos*, Fabaceae). The vestures can be seen through the pit aperture. Scale bars = 2 µm. (**n**, **o** RR Wise)



◘ **Fig. 7.6** **p** Opposite pitting in a tulip tree (*Liriodendron tulipifera*) vessel element with elongate bordered pits. **q** Alternate pitting in a large-tooth aspen (*Populus grandidentata*) vessel element with circular bordered pits. Scale bar in **q** = 25 µm and applies to both panels. (**p, q** RR Wise)

Pit pairs are rarely found singly and usually occur as large fields of pits packed into tight, coordinated arrangements. An opposite arrangement shows linear rows of pits (◘ Fig. 7.6p), while in an alternate arrangement, the pits are staggered in distribution (◘ Fig. 7.6q). Both patterns maximize the amount of cell wall and therefore strength while still providing for significant lateral, vessel-to-vessel, or vessel-to-parenchyma water movement. In evolutionary terms, the alternate pattern is considered to be more advanced than the opposite (see ◘ Fig. 7.5a).

7.7 Most Vessel Elements End in a Perforation Plate and Are Connected to Another Vessel Element

The two adjacent end walls of vessel members may be partially or wholly degraded during development, which opens perforations. Through these perforations, water moves by bulk flow along a continuing series of end-to-end cells that form the multicellular tubelike vessel. Perforation plates may be simple as seen in ◘ Fig. 7.7a–c or complex. Complex perforation plates are referred to as scalariform (◘ Fig. 7.7d, e), reticulate (◘ Fig. 7.7f), or ephedroid (◘ Fig. 7.7g). Simple perforation plates can also be seen in ◘ Fig. 7.5b–e.

A vessel may extend great distances but it will eventually terminate. In leaves, the distal end of the terminal vessel element is blind and does not contain a perforation plate. Refer to ► Fig. 12.2h for an example of a terminal vessel element in a leaf.

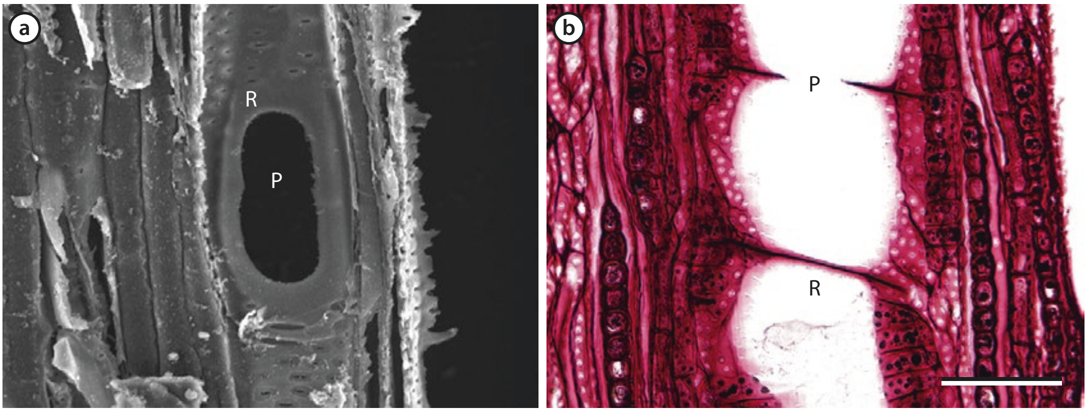


Fig. 7.7 **a**, **b** Oak (*Quercus* sp.) simple perforation plates with large rims. **a** In this view, the plate is inclined and seen end-on. **b** In this view, two *Quercus* perforation plates are seen in side view, one showing the entire rim and the other showing the rim and perforation. P = perforation, R = rim. Scale bar in **b** = 50 µm and applies to both panels. (**a** JM Coulter JM, CR Barnes and HC Cowles HC (1910), public domain; **b** RR Wise)

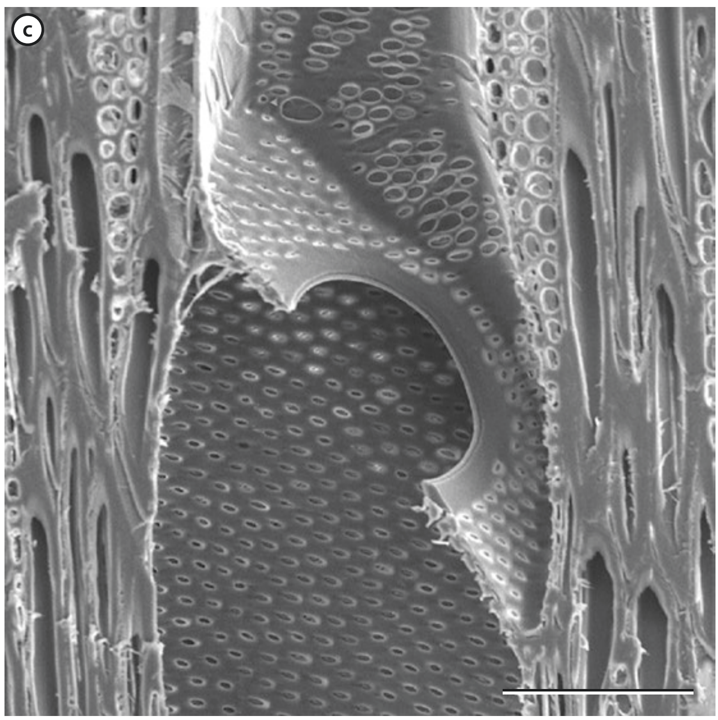


Fig. 7.7 **c** Simple perforation plate in a black walnut (*Juglans nigra*) connecting two vessel elements. In this example, the perforation plate is a combination of a simple pore with a large rim containing numerous pits. Scale bar = 100 µm. (RR Wise)

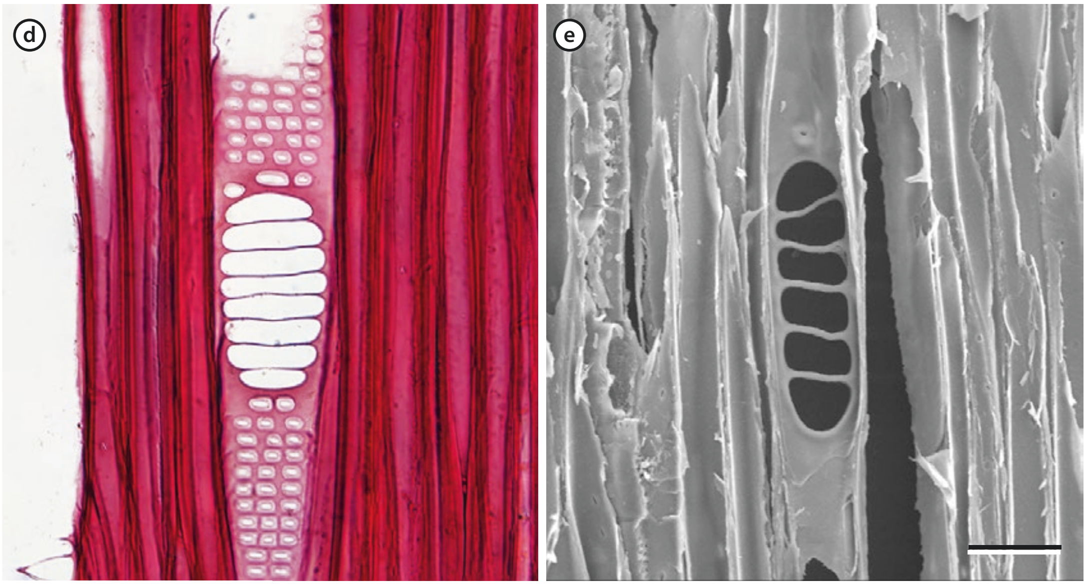


Fig. 7.7 **d**, **e** Scalariform perforation plates in tulip tree (*Liriodendron tulipifera*) vessel elements. Scale bar in **e** = 25 µm and applies to both panels. (**d**, **e** RR Wise)

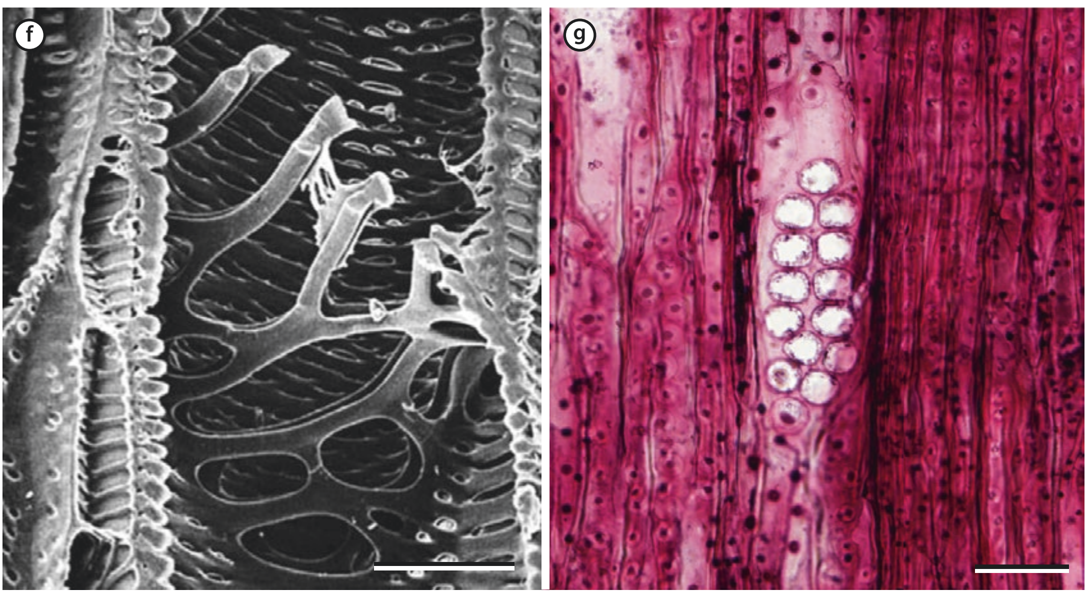


Fig. 7.6 **f** Reticulate perforation plate from the feather duster palm (*Rhopalostylis sapida*). **g** Ephedroid perforation plate from longleaf joint fir (*Ephedra trifurca*) = 10 µm in **f** and 25 µm in **g**. (**f**, **g** RR Wise; **f** from Crang and Vassilyev 2003)

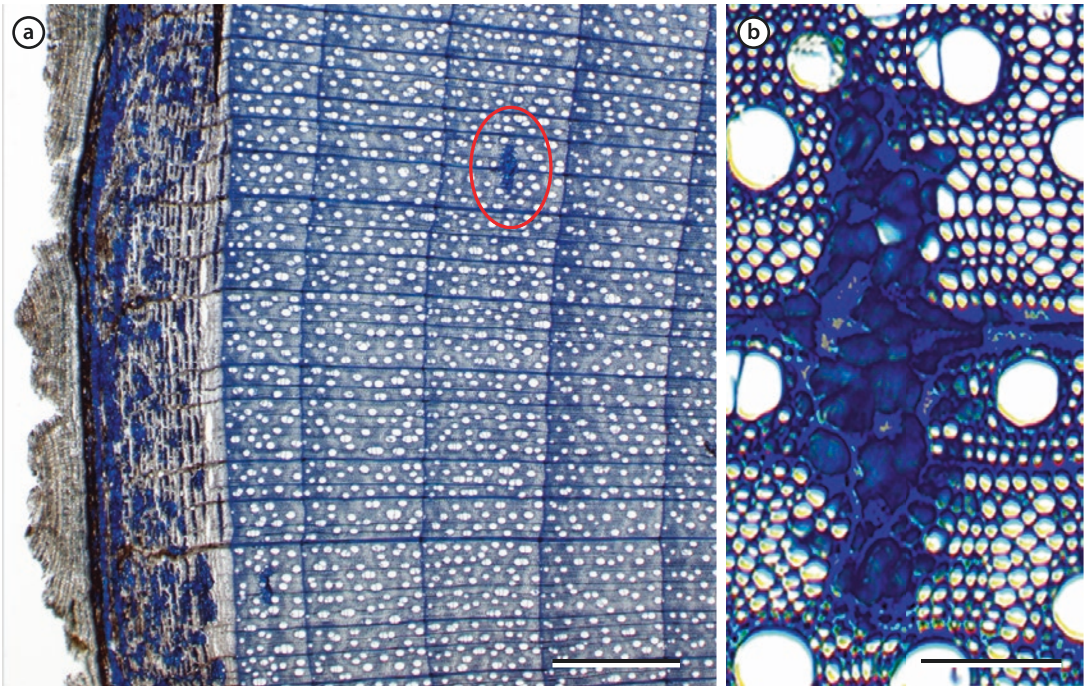
7.8 Xylem Parenchyma Are Living Cells Involved in Xylem Metabolism and Protection

Xylem vessel elements, tracheids, and fibers are dead at maturity. However, xylem parenchyma cells are living. Some of the functions of xylem parenchyma will be discussed in this section. Other aspects are addressed in ► Chap. 15—Wood.

Maple syrup is a well-known product of xylem parenchyma starch storage. Parenchyma starch content increases in the late summer to early fall and that carbohydrate reserve is remobilized in the spring, loaded into the xylem water, and used to support the early heterotrophic growth of leaves. Lacking transpiration (the leaves have not yet expanded), the mechanism of water movement relies on nighttime freezing and daytime thawing, conditions commonly found in the spring. Apoplastic water freezes before symplastic water. The apoplastic ice crystals draw water out of the parenchyma cells during the night. Upon warming, the apoplastic ice thaws and enters the adjacent xylem vessel element or tracheid, thus pressurizing the xylem water and forcing it toward the expanding leaf buds (or the sap spigot, if the tree has been tapped). Stored starches are hydrolyzed to sucrose and loaded into the xylem. This is one of the few instances in which sugars are transported in the xylem and not the phloem.

Xylem parenchyma are also the living cells responsible for response to pathogens and wood repair. The CODIT model (Compartmentalization of Decay in Trees, Morris et al. 2016) postulates that upon attack, trees seal off the damaged areas by the activation of parenchyma cells that divide and differentiate into sclereids (◘ Fig. 7.8a, b). Absent such a repair, pathogens (mainly wood-rotting fungi) and air (which would cause cavitation) could enter and spread through the xylem conducting tissues.

Axial parenchyma cells are oriented parallel along the axis of elongation. Ray parenchyma cells are oriented along the radial axis. Both can be observed in the transverse (cross-sectional) plane. There is considerable variation of parenchyma cellular orientation and shape. Some are square, some are elongated but upright, some are procumbent (longest axis radially oriented), and some are perforated (e.g., *Bathysa meridionalis*, a tropical tree). Perforated ray cells larger than other ray and vessel elements are typically found in uniseriate rays and may be important in horizontal water transport. Most commonly, scalariform perforations in the side walls of ray cells are found and are similar to the end walls of vessel elements.



■ **Fig. 7.8** **a**, **b** Wound repair in sugar maple (*Acer saccharum*) xylem. **a** Low-magnification image showing area of wound repair (red ellipse). **b** Higher-magnification view of repaired area. Note thick-walled sclereids. Scale bars = 500 µm in **a** and 100 µm in **b**. (**a**, **b** RR Wise)

7.9 Chapter Review

■ Concept Review

7.1 *Xylem is a complex tissue containing multiple cell types, each with a specific structure and function.* Xylem cell types include tracheary elements (tracheids and vessel elements which are dead at maturity) and parenchyma (which are alive at maturity). With their thick secondary cell walls, tracheary elements conduct water and provide support. Tracheary elements are divided into two classes. Imperforate tracheary elements are long, narrow, and tapered at the ends. As their name suggests, they lack a perforation. They include tracheids in gymnosperms and tracheids, fiber tracheids, and libriform fibers in angiosperms. Perforate tracheary elements are short and wide and are connected end-to-end via perforations (large holes at the ends of the cell) to form a vessel.

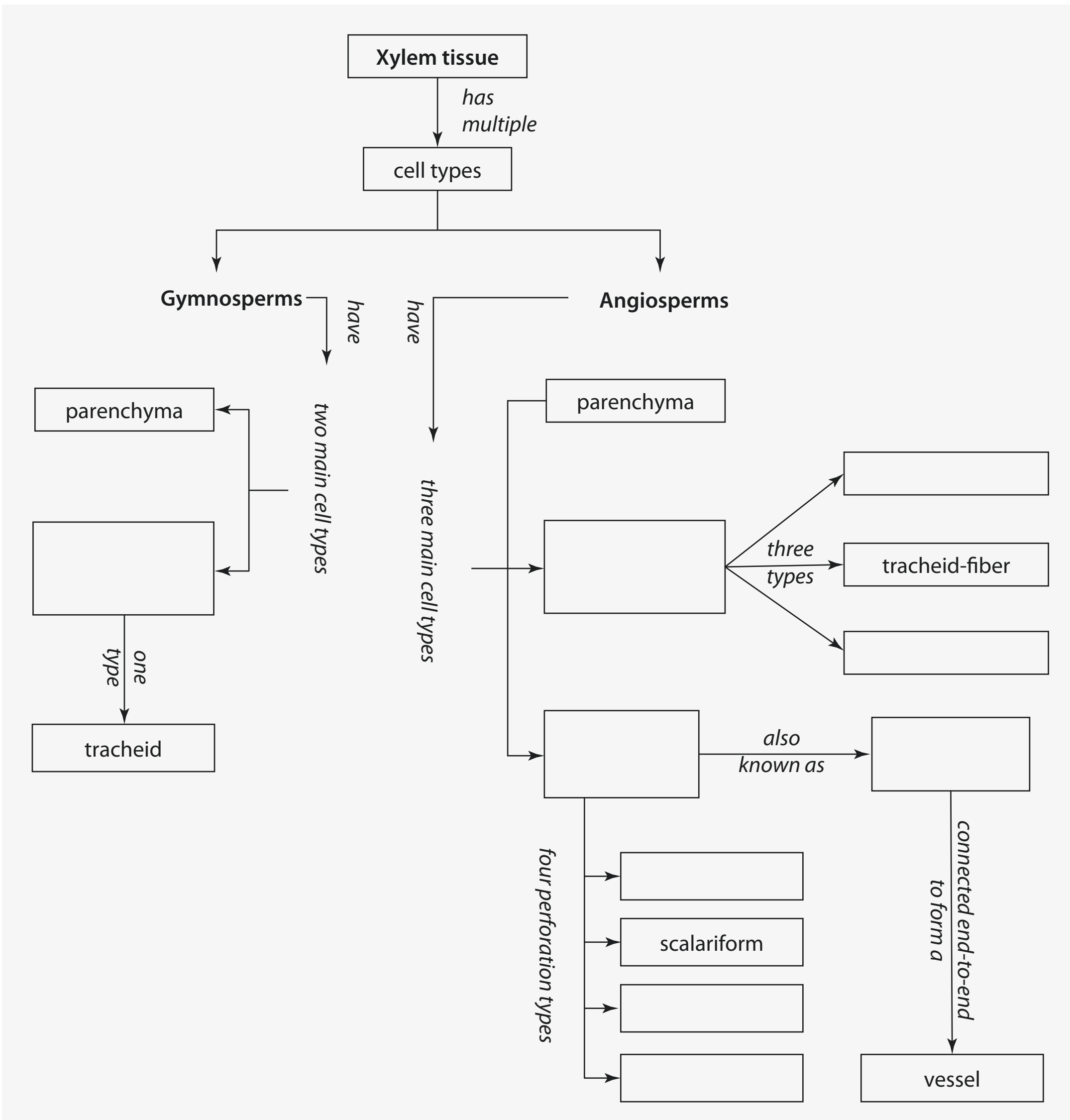
7.2 *The primary functions of xylem are water, mineral conduction, and support.* Transpirational water moves from the soil to the atmosphere via the xylem and is driven by difference in energy between the water in the soil and the water in the atmosphere as described in the cohesion-adhesion-tension model. Xylem water is pulled through the plant and is therefore under tension. As a result cavitation—the formation of a gas bubble that blocks water flow—is a constant threat. The need to minimize cavitation while maximizing water flow has driven almost every aspect of tracheid and vessel element evolution.

7.3 *Tracheids are imperforate tracheary elements and the sole water conductors in gymnosperms.* Gymnosperms tracheids serve the dual role of water conduction and support. Their tapered ends overlap and water movement between tracheids is via pits in the side walls.
7.4 *Angiosperm tracheids, fiber tracheids, and libriform fibers represent a continuum of imperforate tracheid design and function.* Angiosperm imperforate tracheary elements serve mostly for support, although water-conducting tracheids are not uncommon. The three imperforate cell types differ in the number and shape of side wall pits. Tracheids have circular bordered pits. Fiber tracheids have fewer and slit-like pits. Libriform fibers have the least pitting, and those pits are simple. Numerous examples exist of intermediate morphologies. All three cell types are collectively called xylary fibers. Angiosperm wood has a lower percentage of imperforate tracheary elements than gymnosperm wood. To manufacture paper, xylary fibers are digested from angiosperm and gymnosperm wood and formed into thin sheets.
7.5 *Vessel elements are perforate cells and the main water conductors in angiosperms.* The evolution of vessel elements was a major advancement for angiosperms and followed from tracheids, to fiber tracheids, to libriform fibers, to vessel elements. Over evolutionary time, vessel elements evolved to be short and wide with large openings at the ends (perforations).
7.6 *Vessel element side walls are patterned for strength and water movement.* Vessel element side walls have distinct patterns that reflect the balance between the age of the tissue (developing or developed), the need for strength, and the need for the free movement of water. In order of complexity, the five basic patterns are annular, helical (spiral), scalariform, reticulate, and pitted. Pits are holes in the secondary cell wall and may be simple, half-bordered, or bordered. The pit aperture is covered by the pit membrane, which is the remnant of the original primary cell wall. Bordered pits often have a cavitation-limiting valve composed of a margo and torus. Vestured pits have numerous cell wall projections into the pit cavity. Pits may be arranged in an opposite pattern or an alternate pattern.
7.7 *Most vessel elements end in a perforation plate and are connected to another vessel element.* The vessel element end wall is called a perforation. Simple perforation plates have no obstructions. Complex perforation plates have obstructions in a scalariform, reticulate, or ephedroid pattern. The last vessel element in a vessel typically does not have a perforation in its distal end.
7.8 *Xylem parenchyma are living cells involved in xylem metabolism and protection.* Xylem parenchyma cells are the living cells of the tissue and play a variety of roles including storage, pathogen defense, wound repair, and the maintenance of water balance. There are axial parenchyma and ray paren-

chyma. Parenchyma may have perforations that allow rapid exchange of water with adjacent vessel elements.

■ Concept Connections

1. Complete the concept map using the following terms: ephedroid, imperforate tracheary element (x2), libriform fiber, perforate tracheary elements, reticulate, simple, tracheid, fiber tracheid, and vessel elements.



Concept Assessment

2. After primary growth is complete, elements of the protoxylem are
   a. recognized by circular or spiral secondary wall thickenings.
   b. transformed into metaxylem.
   c. active in water conduction.
   d. differentiated into tracheids.
   e. stretched, broken and replaced by metaxylem.

3. The most "derived" perforation plates are considered to be
   a. scalariform.
   b. simple.
   c. oblique and foraminate.
   d. foraminate.
   e. with beaks.

4. Crassulae are represented by
   a. thickened end walls of tracheids.
   b. pitting in vessel members.
   c. primary wall thickenings between bordered pits.
   d. the secondary wall covering a margo and torus.
   e. ray tracheids.

5. Which sequence of progression of secondary cell wall complexity is correct?
   a. scalariform pitting-alternate pitting-opposite pitting-annular thickening-helical thickening.
   b. helical thickening-alternate pitting-annular pitting-reticulate pitting-scalariform pitting.
   c. annular thickening-scalariform pitting-reticulate pitting-alternate pitting-opposite pitting.
   d. helical thickening-reticulate pitting-scalariform pitting-opposite pitting-alternate pitting.
   e. annular thickening-alternate pitting-opposite pitting-scalariform pitting-reticulate pitting.

6. Which is not found in a monocot (e.g., corn) vascular bundle?
   a. metaxylem.
   b. scalarified bundle sheath.
   c. protoxylem lacuna.
   d. metaphloem.
   e. cambium.

7. A bicollateral vascular bundle
   a. has phloem on both sides of the xylem.
   b. has xylem on both sides of the phloem.
   c. is represented by the fusion of two vascular bundles.
   d. possesses no vascular cambium.
   e. has only one layer of xylem and of phloem.

8. Half-bordered pits are found between
   a. ray and axial tracheids.
   b. tracheid and parenchyma cell.
   c. two vessel members.
   d. two tracheids.
   e. two parenchyma cells.

9. Closed vascular bundles are the only form of bundle found in
   a. ferns and other lower plants.
   b. gymnosperms.
   c. eudicots.
   d. monocots.
   e. all plants.

10. In ferns, scalariform thickenings of tracheary elements
    a. do not allow the plant cell to elongate.
    b. are transformed into reticulate thickenings.
    c. form simple pits.
    d. are deposited during the early growth and elongation.
    e. cannot be seen in macerated preparations.

11. What are the most advanced features of derived vessel members?
    a. long, inclined perforation plates, simple openings, no pits.
    b. short, wide cells, simple openings, pits.
    c. long, tapered end walls, pits, reticulate openings.
    d. short, narrow cells, reticulate openings, no pits.
    e. long, scalariform perforation plates, pits, straight end walls.

Concept Applications

12. List the cell types in angiosperm secondary xylem and give the function of each. Compare the structure and function of angiosperm cell types to those found in gymnosperms.

13. Explain the basics of the cohesion-adhesion-tension model. Include in your answer an explanation of cavitation.

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Phloem

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Introduction

Phloem is plant vascular tissue that transports sugars made by photosynthesis from green tissues, where they are manufactured, to parts of the plant where they are needed. That process is called translocation and is described by the Münch pressure flow hypothesis in which osmotically active sugars are loaded at the source and unloaded at the sink. Phloem also plays a role in while-plant communication by being a conduit for plant growth regulators. Pathogenic viruses can also move through the phloem and are the cause of many devastating crop diseases. Phloem has four cell types. Sieve tube elements (STEs) perform the actual translocation of sugars. Companion cells load and unload the sugars into the STEs. Parenchyma cells move water radially and store water. Fibers protect the delicate phloem STEs. The origin, function, and interaction of those cell types are discussed in this chapter.

8.1 Phloem Is a Complex Tissue Containing Multiple Cell Types, Each with a Specific Structure and Function

Angiosperm phloem tissue has four distinct cell types while gymnosperm has two (◘ Table 8.1, ◘ Fig. 8.1a). In angiosperms, the long-distance transport of phloem sap takes place via the **sieve tube elements** (STE, also known as **sieve tube members**). Individual STEs are joined end-to-end to form a **sieve tube**, and sieve tubes travel the length of the plant, from shoot tip to root tip. **Companion cells** (CC) and phloem parenchyma (PP) provide metabolic support for the STE and are involved in the loading and unloading of the molecules to be translocated. STEs, CCs, and PP cells are all parenchyma, with thin primary cell walls. Protection is provided by stout phloem fibers usually positioned to the abaxis (outside) of the other phloem cell types. The four types of cells in the phloem tissue work together to load, transport, and unload molecules while being shielded from damage from the exterior. There can be considerable diversity in the detailed phloem characters such as STE length and width, sieve plate type, and number and arrangement of parenchyma and companion cells (Pace et al. 2015).

Gymnosperm phloem tissue has **sieve cells** and phloem parenchyma, but lacks companion cells and phloem fibers (◘ Table 8.1). The term "sieve cell" is used instead of "sieve tube element" because the sieve cells are connected side-to-side and do not form a sieve tube, as the angiosperm STEs do. In other words, because gymnosperms do not form sieve tubes they, by reasoning, cannot have sieve tube elements. Phloem loading/unloading, which is the responsibility of the angiosperm companion cell (► Sect. 8.4), is accomplished by **albuminous cells** in the gymnosperms (a.k.a. **Strasburger cells**, ► Sect. 8.8). They were named for rich deposits of protein that stain similar to egg albumin (albuminous) and after Eduard Strasburger, a nineteenth-century botanist who first described the cells. Finally, gymnosperms do not make fibers, so they obviously cannot have phloem fibers.

Table 8.1 Phloem cell types and their functions in angiosperms and gymnosperms

Phloem cell type	Function	Angiosperm	Gymnosperm
Sieve tube elements	Translocation of sugars, amino acids and hormones	Yes	Yes
Companion cells	Metabolic support, phloem loading/unloading	Yes	No, but contain albuminous cells
Fibers	Support/protection	Yes	No
Parenchyma	Storage/synthesis	Yes	Yes

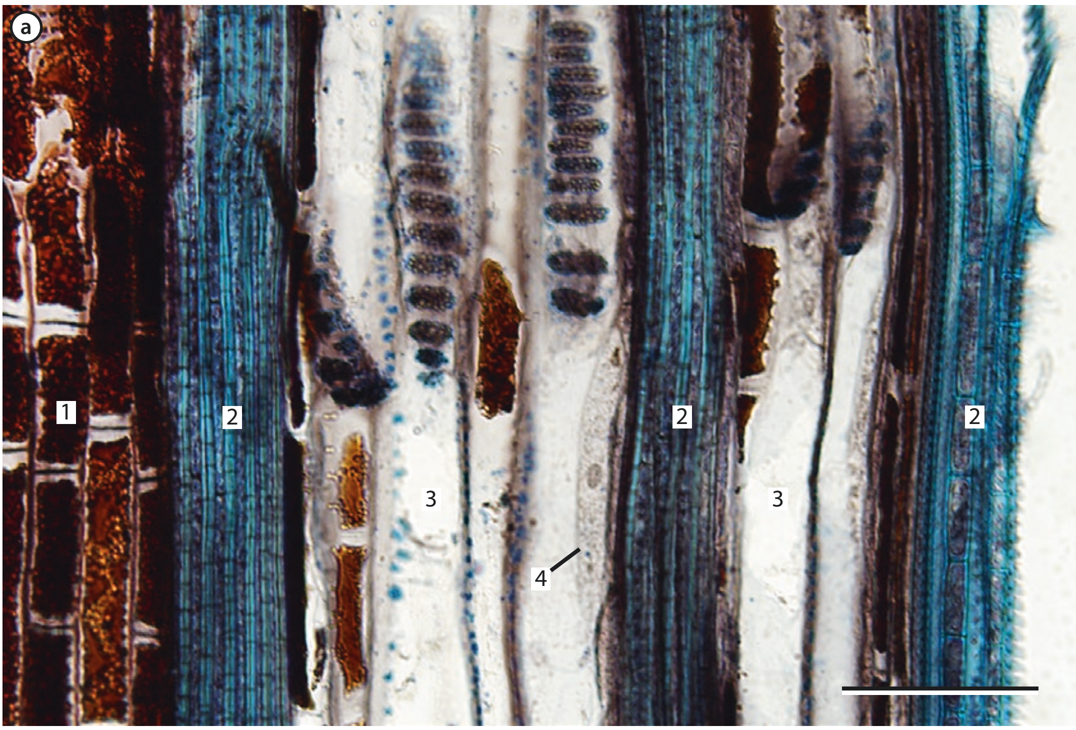
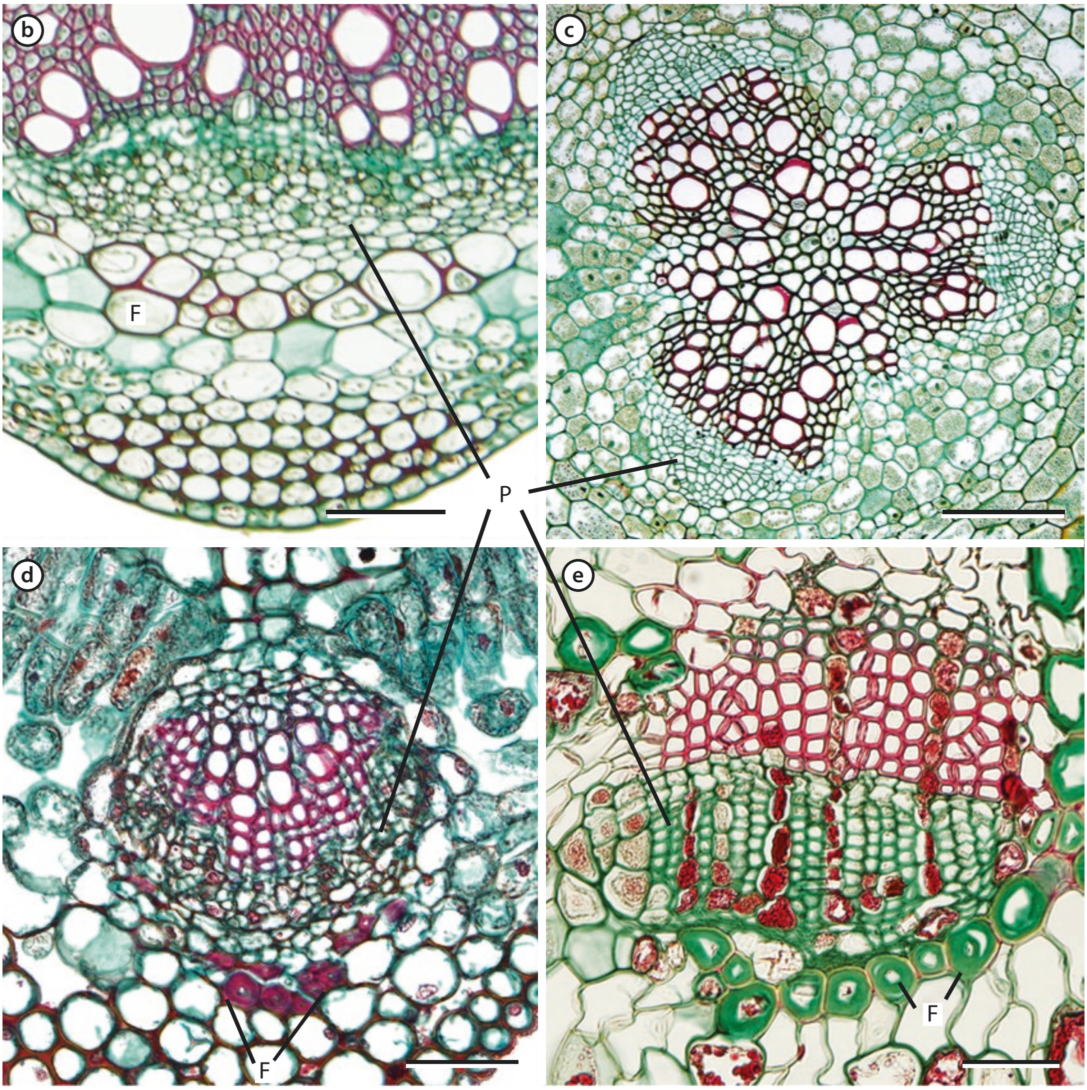


Fig. 8.1 **a** Phloem tissue in a grape (*Vitis* sp.) stem showing the relationship of the four cell types; the stem abaxis is to the left. Phloem parenchyma (1) are darkly stained due to the presence of tannins, fibers (2) are blue, sieve tube elements (3) have slanted **compound sieve plates**, and companion cells (4) have a nucleus and dense cytoplasm. Note that the companion cell shown is shorter than the sieve tube element it serves. Scale bar = 50 µm. (RR Wise)

Plant organs are arranged along an axial (up and down) direction and a radial (from the interior to the exterior) direction, and water and nutrients must flow along both axes. Sieve tube elements and companion cells only run in the axial direction. Radial translocation, which can be significant in a tree trunk with actively growing periderm (refer to ► Chap. 16), occurs exclusively via phloem ray parenchyma (refer to ► Sect. 8.5).

Phloem and xylem tissues are almost always found together because they are derived from the same bifacial meristematic tissue,



◘ **Fig. 8.1** **b**–**e** Abaxial phloem in **b** beet (*Beta vulgaris*) stem, **c** baneberry (*Actaea alba*) root, **d** lilac (*Syringa* sp.) leaf, and **e** pine (*Pinus* sp.) leaf. The abaxial direction for **b, d,** and **e** is toward the bottom of the page. In **c** the abaxial direction is any centripetal direction, because the vasculature is in the center of the root. Phloem (P) is indicated. Xylem conducting cells are the dark red cells to the adaxis of the phloem. Fibers (F) are indicated in **b**, **d,** and **e**. Scale bars = 50 µm in **b**, 100 µm in **c**, and 25 µm in **d** and **e.** (**b**–**e** RR Wise)

the vascular cambium. Therefore, their elements run parallel to each other in vascular bundles. Phloem is usually positioned abaxial to the xylem in leaves, stems, and roots (◘ Fig. 8.1b–e), although other, more complicated arrangements may be found (refer to ► Sect. 11.6—Stems). ◘ Figure 8.1b shows a typical arrangement found in stems in which a vascular bundle contains xylem to the interior and conducting phloem to the exterior, with a cap of phloem fibers external (abaxial) to the conducting phloem.

Roots (◘ Fig. 8.1c) also have abaxial phloem, even though root vasculature architecture (refer to ► Chap. 10—Roots) is distinctly different from that of the stem vasculature (refer to ► Chap. 11—Stems).

Leaves maintain the abaxial phloem position of the stem vasculature, resulting in phloem being positioned toward the "bottom" side of the leaf (◘ Fig. 8.1d, e). Not all phloem tissue produces fibers, but when it does, the fibers are either abaxial to the conducting phloem or intermixed with it (refer to ► Chap. 16—Periderm). Phloem may be the location of secretory ducts (◘ Fig. 13.3c) and laticifers. Phloem, especially the fibers and dead conducting cells, is also a major component of bark, as is described in ► Chap. 16—Periderm.

In the early development of angiosperms, primary phloem is first formed as a growth from procambium parenchyma cells from the apical meristem in what will become the midvein site through extension. These are termed **protophloem** cells and are narrow, enucleate, and mostly without companion cells. As growth of a eudicot embryo takes place, phloem development separately occurs in the root and the cotyledons (a.k.a. seed leaves). Protophloem is formed during cell expansion which also eventually stretches and tears apart the cells. The sieve tube elements are typically narrow and elongated and rarely possess companion cells. Once cell elongation ceases, phloem cells that are formed are termed **metaphloem**, and the cells are wide and long but are not stretched longer with additional cell growth. These cells include sieve tube cells, companion cells, phloem parenchyma as well as phloem fibers.

As secondary growth occurs, **secondary phloem** is derived from the vascular cambium (► Chap. 14) and there is no distinction between protophloem and metaphloem. Sieve tube cells are wide and relatively short, and both phloem parenchyma and phloem fibers are typically found. Parenchyma cells may be companion cells, which are much smaller than the sieve tube cells, densely cytoplasmic and connected to the sieve tube cells via plasmodesmata. However, there are also companion cells that are virtually lacking plasmodesmata, and transfer cells that have greatly irregularly thickened primary walls that move solutes to other sites or for storage.

8.2 Phloem's Main Function Is Photosynthate Translocation

Phloem's main function is the long-distance transport of sugars and other **photosynthates** from the source (mature leaves), or reserves (the cotyledons of germinating seedlings) toward the sinks, e.g., roots, developing reproductive structures (flowers, fruits, and seeds), meristems, and young leaves. The process is called **translocation,** and the aqueous solution being translocated is called **phloem sap** consisting of carbohydrates, minerals, and soluble ions. The distance between source and sink can be significant, and phloem makes a continuous connection between those organs. Consider the distance between the leaves of the tallest tree and its roots. Phloem is also the primary pathway in vascular plants for the movement of amino acids, plant growth regulators, and other compounds that signal and direct responses at sites remote from their origin.

8

Box 8.1 Plants Fight Back—Defenses Against Phloem-Feeding Insects

Some insects indiscriminately feed on plants, while others are much more specific. Aphids are specialists in that the feed specifically on the phloem, termed phloem feeding insects (PFI). They use their piercing stylet to penetrate phloem sieve tube elements in the stem or leaf and feed off the phloem sap. Plants are not without their defenses. Infestation by PFIs induces the expression of a number of biotic stress defense genes. The activation of cell wall proteins and calcium signally proteins are some of the first responses with the plant hormones ethylene, jasmonic acid, and salicylic acid playing signaling roles in mounting the defense response. The combined effect of the defense responses is to inhibit, or at least reduce, the aphid's ability to successfully feed from the phloem strand. Successful PFIs, on the other hand, have evolved mechanisms to overcome the plant molecular defenses.

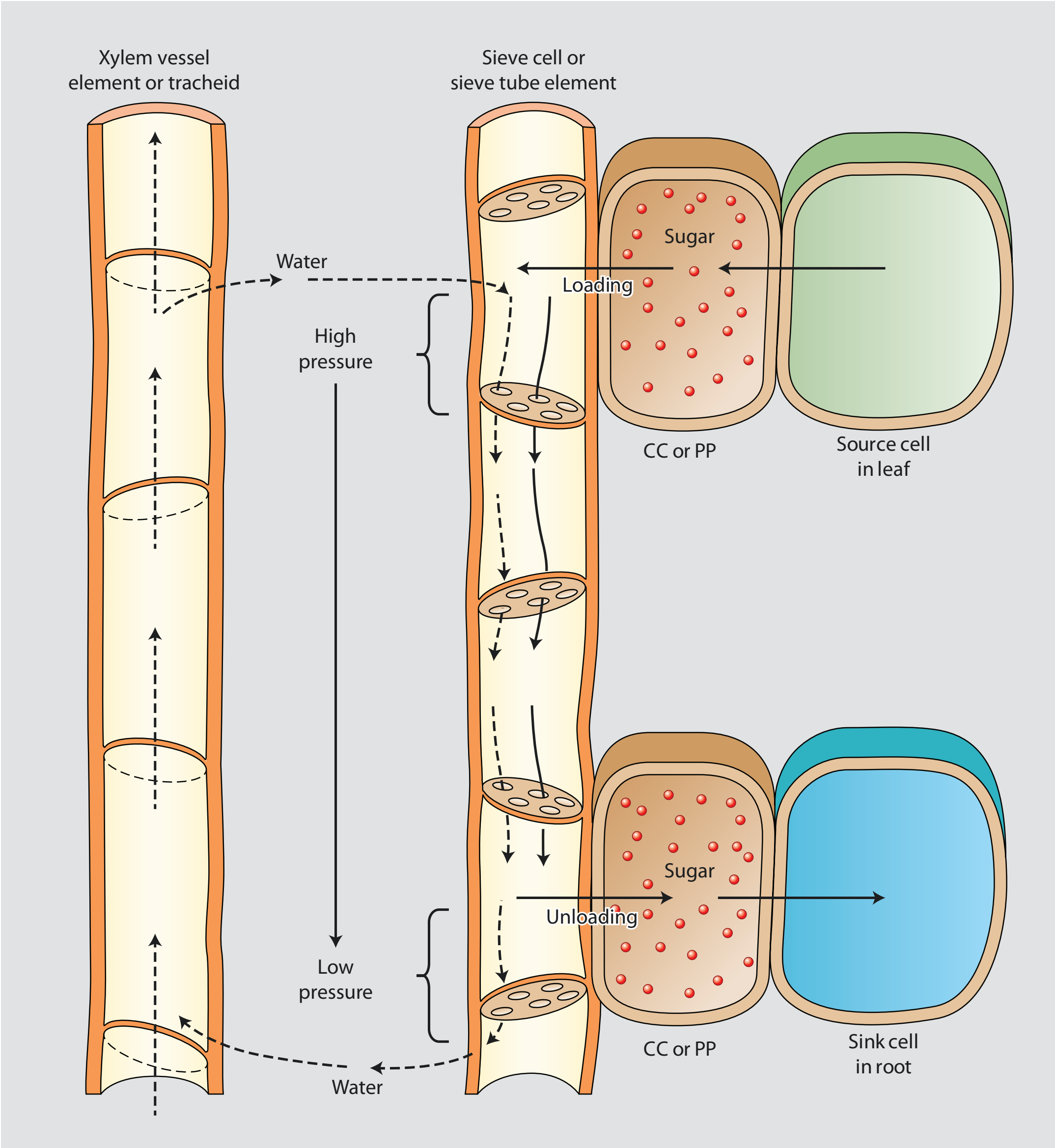
Reference: Foyer et al. (2015)

The mechanism of phloem translocation was first described by the German botanist Ernst Münch in 1926. Those early ideas (now called the Münch pressure flow hypothesis) remain at the core of our modern understanding of the relationship between phloem structure and function. In brief, sugars made by photosynthesis are loaded into the phloem at the source tissues, usually leaves. The sugar is commonly sucrose (a disaccharide), but raffinose (trisaccharide) or stachyose (tetrasaccharide) may also be translocated, depending on the plant species.

The sugars are not only a translocatable form of reduced carbon, but they are also osmolytes, meaning as they go into solution, they lower the osmolarity of the phloem sap. Osmosis then draws water from the adjacent xylem tissues into the phloem, increasing the pressure inside the phloem sieve cell (gymnosperms) or sieve tube element (angiosperms). The pressurized phloem sap is forced toward the sink tissues (which may be tens of meters distant) where the osmotically active sugars are removed and respired or stored in the form of starch in amyloplasts. Removing the sugars causes water to leave the phloem via osmosis and the pressure drops. Therefore, the sugars being translocated are responsible for the pressure gradient between the source and sink tissues which drive the movement of those same sugars (◘ Fig. 8.2).

8.3 Sieve Tube Elements Are Living Cells Responsible for Translocation

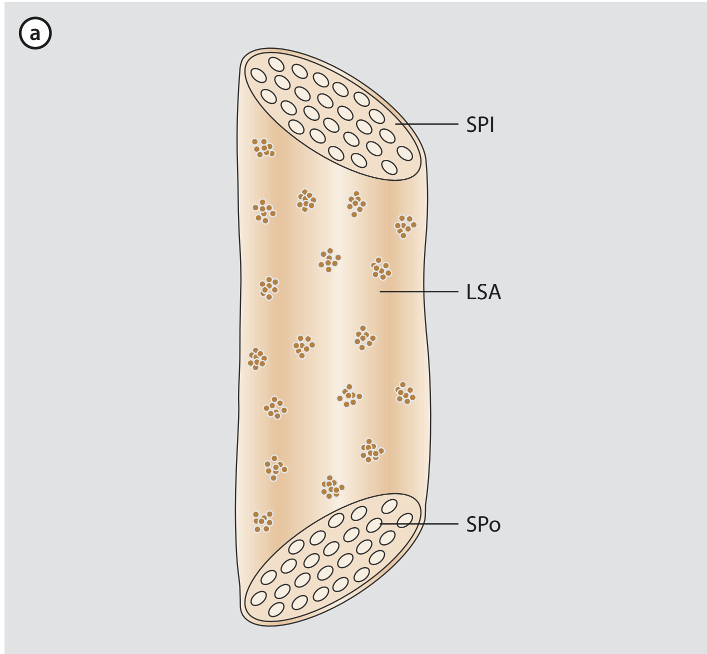
Sieve tube elements (STE), in flowering plants, and **sieve cells** (SC), in gymnosperms (► Sect. 8.2), are the functional components of phloem tissue by which photosynthates and other molecules are distributed around the plant. The angiosperm sieve tube, formed by the end-to-end connection of STEs, is analogous to a vessel in the



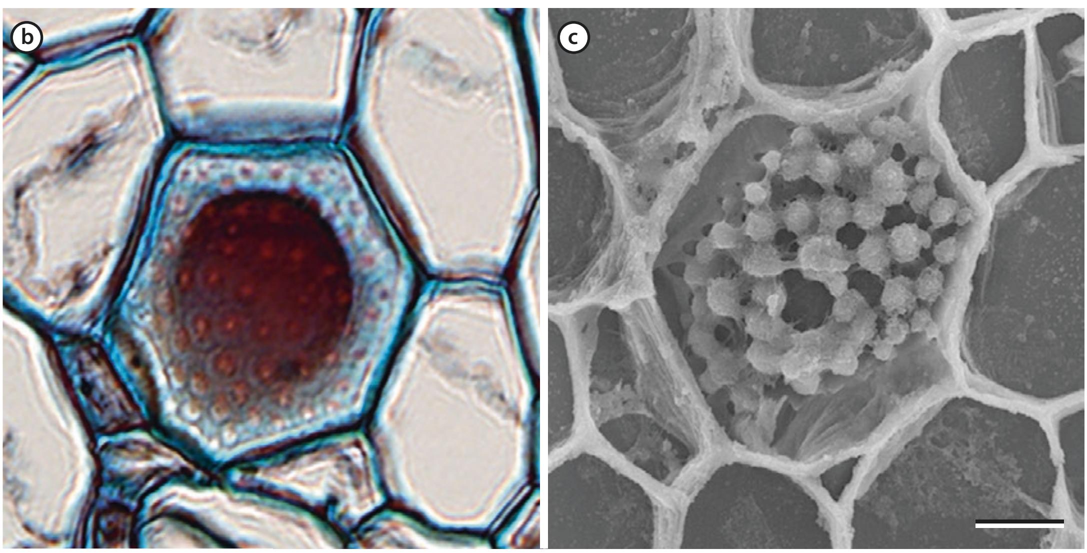
■ **Fig. 8.2** Anatomy and physiology of the Münch pressure flow hypothesis. Sugar loading (top right of figure) from a source cell to a phloem sieve tube element (STE) occurs via either companion cells (CC) or phloem parenchyma (PP), depending on the species. This lowers the water potential of the STE which draws water via osmosis from the neighboring xylem tracheary element and pressurizes the STE. Phloem sap is therefore pushed to the sink tissues, where the sugar is unloaded (by either a CC or PP) (RR Wise)

xylem. Unlike the dead tracheary elements of xylem, however, sieve tube elements are living cells with an intact, osmotically active plasmalemma, a few mitochondria, modified plastids, and an endoplasmic reticulum. In the mature, conducting state, STEs lack cytosol, ribosomes, Golgi apparatus, a nucleus, and the central vacuole with its tonoplast. Thus, the cell lumen is mostly free for phloem sap movement. By contrast, companion cells are rich in cytoplasm and contain a nucleus and other organelles (► Sect. 8.4).

Sieve tube elements (■ Fig. 8.3a) have two types of specialized intercellular communications, **sieve plates** in their end walls

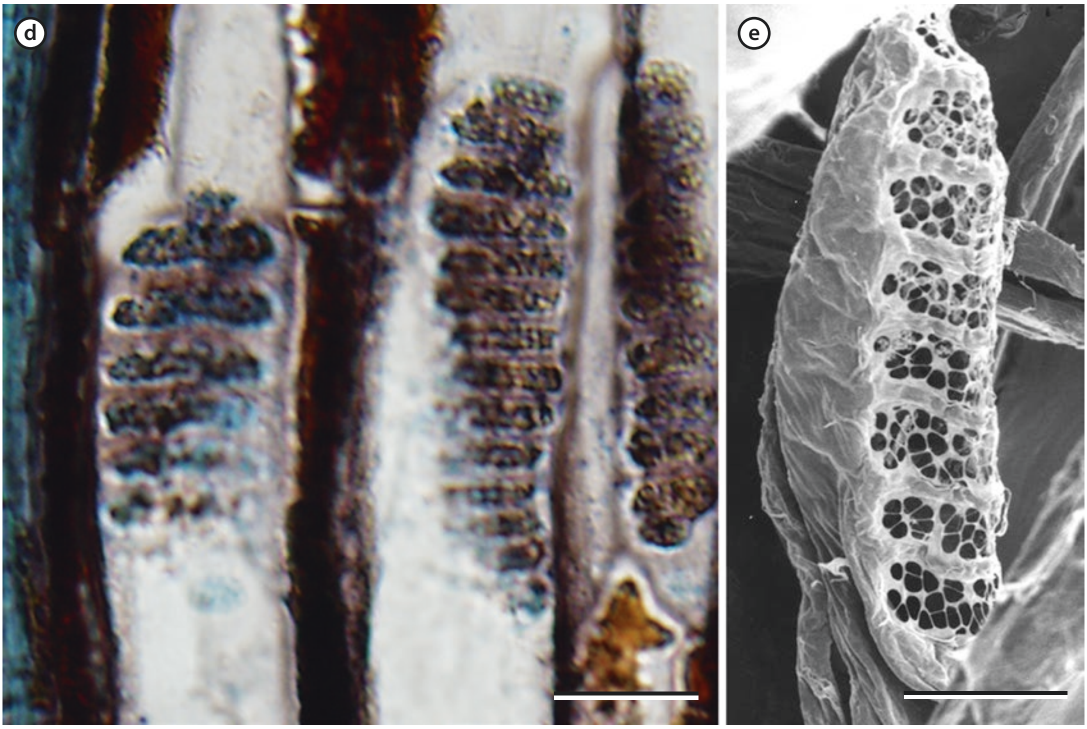


■ **Fig. 8.3** **a** Drawing of a sieve tube element showing the terminal sieve plates (SPl) with sieve pores (SPo) and lateral sieve areas (LSA) (JD Curtis, UW Stevens Point)



■ **Fig. 8.3** **b**, **c** Simple sieve plates in squash (*Cucurbita pepo*) seen face-on. **b** The primary cell wall stains blue in this LM section while the P-protein stains red. Compare this image to the longitudinal section in **g**. **c** Scanning electron micrograph of a sample that was prepared the same as in **b**. Note the companion cells in the 8 o'clock position next to both sieve plates. Scale bar in **d** = 10 µm and applies to both panels. (**b**, **c** RR Wise)

(■ Fig. 8.3b–f) and **sieve areas** in their lateral walls (■ Fig. 8.3g). Both contain numerous **sieve pores**. Sieve pores are modified, enlarged plasmodesmata (see below), and, like plasmodesmata, they interconnect sieve tube elements at both the ends and sides.



◼ **Fig. 8.3** **d**, **e** Compound sieve plates in grape (*Vitis* sp.). **e** Light micrograph of three sieve plates. **f** Scanning electron micrograph of an isolated grape STE from a stem maceration. The specimen experienced some shrinkage during preparation for microscopy. Scale bars = 20 µm in both panels. (**d** RR Wise; Image **e** courtesy of J. D. Curtis)

Sieve plates may be simple, with the entire end wall modified into a sieve area (◼ Fig. 8.3b, c), or compound, consisting of several sieve areas interrupted by intact end wall areas (◼ Figs. 8.3d, e and 8.4e). Non-inclined, simple sieve plates are considered most derived and are adapted for intercellular flow, like straight perforation plates in xylem vessels. On the other hand, inclined compound scalariform sieve plates are considered ancestral, like inclined perforation plates in xylem vessels.

The development of simple sieve plates has been studied in more detail than inclined sieve plate development. During phloem development, plasmodesmata in the walls between future sieve elements are converted into sieve pores usually 0.2–0.4 µm in diameter (but up to 1 µm in some cucurbits). This facilitates the unimpeded flow of the translocation stream between adjacent sieve elements. Like plasmodesmata, the sieve pores are delimited from the cell wall by a plasmalemma membrane which is continuous between the adjacent sieve elements and continuous throughout the length of the sieve tube (◼ Fig. 8.3f). This, in effect, makes the sieve tube a continuous pathway. Development of sieve pores involves the deposition of an amorphous polysaccharide callose in the cell wall around each plasmodesmata that displaces cellulose microfibrils. Due to the subsequent enzymatic digestion of the centers of these cylinders of callose, sieve pores will replace the callose depositions.

A unique filamentous protein termed **P-protein** ("P" derived from "phloem") is formed in the sieve elements of many plants

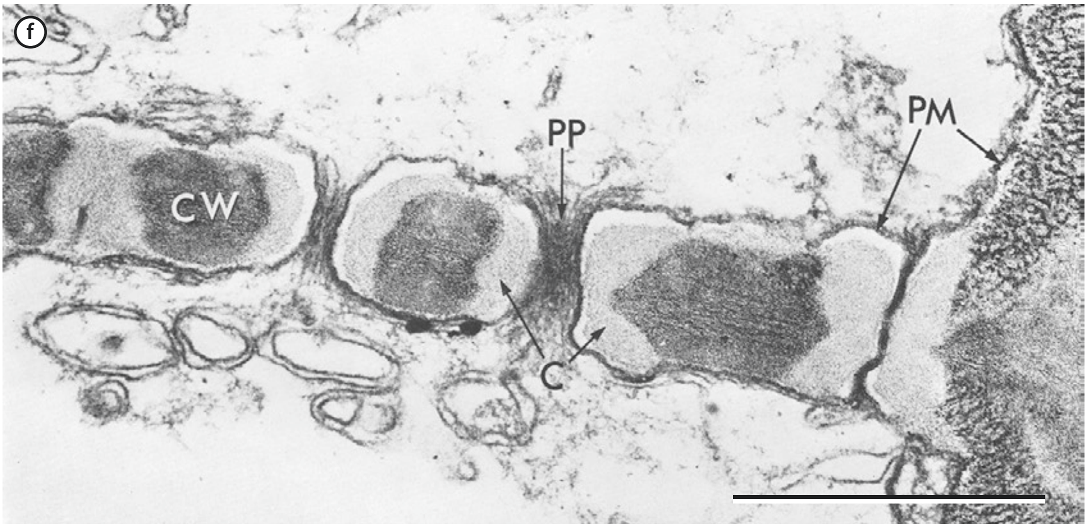


Fig. 8.3 **f** Transmission electron micrograph of a portion of a sieve plate in Arabidopsis showing details of the sieve pores. Seen in cross-section, the areas of cell wall (CW) between the pores appear as isolated islands. Callose (C) lines the pores, while the plasma membrane (PM) surrounds the cells and extends through the sieve pores. Strands of P-protein (PP) are indicated. Scale bar = 1 µm. (Image from Ledbetter and Porter (1970), with permission)

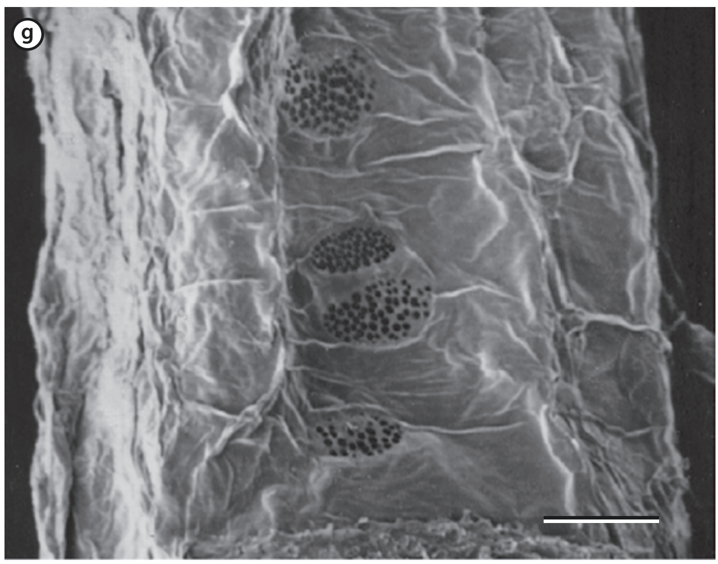


Fig. 8.3 **g** Sieve areas in a grape (*Vitis* sp.) sieve tube element isolated from a stem maceration. STEs are parenchyma cells, and this one shriveled somewhat during specimen preparation, but the sieve areas are clearly visible. Scale bar = 10 µm. (Image courtesy of J. D. Curtis, UW Stevens Point)

during differentiation. It has filaments which are anchored to the periphery of the mature cell and which permeate the sieve element lumen (Fig. 8.3h). After injury to the phloem, P-protein is released from its anchoring sites and accumulates at sieve pores by hydrostatic pressure of the sieve tube sap, blocks the pores, and prevents assimilate loss at the injury site (Figs. 8.3i, j). Such aggregations of P-protein, sometimes also called **slime plugs**, are usually formed during the processing of phloem for light microscopy.

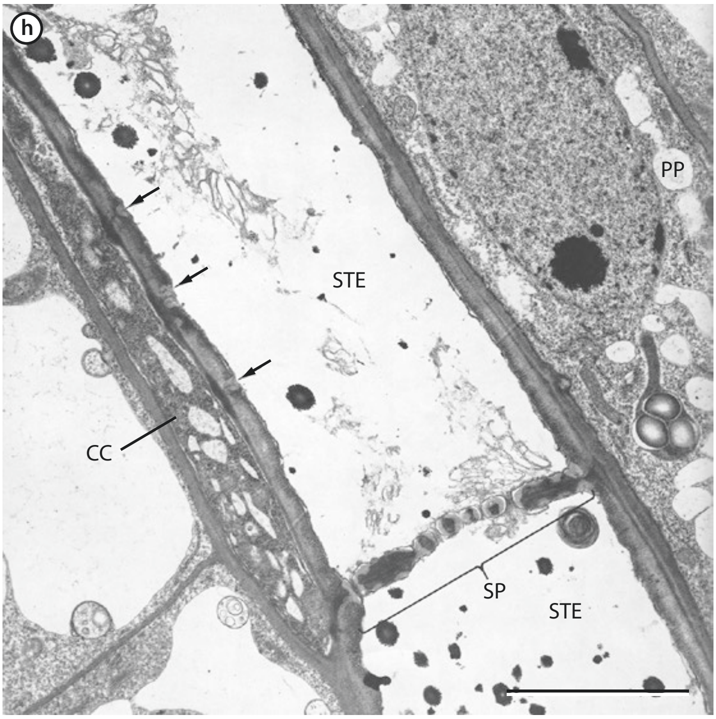


Fig. 8.3 **h** Transmission electron micrograph of portions of two sieve tube elements in an *Arabidopsis* stem. A sieve plate (SP) separates the two sieve tube elements. Plasmodesmata connecting the companion cell (CC) and sieve tube element (STE) are indicated with arrows. The wispy material in the STE lumen is P-protein. A phloem parenchyma (PP) cell lies to the top right. Scale bar = 5 µm. (Image from: Ledbetter and Porter (1970), with permission)

Box 8.2 Dangerous Hitchhikers—Viruses Use Phloem to Spread Throughout a Plant

Phloem is a continuous, living transportation network of vascular tissue that spreads throughout the plant. Viruses enter a plant through damage such as insect bites and make their way, via plasmodesmata, to the phloem sieve tube elements. Plants have numerous defense mechanisms to keep viruses out of sieve tube elements. Once in the phloem, the viruses may spread either as virions in which the viral genome is protected by virus capsid proteins, or as ribonucleoprotein (RNP) complexes in which the viral genome is protected by either viral proteins or host proteins. Susceptible plants are not able to prevent the long-distance viral spread. Resistant plants have molecular mechanisms to block viral passage in the phloem and survive. The fascinating molecular details of this viral-plant arms race are beginning to be elucidated.

Reference: Hipper et al. (2013)

Fig. 8.3 **i**, **j** Longitudinal section of a squash (*Cucurbita pepo*) stem showing P-protein details. **i** Every sieve tube element in the field of view has an accumulation of red-staining P-protein at the lower end of the cell as an artifact of tissue preparation. Phloem sap is under pressure, and the direction of flow was toward the bottom of the image when these samples were collected. Two files of phloem parenchyma (PP) are labeled. **j** A higher magnification view of several sieve tube elements. P-protein has accumulated at the lower end of each STE. Note also the companion cell (*) to the left of the STE in the middle of image **j**. Scale bars = 50 µm in **i** and 20 µm in **j**. (**i**, **j** RR Wise)

8

8.4 Companion Cells Support the Sieve Tube Element and Are Involved in Phloem Loading and Unloading in Angiosperms

Each sieve tube element in angiosperms is accompanied by a single cytoplasmically dense cell called a companion cell. **Companion cells** lie along the sieve element, and, in fact, the two cells together are considered to be a single functional unit called an STE-CC complex. The two cells are the product of longitudinal division from a common phloem mother cell (Fig. 8.4a–d). Phloem mother cells are found in both the procambium (generating primary phloem) and the vascular cambium (generating secondary phloem).

Companion cells have been studied intensively for decades and appear to have a variety of roles depending on species, organ, and developmental stage (Otero and Helariutta 2017), with two basic roles being the most important. First, companion cells provide metabolic support for the sieve tube element. Upon maturation, phloem sieve tube elements undergo partial apoptosis (i.e., programmed cell death). They have a degenerate cytoplasm with minimal organelles and lack a nucleus and ribosomes. In spite of this, phloem STEs can remain alive for decades. The companion

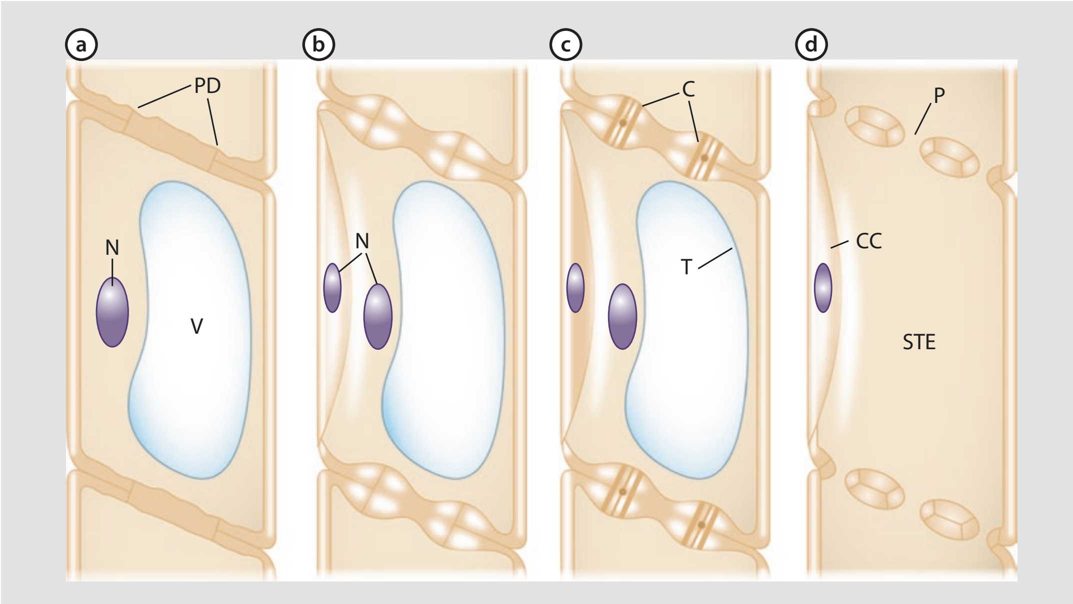


Fig. 8.4 **a**–**d** Development of a sieve tube element (STE) and its companion cell (CC) from a single phloem mother cell. **a** The phloem mother cell has a single nucleus (N), a large vacuole (V) and plasmodesmata (PD). **b** Mitosis generates two cells, each with its own nucleus. **c** The STE nucleus and tonoplast (T) break down. Callose (C) accumulates at the developing sieve pores. **d** In the mature state, sieve tube elements each have an accompanying companion cell and are connected via a sieve plate (SP) containing large sieve pores (P). The CC retains its nucleus and the common wall between the CC and STE has numerous plasmodesmata (not shown). The CC is often shorter than the STE (**a**–**d**, RR Wise)

cell serves to provide the STE with all the necessary biochemical requirements for it to survive. The STE-CC complex represents the ultimate stage in eukaryotic cell compartmentation in that one cell, the STE, relies almost completely on another, the CC, for its basic metabolic needs.

Companion cells also play an important part in loading sieve tubes with photosynthates and other molecules at source tissues and unloading from sink tissues. These are the sugars that drive translocation (refer to ► Sect. 8.2, above). Loading/unloading can have two pathways, depending on the plant and the organ. In **symplastic loading** small monomeric sugars diffuse from a companion cell into a sieve tube element via plasmodesmata in their common wall. Once in the STE, the monomers are polymerized to larger sugars that are too large to diffuse back through the plasmodesmata to the companion cell. This physiological process is called polymer trapping. The polymers are subsequently carried in the phloem sap to a source tissue where they are depolymerized and unloaded. In **apoplastic loading**, **transport proteins** in the CC plasma membrane facilitate unidirectional movement of sugar monomers from the CC cytoplasm into the apoplastic space between the CC and an adjacent STE. Other transport proteins in the STE plasma membrane facilitate unidirectional uptake of the apoplastic sugars into the STE cytoplasm for long-distance translocation.

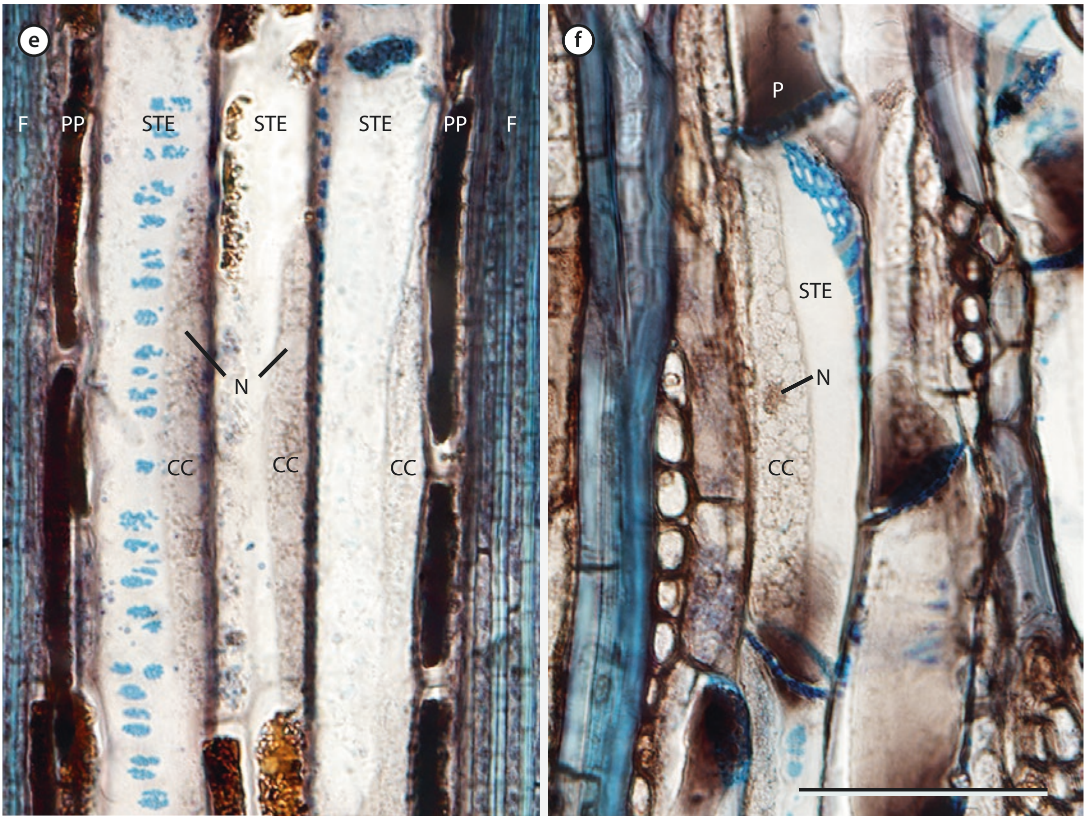
Gymnosperms lack angiosperm-like companion cells and have, instead, specialized cells called **albuminous cells** that are thought to play the same role in phloem loading and unloading (▶ Sect. 8.8). Seedless vascular plants have sieve tube elements, but lack specialized companion cells. Instead, the adjacent phloem parenchymas have numerous plasmodesmata and pores on the STE common walls, indicating that they function in a role similar to the angiosperm companion cell and the gymnosperm albuminous cell (Evert 1990a).

8.5 Phloem Parenchyma Cells Are Involved in Radial Translocation, Xylem/Phloem Coordination, and Storage

Companion cells (▶ Sect. 8.4) and albuminous cells (▶ Sect. 8.8) are parenchyma cells. Indeed, even sieve tube elements qualify as parenchyma cells, although they are highly modified via partial apoptosis. However, phloem tissue contains other parenchyma cells that do not fit into any of the previous categories. Such phloem parenchyma cells play multiple roles in radial translocation, coordination of adjacent xylem and phloem tissues, and storage.

As noted previously, sieve tube elements, companion cells, and phloem fibers run in the axial direction. Phloem parenchyma in secondary tissues, on the other hand, occurs in two orientations or systems. (Tissues in the primary state may have little need for radial transport, due to their small size.) **Axial phloem parenchyma** cells (◘ Fig. 8.4e, f) run up and down the axis of the plant and are part of the vascular bundle containing sieve tube elements, companion cells, and phloem fibers, as well as the adjacent tissues of the xylem. **Ray parenchyma** cells run in a radial direction forming xylem rays to the interior (▶ Chap. 7) and **phloem rays** to the exterior (◘ Fig. 8.5a), meaning that an individual ray is both a xylem ray and a phloem ray, depending on the tissue it penetrates. Ray parenchyma are formed in the vascular cambium by the division of ray initials (▶ Sect. 14.3). Those toward the xylem side are usually short lived, while the phloem ray parenchyma may last considerably longer. Transpirational water moves up the axial xylem from the roots, enters the parenchyma of the xylem ray, and moves in a radial direction into the phloem ray and then to the periderm (◘ Figs. 8.5b, c). Photosynthate is translocated from the source (usually a leaf), through phloem sieve tube elements in the axial phloem, enters the ray parenchyma, and moves in a radial direction out to the living tissues of the periderm (▶ Chap. 16). There are no sieve tube elements in the radial system—all translocation is via the symplasm of the phloem ray parenchyma. In a mature tree, the flux of phloem sap in the radial direction may be significant because it is usually the sole source of water and nutrients for the physiologically active periderm.

Phloem ray parenchyma cells may be elongated in the radial direction, termed **procumbent cells**, or elongated in the axial direction, called **upright** or **erect cells** (◘ Fig. 8.5d, e). Upright cells are usually at the upper and lower margins of the ray.



◘ **Fig. 8.4** **e**, **f** STE-CC complexes. **e** Three sieve tube elements from grape (*Vitis* sp.) are bordered by phloem parenchyma (PP) and fibers (F) to either side. Blue-stained callose marks locations of portions of two sieve plates at the top of the figure and lateral sieve areas in the leftmost STE. Three companion cells (CC) are indicated as two CC nuclei (N). Note that the STEs are considerably longer than the CCs. **f** A single STE-CC complex in elm (*Ulmus americana*) in which the STE and CC have the same length. The brown areas are sieve plate slime plugs made of P-protein (P). Note the CC nucleus (N). Scale bar in **e** = 50 µm and applies to both panels. (**e**, **f** RR Wise)

Phloem parenchymas store starches, tannins, oils, other secondary compounds, and water in both the axial and ray systems. Given their intimate association within the phloem tissue, and that sieve tube elements, companion cells, and phloem fibers have specific and defined roles to play, phloem parenchyma may be seen as the most metabolically flexible of the four phloem cell types. This versatility fits with their multiple roles in storage. Starch storage increases in the autumn, and those carbohydrates are subsequently remobilized to support cambial activity upon the reactivation of the vascular cambium during spring growth in conifers (◘ Fig. 8.5f, Rahman et al. 2016) and ginkgo (Cui et al. 2016). Tannins are well-known **antiherbivory** compounds, and phloem is an attractive target for insect attack. Therefore, many species fill phloem parenchyma cells with tannin deposits (◘ Fig. 8.5g) to deter herbivory. Finally, water from phloem parenchyma may be used to supplement xylem water at times of high transpirational demand (Pfautsch et al. 2015).

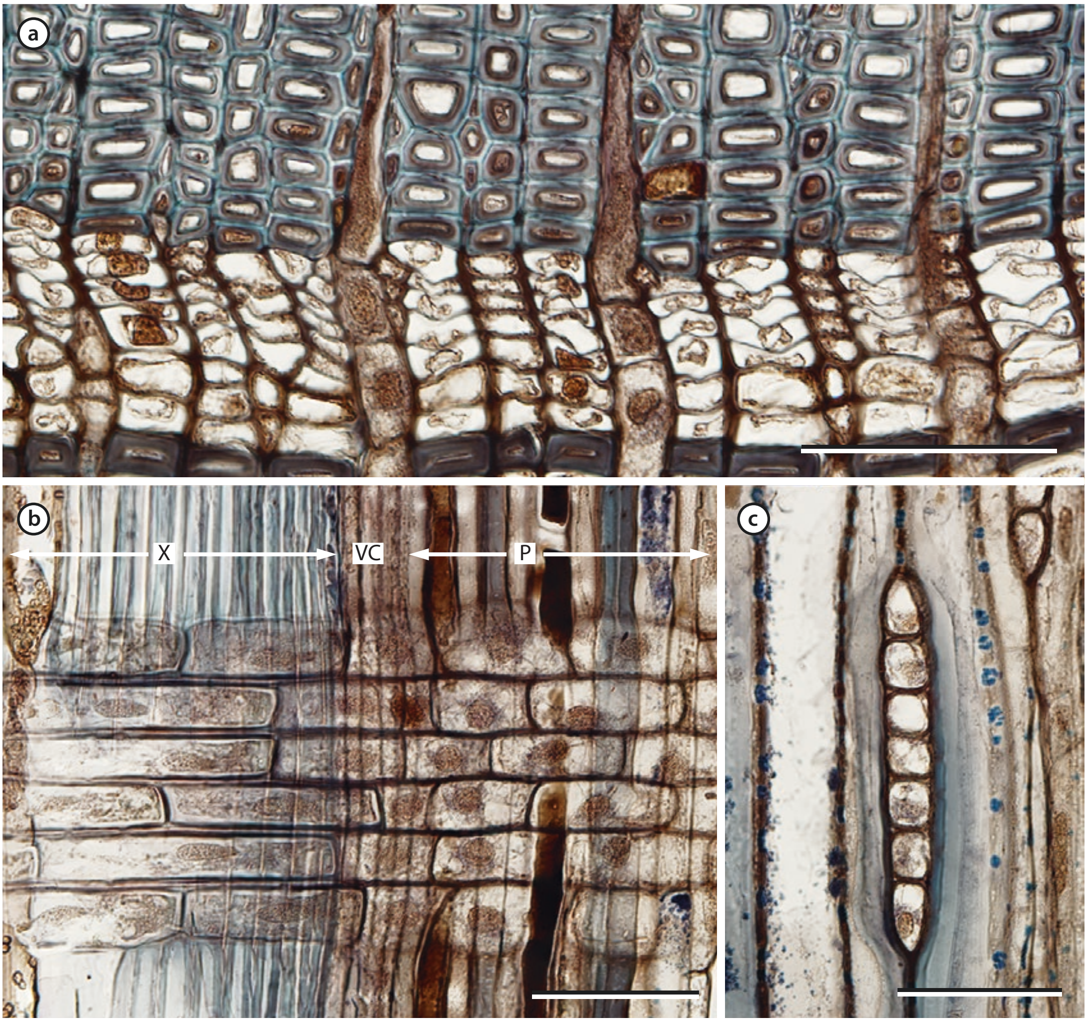
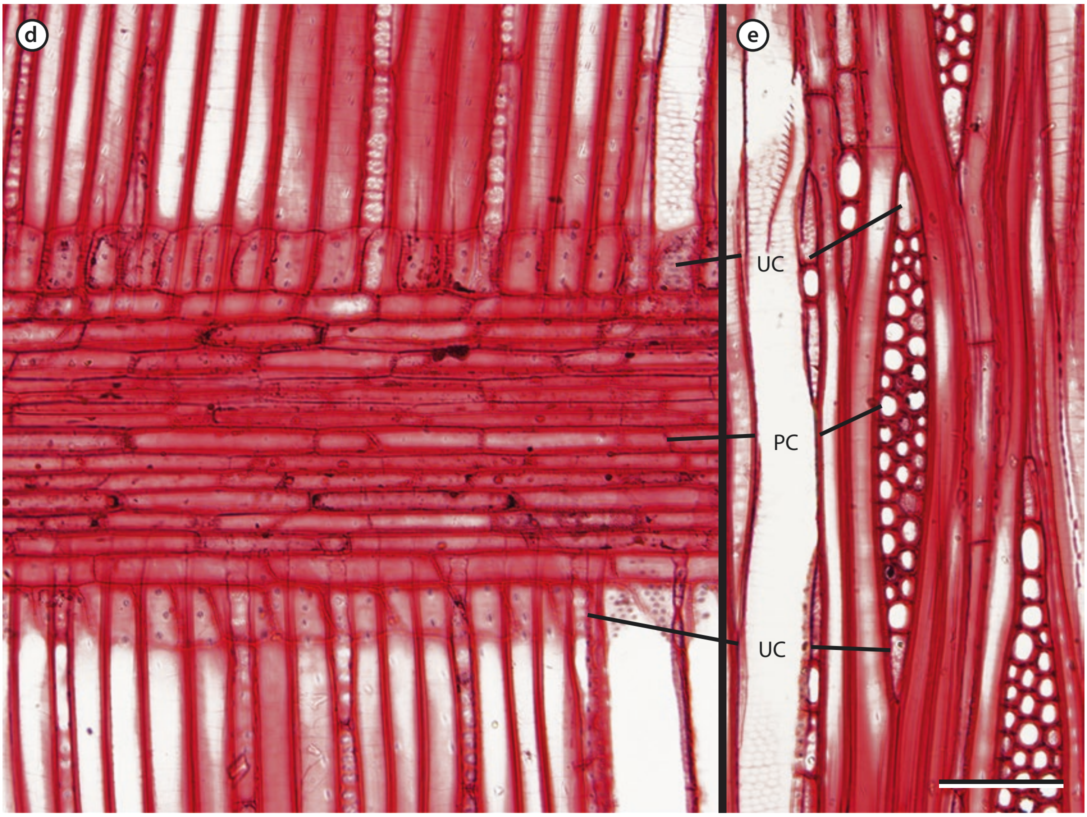
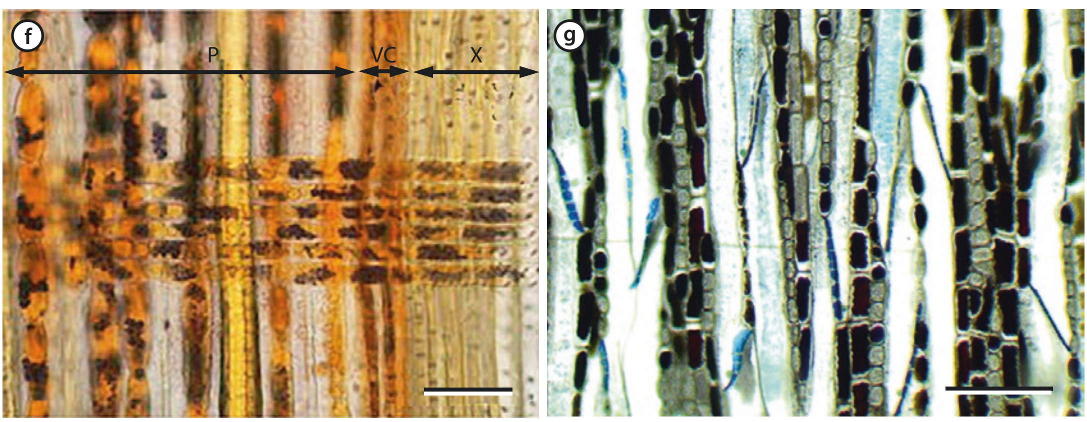


Fig. 8.5 **a** Phloem rays in a coast redwood (*Sequoia sempervirens*) stem. **a** Cross-sectional view showing xylem to the top, phloem to the bottom, and three rays that originate in the xylem and continue through the phloem. The thick-walled cells in the xylem are tracheids and the source of transpirational water. **b** Radial view of a single ray, extending from the xylem (X) into the phloem (P). The vascular cambium (VC) lies between the xylem and phloem, and the periderm would be to the right in the figure. The ray is six cells tall. **c** Tangential view of a single phloem ray which is seven cells tall and one cell layer wide. This is a **uniseriate ray**. The blue dots to the right of the ray are lateral sieve areas in the phloem sieve cells. Scale bars = 50 µm in all three panels. (**a**–**c** RR Wise)

The vascular system may be thought of as having five components: (1) axial xylem, (2) xylem rays, (3) axial phloem, (4) phloem rays, and (5) a mesh of xylem and phloem parenchyma (both derived from the vascular cambium) that integrates and interconnects the other four components. It has recently been proposed that this network of parenchyma plays critical roles in whole-plant coordination of resource transport and, more importantly, resource allocation (Spicer 2014). Anatomical details such as taxon-specific variations in size, shape, and location of parenchyma as well as pits and plasmodesmatal connections to adjacent tissues suggest that the vascular parenchyma is a highly evolved tissue that plays a crucial role in both long-distance and short-distance transport of transpirational



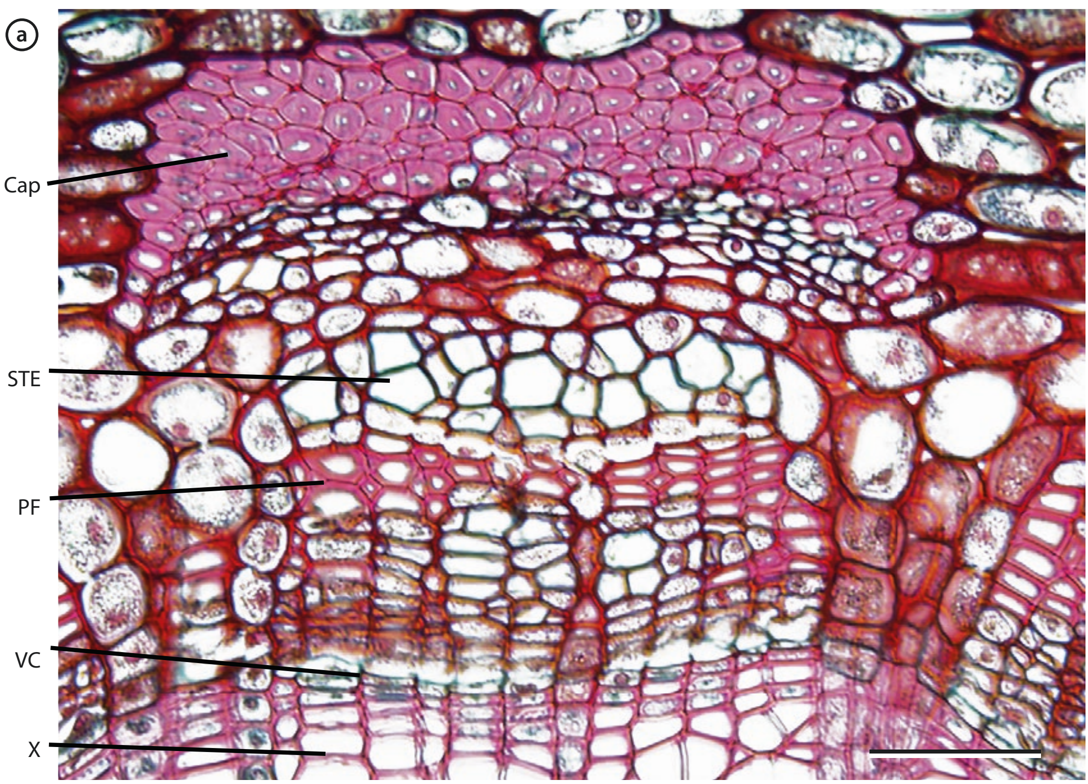
■ **Fig. 8.5** **d**, **e** Procumbent (PC) and upright cells (UC) in xylem rays from holly (*Ilex opaca*) wood. **d** is a **radial section**, and **e** is a **tangential section**. Xylem tissue is shown because the ray cells are more easily seen than in phloem tissues. However, the arrangement is the same in phloem. Scale bar in **e** = 50 µm and applies to both panels. (**d**, **e** RR Wise)



■ **Fig. 8.5** **f**, **g** Phloem storage compounds. **f** Starch has been stained dark brown in phloem parenchyma cells as shown in this radial section of sawara cypress (*Chamaecyparis pisifera*) stem. Axial parenchymas are to the left in the image, and radial parenchyma runs across the image. Both contain starch. **g** Tannin-filled parenchyma cells are dark brown and interspersed among sieve tube elements in this black willow (*Salix nigra*) stem. Scale bars = 100 µm in both panels. (**f** from Rahman et al. (2016), with permission; **g** RR Wise) water and phloem sap. The interconnected parenchymas of xylem and phloem rays therefore take on an important role in whole plant physiology.

8.6 Phloem Fibers Protect the Delicate Sieve Tubes

Technically speaking, all phloem STEs, CCs, and phloem parenchyma are products of the procambium (primary phloem) or the vascular cambium (secondary phloem). However, not all cells termed phloem fibers fit that tight definition. Fibers are sclerenchyma cells found throughout the stems, leaves, and other organs of angiosperms and gymnosperms, and they may have a variety of origins (◘ Fig. 8.1b, d, e and 8.4e). While some fibers are produced by the vascular cambium (◘ Fig. 8.6a), all fibers found within or adjacent to the phloem are often termed phloem fibers based on their location, and not necessarily their origin.



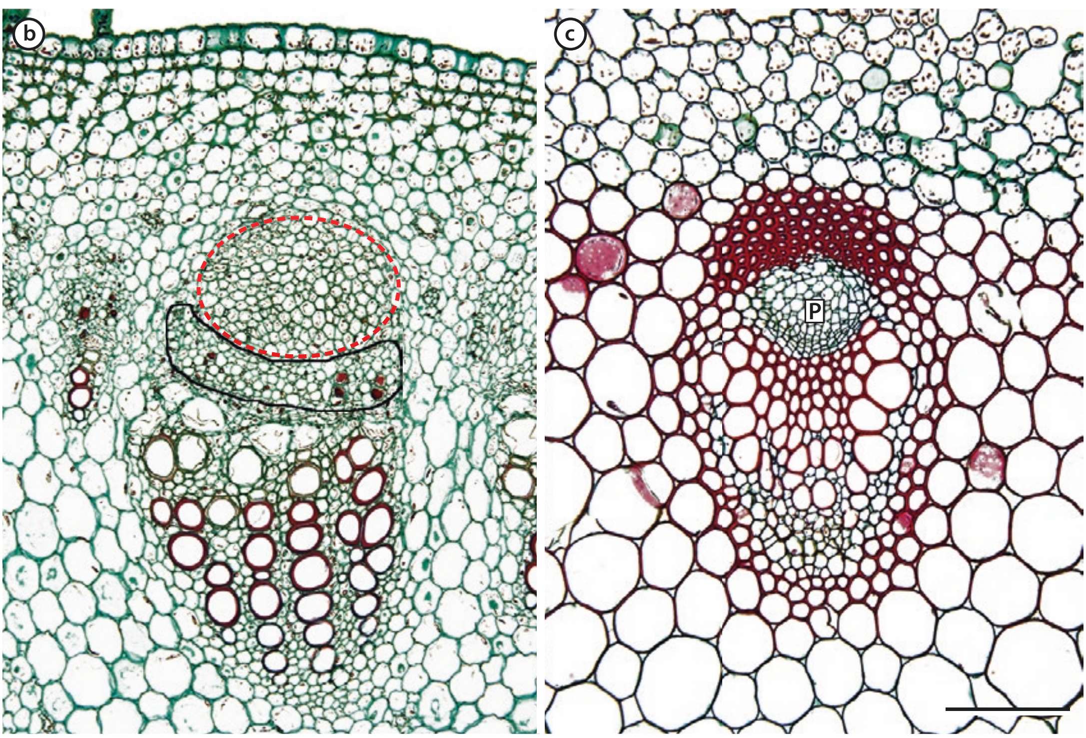
◘ **Fig. 8.6** **a** Tulip tree (*Liriodendron tulipifera*) vascular bundle. *Liriodendron* has a cap of fibers to the exterior of the sieve tube elements. Other phloem fibers (PF) to the interior of the sieve tube elements (STE) were derived from the vascular cambium (VC) and will probably become part of the periderm with time. Their alignment with cells and derivatives of the vascular cambium reveals their origin from the vascular cambium. (X = xylem. Scale bar = 25 µm) (RR Wise)

Regardless of their ontogenetic origin, all phloem fibers are responsible for support and protection. Sieve tube elements are relatively thin-walled parenchyma cells with a function for which no other cell type can substitute. Therefore, they must be protected from wounding, damage caused by bending, and attack by insects. STEs also provide little in the way of support for the stem in either primary or secondary tissues.

Not all phloem tissues have associated fibers; those in the primary state may lack them entirely (◘ Fig. 8.6b). In tissues that do have phloem fibers, it is common for them to form “caps” to the abaxial side of vascular bundles (◘ Fig. 8.6c). Phloem in secondary tissues is protected by the periderm, which is a mixture of phloem fibers, phelloderm, and phellem (refer to ► Chap. 16—Periderm).

8.7 Secondary Phloem Typically Only Functions for One Growing Season

In the elongating stem region, the first nutrient conducting tissues (protophloem) are formed from the procambial strands which are initiated in the apical meristems. The phloem cells lengthen very rapidly to form conducting strands. At about the same time, the first



◘ **Fig. 8.6** **b** A vascular bundle from a cosmos (*Cosmos* sp.) stem showing a lack of fibers in or around the phloem (inside black bounding area), although there is a large cushion of densely packed parenchyma cells to the abaxial side (inside red-encircled bounding area). **c** This vascular bundle from a meadow buttercup (*Ranunculus acris*) stem has a large cap of red-stained fibers to the abaxis of the phloem (P). Scale bar in **c** = 50 µm and applies to both panels. (**b**, **c** RR Wise) strengthening tissues (sclerenchyma fibers) develop on the outside of the phloem. The procambial strand continues to produce vascular tissue beyond the elongating region until only a narrow band of cambium remains. Protophloem sieve tube elements may mature into metaphloem sieve tube elements of the primary phloem, or they may be abandoned and destroyed. The origin and development of proto-/metaphloem and proto-/metaxylem are described together in ► Chap. 11—Stems.

In tissues with only primary growth, the primary phloem serves for the life of that organ, and in woody eudicots, most of the phloem is functional for only a single growing season. However, several reports exist of sieve tube elements functioning for 5 or even 10 years (Evert 1990b, and references therein).

Secondary thickening occurs to some degree in most eudicotyledons and is especially notable in those with perennial (or persistent) aerial parts (i.e., woody plants). ► Chapter 15—Wood—discusses secondary thickening in detail. Secondary thickening involves the laying down of extravascular and strengthening tissue necessitated by the increased size of the plant (◘ Fig. 8.6d, e). Some of the cells of the medullary rays become active and join with the cambium of the vascular bundles to form a meristematic ring. Secondary phloem (along with xylem) tissues are then formed. The xylem tissues build up inside the cambium and force it and the phloem further from the center. Thus, a tree trunk consists mainly of xylem tissue, with a thin layer of phloem near the outside. In most temperate ecosystems, the xylem shows **annual rings**. In the spring, when the sap is rising, the xylem consists mainly of large vessels, but in autumn there is a high proportion of fibers and smaller vessels.

In cross-sectional view, spring and autumn woods are distinctively different, producing a ringed effect. Secondary phloem does not build up a thick layer because the cells do not have thickened walls and, being outside of the trunk, become crushed by the pressure of the expanding xylem tissue and must be replaced each growing season. These forces usually break down the epidermis also, and its protective function is assumed by the phellem (protective nonliving cells). That corky tissue is formed from a layer of cortex which became meristematic. The phellem is a dead tissue and cuts off food from all tissues outside of it forming dead bark (refer to ► Chap. 16—Periderm). ◘ Figure 8.7 illustrates the progress of the phloem development over the course of progressive seasonal growth stages.

8.8 Gymnosperm Phloem Is Simpler Than Angiosperm Phloem

The anatomy of gymnosperm phloem is simpler with fewer cell types than that found in angiosperms (◘ Table 8.1), with gymnosperms only having two or three (depending on how one chooses to count them) cell types. Angiosperm phloem has sieve tube elements, companion cells, phloem parenchyma, and phloem

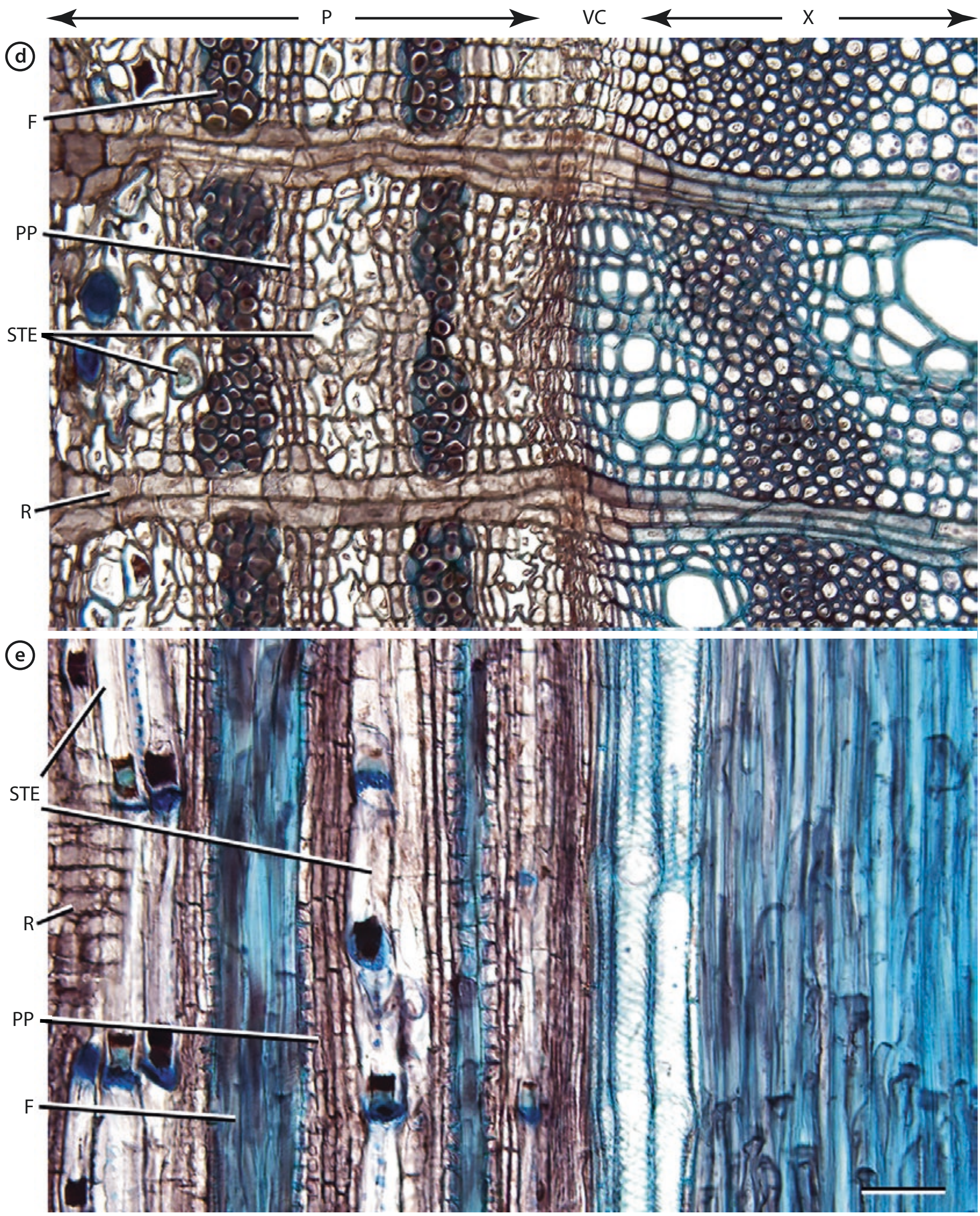


Fig. 8.6 **d**, **e** Secondary phloem in the stem of black locust (*Robinia pseudoacacia*) in **d** cross-section and **e** radial section. Phloem (P) is to the left and xylem (X) is to the right in both panels. The two images are of separate sections and are aligned to show correspondence between the two sectional views. Fibers (F), phloem parenchyma (PP), sieve tube elements (STE), and rays (R) are indicated in both panels. Scale bar in **e** = 25 µm and applies to both panels. (**d**, **e** RR Wise)

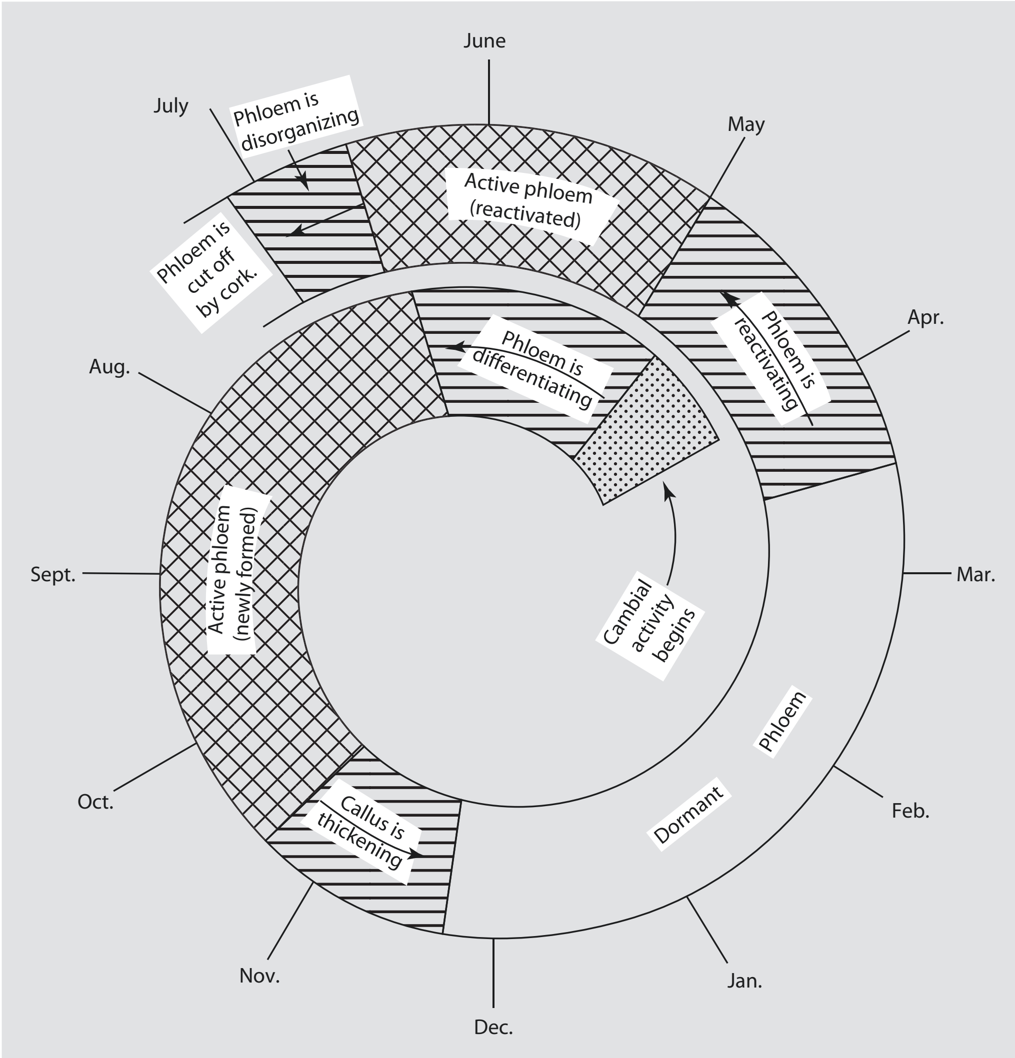


Fig. 8.7 An annual cycle of phloem activity as found in seed plants from a temperate climate zone. Begin in the center with spring cambial activity and follow the spiral to a second year of growth. After that, succeeding year's growth will be similar. (Designed by Dr. L.K. Mann and redrawn from Esau (1948) Hilgardia 18:217–296)

fibers. Gymnosperms have sieve cells and phloem parenchyma. Gymnosperms lack fibers, and albuminous cells (a.k.a. Strasburger cells) (Sauter 1980) take the place of companion cells. Albuminous cells are most commonly found along phloem rays (Fig. 8.8).

Gymnosperm sieve cells have tapering ends, and phloem sap transport is through sieve areas in overlapping side walls. Thus, a sieve tube (the end-to-end connection of the angiosperm sieve tube elements) cannot be formed, and phloem translocation typically has a higher resistance to flow (Liesche et al. 2015). Gymnosperm sieve cells are also usually narrower and longer than angiosperm sieve tube elements.

The angiosperm companion cell is a sister cell to the sieve tube element. The two start out as a single cell, and then later in development, they divide into two, connected cells (► Sect. 8.4).

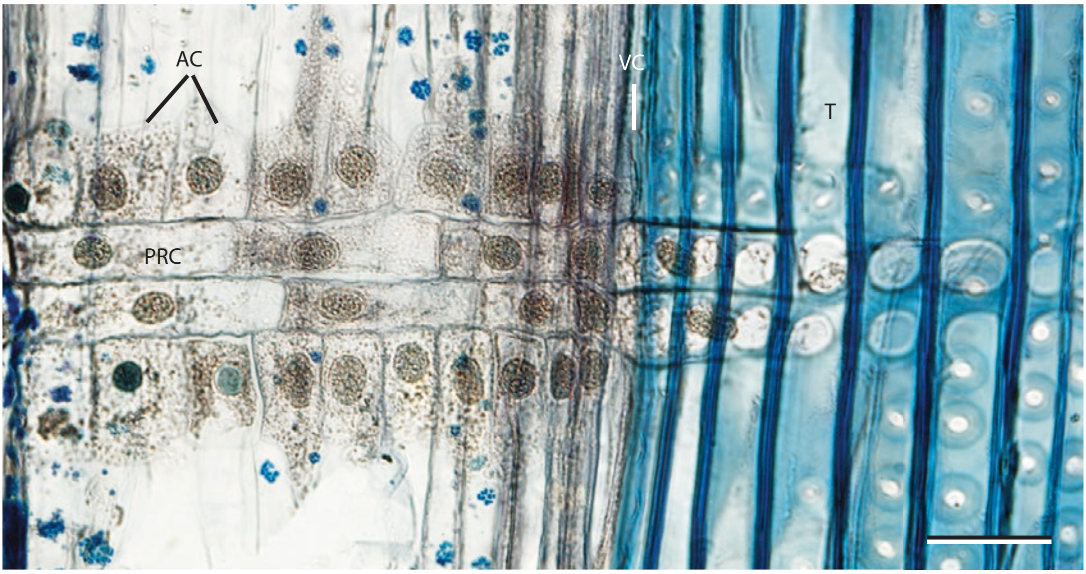


Fig. 8.8 Albuminous cells (AC) line the top and bottom of a phloem ray made of procumbent ray cells (PRC). The vascular cambium (VC) separates the phloem to the left from the xylem tracheids (T) to the right. Scale bar = 50 µm. (RR Wise)

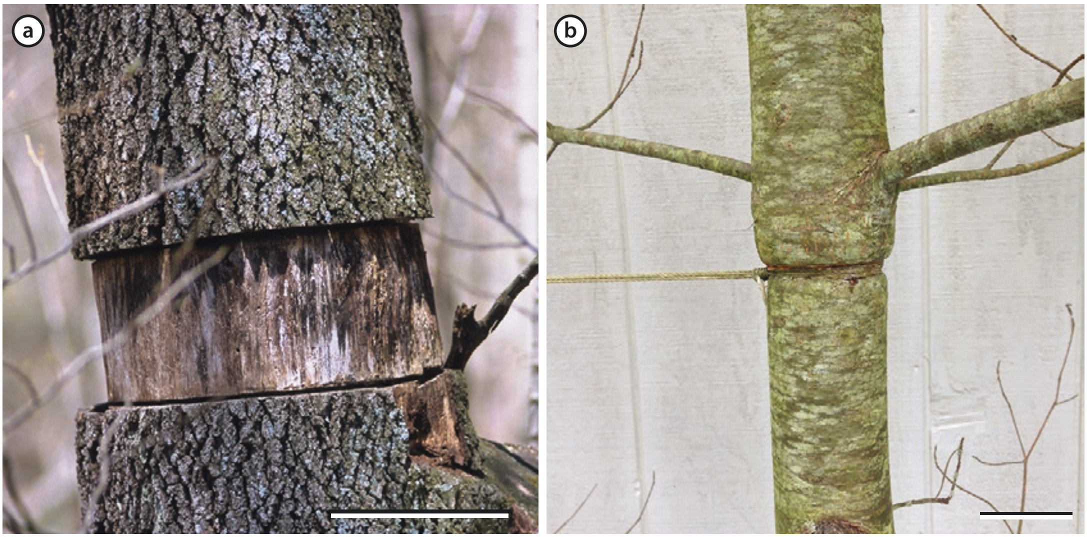
Gymnosperm albuminous cells, on the other hand, are not derived from the same mother cell as the sieve cell; they are derived from separate cells. Albuminous cells do, however, perform many of the same functions for a sieve cell as a companion cell performs for a sieve tube element—phloem loading/unloading and metabolic support.

Gymnosperm phloem parenchyma is similar in structure and function as the angiosperm analog.

The simpler nature of the gymnosperm vascular tissues, as compared to that found in angiosperms, does not mean that gymnosperms are not as successful at moving water and photosynthate throughout the plant. Indeed, the tallest trees are gymnosperms, so they must be pretty good at hydraulics. However, limits to their phloem (and xylem) versatility have restricted the ecological range and potential habitats of gymnosperms.

8.9 Girdling Inhibits Phloem Translocation and Can Kill a Tree

Girdling involves the removal of a ring of bark around the entire circumference of a stem or tree trunk (Fig. 8.9a). The removal includes the cork cambium, bark, secondary phloem, and possibly portions of the secondary xylem. When this takes place around a tree trunk, the entire tree will die. Girdling can be performed on stems as well as the tree trunk and can be done below the soil surface or around the root. It may be caused by animals or insects in the process of herbivory, or by foresters to thin forests. However, horticulturists may utilize girdling in order to obtain a larger yield of cer-



◘ **Fig. 8.9** **a** Girdling of this tree trunk involved removing the bark, cambium, and likely the sapwood in a ring around the trunk. This will kill the tree due to cutting off the flow of sap and nutrients. **b** If not removed, the string tied around this white pine (*Pinus strobus*) stem will eventually girdle and kill the tree. Note the swollen stem diameter above the girdle. Sugars accumulate above the girdle and cause the stem to swell. Scale bars = 10 cm in **a** and 5 cm in **b**. (**a** Image courtesy of the Wisconsin Department of Natural Resources, CC BY ND-2.0; **b** RR Wise)

tain fruits. This is commonly utilized with grapes, apple, avocado, and citrus trees. In these cases, more careful girdling is employed not to kill the plant but to remove bark from a branch in which all the carbohydrates and minerals produced by the leaves are unable to be transported down to the root system, but rather are taken up by the fruit which may become larger and sweeter than usual.

Girdling was used by Marcello Malpighi in 1686 to demonstrate that sugars moved through the phloem and water through the xylem.

In some cases, merely tying a string about a tree will eventually cause girdling as secondary growth increases the trunk diameter (◘ Fig. 8.9b). Indeed, even other plants, primarily vines (English ivy, wisteria, etc.), may climb and encircle the stem and cause a disruption of the bark sufficient to girdle and kill the tree.

8.10 Chapter Review

■ Concept Review

8.1. *Phloem is a complex tissue with multiple cell types, each with a specific structure and function.* Primary phloem develops from the procambium; secondary phloem develops from the vascular cambium. Angiosperm phloem consists of sieve tube elements, companion cells, fibers, and parenchyma. Gymnosperm phloem only has sieve cells and phloem parenchyma. In almost every instance, phloem and xylem always occur together, because they are derived from the same, bifacial meristems. Phloem is to the outside, abaxial to the xylem.

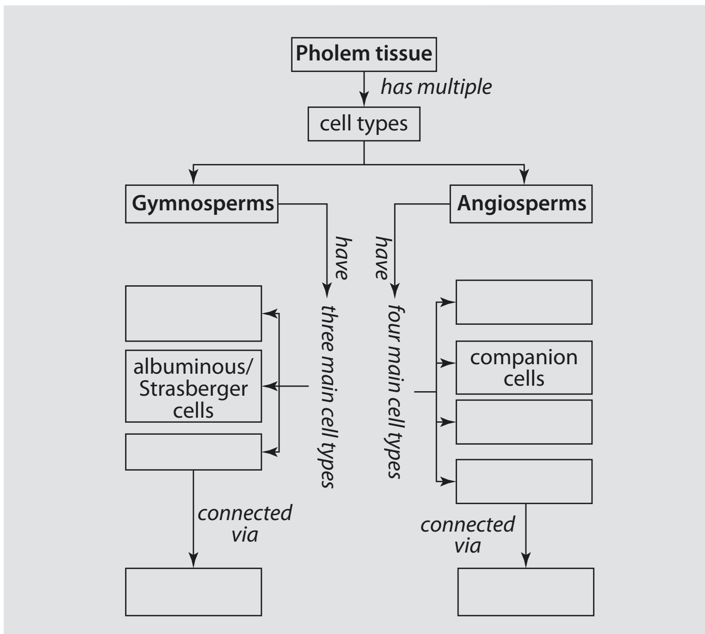
8.2. *Phloem's main function is photosynthate translocation.* Photosynthate (the product of photosynthesis) is translocated via the phloem from autotrophic tissues (called "sources," typically leaves) to heterotrophic tissues (called "sinks," typically roots and developing fruit) via the sieve cells and sieve tube elements of the phloem via a mechanism described by the Münch pressure flow hypothesis. Sugars are actively loaded at the source and actively unloaded at the sink. Water follows the sugars via osmosis, which pressurizes the sieve tube and drives the system.
8.3. *Sieve tube elements are living cells responsible for translocation.* Sieve tube elements contain a living plasmalemma and minimal internal organelles. They are connected at the ends via sieve plates (simple or inclined) and at the sides via sieve areas. Both contain sieve pores. Sieve pores develop from enlarged plasmodesmata and the deposition of callose. The callose is degraded to enlarge the pore. P-protein filaments are loosely attached to the interior of the sieve tube element. They are released upon damage to the sieve tube and plug the sieve pores (forming a slime plug), thus isolating the injury.
8.4. *Companion cells support the sieve tube element and are responsible for phloem loading and unloading in angiosperms.* Companion cells (CC) develop from the same phloem mother cell as the sieve tube element (STE). Together they form the STE-CC complex. Companion cells provide metabolic support to the minimally alive STE, and they are the site of phloem loading and unloading. Loading/unloading may be symplastic (via plasmodesmata) or apoplastic (across the plasmalemma).
8.5. *Phloem parenchyma cells are involved in radial translocation, xylem/phloem coordination, and storage.* Ray parenchyma is the conduit for the movement of water and photosynthate from the stem or root interior to the living periderm at the stem or root exterior. Procumbent phloem ray parenchyma cells are elongated in the radial direction. Upright cells are elongated in the axial direction. Phloem parenchyma may store starches, tannins, oils, and water. The axial and radial xylem and phloem cells work together as a complex tissue that is integrated and interconnected by the xylem and phloem parenchyma cells.
8.6. *Phloem fibers protect the delicate sieve tubes in primary tissues.* Phloem STE, CC, and parenchyma are defined as having arisen from the vascular cambium. However, phloem fibers are defined as fibers in or near the phloem, regardless of their ontogenetic origin. Phloem fibers serve to protect and support the fragile STE-CC complexes.
8.7. *Secondary phloem only functions for one growing season.* Secondary phloem is generated by the vascular cambium. Because the phloem lies to the exterior of the xylem, it is forced outward and crushed by the growing xylem tissue to the interior. The crushed phloem becomes incorporated into the phellem, or bark, of the stem and root.

8.8. *Gymnosperm phloem is simpler than angiosperm phloem.* Although gymnosperm phloem has fewer cell types than angiosperm phloem, all of the major phloem functions are present. However, this limitation restricts the ecological niches available to gymnosperms.

8.9. *Girdling inhibits phloem translocation and can kill a tree.* Girdling is the stripping away of all tissues from the outer bark of a tree down to the xylem, or applying a tourniquet around the stem. Because phloem is the only route for photosynthate translocation from the shoot downward, girdling will usually starve the roots and eventually kill the tree.

Concept Connections

1. Complete the concept map using the following terms: phloem fibers, phloem parenchyma (x2), sieve areas (lateral), sieve cells, sieve tube elements, and sieve plates (terminal).



Concept Assessment

2. In most angiosperms, primary phloem
   a. is organized into annual rings.
   b. replaces secondary phloem.
   c. possesses axial rays.
   d. is derived from the vascular cambium.
   e. is eventually torn apart.

3. In gymnosperms, ______________ serve the same role as the angiosperm companion cells.
   a. sieve tube elements.
   b. sieve cell.s

c. albuminous cells.
d. parenchyma.
e. phloem fibers.

4. P-protein appears to function in
a. the movement of assimilates (sugars) throughout the sieve tube.
b. conveying information from the companion cell to the sieve element.
c. providing a site for the accumulation of callose.
d. plugging sieve plates upon mechanical damage.
e. enzymatic activities.

5. Upon maturity, sieve tube elements are missing
a. nuclei.
b. cytoplasm.
c. p-protein.
d. callose.
e. sieve pores.

6. Phloem parenchyma include
a. companion cells.
b. sieve tube elements.
c. axial parenchyma.
d. ray parenchyma.
e. all of the above.

7. Phloem fibers are so designated based on
a. their derivation from the procambium.
b. their derivation from the vascular cambium.
c. their location in or near the phloem.
d. the organ in which they are found (leaf, stem, or root).
e. the structure of their secondary cell walls.

8. Angiosperm phloem cell types include
a. sieve tube elements, collenchyma cells, and fibers.
b. companion cells, collenchyma cells, fibers, and parenchyma cells.
c. sieve tube elements, albuminous cells, and parenchyma cells.
d. sieve tube elements, companion cells, parenchyma cells, and fibers.
e. sieve tube elements and parenchyma.

9. Sieve pores originate from
a. callose deposits.
b. plasmodesmata.
c. microtubules.
d. sieve plates.
e. companion cells.

10. Secondary phloem lives an average of
    a. 1 month.
    b. 1 year.
    c. 2 years.
    d. variable, depending on rainfall.
    e. one growing season.

11. The main function of phloem is to
    a. translocate photosynthate.
    b. provide water for transpiration.
    c. store carbohydrates for use during the winter.
    d. store water for use during arid periods.
    e. provide a means to transport carbohydrates from roots to leaves.

Concept Applications

12. List the cell types in angiosperm secondary phloem and give the function of each. Compare the structure and function of angiosperm cell types to those found in gymnosperms.

13. Explain the basics of the Münch pressure flow hypothesis. Include in your answer the difference between symplastic loading and apoplastic loading.

8

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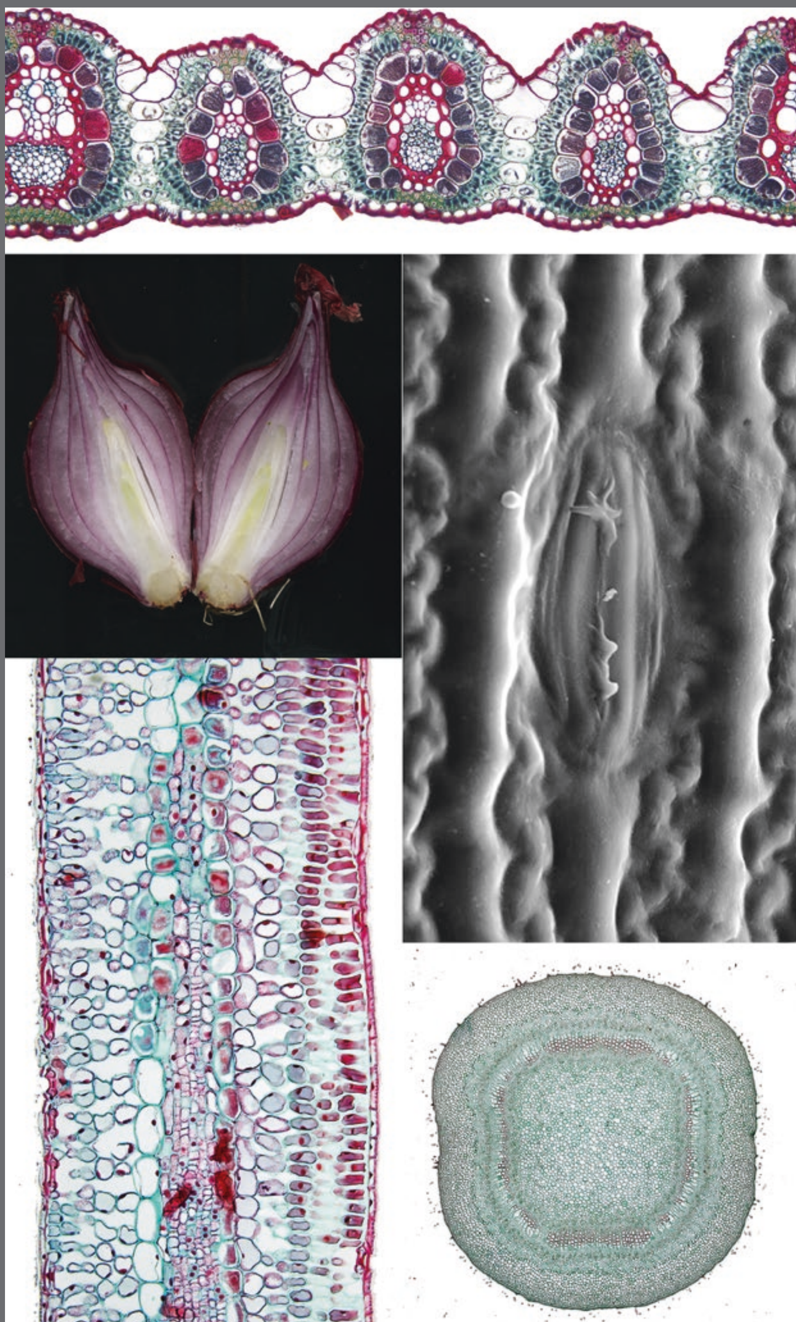
Primary Vegetative Growth



Light micrograph of a brome grass (*Bromus* sp.) leaf. Photograph of an onion (*Allium* sp.) cut in half. SEM of a Pennsylvania sedge (*Carex pensylvanica*) stomate. LM of a fir (*Abies* sp.) leaf in longitudinal section. LM of a milkweed (*Asclepius* sp.) stem in cross section. (All images by RR Wise.)

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Epidermis

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Introduction

The epidermis is the outer layer of cells of all aboveground (i.e., aerial) organs that are in the primary stage of growth. The epidermis persists throughout the life of leaves and flowers, because these organs do not have secondary growth. However, the epidermis may be replaced by a periderm when secondary growth occurs; this topic will be discussed in ► Chap. 16: Periderm.

The two primary functions of the epidermis on the leaf, flower, and stem are to limit water loss and to control gas exchange. The epidermis also plays a role in protecting the plant from biotic threats such as bacteria, fungi, and herbivores, as well as from abiotic stresses of high light and atmospheric pollution.

The shoot and leaf epidermises are derived from the protoderm of the shoot apical meristem (► Chap. 4). Subsequent developmental events lead to the origin of the different epidermal cell types – pavement cells, guard cells, trichomes, and idioblasts. This chapter will focus on the epidermis of the aerial parts of the plant, namely, the leaf and stem.

The outer tissue layer in roots is adapted almost entirely for water and ion absorption and anchorage. Given these differences in structure and function, the term *rhizodermis* is used for the root outer cell layer and is more completely discussed in ► Chap. 10: Roots.

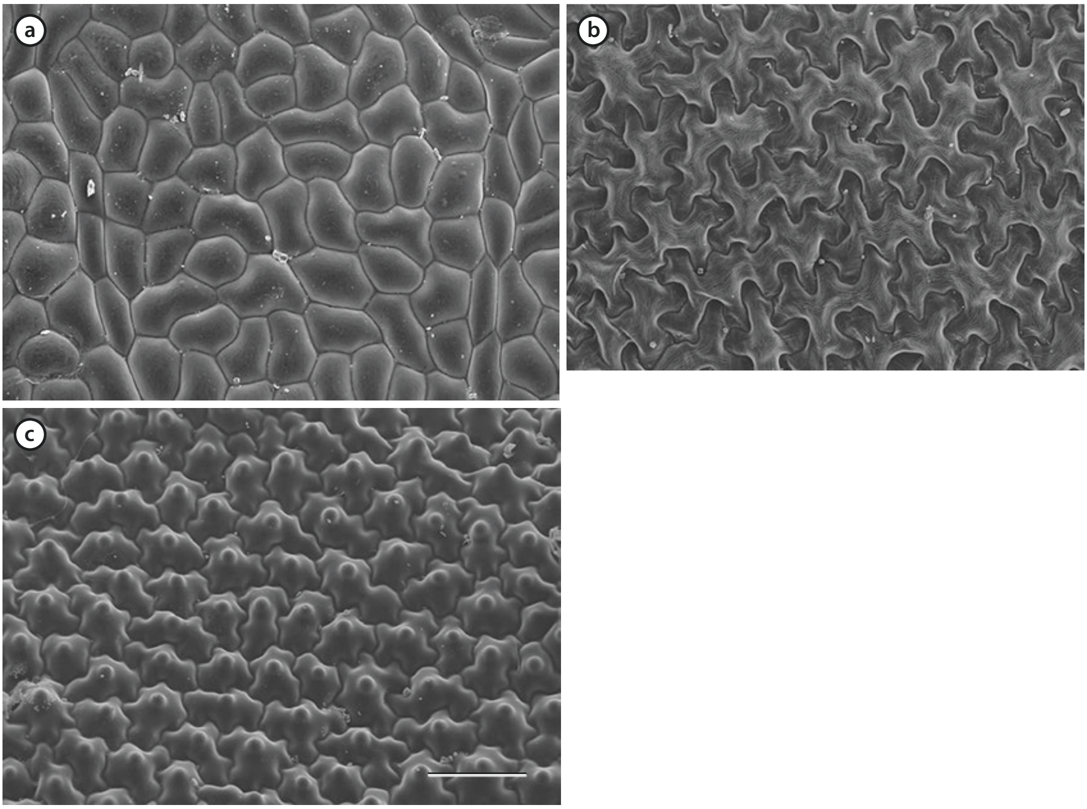
9.1 Pavement Epidermal Cells Cover Leaf and Stem Surfaces

The majority of the cells on most leaf and stem surfaces are relatively non-differentiated parenchyma cells called **ground cells** or pavement cells (◘ Fig. 9.1a–c). Pavement cell patterns vary between and among species and even between the two surfaces of the same leaf. Regardless of patterning, pavement cells are tightly packed with no intercellular spaces, thus providing a means to minimize the loss of water and prevent the entrance of microbial or fungal pathogens from outside of the plant.

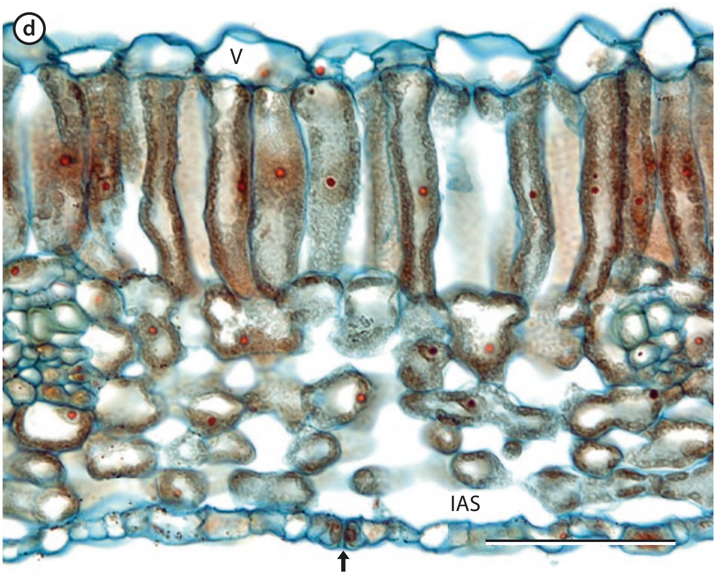
In leaves, epidermal cells form a continuous layer over both the abaxial and adaxial surfaces and may have significantly different sizes and shapes depending on which leaf surface they cover (◘ Fig. 9.1d). In contrast to the interior leaf mesophyll cells, pavement cells appear to be empty. In fact, more than 90% of their internal contents are due to a large central vacuole with only a thin layer of cytoplasm around the periphery of the cell. With the exception of guard cells (refer to ► Sect. 9.3), epidermal cells do not contain chloroplasts.

In accordance with the protective function of the tissue, the cell walls, especially the outer tangential cell walls, may be very thick and occupy a large volume equal to about 10–20% of the total cell volume (◘ Fig. 9.1e, f).

Anthocyanins are water-soluble red or purple pigments typically found in the epidermal or hypodermal cell vacuoles; the **hypodermis** is composed of one or more cell layers located beneath the



◘ Fig. 9.1 **a**–**c** Epidermal pavement cells on the adaxial surface of leaves from **a** box elder (*Acer negundo*), **b** trillium (*Trillium* sp.), and **c** the leopard plant (*Ligularia* sp.). Note the tight-fitting nature of the cells and the lack of stomata. Scale bar = 100 μm for all three panels. (**a**–**c** RR Wise)



◘ Fig. 9.1 **d** Cross-section of potato (*Solanum tuberosum*) leaf showing a single layer of epidermal cells on the abaxial and adaxial surfaces. Large vacuoles (V) can be seen in the adaxial surface, while the **spongy mesophyll** layer of the leaf contains numerous intercellular air spaces (IAS). A guard cell pair in the abaxial surface is indicated by the arrow. Scale bar = 50 μm. (RR Wise)

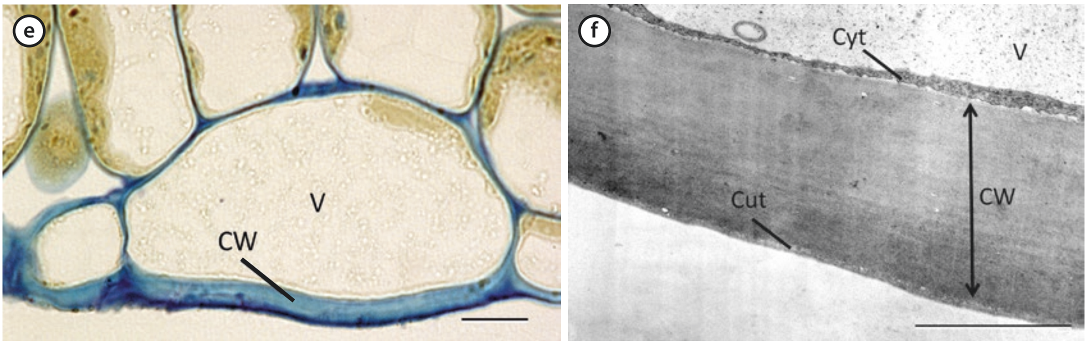


Fig. 9.1 **e**, **f** Abaxial epidermal cells of the lyre-leaved sand cress *Arabidopsis lyrata*). **e** LM indicating the large vacuole (V) and thick outer cell wall (CW). Scale bar = 50 µm in **f** TEM shows a thin cytoplasmic layer (Cyt) adjacent to the cell wall that is covered by a thin cuticle (Cut). Scale bar = 5 µm. (**e**, **f** RR Wise)

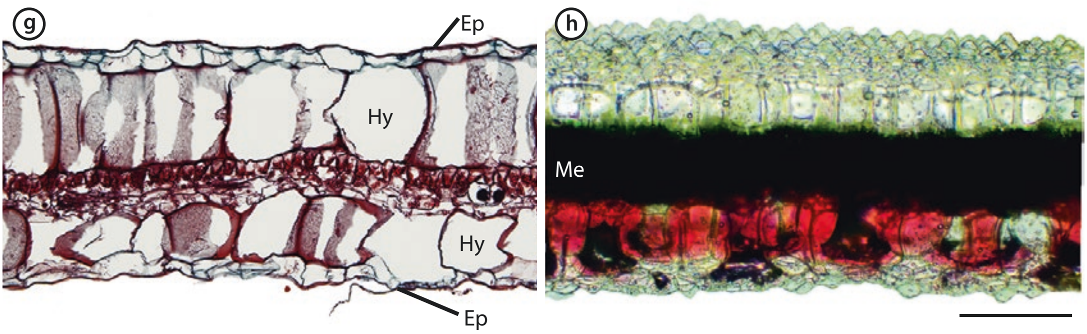
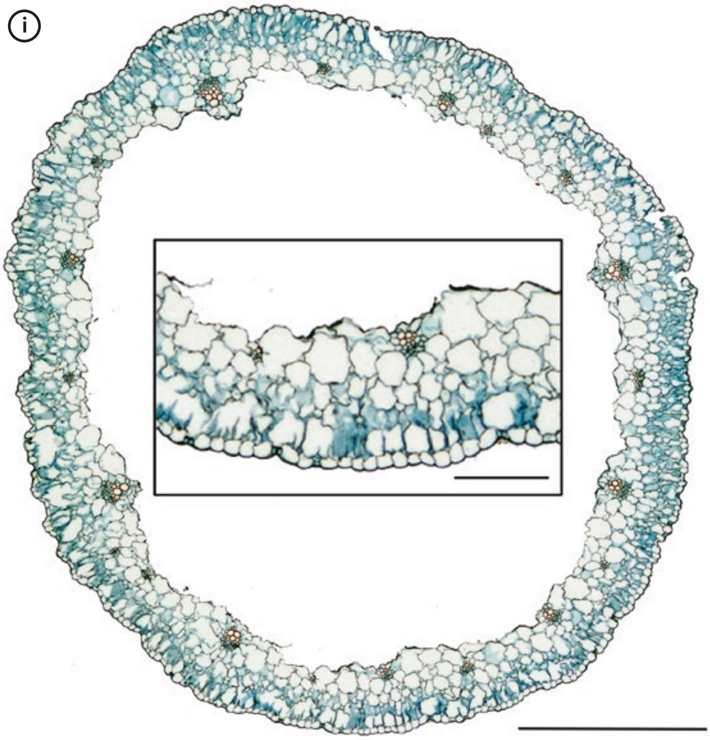


Fig. 9.1 **g**, **h** Cross-sections of begonia (*Begonia* spp.) leaves. These two species of begonia have slightly different leaf anatomies, but contain the same tissue layers—two outer layers of epidermis (Ep) with subjacent hypodermises (Hy) and a layer of mesophyll (Me) made of chlorenchyma. **g** Thin section of a fixed and stained leaf showing the five distinct tissue layers. **h** Thick section of a fresh leaf showing red anthocyanins in the abaxial hypodermis and chloroplasts in the mesophyll. A thick section must be used; otherwise the anthocyanin-containing cells would be cut open and lose their pigments. Scale bar = 50 µm for both photos. (**g**, **h** RR Wise)

epidermis but do not resemble the cortex or other ground tissue. Recall that plants use pigments for a variety of purposes and that a red pigment absorbs blue light and reflects red light. Anthocyanins in the adaxial epidermis of plants from high-light environments serve to reduce the amount of blue and ultraviolet light that penetrates to the leaf interior, thus limiting photoinhibition, a light-dependent loss of photosynthetic function. On the other hand, plants that have adapted to shaded environments, such as many species of *Begonia*, may have anthocyanins in the abaxial epidermis (Fig. 9.1g, h). Therefore, any red light that makes it through the leaf without being absorbed is reflected back up into the leaf to be absorbed by chlorophyll, increasing the efficiency of light capture for photosynthesis.

While most leaves have two surfaces, and thus two epidermises, tubular leaves, such as those found in onion, leeks, and garlic, are



■ **Fig. 9.1** **i** Tubular leaf of onion (*Allium cepa* sp.) shown in cross-section with a single, abaxial epidermis (scale bar = 1 mm). The inset shows the lack of an inner epidermal layer (0.25 mm). (RR Wise)

the exception to the rule and only have one epidermis on the abaxial outer surface (■ Fig. 9.1i). The adaxial leaf surface, in this instance, directly abuts the abaxis of a leaf to the interior and is composed of leaf mesophyll cells with no cuticle or other covering. Tubular leaves are considered in more detail in ► Sect. 12.3.

Although a single epidermal layer covers the leaves of most plants, a few species such as fig (*Ficus* sp.) possess multiple layers of epidermal cells (■ Fig. 9.1j). In the adaxial surface, four layers, two thin and two thick, are observed, and on the abaxial surface, there are three layers of increasing thickness. Such types of multiple epidermal cell layering occur primarily in tropical plants, in which the enlarged epidermal cells are adapted for water storage and also aid in light-scattering within the leaf.

Young stems of herbaceous plants have an epidermis similar to that found on leaves. Such stems have pavement epidermal cells, stomata, and a cuticle (■ Fig. 9.1k) and may have trichomes (not shown). The stomata control gas exchange for the chlorenchyma—chloroplast-containing parenchyma cells that underlie the epidermis. Subsequent secondary growth may replace the epidermis with a periderm as the stem matures (refer to ► Chaps. 11 and 16).

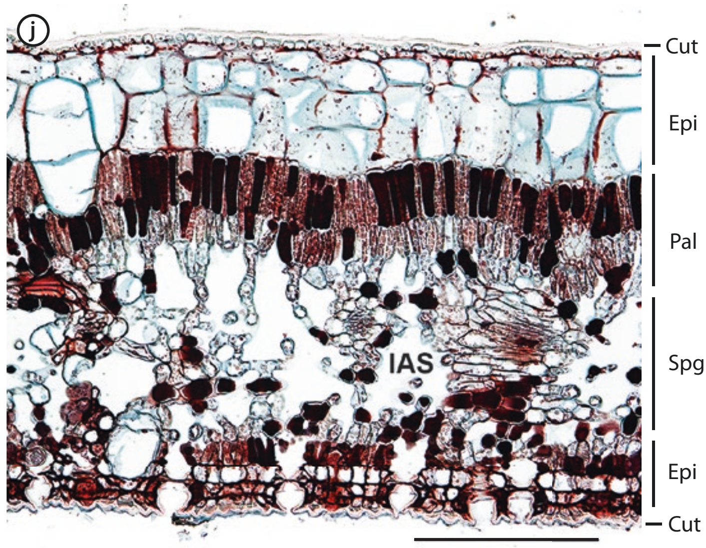


Fig. 9.1 **j** Rubber tree (*Ficus* sp.) leaf in cross-section showing a *multiple epidermis* (Epi) on both the adaxial and abaxial surfaces. Note the double layer of palisade (Pal) mesophyll cells that are stained red and the extensive array of loose, spongy tissue (Spg) with copious intercellular air spaces (IAS) and portions of vascular tissue. Even at this relatively low magnification, the thick cuticle (Cut) is apparent on both leaf surfaces. Scale bar = 50 µm. (RR Wise)

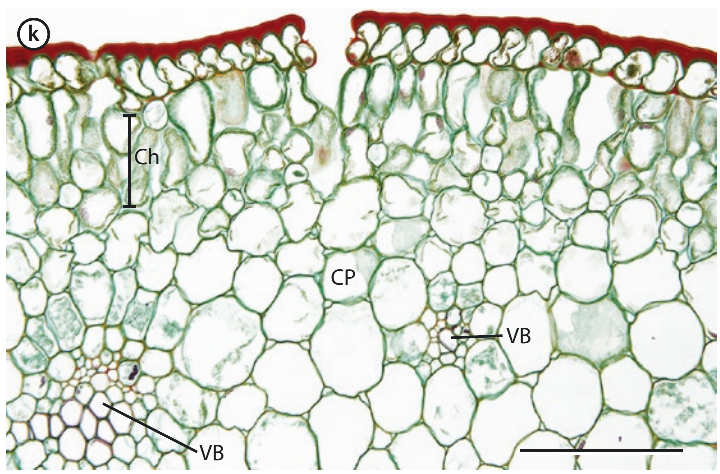


Fig. 9.1 **k** Castor bean (*Ricinus communis*) stem in cross-section showing a layer of pavement cells with stomata. The cuticle, stained in dark red, forms a continuous surface layer over the epidermis. Note also a layer of chlorenchyma (Ch) adjacent to the epidermis, cortical parenchyma (CP), and vascular bundles (VB). Scale bar = 100 µm. (RR Wise)

9.2 Stomata Are Dynamic Pores That Control Gas Exchange

Guard cells, and the **stomatal pore** they define, control the exchange of carbon dioxide, oxygen, and water vapor between the leaf and the atmosphere. Guard cells are a pair of specialized epidermal cells

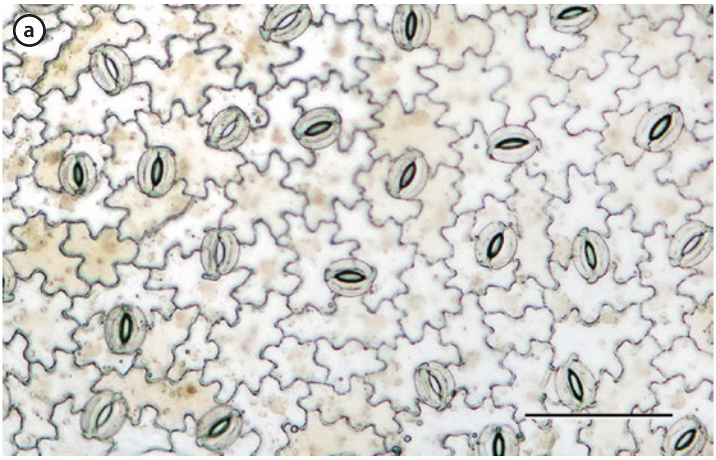


Fig. 9.2 **a** General view of guard cells and stomata in a surface view of the abaxial epidermis peel from purple cone flower (*Echinacea purpurea*). The guard cells appear as two kidney-shaped cells surrounding the stomatal pore through which gases CO_2, O_2, and H_2O exchange between the external environment and the internal leaf airspaces. Scale bar = 100 µm. (RR Wise)

that are distinguished from pavement cells in their ability to change shape. When guard cells take up water in the process described below, they swell due to increased turgor pressure and bend, thus opening a pore between the two cells and creating a hole in the leaf surface. That hole is called a *stoma* from the Greek word for "mouth" or *stoma* (pl. stomata). Technically speaking, a stoma is not a structure; it is the pore that results when guard cells fill with water, bend, and create an opening. However, it is a common practice to refer to a pair of guard cells as a "stoma." In this aspect, ◘ Fig. 9.2a shows 24 guard cell pairs or 24 stomata.

Stomatal density is the number of stomata per unit area of leaf surface, and it varies greatly among species, habitat, and plant organ. While most discussions of stomata focus exclusively on leaves, fruit such as bean pods, herbaceous stems, and floral sepals may also contain functional stomata.

Guard cells are distinguished from the pavement epidermal cells by their green color and unique shape (◘ Fig. 9.2b). Guard cells contain many chloroplasts that are fully capable of photosynthesis and typically contain photosynthetically derived starch grains (Sect. ► 3.5.10).

With the aid of transmission electron microscopy (◘ Fig. 9.2c), it can be seen that each guard cell contains a dense cytoplasm, numerous small organelles such as mitochondria, small vacuoles, and chloroplasts with a large number of starch grains. The number and size of the starch grains will vary considerably with the intensity of light and time of day. Note also the unevenly thickened cell walls with the cell wall facing the stomatal pore being the thickest.

Stomata act as dynamic barriers between the atmosphere and the leaf intercellular air spaces that permeate the spongy mesophyll layer common to most eudicot and monocot leaves (◘ Fig. 9.2d). Cuticular ledges made of wax deposits bound an

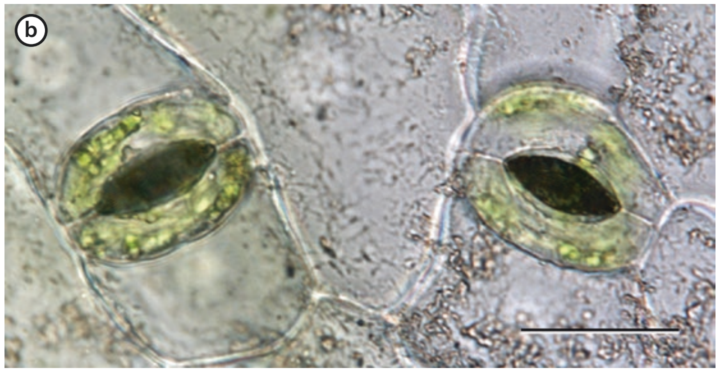
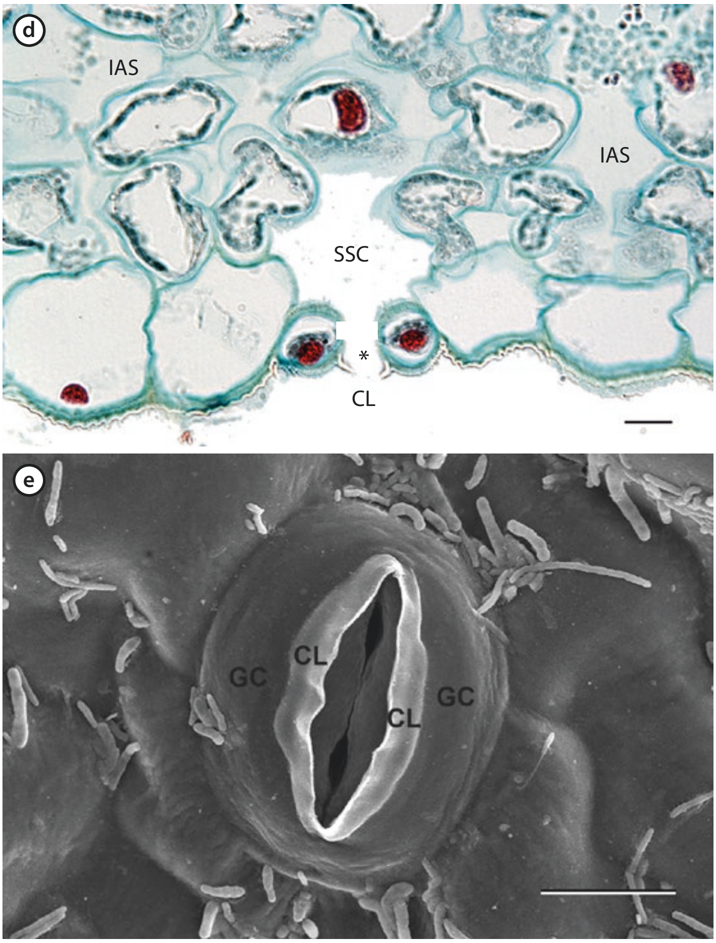


Fig. 9.2 **b** Two stomata from a hosta (*Hosta* sp.) abaxial leaf peel showing chloroplasts in the curved guard cells. The stoma appears dark due to an air bubble that was trapped in the opening during preparation. Chloroplasts can be viewed as green spherical structures within each guard cell. See below for discussion. Scale bar = 25 µm. (RR Wise)

Fig. 9.2 **c** Fine structure of guard cells from a cottonwood (*Populus deltoides*) leaf seen in paradermal section, i.e., parallel to the surface of the leaf. Chloroplasts are visible as bodies containing clusters of large, dark starch grains. M = mitochondrion, V = vacuole. Scale bar = 10 µm. (Crang and Vassilyev 2003)



■ **Fig. 9.2** **d** Flax (*Linum* sp.) leaf cross-section showing a guard cell pair, intercellular air spaces (IAS), substomatal cavity (SSC), antechamber (*), and cuticular ledges (CL). **e** Surface view of a ground ivy (*Glechoma hederacea*) leaf showing guard cells (GC) with cuticular ledges. Rod-shaped bacteria are present on the leaf surface. Scale bars = 10 µm in both panels. (**d**, **e** RR Wise)

area called the **antechamber** to the outside of the guard cells (■ Fig. 9.2d–f). The **cuticular ledges** and antechamber play a passive role in regulating water vapor loss from the leaf, while the daily opening and closing of the stomatal pore by the actions of the guard cells play an active role.

Guard cells are sensitive to light, atmospheric humidity, leaf water status, time of day, and the plant growth regulator **abscisic acid** (abbreviated as "ABA"). Stomata open in response to the proper combination of physiological and environmental cues. Stomata on most plants typically open at dawn and close in midafternoon, although there are many variations on that central theme. Opening is initiated by the transport of potassium ions into guard cells from adjacent subsidiary cells (■ Fig. 9.2g–j). This causes an accompanying influx of water via osmosis, which causes the guard cells to swell. Guard cell pairs are attached at the two ends. The thick inner guard cell walls (the walls facing the pore) resist stretching, while the thinner outer

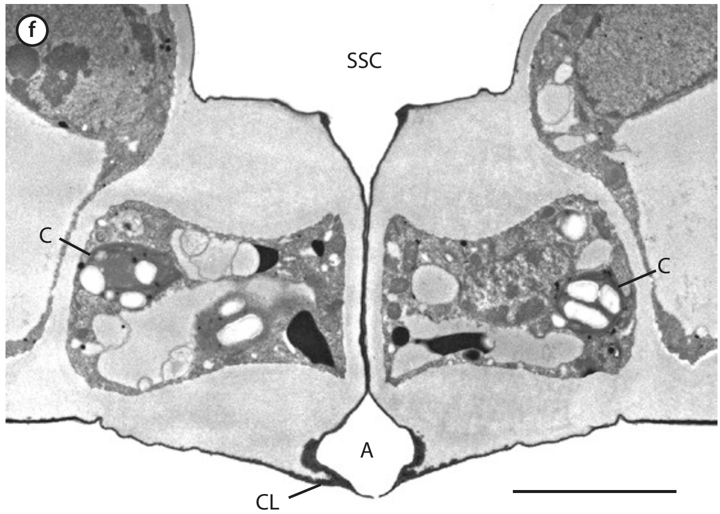


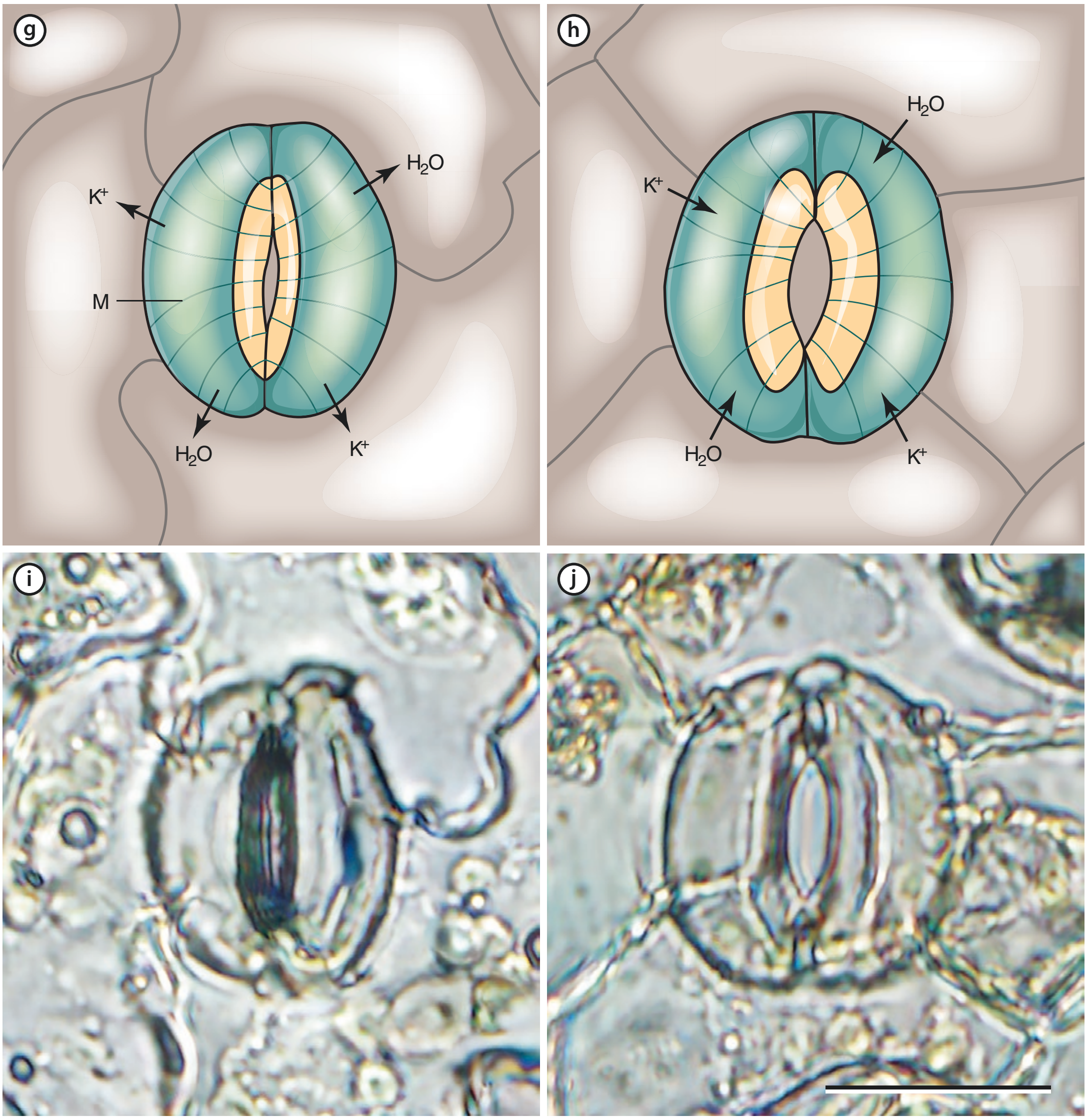
Fig. 9.2 **f** Transmission electron micrograph of a cotton (*Gossypium hirsutum*) leaf guard cell pair in cross-section. Two chloroplasts (C) are in the left guard cell, and one chloroplast with three starch granules can be seen in the right guard cell with both cells containing dense cytoplasm. A substomatal cavity (SSC) connects to the intercellular air spaces of the mesophyll. The compartment below the surface of the exterior wall is an antechamber (A) limited at the bottom by tapered cuticular ledges (CL). The walls are unevenly thickened and show especially on the inner surfaces the helicoidal pattern of cellulose microfibril orientation. A, antechamber; CL, cuticular ledge; SSC, substomatal cavity. Scale bar = 10 µm. (RR Wise)

walls expand. Cellulose microfibrils in the sidewalls wrap around the wall in a radial fashion, termed **radial micellation**. The combination of guard cell wall anatomy coupled with potassium-driven water uptake causes the guard cells to bend, and thus the stomatal pore enlarges. Stomatal opening can take place on a 5- to 10-minute time scale. The potassium slowly diffuses out, and by midafternoon most stomata have closed for the day.

9.3 Guard Cells and Subsidiary Cells Make Up the Stomatal Complex

While guard cells regulate the stomatal pore, they can only do so by exchanging potassium ions and water with adjacent epidermal pavement cells. Those cells are called **subsidiary cells** because they work closely with the guard cell and are therefore functionally distinct from the other epidermal pavement cells. The combination of the guard cells with associated subsidiary cells is called the **stomatal complex**.

The number and orientation of subsidiary cells vary. Thus, there are distinct and recognizable patterns of organization between guard cells and subsidiary cells. Dozens of morphological types, with numerous intermediates and subtypes, have been recognized by anatomists in the field of **stomography** (Baranova 1992). Such depth is beyond the scope of this book, and only a few examples



◘ **Fig. 9.2** **g**–**j** Stomatal anatomy as it drives opening. **g** and **h** are interpretations of the images of closed and open stomata from a purple coneflower (*Echinacea purpurea*) leaf shown in **i** and **j**. Closure is accompanied by an efflux of potassium and water. Opening is driven by the uptake of potassium and water. (**g**–**j** RR Wise)

will be discussed. However, in the hands of experts, detailed stomatographic studies may be of value for taxonomic purposes, for the identification of spices and drugs if only ground leaf powder is available for examination, and for reconstructions of past climatic conditions (McElwain and Steinthorsdottir 2017). It should be noted that two or more of the individual patterns given below, with intermediates, might be found in a single species. Eight of the major patterns are listed in ◘ Table 9.1, and illustrated in the following figures.

The cells of the stomatal complex differentiate during leaf development, and several pathways of stomatal development can be recognized. If guard cells and the neighboring subsidiary cells have a

Table 9.1 Eight major types of stomatal complexes

Type	Description
Floating	A single subsidiary cell surrounds the guard cell pair (Fig. 9.3a, b)
Paracytic (parallel-celled)	Two subsidiary cells border the stomatal complex with their long axes parallel with the long axes of the guard cell pair (Fig. 9.3c, d)
Diacytic (cross-celled)	Two subsidiary cells border the stomatal complex with common walls at right angles to the long axes of the guard cell pair (Fig. 9.3e, f)
Triacytic (three-celled)	Three subsidiary cells adjoin the guard cell pair (Fig. 9.3g, h)
Anisocytic (unequal-celled)	Three subsidiary cells adjoin the guard cell pair; one cell is considerably smaller or larger than the other two (Fig. 9.3 i, j)
Tetracytic (four-celled)	Four subsidiary cells adjoin the guard cell pair (Fig. 9.3k, l)
Anomocytic (irregular-celled)	Subsidiary cells are indistinct from the pavement cells (Fig. 9.3m, n)
Graminaceous	Found in the grass family—guard cells are dumbbell shaped and subsidiary cells lie parallel in a paracytic fashion (Fig. 9.3o, p)

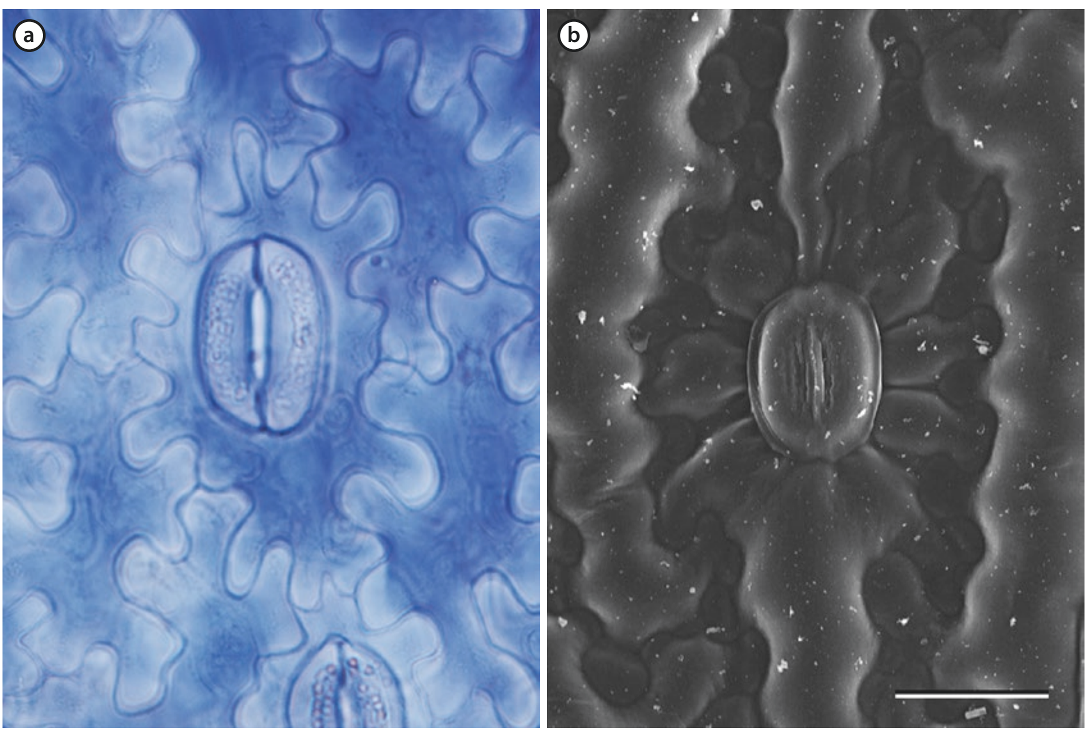
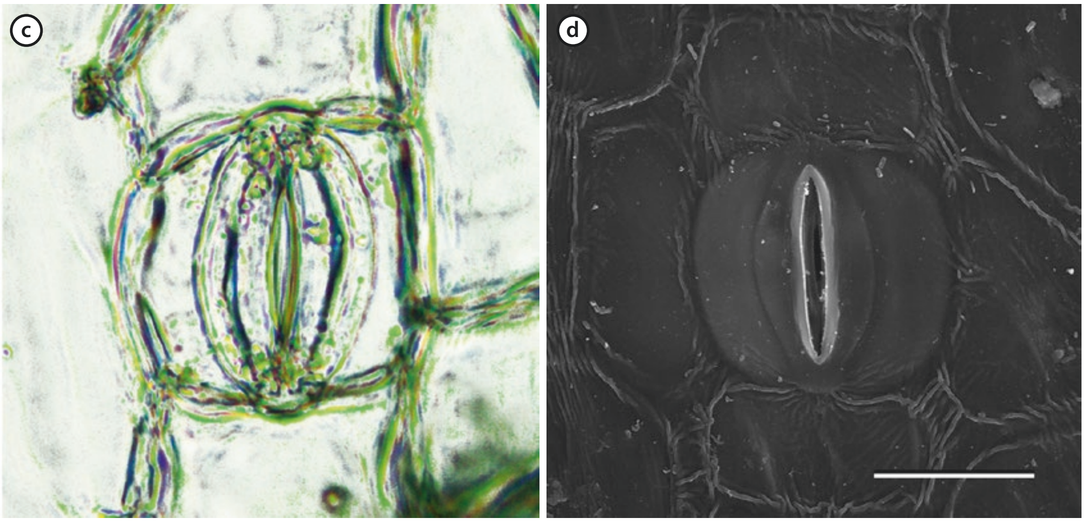
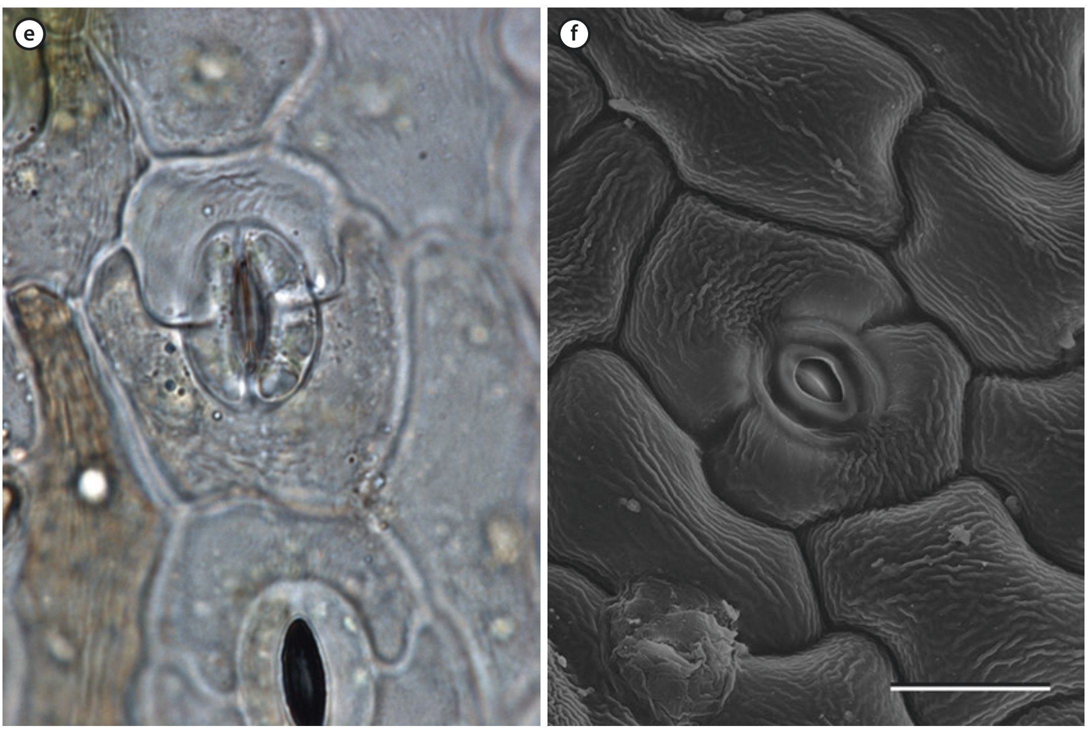


Fig. 9.3 **a**, **b** "Floating" stomata from a leaf of the fern *Anemia phyllitidis*. The two guard cells are completely surrounded by a single subsidiary cell. Scale bar = 50 µm. (**a**, **b** RR Wise)



■ **Fig. 9.3** **c**, **d** Paracytic stomatal complex from a water hyacinth (*Eichhornia crassipes*) leaf. Each guard cell pair is contacted by two subsidiary cells that run parallel to the guard cells. Scale bar = 25 µm. See also ■ Fig. 9.2b. (**c**, **d** RR Wise)



■ **Fig. 9.3** **e**, **f** Diacytic stomatal complexes from a Queen Anne's lace (*Daucus carota*) leaf. Each guard cell pair is contacted by two subsidiary cells; common walls are perpendicular to the long axis of the guard cell pair. Scale bar = 25 µm. (**e**, **f** RR Wise)

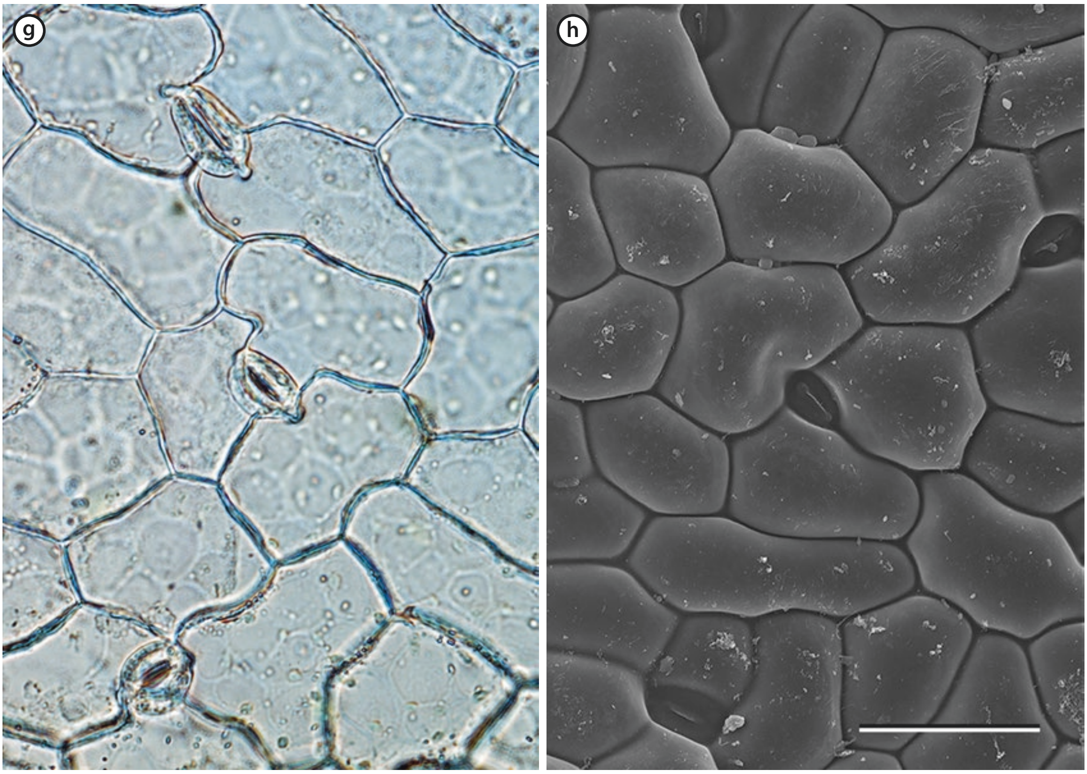


Fig. 9.3 **g**, **h** Triacytic stomatal complexes from a foxtail amaranth (*Amaranthus caudatus*) leaf. Each guard cell pair is contacted by three subsidiary cells Scale bar = 50 µm. (**g**, **h** RR Wise)

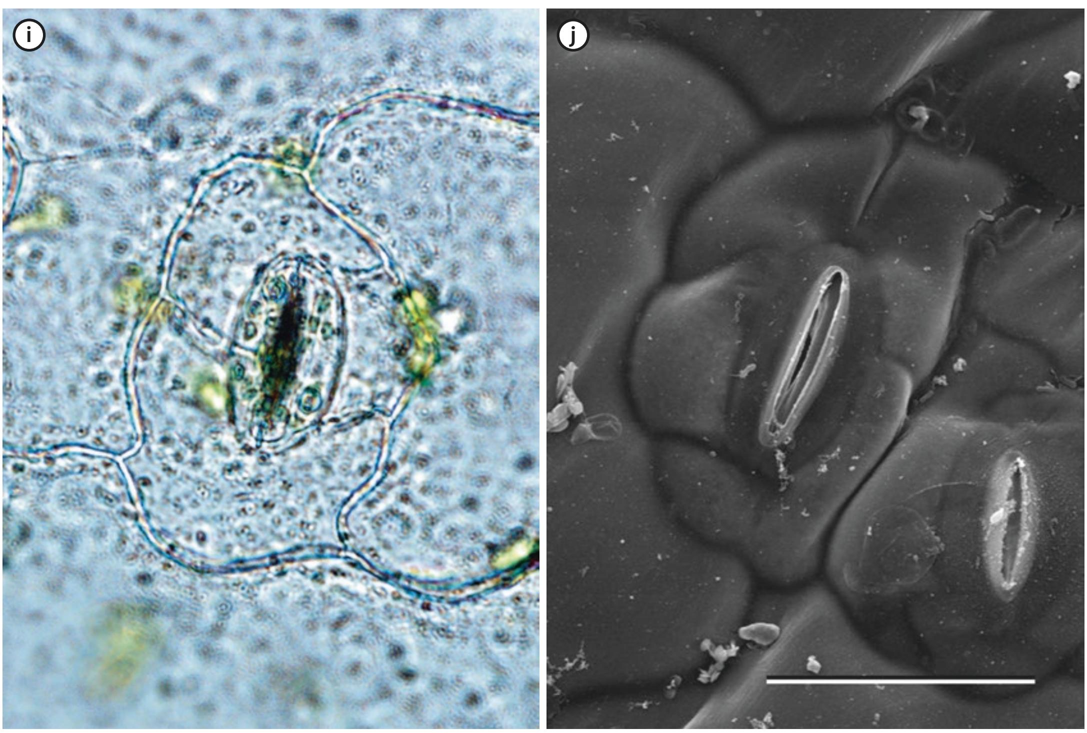


Fig. 9.3 **i**, **j** Anisocytic stomatal complexes from an autumn joy sedum (*Sedum spectabile*) leaf. Each guard cell pair is contacted by three subsidiary cells of significantly different sizes. Scale bar = 50 µm. (**i**, **j** RR Wise)

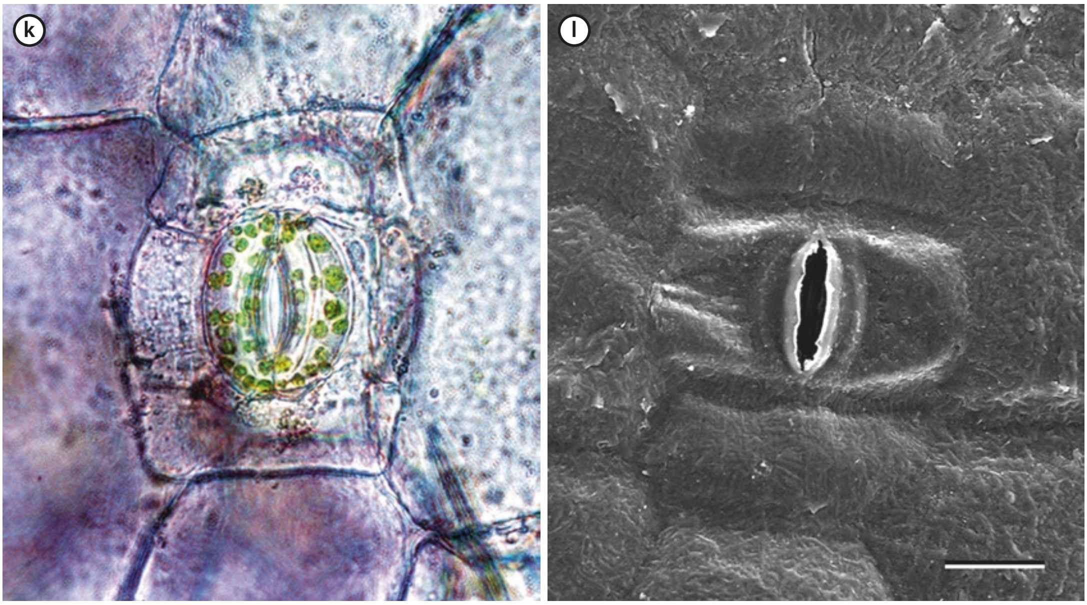


Fig. 9.3 **k**, **l** **Tetracytic stomatal** complexes from a Moses-in-a-boat (*Tradescantia spathacea*) leaf. Each guard cell pair is surrounded by four subsidiary cells. Note the presence of purple anthocyanins in pavement epidermal cells to the left. Scale bar = 25 µm. (**k**, **l** RR Wise)

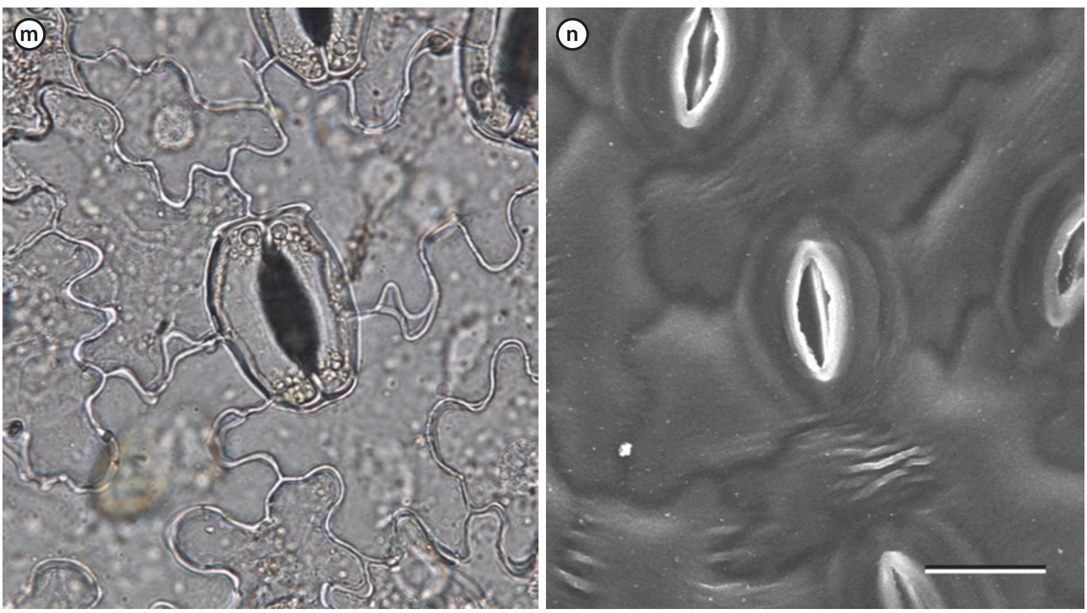


Fig. 9.3 **m**, **n** Anomocytic stomatal complexes from a peony (*Paeonia* sp.) leaf. The subsidiary cells are variable in number and are indistinguishable from the pavement cells. Scale bar = 25 µm. (**m**, **n** RR Wise)

common origin, then the development is referred to as **mesogenous**. If one or more, but not all of the, neighboring cells are of common origin to the guard cells, the relationship is designated as **mesoperigenous**. Finally, if there is no common development between the neighboring and subsidiary cells with the guard cells, the development is referred to as **perigenous**.

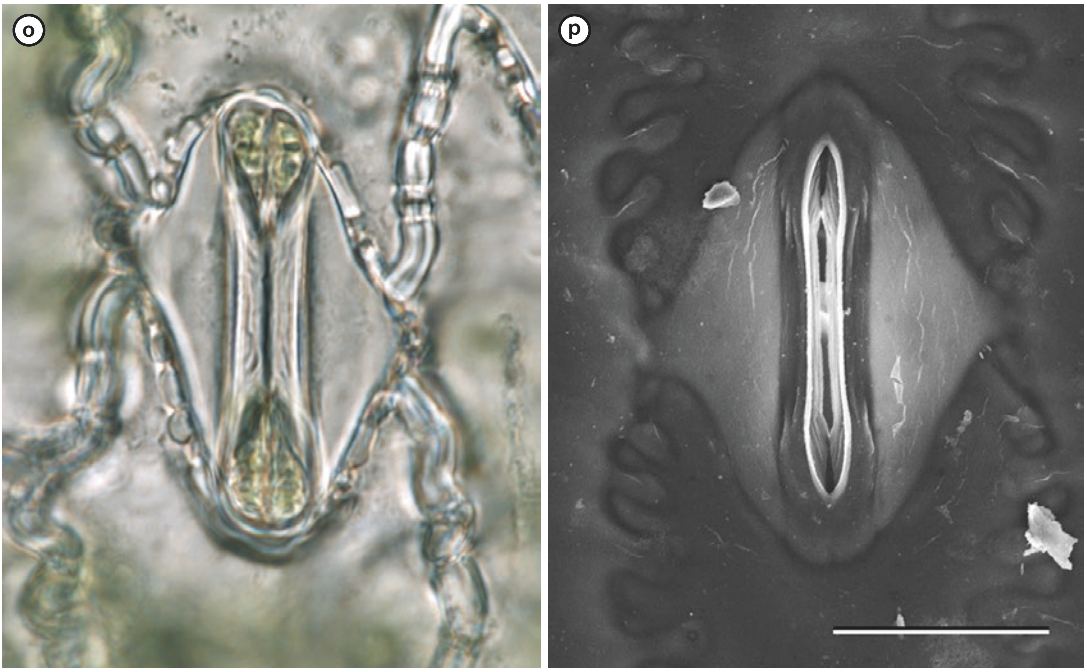


Fig. 9.3 **o**, **p** Graminaceous stomatal complexes from a maize (*Zea mays*) leaf. The guard cells are long with bulbous ends. The subsidiary cells are triangular shaped and, by definition, are in a paracytic arrangement. Scale bar = 25 µm. (**o**, **p** RR Wise)

Box 9.1 Control of Stomatal Patterning

The distribution of stomatal complexes across the leaf surface is under strict genetic control. Stomatal patterning follows the "one-cell spacing rule" in which stomatal complexes almost never touch one another. Proper density and spacing of stomata is controlled by cell-to-cell signaling between cells at the shoot apical meristem, specifically in the protoderm.

Steps in the pathway: A single protodermal cell is triggered to differentiate into a meristemoid mother cell (MCC). The MCC divides, and one daughter cell eventually develops into a guard mother cell (GCM) and then the two guard cells (GC). The other MCC daughter cell produces the 2–4 subsidiary cells. Thus, a single MCC yields all the cells of the mature stomatal complex. This developmental pathway is under the control of several gene products.

Control of spacing: The signals that trigger a protodermal cell to enter the MCC to GC developmental pathway come from the underlying mesophyll cells in the shoot apical meristem. However, once an individual MCC is initiated, it immediately produces chemical signals (EPF gene products) that inhibit neighboring protoderm cells from becoming MCCs. Hence, the one-cell spacing rule is enforced, and the spatial pattern of stomatal distribution is dictated.

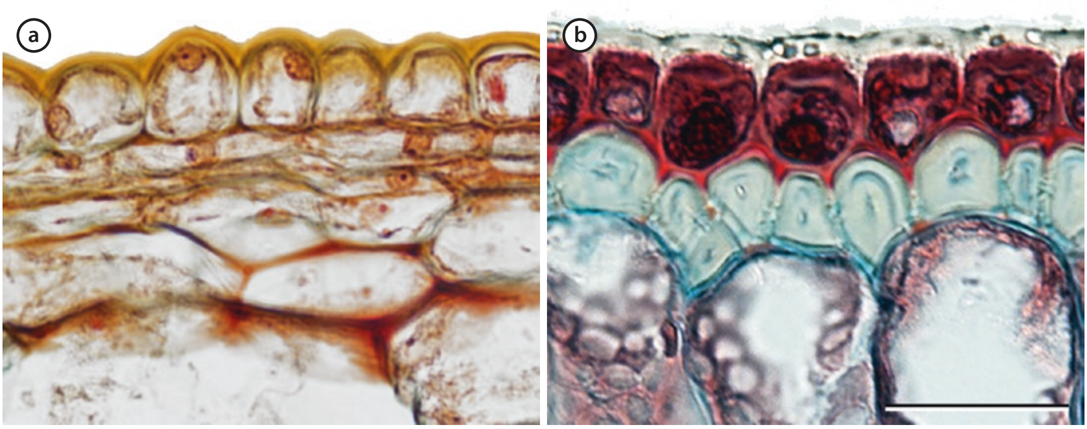
Reference: Torii (2015).

9.4 The Cuticular Membrane Protects the Plant Surface

The **cuticular membrane** (a.k.a. cuticle) is a coating of wax and oil that covers the epidermis of the aerial portions of a plant—the leaf, stem, and fruit (◘ Fig. 9.4a, b; several examples of stem cuticles are shown in ► Chap. 11). Root cells are incapable of synthesizing cuticular components (Jeffree 2006). [Note: the cuticular membrane should not be confused with the cell membrane (► Sect. 3.3)]. Evolution of the cuticle was a major step in the colonization of land by plants because it prevents desiccation of those portions of the plant exposed to the air. The cuticle may also inhibit the attachment of fungal and bacterial pathogens, help shed water, and block the passage of certain wavelengths of ultraviolet radiation (Mulroy 1979). Leaves or fruits with a thick coating of waxes are said to be **glaucous** (Latin for "blueish gray"), such as can be seen on plums and grapes.

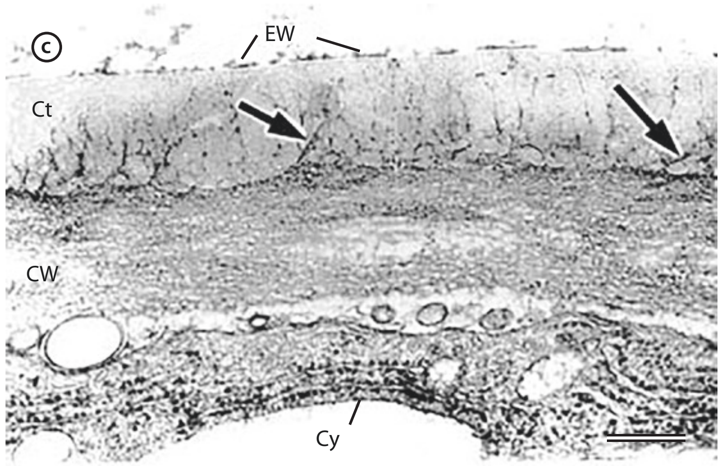
Cutins are the main component of the cuticle and are found in practically every plant cuticle. In terms of chemical composition, cutins are hydrophobic polyesters containing 16 to 18 carbons (C_{16}–C_{18}). **Cutan** differs chemically from cutin in that it is a hydrophobic hydrocarbon, not a polyester, and composed of long-chain (up to C_{33}) polymers. Cutan typically is a minor component of most cuticles but predominates in drought-adapted plants and fossil plants (Boom et al. 2005). The cuticle is also impregnated with and covered by **epicuticular waxes,** a class of polymeric long-chained (C_{29} to C_{33}) hydrocarbons (Jetter et al. 2006). The components of the cuticle are synthesized by epidermal cells and secreted to the cell surface, resulting in a layered and intermingled ultrastructure (Jeffree 2006) with quite variable characteristics (◘ Fig. 9.4c, Jetter and Riederer 2016).

Epicuticular waxes often vary greatly in structure, distribution, and frequency depending on the species, plant organ, and habitat. They may appear as droplets, plates, or fine strands on leaf surfaces (◘ Fig. 9.4d–i). Each of these different configurations affects the physical properties of the cuticle.



◘ **Fig. 9.4** **a**, **b** Cuticles on **a** tomato (*Solanum lycopersicum*) fruit and **b** China fir (*Cunninghamia lanceolata*) leaf. Scale bar in **b** = 25 µm and applies to both panels. (**a**, **b** RR Wise)

Frequently, the deposition of the cuticle and cuticular waxes is not uniform, and ridges may be observed extending over the surface of pavement epidermal cells in an orderly arrangement (◘ Fig. 9.4j, k). Such wax-coated ridges are thought to play a role in the light-scattering, water-shedding, and pathogen-inhibiting properties of cuticles mentioned above.



◘ **Fig. 9.4** **c** Transmission electron micrograph of a willow (*Salix fragilis*) leaf epidermal cell showing a thick cuticle (Ct), primary cell wall (CW), and cytoplasm (Cy). The cuticle is observed as a thick layer, in which there are a large number of branching or dendritic channels (*arrows*). Small traces of epicuticular waxes (EW) can be observed on the surface of the cuticle. Scale bar = 1 µm. (Crang and Vassilyev 2003)

Box 9.2 From Surf Boards to Candy: Applications of Epicuticular Waxes

Epicuticular waxes abound all around you. The blue color of the blue spruce (*Picea pungens*) needles results from the optical properties of wax. Epicuticular waxes even give grapes and plums a dull sheen. A very popular commercial application of waxes originates in the wax palm (*Copernicia prunifera*). Carnauba wax is extracted from wax palm leaves. Carnauba wax is used in a variety of products including the coatings of many candies, dental floss, and even automobile and surfboard wax.

Scientists have experimented with ways to improve the use of waxes to preserve fruits. Jo et al. (2014) coated apples with carnauba wax mixed with lemongrass essential oil that provides water holding and antimicrobial protection, respectively. Apples that were coated with the mixture lost less water than non-treated apples. The treated apples had fewer microorganisms on surfaces relative to non-treated apples. Perhaps we shall see more essential oils used with wax to help to increase the shelf life of fruits and vegetables in the future.

Reference: Jo et al. (2014)

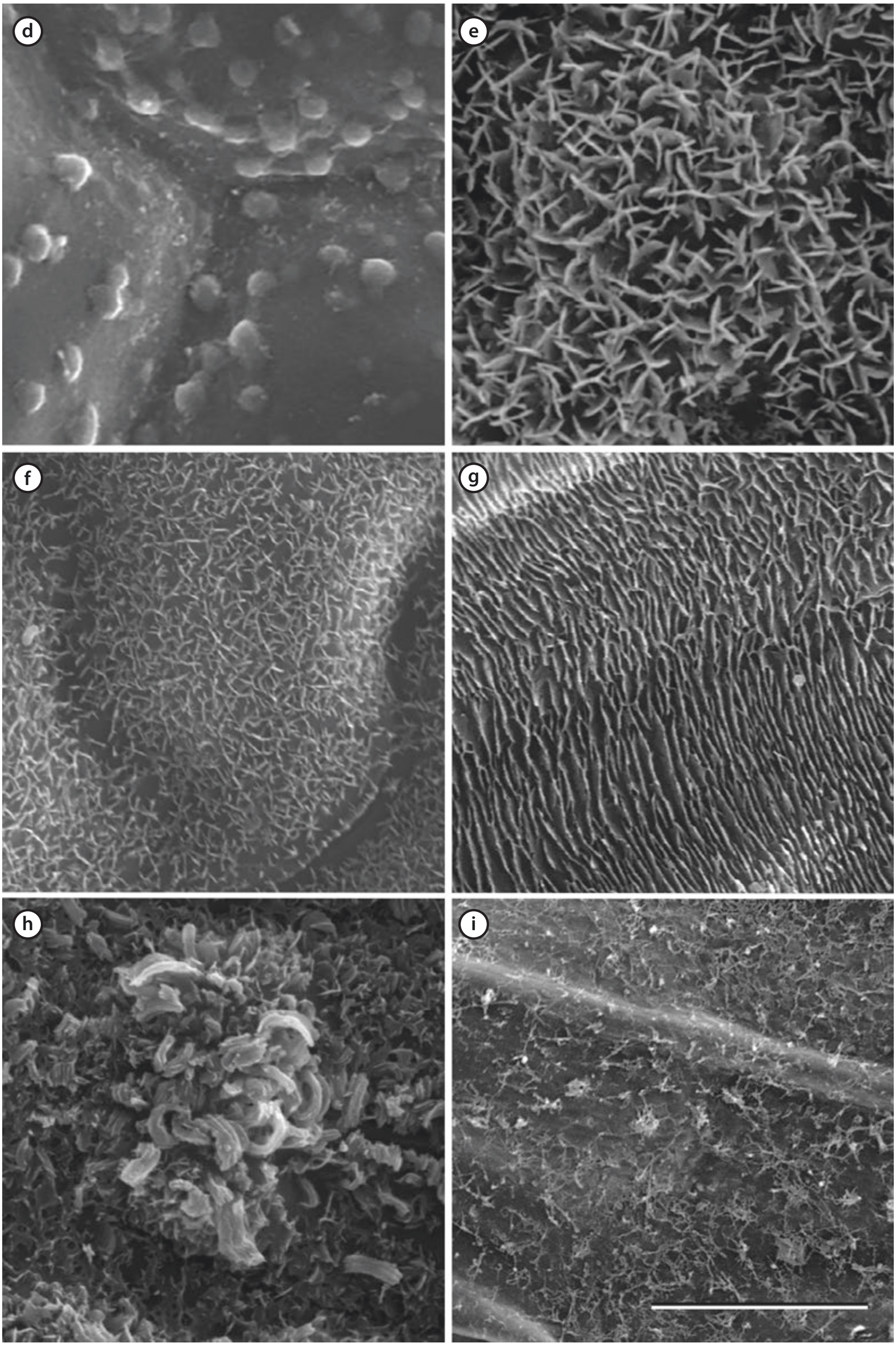


Fig. 9.4 **d**–**i** Waxes on surfaces of leaves from **d** broadleaf plantain (*Plantago major*), **e** Kentucky coffee tree (*Gymnocladus dioicus*), **f** soybean (*Glycine max*), **g** day lily (*Hemerocallis* sp.), **h** big blue stem grass (*Andropogon gerardii*), and **i** daffodil (*Narcissus* sp.). Scale bar = 20 μm for all micrographs. (**d**–**i** RR Wise)

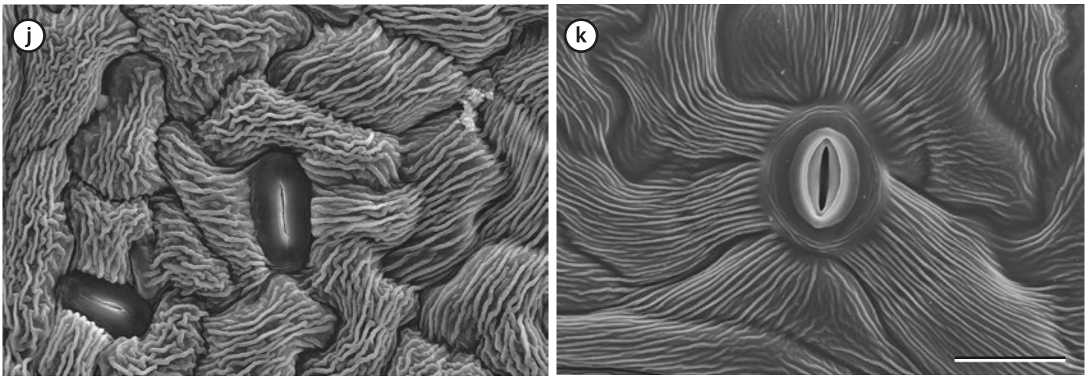


Fig. 9.4 **j**, **k** Irregular cuticular thickenings form ridges on the leaves of **j** horse chestnut (*Aesculus hippocastanum*) and **k** mock orange (*Philadelphus coronarius*). Scale bar in **k** = 25 µm and applies to both panels. (**j**, **k** RR Wise)

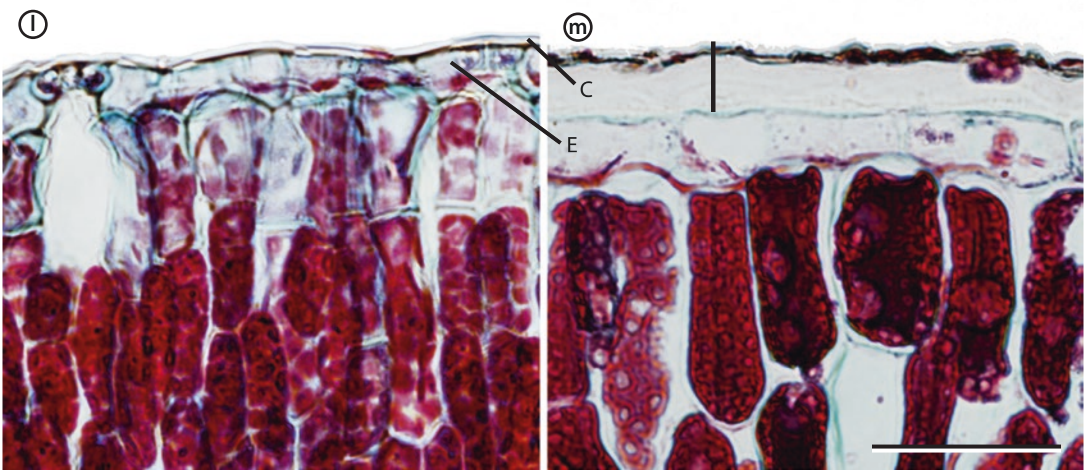


Fig. 9.4 **l**, **m** Cuticles on an aquatic leaf and an evergreen leaf. **l** The cuticle (C) on the aquatic water lily (*Nymphaea odorata*) leaf is less than 1 µm thick. It appears as a clear zone to the exterior of the dark epidermal (E) cell wall. **m** The evergreen kinnikinnick (*Arctostaphylos uva-ursi*) leaf cuticle is about 9–10 µm thick. The dark deposits on the surface of the cuticle are epicuticular waxes. Scale bar in **m** = 25 µm and applies to both panels. (**l**, **m** RR Wise)

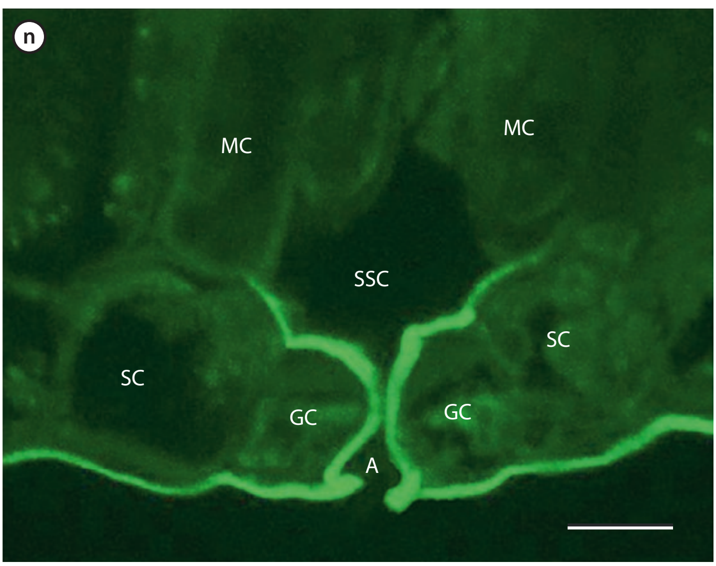
9

Plant roots take up water from the soil. That water travels through the xylem to the aboveground parts and is lost to the atmosphere via stomata in the process of transpiration. Stomatal control over transpiration can only be effective if there is no other pathway for water to escape the plant. A major role of the epidermis, therefore, is to prevent non-stomatal water loss, or **cuticular transpiration**. Cuticular transpiration is generally higher in fruit than in leaves, varies greatly between and among species and environmental conditions, and is almost always a very small percentage of stomatal transpiration (Burghardt and Riederer 2006; Kerstiens 1996). Not only does the cuticle block the loss of water; it also is a barrier to the uptake of water-soluble herbicides. Therefore, most herbicide formulations contain surfactants, detergent-like molecules that increase the "wettability" of a leaf and allow for the penetration of the active herbicidal compound across the cuticle and into the leaf.

Cuticle thickness varies by species and habitat, indicating that cuticular transpiration, although low, must be controlled in response to the water availability. The lower, abaxial epidermis of floating leaves (**hydrophytes**) is typically covered with a mucilaginous layer of pectic compounds, whereas the upper, adaxial surface has a thin cuticle (◘ Fig. 9.4l). Leaves of plants growing in deep shade (not shown) tend to have relatively thin walls and cuticles, as water stress is reduced in shaded environments. Alternatively, in plants growing in dry habitats (**xerophytes**), the epidermal cell wall, cuticle, and wax layers are usually quite thick (◘ Fig. 9.4m).

Only epidermal cells are capable of synthesizing components of the cuticular layer, but they can do so to both the exterior and interior of the leaf resulting in and external cuticle and, in some plants, an **internal cuticle** (◘ Fig. 9.4n). The internal cuticle allows epidermal cells to control water loss from the surface of the epidermal cells that are exposed to the interior of the leaf and plays a role in whole leaf control of transpiration (Wullschleger and Oosterhuis 1989).

Although in most cases the cuticle forms a continuous layer over the epidermal cells, in some rare situations, such as in some **secretory cells**, small openings are formed. This situation is often characteristic of digestive glands from carnivorous plants (Vassilyev 1988). ◘ Figure 9.4o shows the outer cell wall of a digestive gland secretory cell from the Portuguese sundew. Extensions of the cell wall may provide branching into a series of channels through which a mucopolysaccharide called "slime" is secreted to the surface of the leaf through the opening in the cuticle. The slime traps the insects and contains the digestive enzymes used for breaking down the prey.



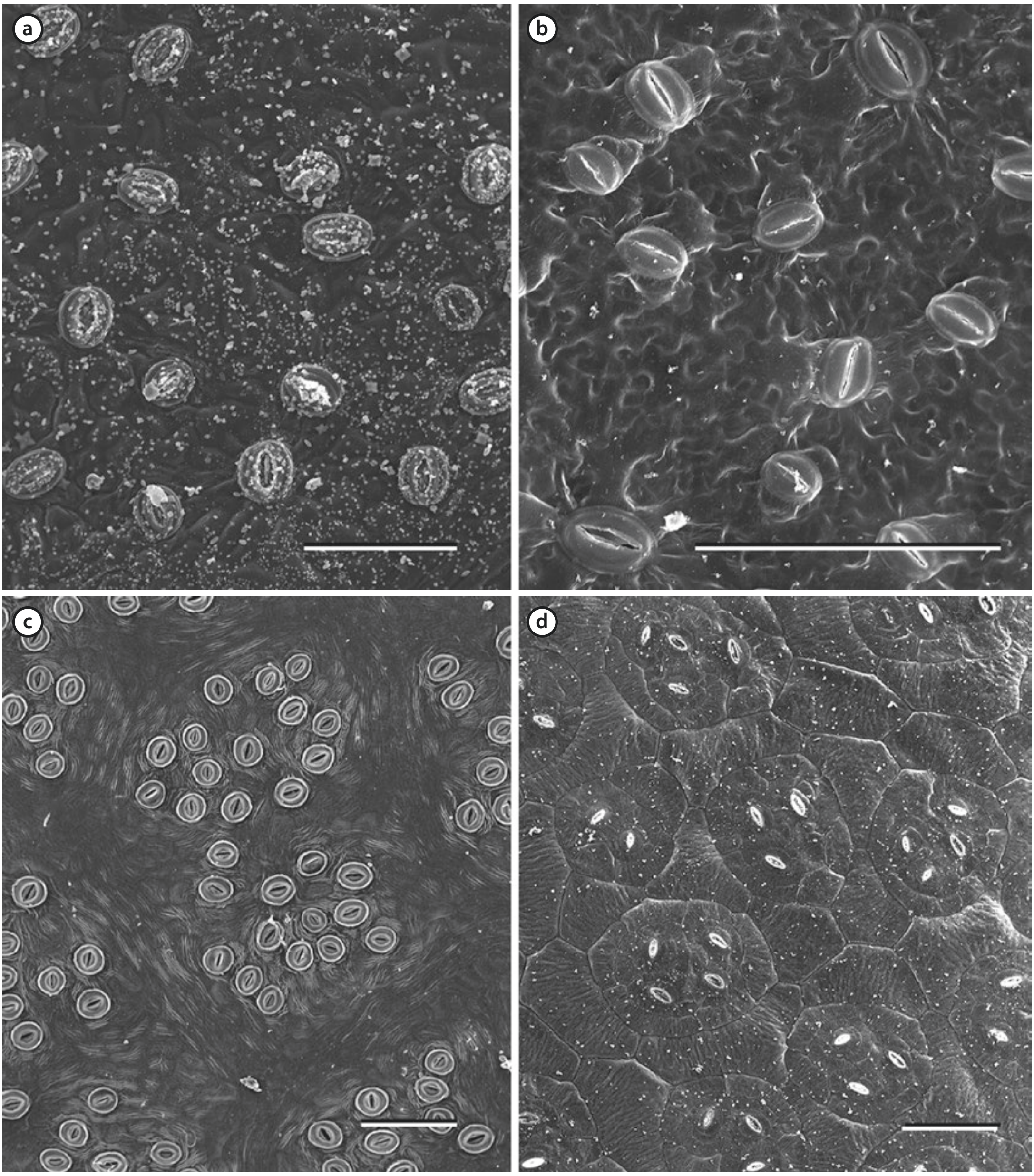
◘ **Fig. 9.4** **n** Confocal laser scanning micrograph of a cotton (*Gossypium hirsutum*) guard cell pair seen in cross-section. The specimen has been treated with a stain that only fluoresces when in contact with a hydrophobic molecule to emphasize the external and internal cuticle. Thus, the cuticle can be seen to cover the exterior of the leaf, make up the cuticular ledges, and extend to the interior of the substomal cavity to the point where the epidermal subsidiary cell meets a leaf mesophyll cell. A, antechamber; GC, guard cells; MC, mesophyll cells; SC, subsidiary cells; SSC, substomatal cavity. Scale bar = 10 μm. (RR Wise)

Fig. 9.4 **o** Surface of a Portuguese sundew (*Drosophyllum lusitanicum*) digestive gland secretory cell. CW, cell wall; PM, plasma membrane. The cuticle is dark in this transmission electron micrograph, and an opening in the cuticle is indicated by the arrow. Scale bar = 1 µm. (Image courtesy of AE Vassilyev, Komarov Botanical Institute, St. Petersburg, Russia)

9.5 Stomata Vary in Distribution and Depth

All leaves, with the exception of spines, have stomata, but their distribution, density, and relative number on each surface vary greatly. Floating leaves, for obvious reasons, only have stomata on the adaxial, or upper, surface. This distribution is called **epistomatic**. Leaves with stomata on only the abaxial surface are called **hypostomatic**, and examples include many eudicots such as Oleander (*Nerium oleander*). **Amphistomatic** leaves have stomata on both the adaxial and abaxial surfaces. Monocot leaves are often oriented in a vertical fashion; thus there is no "lower" or "upper" surface, and, not surprisingly, monocots typically are amphistomatic with an equal distribution of stomata on abaxial and adaxial surfaces. Even though eudicots can also be amphistomatic, there may not be the same number on each surface. Cotton (*Gossypium hirsutum*), for instance, has the majority of the stomata on the leaf abaxis. This is thought to take advantage of the higher humidity found in the lower, and shaded, surface of the eudicot leaf. Unequal distribution with more stomata on the abaxis is the predominant form in amphistomatic eudicots.

Stomata open onto a substomatal cavity, an air-filled space inside the leaf. Therefore, stomatal placement and distribution must be in concert with the underlying structure of the leaf mesophyll tissue. Many plants show a seemingly random pattern of stomatal distribution across their leaves, or at least no recognizable pattern is obvious (Fig. 9.5a, b). Hawthorn and begonia are known for their clustered stomata, in which groups of stomata are surrounded by a field of pavement cells (Fig. 9.5c, d). Plants with parallel vasculature, for example, conifer needles and many monocot leaves, typically have stomata arranged in linear rows (Fig. 9.5e, f).



◘ **Fig. 9.5** **a**–**f** Random stomatal distribution on **a** peach (*Prunus persica*) and **b** potato (*Solanum tuberosum*) leaves; clustered stomata on **c** thornless cockspur hawthorn (*Crataegus crusgalli*) and **d** begonia (*Begonia* sp.) leaves; and linear stomatal distribution on **e** white pine (*Pinus strobus*) and **f** foxtail (*Setaria viridis*) leaves. Scale bar in each panel = 100 µm. (**a**–**f** RR Wise)

The diffusion of water vapor from the leaf interior to the atmosphere (e.g., transpiration) is strongly influenced by the size of the stomatal opening (discussed above in ► Sect. 9.2) and the length of the diffusional pathway between the stomatal pore and the bulk atmosphere. The longer the pathway, the greater the resistance to water vapor loss. In some species, guard cells are sunken below the surface (◘ Fig. 9.5g, h). Trichomes (discussed below in ► Sect. 9.6) also increase the length of the diffusional pathway by trapping air against the leaf surface, thereby reducing water loss.

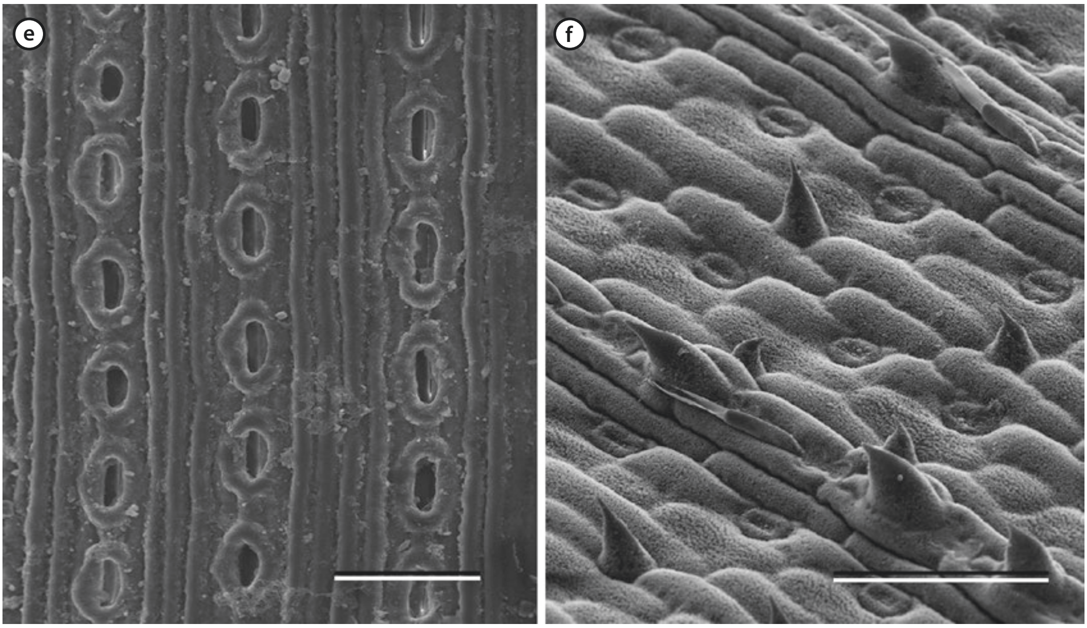


Fig. 9.5 (continued)

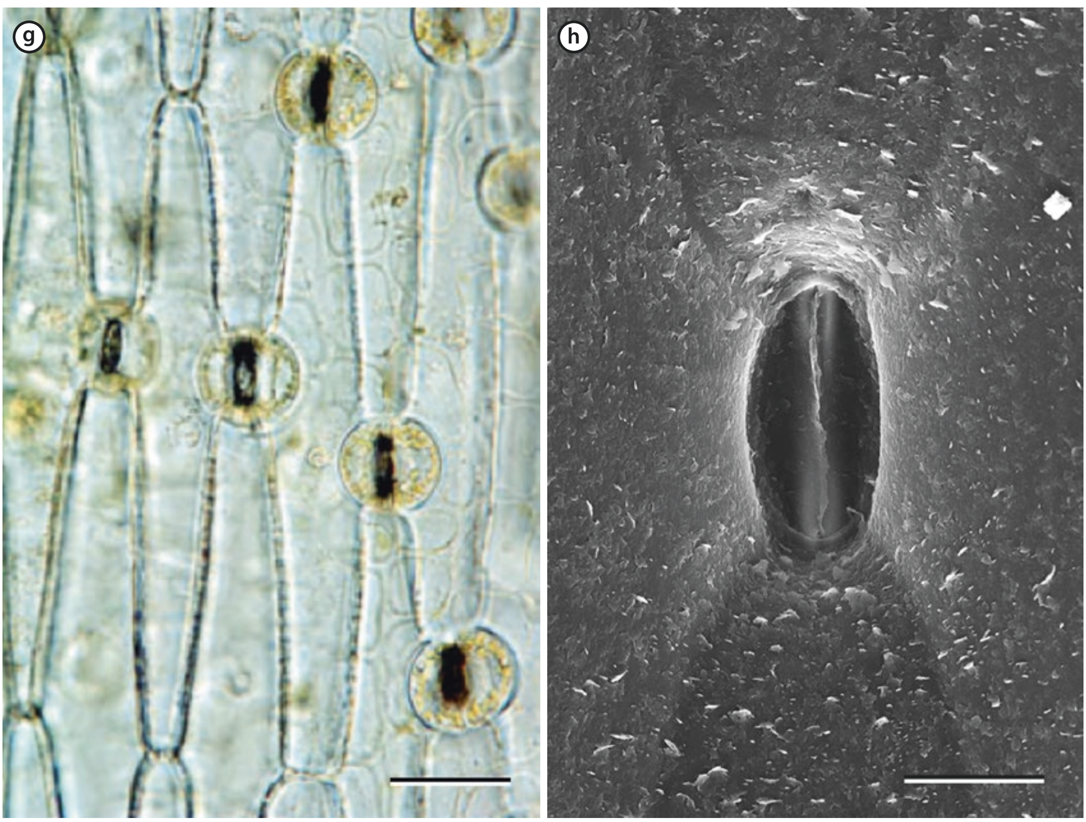


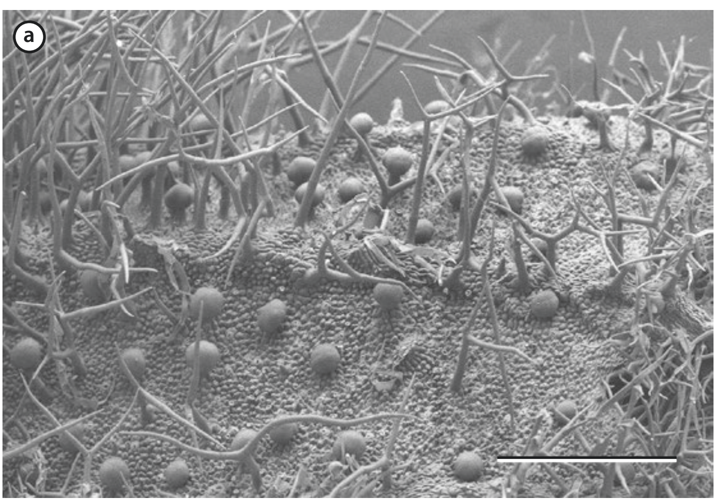
Fig. 9.5 **g**, **h Sunken stomata** on an iris (*Iris domestica* sp.) leaf. Subsidiary cells can be seen in the left panel and are in a paracytic arrangement. Scale bars = 50 µm on the left and 10 µm on the right. (**g**, **h** RR Wise)

9.6 Trichomes Protect the Leaf from Biotic and Abiotic Stresses

Trichomes are unicellular or multicellular extensions of the epidermis found on leaves and stems of many ferns, gymnosperms, and angiosperms. When found in abundance, they constitute a character called **pubescence**, meaning covered with a fine fur or hairs. Trichomes may be divided into two main types, nonglandular (this section) and glandular (► Sect. 9.7). Many species have both types of trichomes on the same leaf surface, as seen in ◘ Fig. 9.6a.

As a part of the epidermis, trichomes play crucial roles at the interface between plant and the environment. First, the presence of trichomes raises the humidity of the air directly in contact with the leaf surface by increasing the **boundary layer resistance** to water vapor movement from the leaf to the atmosphere. This has a major impact on rates of transpiration of plants in arid environments. For example, the European olive, a hypostomatic Mediterranean species, has a thick layer of peltate trichomes on the leaf abaxis (◘ Fig. 9.6t–v) that leads to a reduction in water loss via transpiration. Second, trichomes can reduce the amount of light entering the leaf mesophyll by reflecting and scattering incoming solar irradiance. Plants in high-light environments often have a dense covering of trichomes; many bromeliads (e.g., *Tillandsia* sp.) are a good example (◘ Fig. 9.6r, s). Third, trichomes can present both mechanical and chemical barriers to herbivorous attack. In combination with surface waxes and thicker outer cell walls, the feeding success of smaller insects can be deterred by the structural impediments of nonglandular trichomes. The chemical defenses of trichomes will be discussed in ► Sect. 9.7, Glandular Trichomes.

The architecture of nonglandular trichomes varies greatly among different plant taxa and organs. The simpler trichomes are



◘ **Fig. 9.6** **a** Nonglandular (tall, branched structures) and glandular (short round structures) trichomes on the surface of a Russian sage (*Perovskia atriplicifolia*) leaf. Scale bar = 500 µm. (RR Wise)

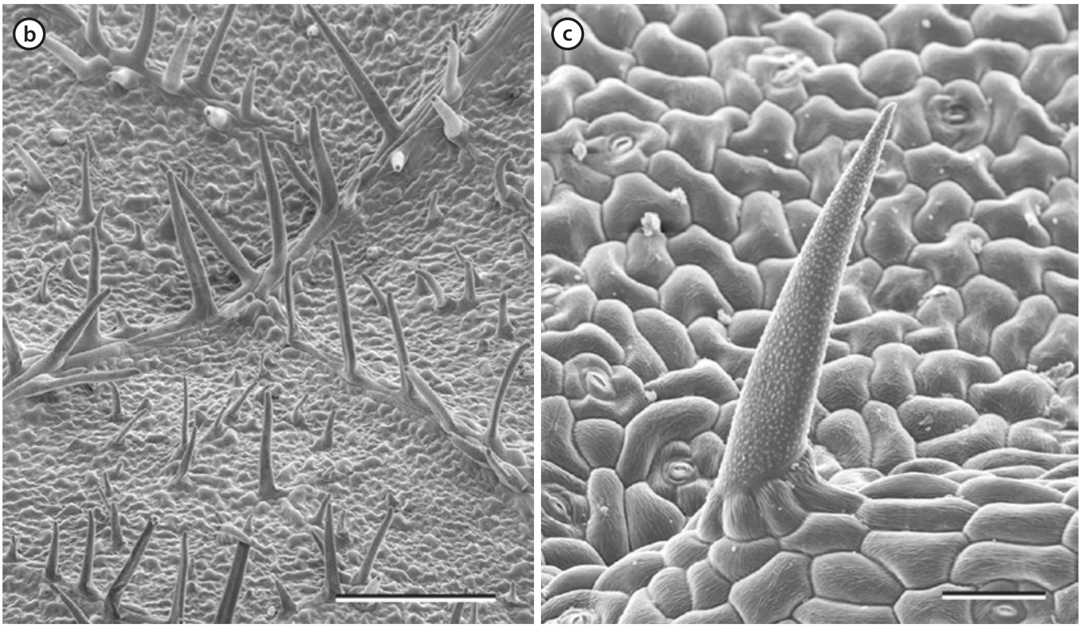


Fig. 9.6 **b**, **c** Unicellular, unbranched trichomes on leaves of **b** false Solomon's seal (*Maianthemum racemosum*) and **c** carrot (*Daucus carota*). Scale bars = 500 μm for **b** and 100 μm for **c**. (**b**, **c** RR Wise)

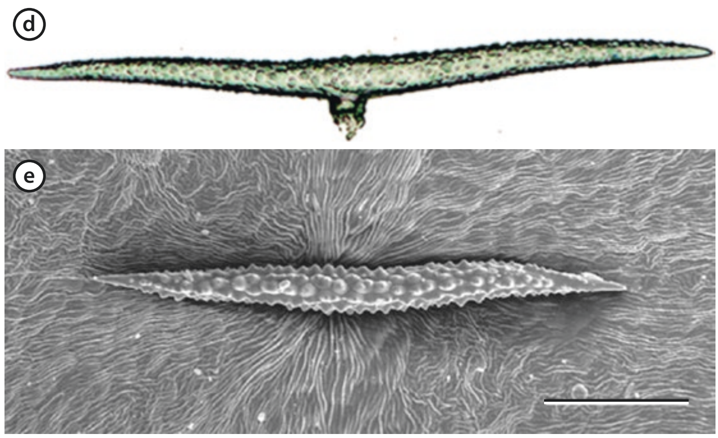


Fig. 9.6 **d**, **e** Unicellular, needle-shaped, two-armed (dolabrate) trichome from the leaf of dogwood (*Cornus* sp., Cornaceae) as seen with **d** light microscopy and **e** scanning electron microscopy. The surface bumps are calcium oxalate deposits. Scale bar = 100 μm for both panels. (**d**, **e** RR Wise)

classified based on three characters: (*1*) number of cells, unicellular vs. multicellular; (*2*) branching, unbranched or branched; and *3*) the number of rows of cells: uniseriate, one row of cells; biseriate, two; or multiseriate, many (Fig. 9.6b–k). Those trichomes with a more complicated structure, all of which are multicellular, are in categories called **candelabra** (highly branched), **stellate** (star-shaped), and **peltate** (round or shield-shaped) with the attachment point in the middle (Fig. 9.6l–v). Peltate trichomes may be stalked or unstalked.

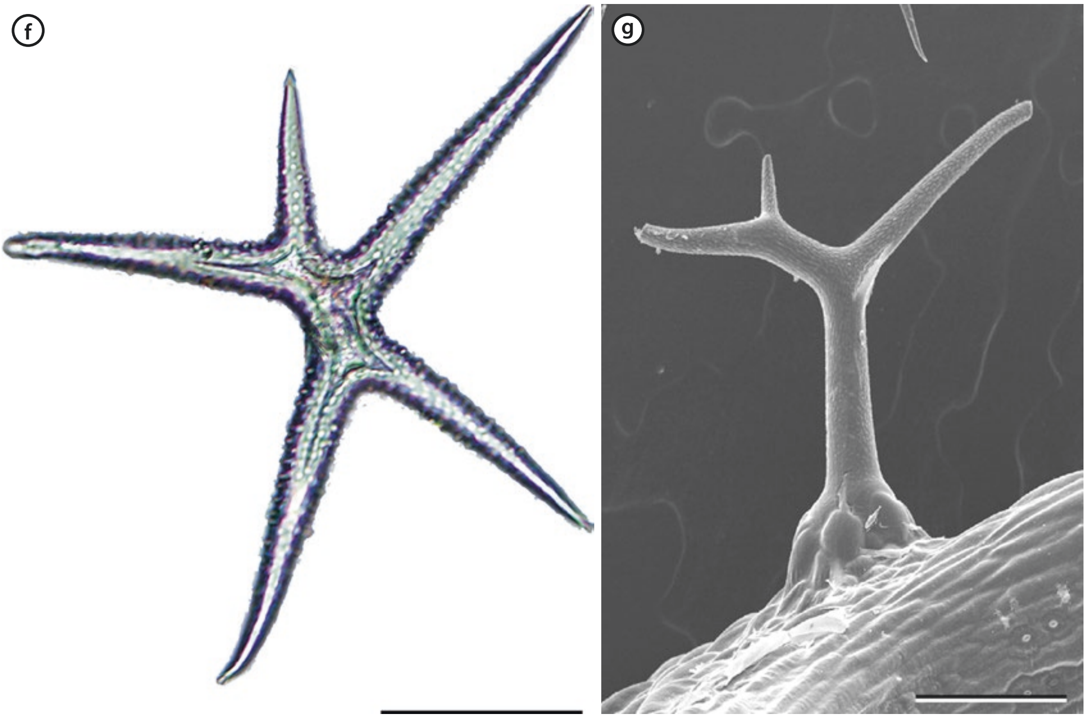


Fig. 9.6 **f**, **g** Unicellular, branched trichomes. **f** Top view of an isolated unicellular, branched trichome with five branches (5-furcate) of shepherd's purse (*Capsella bursa-pastoris*). The trichome is studded with calcium oxalate crystals. **g** Side view of a trifurcate unicellular trichome from the lyre-leaved sand cress (*Arabidopsis lyrata*). Both species are in the Brassicaceae. Scale bars = 100 µm in both panels. (**f**, **g** RR Wise)

Box 9.3 Cotton Fabrics Originate from Unicellular, Nonglandular Trichomes Associated with the Seed Coat

Like stomatal patterns (► Sect. 9.5), the complex nomenclature has practical applications in the classification and identification of plant-based products. Nonglandular trichomes from cotton (*Gossypium* spp.) seeds have been used by humans for textile making in both the old and new worlds since antiquity. Strong historical evidence indicates that cotton was independently domesticated in the Near East, the Far East, and the New World as far back as 5000 BC. The genus *Gossypium* contains about 50 species, but only four are grown for commercial cotton fiber production: upland cotton (*G. hirsutum*), creole cotton (*G. barbadense*), tree cotton (*G. arboreum*), and Levant cotton (*G. herbaceum*).

The unicellular, unbranched trichomes (Fig. 9.6w, x), typically called fibers, originate from the seed coat and can reach lengths of up to 3 centimeters, making them some of the longest plant cells known. These hairs elongate and then die at maturity within the mature fruit capsules and become the source of the commercial cotton fibers. While they develop secondary walls, they are not lignified.

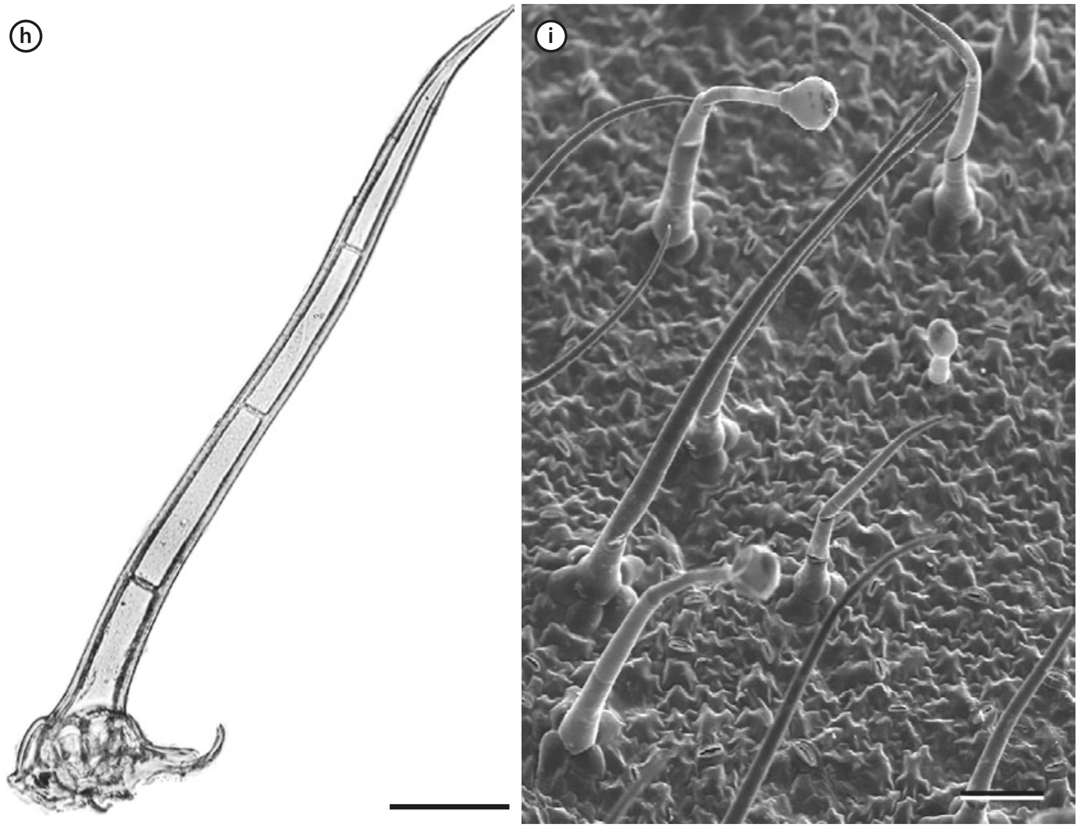


Fig. 9.6 **h**, **i** Multicellular, unbranched, uniseriate trichomes from the **h** petiole and **i** leaf of geranium (*Pelargonium* sp., Geraniaceae). Glandular trichomes are also present on the geranium leaf (see round structures at apex of trichome). Scale bars = 100 µm in both panels. (**h**, **i** RR Wise)

9.7 Glandular Trichomes Secrete a Variety of Oils, Resins, and Toxins

Many plants produce **glandular trichomes** that secrete an essential oil, nectar, salts, slime, or other substances that act as mini-factories that produce a wide variety of complex organic compounds on plant surfaces. The odor of tomato and potato leaves is from the essential oils stored in such glandular trichomes that are released upon rupture of the glands. Tetrahydrocannabinol, the main psychoactive ingredient in marijuana's (*Cannabis sativa*) leaves and floral parts, is produced in glandular trichomes that originate in the epidermis. Given that many of the compounds produced by glandular trichomes are toxic, psychoactive, or just bad tasting, their presumed function in almost every case is to deter herbivory. Thus, the surface location of glandular trichomes has two advantages. First, they serve as the initial line of defense—herbivores have to eat their way through the epidermis to get to the mesophyll. Second, the toxic chemicals are sequestered away from the leaf mesophyll where their release could cause as much damage to the host plant as to the invading herbivore.

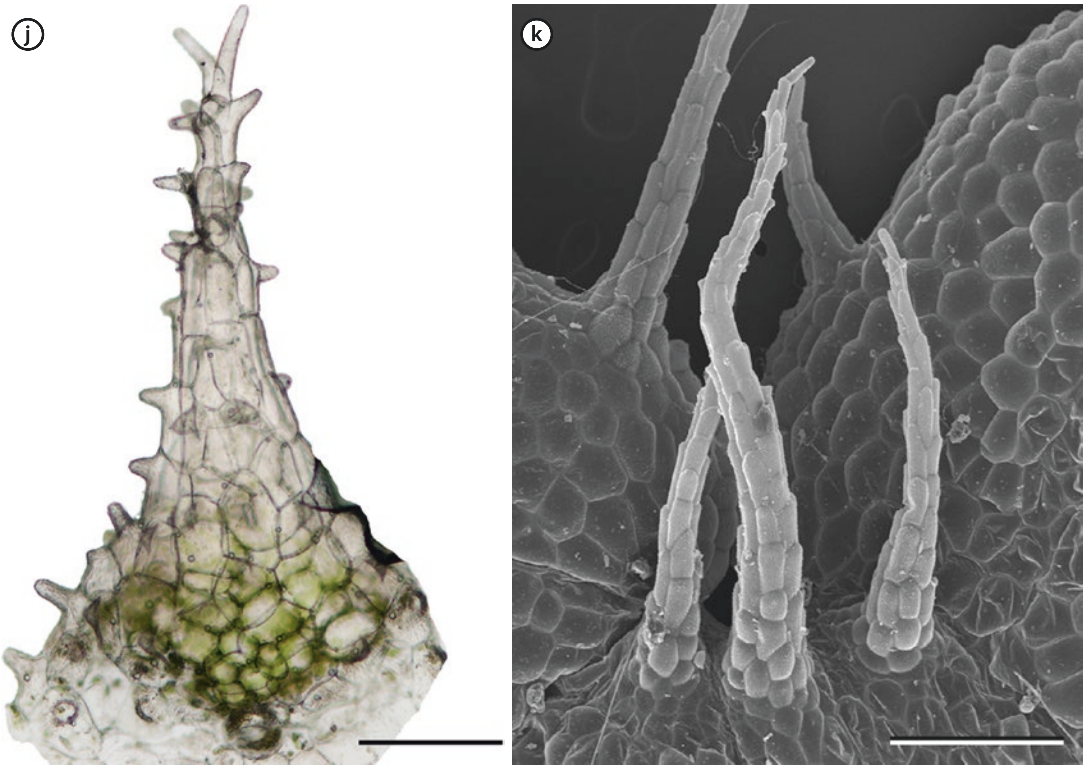


Fig. 9.6 **j**, **k** Multicellular, unbranched, multiseriate trichomes of begonia (*Begonia* sp., Begoniaceae). Scale bar = 250 μm for **j** and 500 μm for **k**. (**j**, **k** RR Wise)

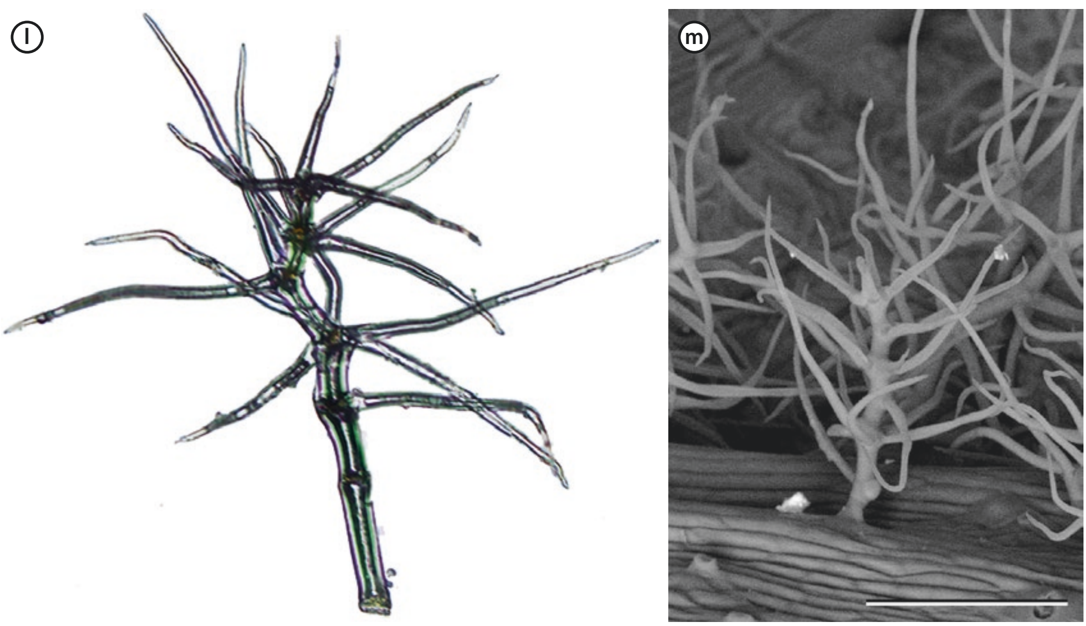


Fig. 9.6 **l**, **m** Multicellular, branched, candelabra leaf trichomes of sycamore (*Platanus occidentalis*, Platanaceae). Scale bars = 250 μm in both panels. (**l**, **m** RR Wise)

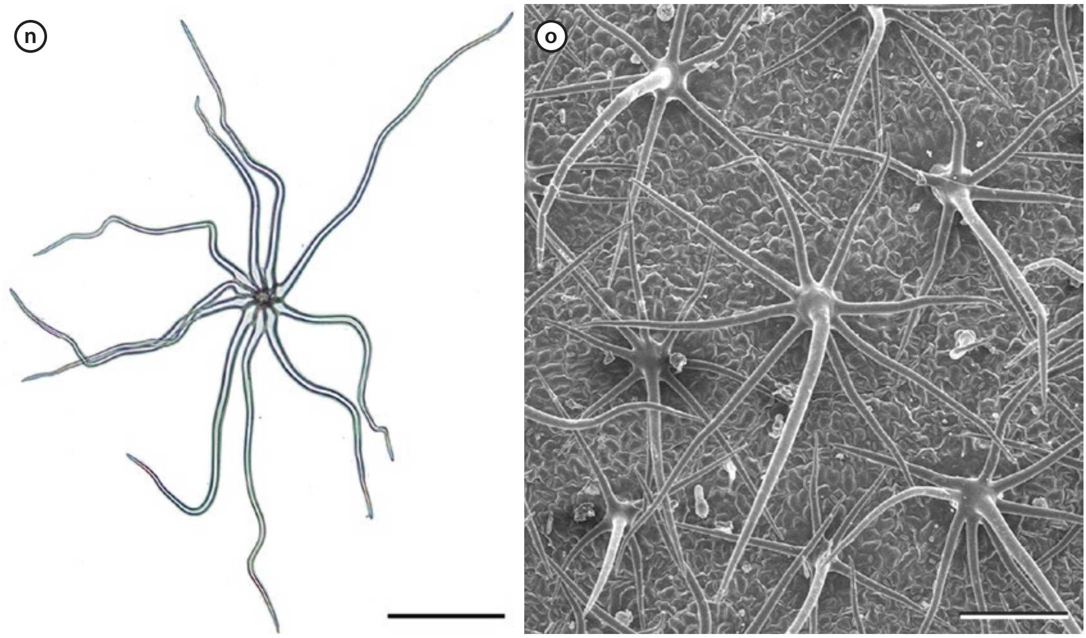


Fig. 9.6 **n**, **o** Multicellular, branched, stellate trichomes with simple processes from the leaves of **n** Canada buffaloberry (*Shepherdia canadensis*, Elaeagnaceae) and **o** eggplant (*Solanum melongena*, Solanaceae). Scale bars = 100 µm in (n) and 250 µm in **o**. (**n**, **o** RR Wise)

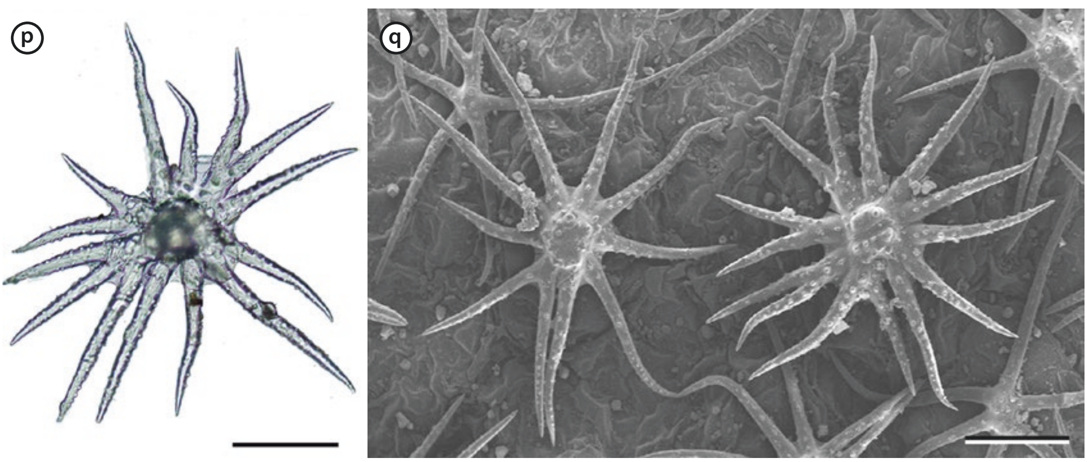


Fig. 9.6 **p**, **q** Multicellular, branched, stellate trichomes with bifurcated processes from leaves of the round-leaf bladderpod (*Physaria ovalifolia*). Scale bars = 250 µm in both panels. (**p**, **q** RR Wise)

Glandular trichomes may be as varied in form as nonglandular trichomes and appear as stalked or unstalked structures (Fig. 9.7a). The glands themselves may be unicellular or multicellular (Fig. 9.7b, c).

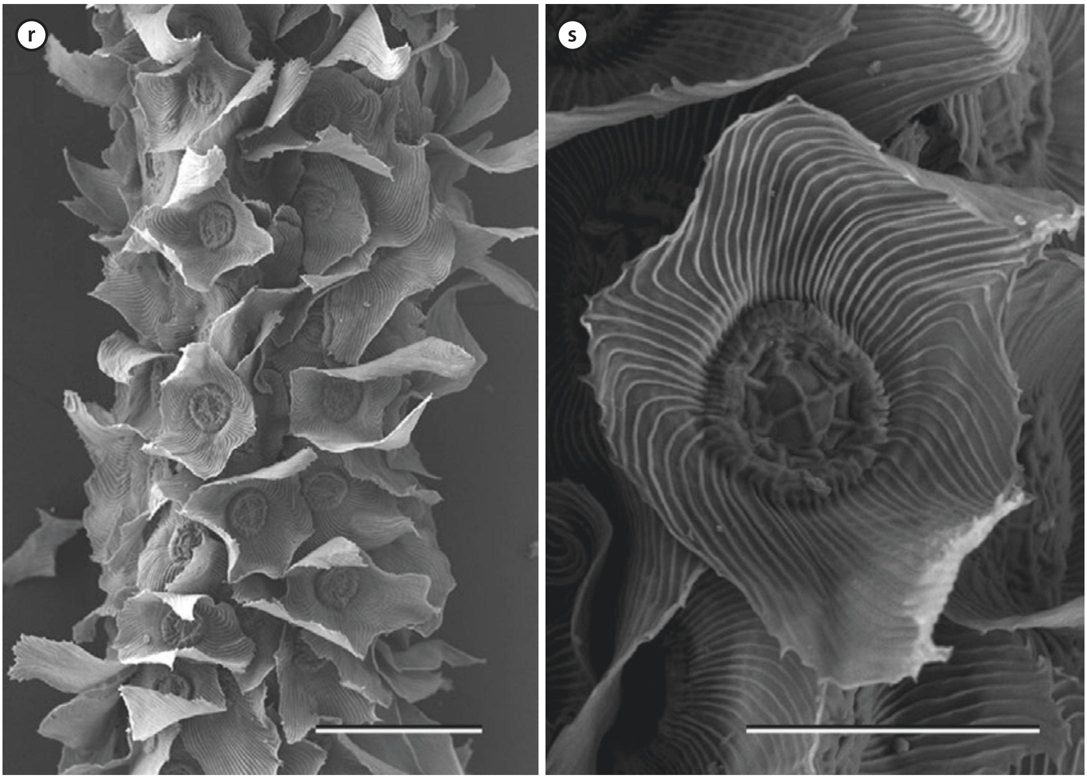
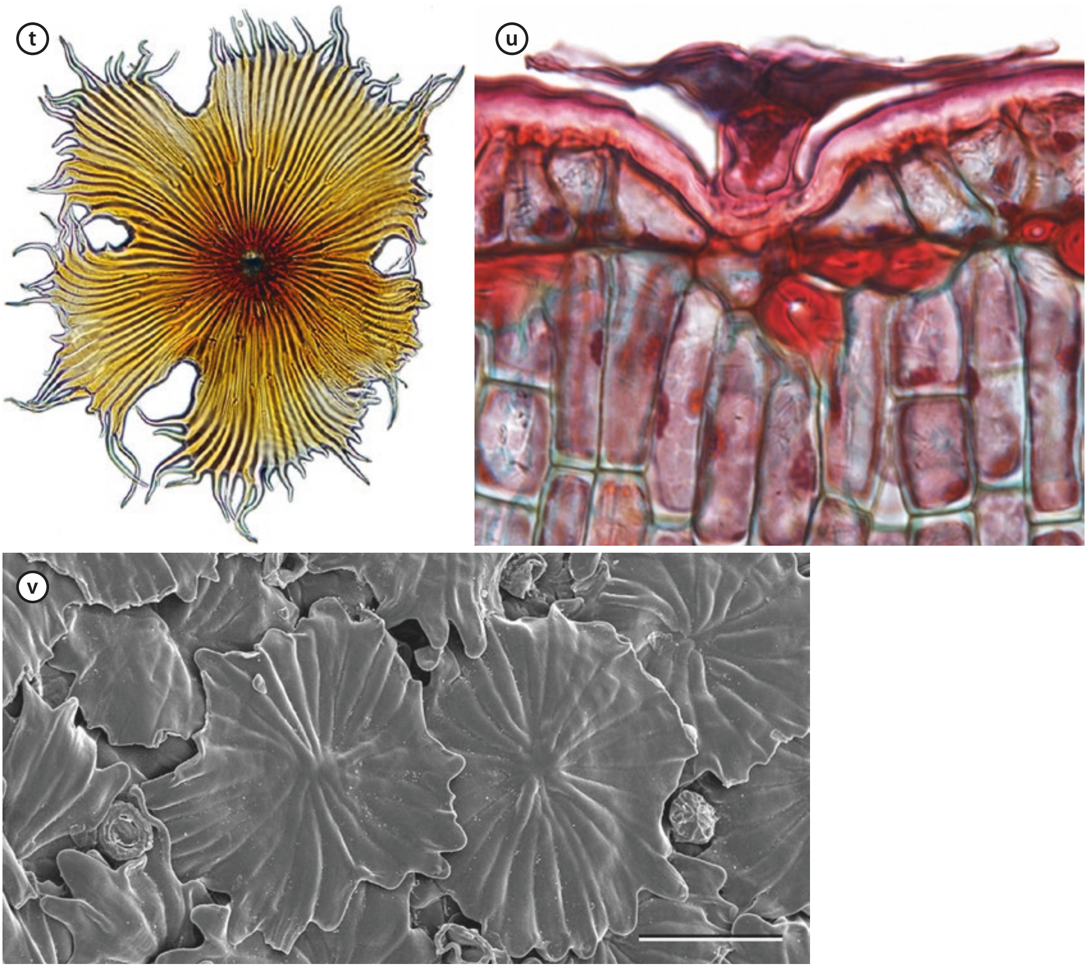


Fig. 9.6 **r**, **s** Multicellular, unstalked, peltate trichomes from Spanish moss (*Tillandsia usneoides*, Bromeliaceae). Scale bars = 500 µm in **r** and 200 µm in **s**. (**r**, **s** RR Wise)

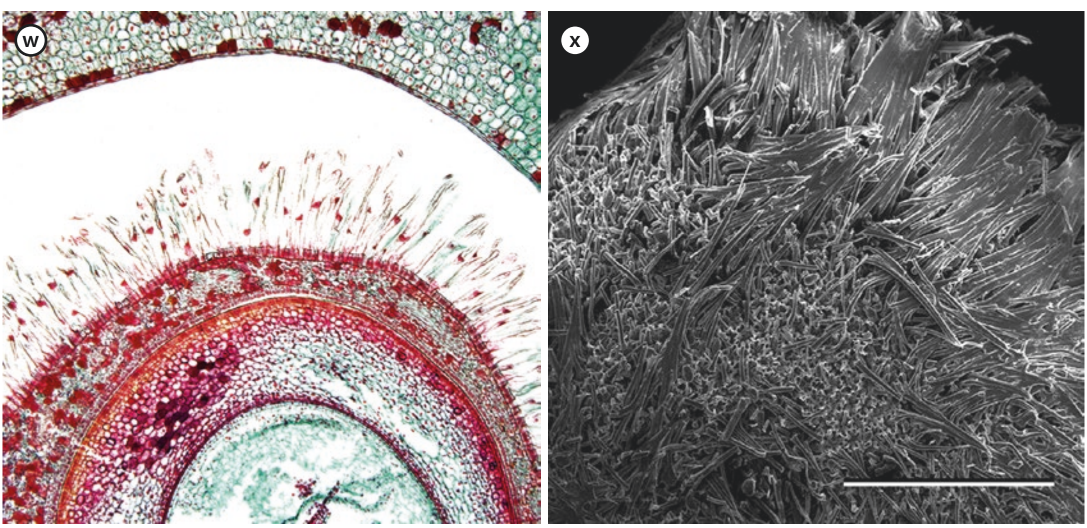
9.8 Idioblasts Are Unusual Cells in the Epidermis and May Contain Elemental Deposits

An **idioblast** (from the Greek "idios" meaning separate or unique) is an isolated cell in a tissue that is surrounded by other more homogenous cells. By this definition, guard cells and trichomes are technically idioblasts; however, most texts, including this volume, have chosen to treat them as separate, distinct cell types.

An example of another idioblast is the epidermal **silica cell**. This cell type is found in many grasses where the epidermal cells accumulate **silica bodies** (◘ Fig. 9.8a, b). While silica cells are widespread in grasses, their function is unclear. Some hypotheses suggest that silica is used as a plant defense to deter insect herbivory due to the indigestibility and abrasiveness of silica (Massey et al. 2006). Other hypotheses suggest that perhaps silica cells serve as light pipes and direct solar irradiance to the leaf mesophyll, but these have not been supported by experimental evidence. It should be noted that their distinctive structure and persistence in the fossil record makes them useful for determining grass distribution and abundance in paleoenvironments and can also give some clues regarding the paleodiet of humans and other omnivores based on dental wear patterns (El Zaatari et al. 2011). Additional epidermal idioblasts are discussed in ► Chap. 13—Secretory Structures.



■ **Fig. 9.6** **t**–**v** Multicellular, stalked, peltate trichomes from **t** a soapberry (*Shepherdia canadensis*) leaf and **u**, **v** a European olive (*Olea europaea*) leaf. The two small, round structures in **v** are the stalks of trichomes that have broken off the leaf surface. Both species are in the Elaeagnaceae. Scale bar in **v** = 50 μm for all three panels. (**t**–**v** RR Wise)



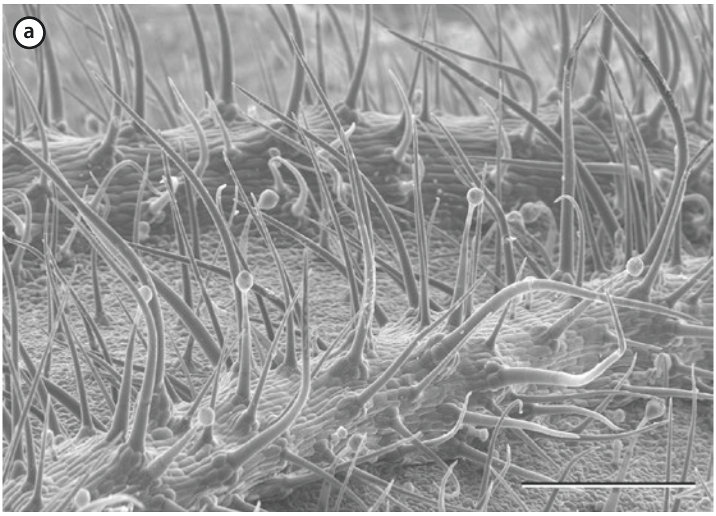


Fig. 9.7 **a** Glandular (note gland on tip of trichome) and nonglandular (sharply pointed) stalked trichomes on the surface of a geranium (*Pelargonium* sp.) leaf. Scale bar = 0.5 μm. (RR Wise)

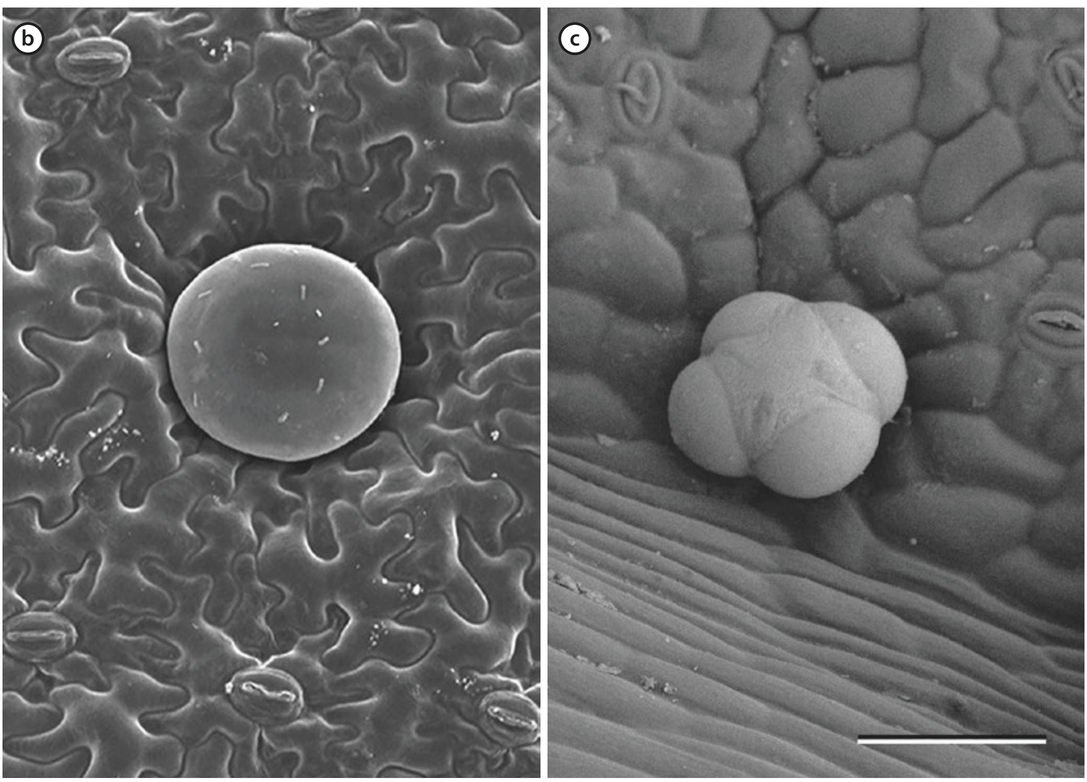


Fig. 9.7 **b**, **c** Unstalked glandular trichomes. **b** Unicellular gland in mint (*Mentha* sp.), **c** multicellular gland in black walnut (*Juglans nigra*). Scale bar in **c** = 50 μm for both panels. (**b**, **c** RR Wise)

Fig. 9.6 **w**, **x** Unicellular trichomes on **w** cotton (*Gossypium hirsutum*) and **x** tomato (*Solanum lycopersicum*) seed coats. Note the presence of a nucleus in each cotton trichome cell in **w**. Scale bar = 500 μm for both panels. (**w**, **x** RR Wise)

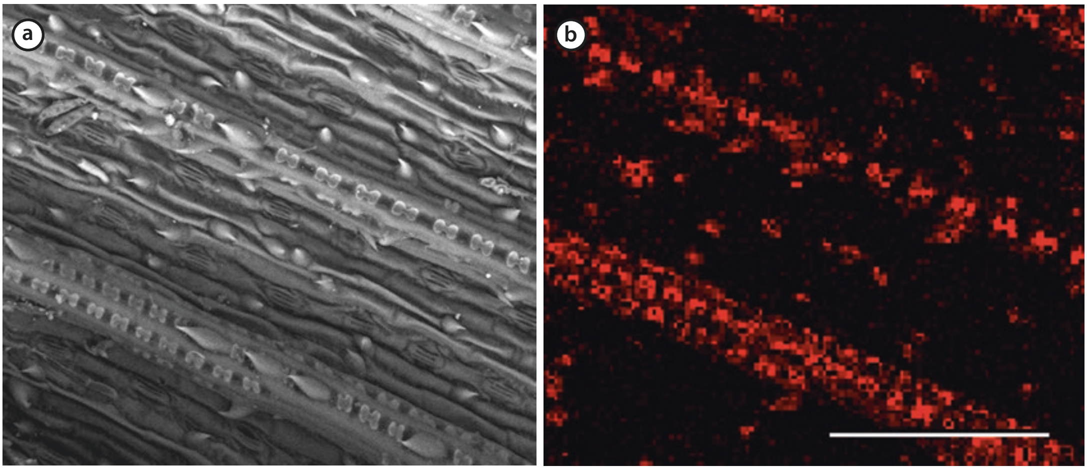


Fig. 9.8 **a** Silica cells on the surface of a foxtail (*Setaria viridis*) leaf as observed with scanning electron microscopy. **b** X-ray microanalysis was used in conjunction with SEM to localize high concentrations of silicon (shown in red) in the silica cells. Scale bar = 100 µm. (**a**, **b** RR Wise)

9.9 Chapter Review

Concept Review

9.1. *Pavement epidermal cells cover leaf and stem surfaces.* Tightly packed parenchyma cells, of various patterns and shapes, cover and protect most plant surfaces. They may contain red or purple anthocyanins as an adaptation to high- or low-light conditions. Tropical plants may have two or three layers of epidermal cells for water storage or light scattering.

9.2. *Stomata are adjustable pores that control gas exchange.* Pairs of guard cells surround and define the adjustable pores on the leaf and stem surfaces that are called stomata. Stomata may also be found on some fruit and floral parts. Guard cells are the only epidermal cells to contain chloroplasts, which are fully functional and play a large role in stomatal functioning. The light-dependent movement of water and ions drives stomatal opening into the guard cells, causing them to swell and bend. Guard cells secrete epidermal waxes to both the exterior and the interior surfaces of the leaf. Waxes to the interior are called the internal cuticle.

9.3. *Guard cells and subsidiary cells make up the stomatal complex.* Guard cells must exchange water and ions with adjacent epidermal cells, i.e., subsidiary cells, and together they form a stomatal complex. The number and arrangement of subsidiary cells varies in a species-dependent manner. Dozens of distinct patterns have been described. Eight of the major patterns are floating, paracytic, diacytic, triacytic, anisocytic, tetracytic, anomocytic, and graminaceous.

9.4. *The cuticular membrane protects the plant surface.* The cuticular membrane (a.k.a. cuticle) covers all aerial surfaces of the plant. It is composed of cutin, cutan, and waxes. The waxes have different shapes. One of the major purposes of the cuticle is to prevent non-stomatal water loss from the leaf—called cuticular transpiration. Cuticle thickness varies based on plant habitat, thinner in moist or aquatic habitats and thicker in evergreen or arid habitats.

9.5. *Stomata vary in distribution and depth.* Stomata may be epistomatic (only found on adaxial leaf surface), hypostomatic (abaxial surface), or amphistomatic (both surfaces). Stomata may be randomly distributed across the leaf and stem surface, or they may display distinct patterns. Stomata may be sunken below the leaf surface to reduce transpiration.

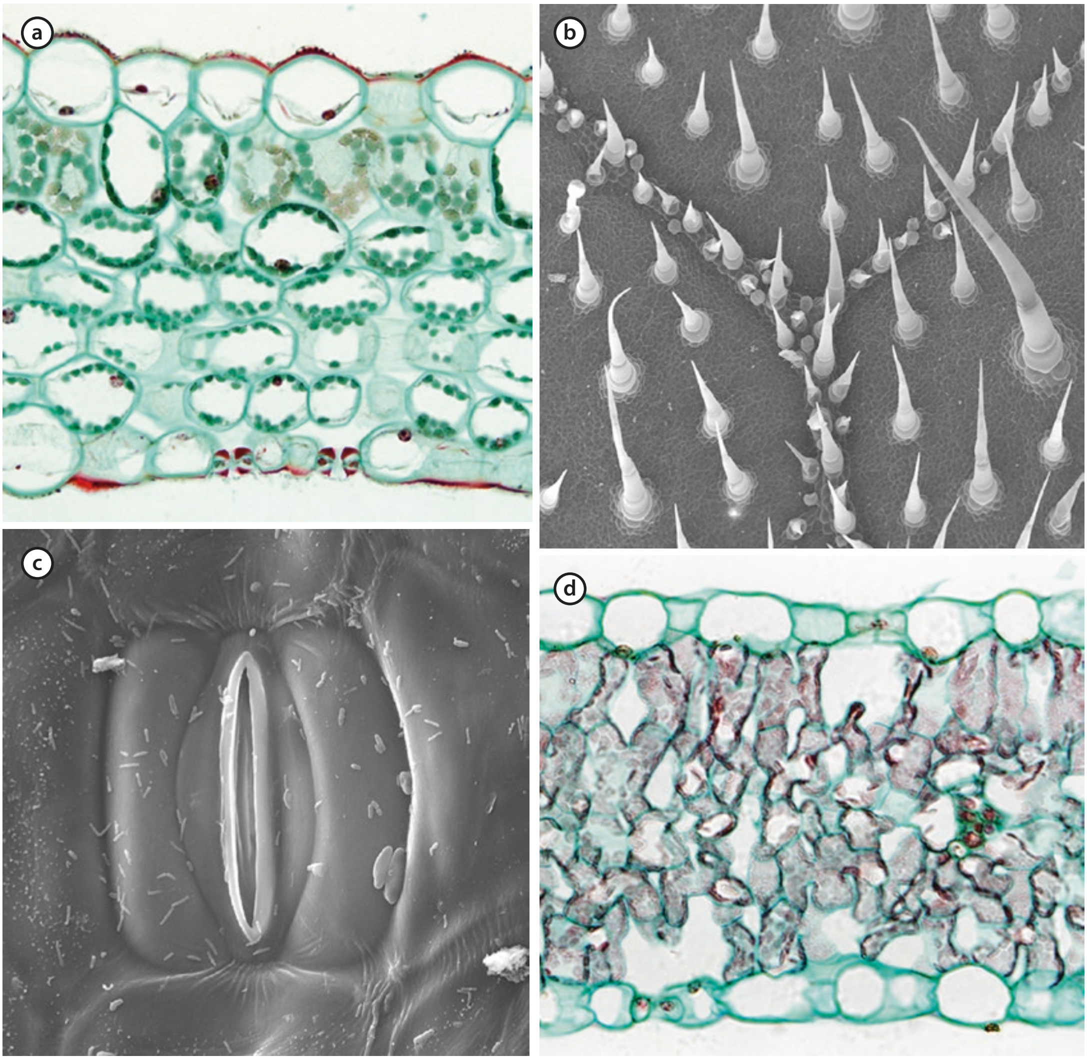
9.6. *Nonglandular trichomes protect the leaf from biotic and abiotic stresses.* Trichomes arise from epidermal cells and may be nonglandular or glandular. Nonglandular trichomes may reduce transpiration, scatter incoming light, or deter herbivory. Trichome architecture is species-specific. In addition to unbranched trichomes, other varieties include branching, forking, single-celled, or multicelled.

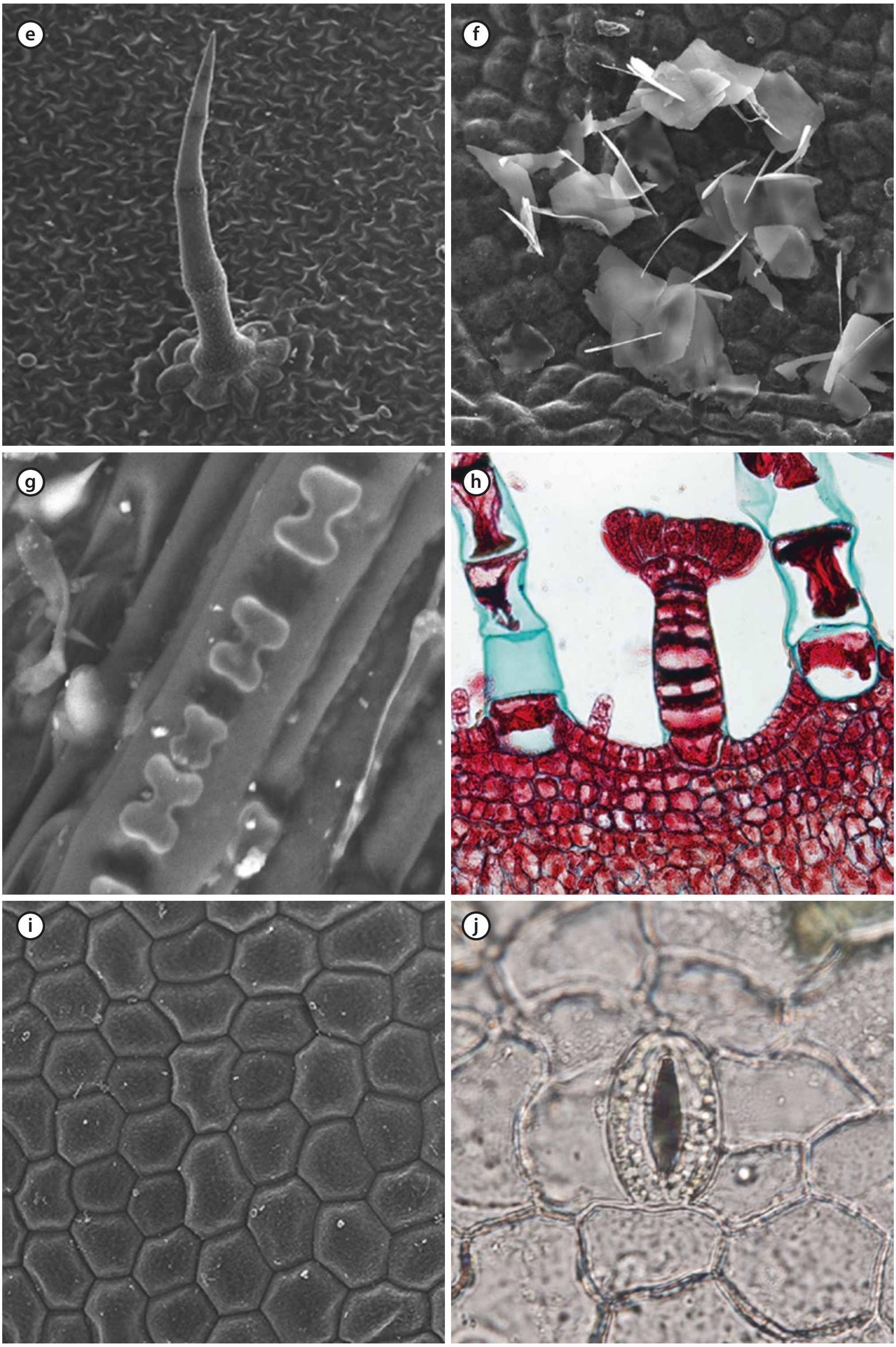
9.7. *Glandular trichomes secrete a variety of oils, resins, and toxins.* Glandular trichomes originate from the epidermis and contain a wide variety of toxic or psychoactive compounds that discourage animals from feeding on the leaf or stem. They may be stalked or unstalked and contain from one to many cells.

9.8. *Idioblasts are unusual cells in the epidermis and may contain elemental deposits.* Many plants, particularly grasses, have silicon-containing cells (silica bodies) in the leaf epidermis. The silicon can be detected and imaged using X-ray elemental microanalysis in conjunction with scanning electron microscopy. While the functions of such silicon accumulations are not well understood, they persist in the fossil record and can be useful in the field of paleoclimatology.

Concept Connections

1. Match the proper descriptor (i–x) with the correct figure (a–j).




e
f
g
h
i
j

(i) anomocytic stomatal complex.
(ii) pavement cells.
(iii) multicellular nonglandular trichome.
(iv) epidermal waxes.
(v) glandular trichome.
(vi) silica bodies.
(vii) hypostomatic.
(viii) paracytic stomatal complex.
(ix) nonglandular trichomes.
(x) amphistomatic.

Concept Assessment

2. Nonspecialized cells that cover the leaf surface are called
   a. subsidiary cells.
   b. guard cells.
   c. meristemoid mother cells.
   d. pavement cells.
   e. blocking cells.

3. Surfactants help break down
   a. the waxy cuticle.
   b. calcium-containing cystoliths.
   c. stomatal complex.
   d. mucilage on hydrophytic leaves.
   e. anthocyanins in the epidermis.

4. Leaves with stomata on only the adaxial side are referred to as
   a. amphistomatous.
   b. hyperstomatic.
   c. epistomatous.
   d. mesostomatous.
   e. hydrostomatous.

5. Dendrites help deliver ____________ to the leaf surface.
   a. cuticle precursors.
   b. water and ions.
   c. guard cells.
   d. toxic antiherbivory compounds.
   e. digestive enzymes.

6. An anomocytic stomatal complex is characterized by having
   a. a single cell surrounding the guard cell pair.
   b. two subsidiary cells parallel to the guard cells.
   c. two subsidiary cells at right angles to the guard cells.
   d. three subsidiary cells in contact with the guard cells.
   e. four or more cells in contact with the guard cells.

7. The internal cuticle mainly controls
   a. water loss down the stem to the roots.
   b. non-stomatal water loss (cuticular transpiration).
   c. water loss to the interior of the leaf, near the stomatal pore.
   d. the secretion of water via hydathodes.
   e. the entry of pathogenic bacteria.

8. X-ray microanalysis in conjunction with SEM can be used to image
   a. cell walls and vacuoles.
   b. water and carbohydrates.
   c. heavier, non-carbon elements.
   d. cystoliths and silica bodies.
   e. c and d.

9. A flattened, umbrellalike trichome with a short stalk is termed
   a. peltate.
   b. radiating.
   c. tufted.
   d. stellate.
   e. branched—unicellular.

10. The epidermis is derived from the
    a. calyptrogen.
    b. corpus.
    c. rib meristem.
    d. procambium.
    e. protoderm.

11. Pavement cells lack
    a. chloroplasts.
    b. cuticle.
    c. epicuticular waxes.
    d. mitochondria.
    e. vacuoles.

Concept Applications

12. Chaparral plants are highly flammable. Research "chaparral" on the Internet, and explain, in terms of leaf epidermis and the habitat in which they grow, why this is the case.

13. How can stomatal density (number of stomata per unit of leaf area) of fossil plant leaves be used to estimate ancient atmospheric carbon dioxide levels?

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Roots

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R. Crang et al., *Plant Anatomy*, https://doi.org/10.1007/978-3-319-77315-5_10

Introduction

The function of modern-day roots has not essentially changed from their early evolutionary development, i.e., the uptake of water and minerals as well as anchorage for the stabilization of shoot development and growth, but also food storage, the production of plant growth regulators, and aeration. Roots have an anatomy that is distinctly different from that of shoots, as dictated by the substrate in which they grow—air vs. soil. Stems have nodes from which they can produce stems, leaves, flowers, or roots. Roots lack nodes and can only produce lateral roots. The root cap protects the growing tip as it pushes through the soil. Lateral roots originate from the interior of the root, some distance from the tip, as opposed to leaf initiation which is from the shoot tip. Roots adjust their growth in response to gravity, water, and nutrition. They are insensitive to light, unlike the very light-sensitive shoot. Root vasculature is characterized by a central, often solid in eudicots and pithy in monocots, mass of xylem surrounded by individual patches of phloem. Symbiotic associations with certain bacteria and fungi greatly enhance nutrient acquisition and uptake.

10.1 Roots and Root Systems Serve Multiple Purposes

Roots have multiple functions. Roots anchor plant to the substrate, even in the most precarious situations (◘ Fig. 10.1a). The epiphytic strangler figs start as a germinating seed on a limb or trunk and grow their roots down to the soil, completely encircling the host plant (◘ Fig. 10.1b). The host plant is only used as a source of support; no water or nutrition is derived from it by the strangler fig. Roots of many plants maintain a role in the storage of nutrient substances, many of which serve as a source of foods for animal and human needs. Beetroot (*Beta vulgaris*), carrot (*Daucus carota*), parsnip (*Pastinaca sativa*), radish (*Raphanus sativus*), and sweet potato (*Ipomea batatas*) are but a few major root crops. While most of these nutrients are carbohydrate, some roots store oils, proteins, and fats as well as mineral nutrients such as phosphates and sulfates. Horseradish (◘ Fig. 10.1c) stores irritating chemical compounds that serve as an anti-herbivory defense and a spicy flavoring. Stored carbohydrates are important in non-crop species for stem regeneration after heavy pruning (Vriet et al. 2014) and in the production of leaves and flowers by fruit trees in the spring (Tromp 1983). Succulent roots store water in large parenchyma cells (Hearn et al. 2013), in a manner analogous to that found in succulent leaves (► Sect. 12.7). Plants growing in wet or marshy areas, such as mangrove (◘ Fig. 10.1d), put out a large number of adventitious "**prop**" roots that contain a large amount of internal aerenchyma. The roots both provide support and help aerate those portions of the root system that are submerged in the low oxygen substrate (Purnobasuki and Suzuki 2005).

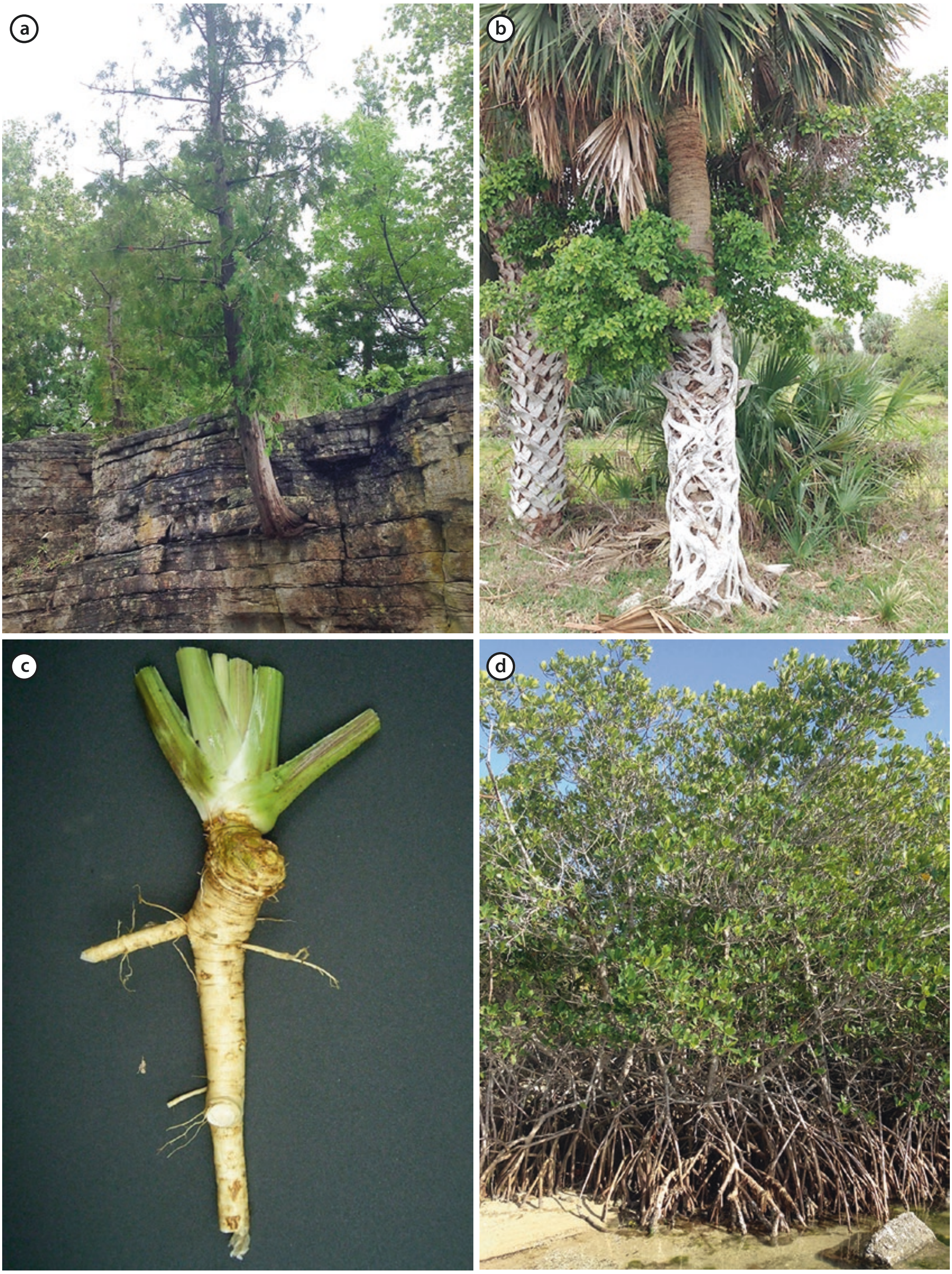

Fig. 10.1 **a** White cedar (*Thuja occidentalis*) anchored to a cliff face by its root system. **b** Strangler fig (*Ficus banyan*) roots wrapped around a palm. The fig leaves are at the top of the root system, about halfway up the palm trunk. **c** Horseradish (*Armoracia rusticana*) storage root, harvested and with most of the leaves cut off. **d** Red mangrove (*Rhizophora mangle*) prop roots. (**a**, **b**, **d** RR Wise; **c** F Vincentz, CC BY-SA 3.0)

Nongreen parasitic plants that lack the chlorophyll necessary for photosynthesis must develop parasitic growths called **haustoria** (threadlike growths of a parasitic plant), which enter into the water- and food-conducting tissues of a host plant in order to obtain their nutrition (Fig. 14.7a). This requires a fusion of the vascular systems of the host and parasite and is discussed in ▶ Chap. 14—Vascular Cambium.

Although it might be most convenient to view plant anatomy as a series of structural/functional parts, nevertheless one should not lose sight of the fact that plants represent integrated systems just as in the case of all living organisms. To this end, while unique in many ways, the organs of a plant must communicate with each other to produce a viable and successful organism. Employing molecular physiology, we are starting to learn more about the reciprocal exchange of information and needs of plants. Thus, roots and shoots exchange plant growth regulators (a.k.a. hormones) which carry such information to provide for growth, differentiation, and resistance to herbivory (Jackson 2002; Takei et al. 2002). The risk of herbivory varies from one part of the plant to another. For example, roots are less likely to be attacked by insect herbivores than leaves, whereas leaves have a far lower likelihood of threat from fungi, bacteria, and nematodes than subterranean roots. Changes in plant growth regulator levels are significant in repair to structural damage in root tips and shoot apical meristems to bring about repair and renewed growth. Following herbivore damage such regulators as abscisic acid, auxins, cytokinins, ethylene, and gibberellins are believed to play key roles in communication trafficking and in directing appropriate repair (Kaplan et al. 2008).

Water uptake represents one of the primary functions of roots. The amount of water taken up per plant community or individual plant for transpiration varies tremendously based on a host of factors (including the method used to measure that water movement). In an extensive literature survey, Wullschleger et al. (1998) reported water usages on a per plant basis ranging from the low teens to several hundred kg H_2O day^{-1}. *Eperua purpurea*, a tropical tree in the Leguminaceae, topped the list with a value of 1180 kg H_2O day^{-1} or over 300 gallons a day.

While mineral nutrient uptake may typically follow the same passive pathway as water in root systems, in many cases the plant **root hairs** and surface cells may expend energy in order to take up and concentrate mineral ions. This includes minerals such as nitrates, phosphates, and potassium which cannot be absorbed across the plasma membrane without such a chemiosmotic force. Nitrogen enters the root as nitrate (NO_3^-) or as ammonium ions (NH_4^+), whereas phosphorus enters as PO_4^{3-}, calcium as Ca_2^+, and potassium as K^+. Inorganic ions pass from cell-to-cell through plasmodesmata for the most part, but from the cytoplasm of the pericycle cells (just inside the endodermis) to the xylem transport is mostly by means of active transport. When incorporated into the xylem of roots, minerals may exit and enter cells that require them.

Water and ions are taken up from the soil, move radially through the cortex to the stele (a.k.a. **central cylinder**), and then

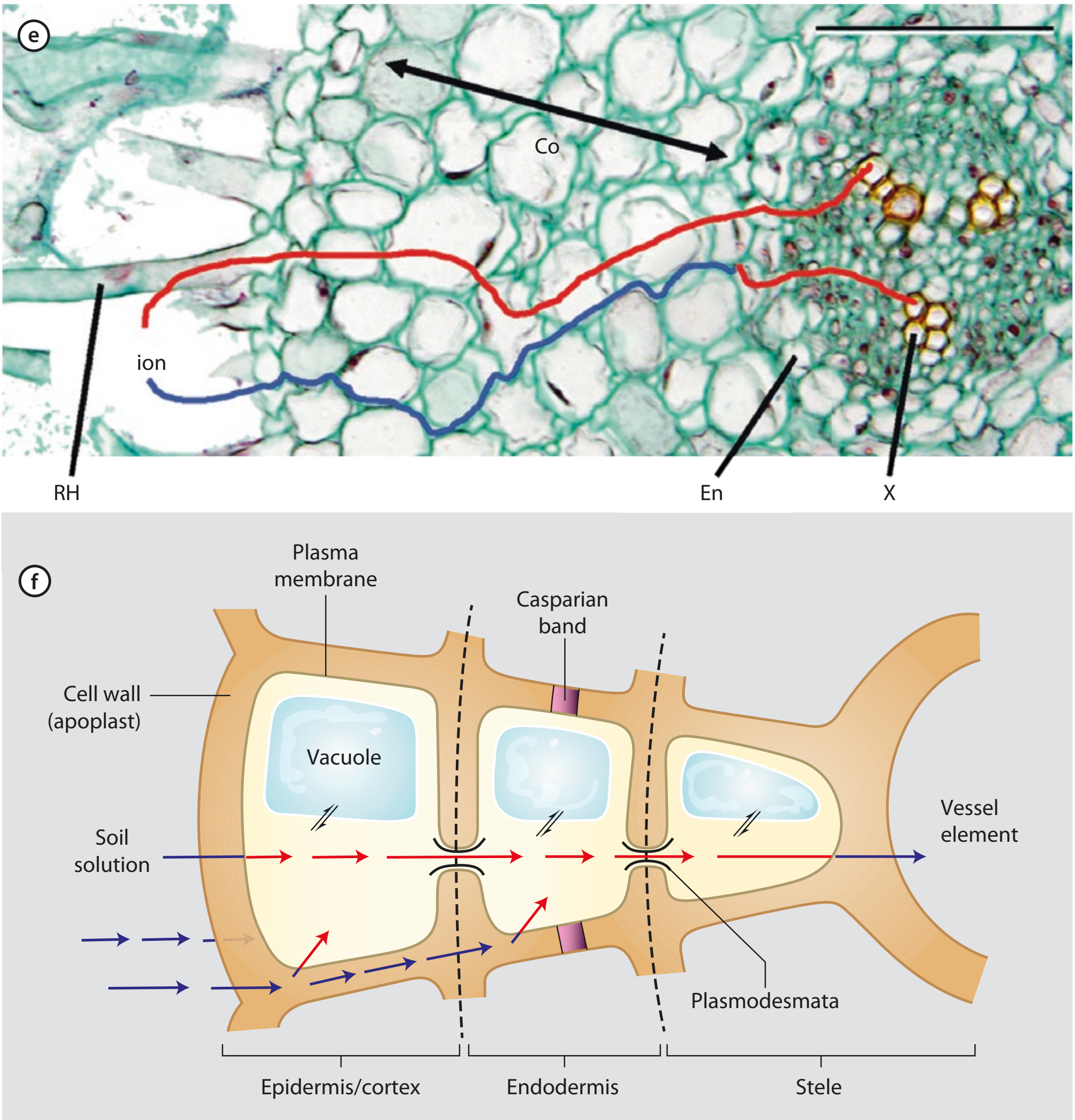

Fig. 10.1 **e**, **f** Water and ion uptake by plant roots may take **e** a symplastic pathway (red arrows) or **f** an apoplastic pathway (blue arrows) from the soil water, through or around the root hair (RH), cortex (Co), to the endodermis (En). The Casparian strip in the endodermis forces apoplastic water and ions to cross the plasma lemma and enter the symplast of the endodermis from which they then move via plasmodesmata into the xylem tracheary elements (X) in the stele. Scale bar in **e** = 50 µm. (Modified from F Vincentz, CC BY-SA 3.0)

move in an axial direction to the shoot. Figure 10.1e, f shows the two anatomical pathways of water and mineral ion uptake in roots. When following the **symplastic pathway**, water and mineral ions move across the root hair plasma lemma and immediately enter the root hair cytoplasm. They then travel cell-to-cell via plasmodesmata through the cortex, endodermis, and into the living parenchyma cells of the stele. Ion uptake requires an energy source (ATP or membrane potential) and specific membrane-bound transport proteins, the presence and permeability of which are under control by the cell. The plant, therefore, has the ability to exclude or concentrate certain ions. The "decision" on which ions the plant takes up is made at the root hair. In the **apoplastic pathway**, water and ions passively enter the cell wall space of the cortex and diffuse to the cell wall space of the endodermis. There, the **Casparian strip** (refer to ► Sect. 10.1) blocks further apoplastic movement, and the ions must be transported across the plasma lemma of the endodermal cells to enter the symplasm and move on to the stele. In this case, the "decision" on which ions the plant takes up is made at the endodermis.

10.2 Root System Morphology Is Diverse and Adapts to Soil Conditions via Compensatory Growth

Root morphology may be largely classified into two groups. Monocots typically produce a fine but dense network of roots termed a fibrous root system (◘ Fig. 10.2a). Fibrous roots, most typical of grasses, do not grow as deep into the soil as taproots and usually are found where water and phosphates are more abundant and thus grow more in a horizontal pattern. Fibrous roots also often form a complex with soil particles that aids in the prevention of erosion. Eudicots, on the other hand, mostly possess a taproot system (◘ Fig. 10.2b) in which the primary root grows downward in the soil and develops smaller lateral roots. Such taproot systems are often found in dry soils and grow deep toward underlying water

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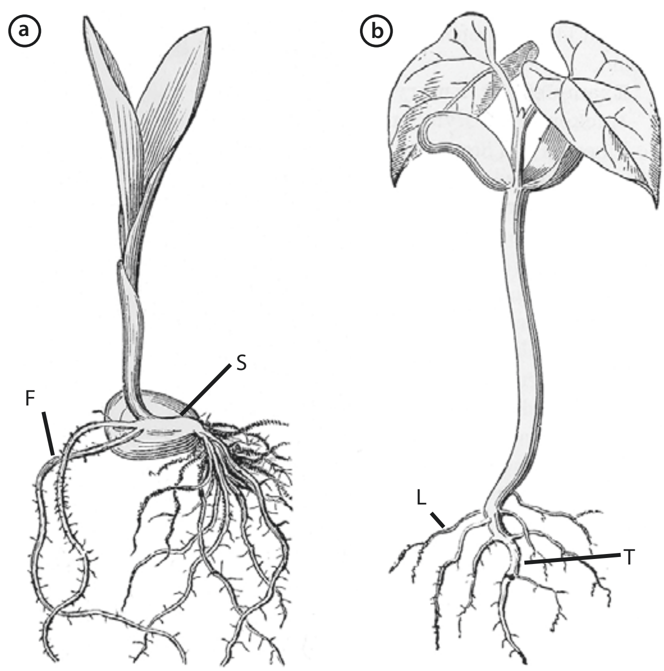
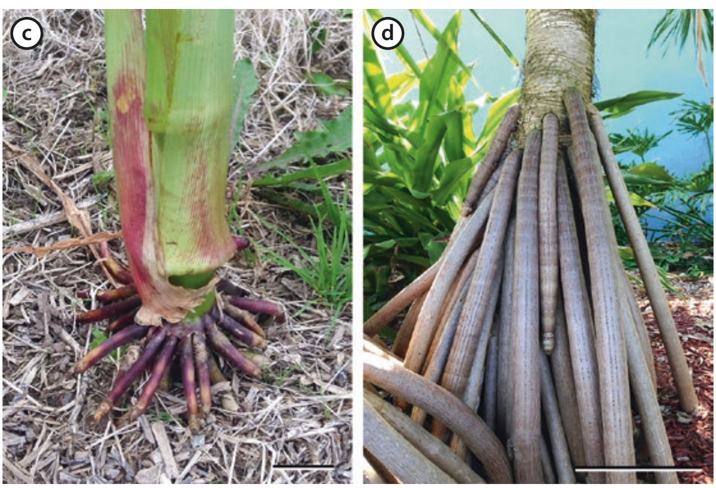


◘ **Fig. 10.2** **a**, **b** Drawings of **a** maize (*Zea mays*-monocot) and **b** bean (*Phaseolus vulgaris*-eudicot) seedlings. F, fibrous root; S, stem; L, lateral root; T, taproot. Scale bars = xx µm. (**a**, **b** A Grey (1887), public domain) and nitrogen sources. The fact that the last tracheophytes to arise, namely, the eudicots, have a taproot system and the ferns have fibrous systems indicates that the fibrous root system evolved first. The fibrous/tap distinction may be lost in perennial plants such as trees as the root system develops and adapts to local soil conditions.

During seedling germination, the first organ to develop from both monocots and eudicots embryos is the **radicle** (refer to ▶ Chap. 19). In eudicots, the radicle continues to elongate, develops an apical meristem and root cap, and becomes the taproot from which lateral roots subsequently arise.

Development of the monocot root system is more complicated. Maize is a prototypical annual grass. Maize produces two root systems. The first includes the radical and a series of 3–6 seminal roots. Seminal roots are adventitious lateral roots that arise from the embryonic stem. At germination, a true root develops from the radicle, and the seminal roots elongate. Together, they are called the primary root system and are only present during early seedling development. The secondary root system is composed of adventitious roots that arise later from nodes higher on the developing shoot, some from nodes below the ground and some from nodes above ground. Those roots arising above ground are called prop roots (◘ Fig. 10.2c). Prop roots can be quite extensive, as can be seen in screw pine (◘ Fig. 10.2d). The maize primary root system aborts after the first few weeks of growth and after the secondary root system has become established. Therefore, all the roots on a mature maize plant are adventitious. Typically, adventitious roots are the sole source of roots in vegetative propagation in which sections of rootless stem tissue are induced to grow roots from existing nodes (Steffens and Rasmussen 2016).

Roots show compensatory growth inasmuch as the architecture is not stable. Roots also respond almost exclusively to variations in soil texture, moisture, nutrients, aeration, and biota. Roots are



◘ **Fig. 10.2** **c** Secondary, adventitious roots arising from a maize (*Zea mays*) stem at a level above the soil. **d** Adventitious roots of screw pine (*Pandanus utilis*) growing from the stem. These new roots serve a primary function of stabilizing the plant in strong winds or during heavy rain spells. Scale bars = 2 cm in **c** and 20 cm in **d**. (**c**, **d** RR Wise) also subject to additional possible abiotic stresses such as drought, flooding, salinity, and extreme temperatures. We are learning that root system defenses to such stresses involve anatomical, cellular, and molecular mechanisms.

Box 10.1 Root Hydrotropism Involves the Action of ABA in the Root Cortex

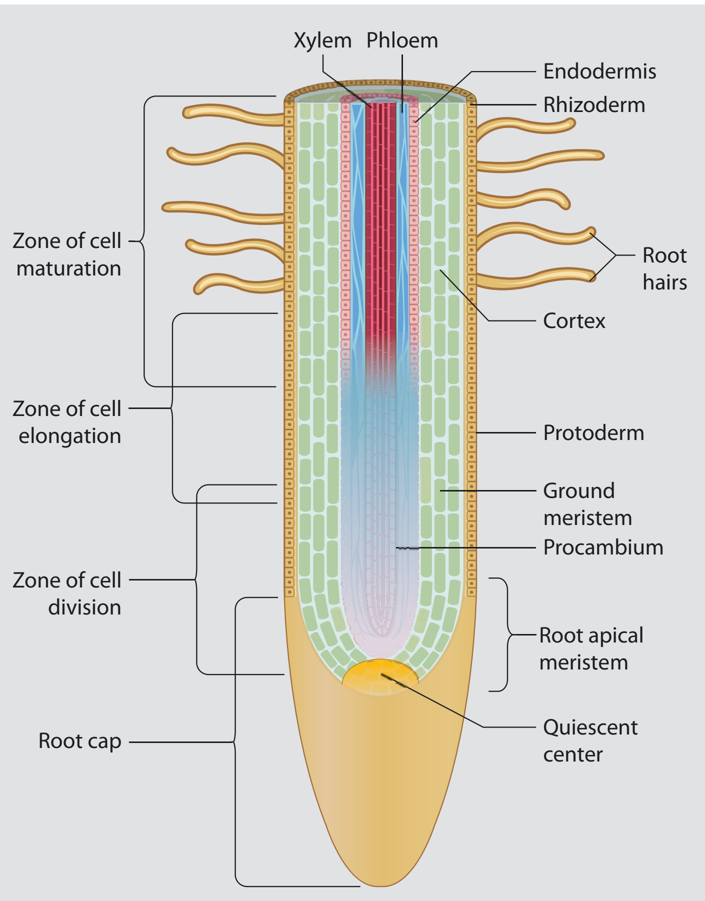
Tropisms are growth-driven movements. Phototropism, seen almost exclusively in shoots, is growth toward or away from light. Gravitropism, found in both roots and shoots, is growth toward or away from gravity. Hydrotropism is growth of the root tip toward soil water, allowing roots to actively seek out areas of the soil that contain more moisture. Phototropism and gravitropism have been well studied. Indeed, Charles Darwin performed the first phototropism experiments in the 1800s. Both the plant hormone (auxin) and tissues involved (endodermis, root cap) have been well-defined for both tropic responses. However, until recently, the signaling pathway for hydrotropism was virtually unknown other than the knowledge that abscisic acid (ABA) was involved, not auxins. In a series of elegant experiments, Dietrich et al. (2017) have elucidated the role of ABA in hydrotropism and identified the root cortex as the tissue wherein the physiological response takes place. First, they used laser ablation (which kills cells) and surgical excision to demonstrate the root cap is not involved in hydrotropism. Second, they used mutants lacking the hydrotropic response to probe which genes are active in which tissues during hydrotropism. The ABA signaling pathway is known to follow these steps: ABA inhibits a class of receptor proteins known as PYR/PYL/RCARs. When active, those proteins suppress the activity of PP2C kinases. The PP2C kinases would normally dephosphorylate, and inactivate, SnRK2s, which activate transcription factors, leading to a growth response. In the presence of ABA, therefore, SnRK2 activity is maintained, and the growth response proceeds. Gene constructs of known ABA signaling proteins and tissue-specific promotors were then used to "turn on" the response in the root cap, epidermis, endodermis, or cortex. Hydrotropism was only restored in the mutants when the cortex signaling pathway was activated, thus demonstrating a tissue-level location of the hydrotropism response very different from that for phototropism and gravitropism.

Reference: Dietrich et al. (2017).

In the monocot families Asphodelaceae, Agavaceae, and Cactaceae and a few herbaceous perennial eudicots, the major roots have the capability of undergoing a contraction of length after establishment. Such roots are termed **contractile roots** and are often responsible for pulling the plant deeper into the soil and protecting the plant from excessive sun and heat, as described for the "living rock" plant (Garret et al. 2010). In contractile roots, the radial longitudinal walls not only shorten but become thicker in the process of contraction. The process of shrinkage may take several weeks but may account for as much length contraction as 50%.

10.3 Primary Growth of Roots Involves Formation of Tissues and Their Organization

The root apical meristem is the source of new cells for the root (▶ Sect. 4.11), and ◘ Figure 10.3a shows the relationship of the RAM to the tissues of the primary root. The RAM generates the daughter cells that become the three other root meristems. The procambium produces the vascular tissues of xylem and phloem, the protoderm produces the rhizodermis, and the ground meristem produces the cells of the cortex. The growing root tip may be further



◘ **Fig. 10.3** **a** Diagram of a root tip. The root cap and three zones of differentiation (division, elongation, and maturation) are labeled to the left. The four meristems (RAM, procambium, ground meristem, and protoderm) are labeled to the lower right. The six mature tissues (cortex, root hairs, rhizodermis, endodermis, xylem, and phloem) are labeled to the top right. (Redrawn from Crang and Vassilyev 2003) divided into four zones – the root cap (treated further in ► Sect. 10.4), the zone of division, the zone of elongation, and the zone of maturation.

The zone of division (which arises directly from the RAM) is just behind the root cap and generates cells of both the root cap and the root proper. While it may be largely a semantic distinction, the RAM may be thought of as the quiescent center (► Sect. 4.11) and its immediate, undifferentiated daughter cells. Those products subsequently differentiate into the protoderm, procambium, and the ground meristem, and it is those three meristems that make up the zone of division. If physical damage occurs to the quiescent center, or if it is nutritionally stressed, root tip growth may be arrested or (with partial damage to the quiescent center) abnormal growth may occur (e.g., forked development). Cells that are active in division are essentially isodiametric cubes with large nuclei, but with few and small vacuoles. A central pith tissue is developed in grasses and many other monocots but is not normally found in eudicot plants because of compression forced by the establishment of the central **vascular cylinder**.

At the upper end of the zone of cell division (i.e., toward the stem) is a gradual change into a zone of elongation. True to its name, cells in this zone undergo elongation prior to full differentiation, and this elongation is responsible for an increase in length of the root. Little to no secondary cell wall is laid down yet, and the cells do not function in water or ion uptake.

The zone of maturation is where differentiation of tissues takes place, involving vascular tissues, cortical parenchyma, and the rhizodermis. Stele formation begins with the maturation of primary xylem, primary phloem, and the endodermis allowing for the uptake, and transport, of water and ions. Root hairs, which play a critical role in water uptake (► Sect. 10.5), begin to appear. Root hairs can only develop after root elongation has ceased, or else they would be torn off as the root advanced through the soil. The growth of root hairs greatly increases the area of the root allowing for efficient uptake of water and mineral substances (Grierson et al. 2014), which can be delivered to the stele.

10.4 The Root Tip and Root Cap Control Rate and Direction of Root Growth

The early developing root that grows from a root apical meristem is protected by a renewing coat of terminal parenchyma cells designated as a **root cap** (◘ Fig. 10.4a–c). The origin of the root cap from the root apical meristem is described in ► Sect. 4.11.

In floating aquatic plants such as duckweed (◘ Fig. 10.4a), the root cap is quite distinct from the root tip, the only point of contact being at the tip of the root, which is where the root cap cells are generated. Duckweed (*Lemna* sp.) is a floating aquatic plant, and its root cap is a reasonably stable structure because it is not worn away by soil abrasion. In other plants, the root cap may be less evident and tightly adhered to the root tip (◘ Fig. 10.4b, c).

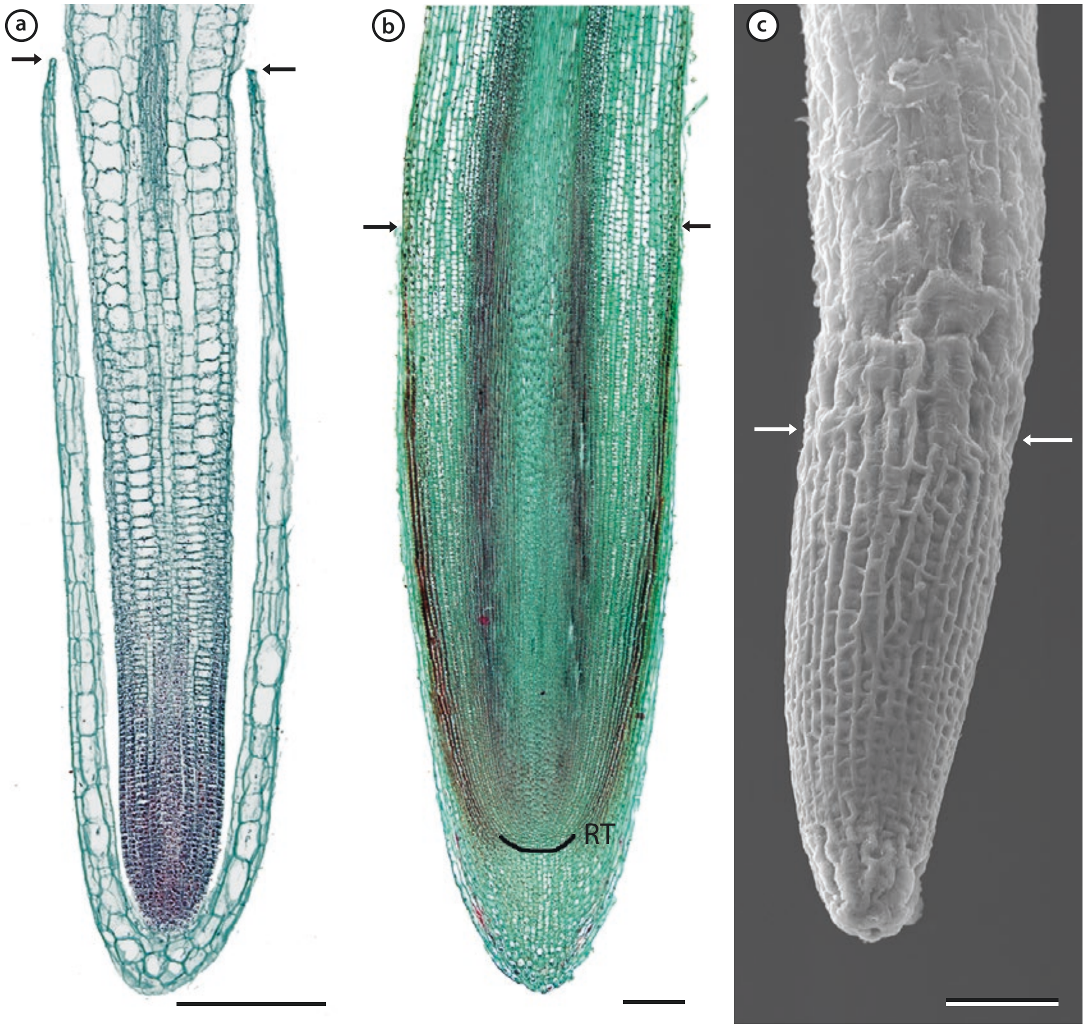


Fig. 10.4 **a**–**c** Root tips with root caps. **a** The duckweed (*Lemna* sp.) root cap, seen in longitudinal section, is easily distinguished from the root tip. **b** Longitudinal section of pea (*Pisum sativum*) root tip and **c** SEM of thale cress (*Arabidopsis thaliana*) root tip. The terminus of the pea root tip (RT) is shown by the black line in **b,** and the upper extent of all three root caps is indicated by single-headed arrows. Scale bars = 100 µm in **a** and **b** and 50 µm in **c**. (**a**–**c** RR Wise)

The zone of division encompasses the protoderm that becomes the rhizodermis (a.k.a. epidermis) of the root, the ground meristem that develops into the cortex, and the procambium that in turn produces primary xylem and phloem. The outer root cap cells produce a slimy substance called **mucigel** via **exocytosis** from numerous dictyosomes that traverse the cell wall and pass to the outside surface of the root. The mucigel lowers friction between the root and soil particles during root growth and contains root cap cells that have been sloughed off (Fig 10.4d). Those cells maintain a living protoplasm even after detachment from the root cap but eventually are lost and die. Mucigel is a lubricating product composed primarily of glycoprotein-rich compounds and pectins. It also contains carbohydrates and proteins that aid in the support of bacterial growth (Fig. 10.4d, e). The mucigel/microbe/rhizosphere is an ecosystem in and of itself that benefits both the plant and the microbes (York et al. 2016).

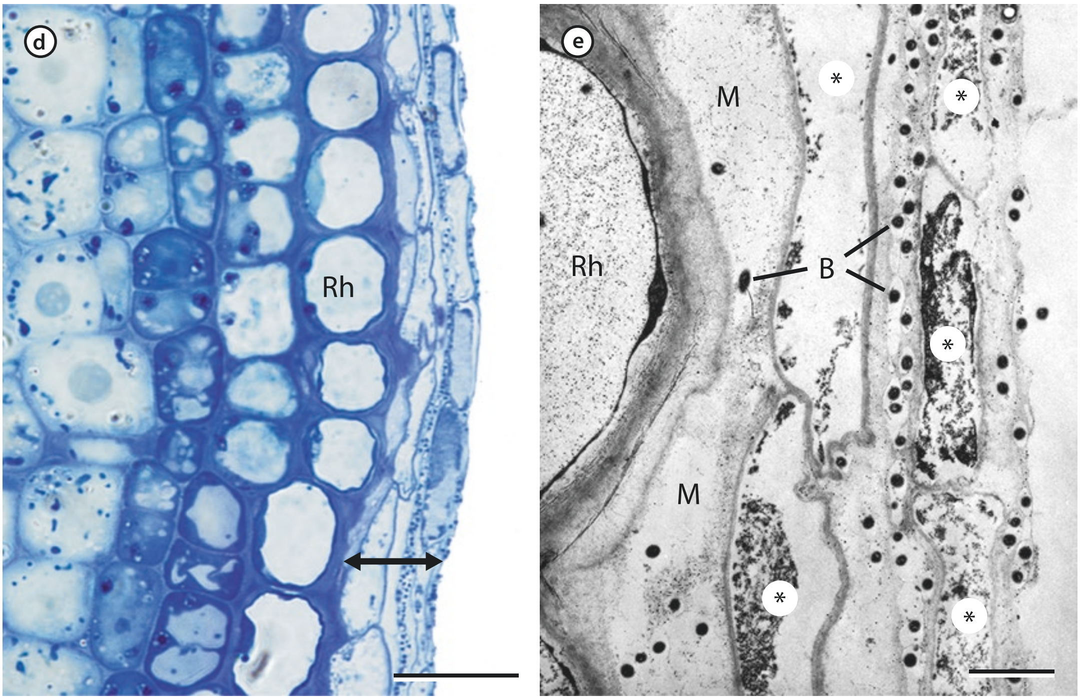


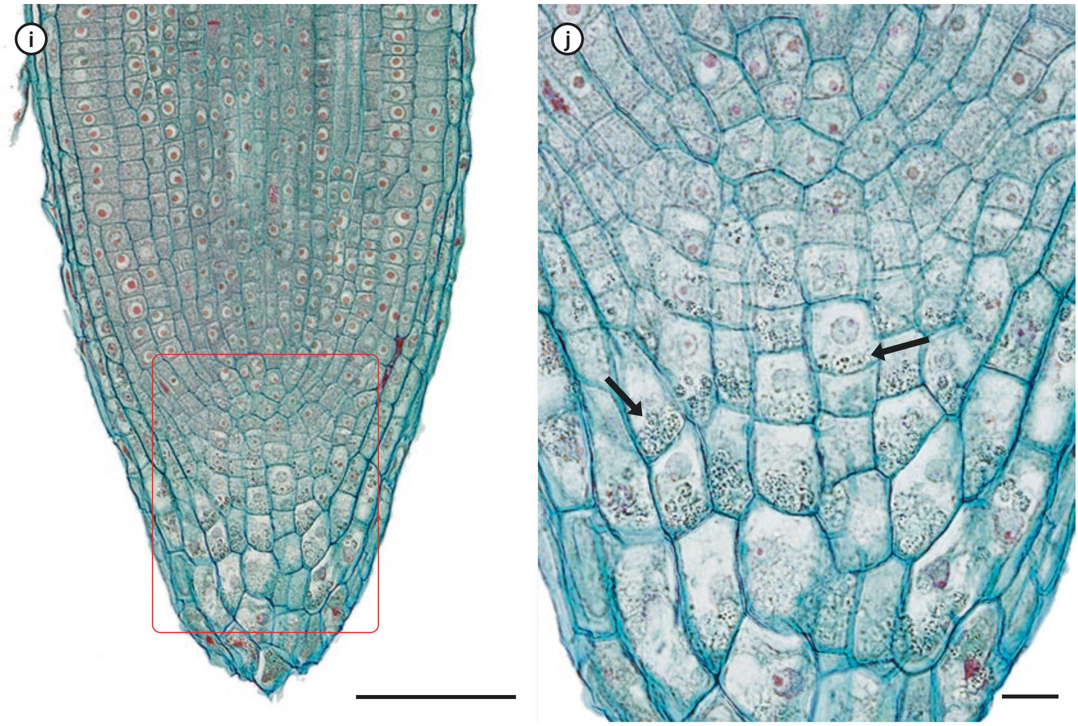
Fig. 10.4 **d** LM of the margin of a sweet potato (*Ipomea batatas*) root tip. The root cap cells and mucigel (double-headed arrow) lies to the outside of the rhizodermal (Rh) of the root proper. **e** TEM of bacteria in mucigel of sweet potato root tip showing one large rhizodermal cell (Rh). Five root cap cells are indicated by (*). Numerous bacteria (B) are scattered throughout the mucigel (M). Scale bars = 10 µm in **d** and 2 µm in **e**. (**d**, **e** RR Wise)

Gravity is one of the major environmental cues sensed by roots. Positive **gravitropism** describes growing in the direction of the gravitational vector, i.e., down. The embryo has a definite shoot end (plumule) and root (radicle) end (refer to ► Chap. 19). During germination, the radicle emerges first and grows down (Fig. 10.4f), with the shoot emerging slightly later. If the seed is germinated with the radicle pointing up, the root still grows down, and the shoot (lagging behind) grows up (Fig. 10.4g). A seed germinated in the upright position develops normally, but when oriented perpendicular to gravity, senses the change and once again grows downward (Fig. 10.4h).

Gravisensing takes place in the **columella**, a region of specialized cells at the center of the root cap (Fig. 10.4i). Cells of the columella have a large number of amyloplasts (Fig. 10.4j). As described in ► Sect. 3.5.4, amyloplasts are starch-containing plastids. For the vast majority of amyloplasts in a plant, the stored starch, upon remobilization, represents a major food source for both plants and animals because starch is a polymer of high-energy glucose monomers. Starch is also heavy, and the amyloplasts in the columella sink, or settle, in response to the gravitational vector. Therefore, the amyloplasts of the columella are usually referred to as **statoliths**, meaning "static rock," to differentiate them from those amyloplasts that function exclusively in starch storage. Likewise, the statolith-containing cells of the columella are termed **statocytes** to highlight their function in gravisensing.

◘ **Fig. 10.4** **f**–**h** Maize (*Zea mays*) seeds germinated while facing different gravitational vectors. **f** Seed was positioned with radicle end pointed down, toward the gravitational vector. The root (R) grew toward gravity (down), and the shoot (S) grew away from gravity (up). Note that the root, which started growing first, is longer than the shoot. **g** The seed was germinated with the radicle end pointed up. The root grew up until it developed a root cap, then it sensed gravity and grew down. The shoot grew up. **h** Germination was started with the seed radicle pointing down, as in **f**. After 4 days, the seed was rotated 90° counterclockwise. The root grew down (to the right) initially, then changed direction upon reorientation of the seed. Scale bar = 1 cm. (**f**–**h** RR Wise)

The change in growth direction seen in ◘ Fig. 10.4h can be followed experimentally. When a plant is positioned on its side, such that the root tip is perpendicular to the direction of gravity, the statoliths sink to the new bottom cell wall. In a short time (e.g., a few hours), the shoot or root will show growth in the new vertical direction (refer to ◘ Fig. 10.4a–c). In *Arabidopsis* sp., laser ablation of the central columella cells with the most amyloplasts caused the strongest inhibitory effect on root bending (Blancaflor et al. 1998). When amyloplasts settle to the bottom of the gravity-sensing cells in the columella, they physically contact the endoplasmic reticulum (ER). This causes the release of calcium ions from inside the ER. Such calcium signaling in the cells in turn brings about polar transport of the plant hormone indole acetic acid (IAA) to the bottom of the cell. Polar IAA transport from cell-to-cell is mediated by transmembrane transporters. In roots, a high concentration of IAA inhibits



■ **Fig. 10.4** **i, j** Tomato (*Solanum lycopersicum*) root tip in longitudinal section. **i** The red box indicates the area of Figure 10.5. It includes the bottom of the root tip and the region of the columella. **j** Starch-containing amyloplasts (arrows) have settled to the bottom of the columella cells. Scale bars = 50 µm in **i** and 5 µm in **j**. (**i, j** RR Wise)

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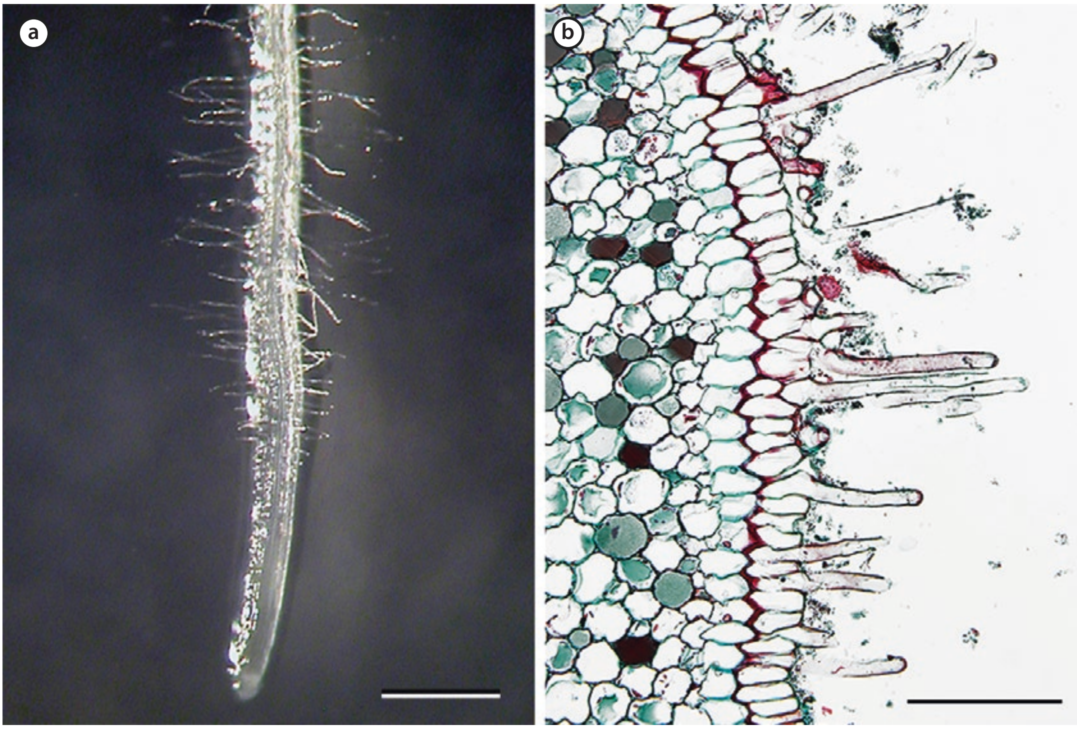
cell elongation. The effect slows cell elongation on the lower side of the root, while cells elongate normally on the upper side resulting in positive gravitropism. IAA has the opposite effect in shoots, where a higher concentration at the lower side of the shoot stimulates cell expansion and causes the shoot to grow upward (negative gravitropism). The role of the shoot endodermis in negative gravitropism is described in the Stems Chapter, ► Sect. 11.5.

The growth phenomenon described above results in positive gravitropism. However, not all roots grow straight down. In secondary, tertiary and higher-order lateral roots, the root cap senses the gravitational vector per normal but directs a different growth response. Some roots exhibit ortho-gravitropism and grow parallel to gravity. Others are diagravitropic (grow 90° from parallel), plagiogravitropic (~45° from parallel), or agravitropic (no response to gravity at all). All of these responses combine to direct the final three-dimensional shape of the overall root system.

10.5 The Root Rhizodermis Interacts Directly with the Soil

It should be noted that many authors use the term "epidermis" for the outermost layer of root tissues in the primary state of growth. However, it is more appropriate to utilize the term rhizodermis



◘ **Fig. 10.5** **a** Root hairs on the primary root of the lyre-leaved cress (*Arabidopsis lyrata*). Note that root hairs are not found at the root tip; the hairless regions represent the zones of division and elongation. **b** Cross-section of an anthurium (*Anthurium* sp.) root showing root hairs. Scale bars = 200 µm in **a** and 100 µm in **b**. (**a**, **b** RR Wise)

(sometimes called the **epiblem**), since this tissue in root systems functions very differently from that of stems and leaves. In its underground state, the rhizodermis has no stomata, it is specialized for the absorbance of water and mineral substances, it produces mucigel as a lubricant, and it is never covered by a cuticle but develops short-living root hairs. Secondary development may lead to multiple layers and heavy sclerification. Because of these significant structural and functional differences with the epidermis of leaves and stems, the designation of "rhizodermis" will be employed in this text regarding root anatomy.

A rhizodermis differs from the root periderm in that the rhizodermis arises during primary growth from the protoderm, or from protoderm derivatives. The periderm arises from a phellogen that develops de novo in the root **pericycle**. Initiation and development of the root phellogen is discussed in ► Sect. 16.2.

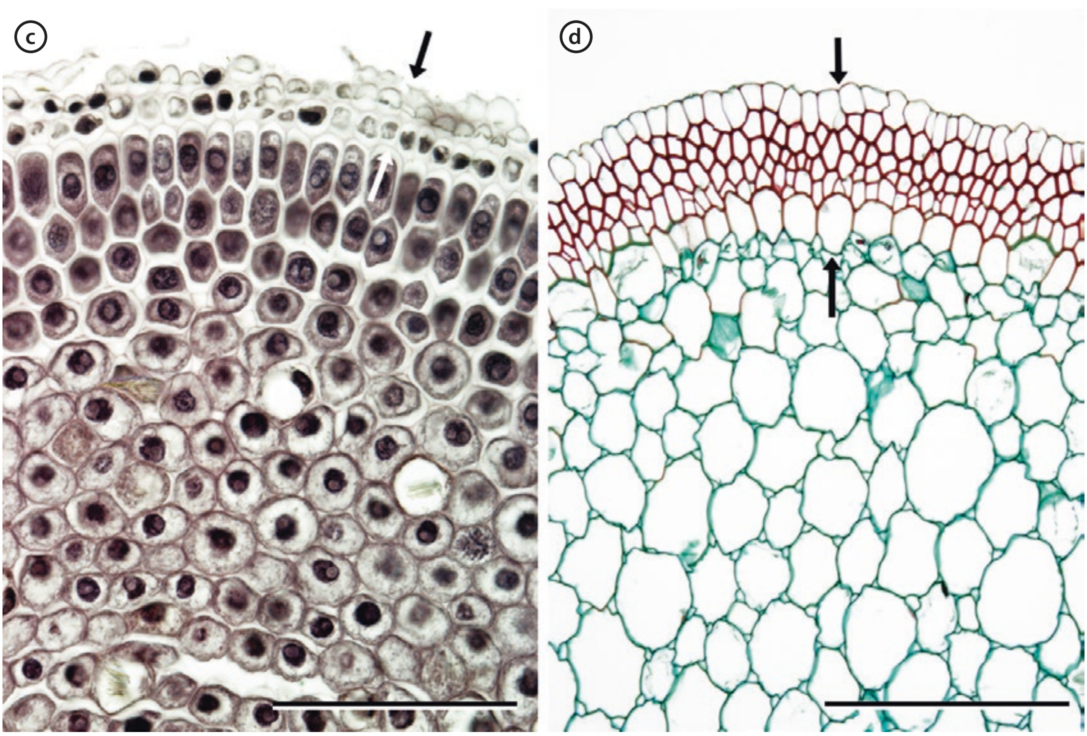
The rhizodermis in the primary state of growth is quite different anatomically from that in the secondary state of growth. Primary growth represents an opportunity for roots to increase in length in search of exploitable resources of water and minerals. Therefore, they are specialized for uptake with root hairs being a major route for the entry of water and minerals. Secondary growth involves strengthening the root to provide maximum anchorage.

Root hairs begin to develop near the root tip (◘ Fig. 10.5a, b) but only after that area of the root has achieved maximum elongation (refer to ► Sect. 10.3). They arise from rhizodermal cells positioned over the radial cell wall between cortical cells. The root hairs start from a protuberance at the apical end of elongate rhizodermal cells via tip growth (Ryan et al. 2001). For growth to occur, there is a demand for a rich Ca^{+2} gradient and dictyosome transport producing vesicles with newly formed cell wall materials to fuse with the cell membrane. Cells of the rhizodermis giving rise to root hairs are termed **trichoblasts**, whereas those that do not produce root hairs are designated as **atrichoblasts**. Most root hairs only survive for 1 or 2 days but by that time the root tip has elongated and new root hairs have developed (Grierson et al. 2014).

It is no coincidence that the zone of maturation, where root hairs develop, is also the area where the developing stele is the most permeable. Xylem, phloem, and the endodermis mature at this same level, giving the water and ions taken up by the root hairs a path of least resistance to the xylem transpirational stream.

Upon further development, multiple rhizodermal layers may arise, as is common in the irises (◘ Fig. 10.5c). The multiple layers are not a true periderm because they are the products of cell divisions in the rhizodermis, not in the phellogen (refer to ► Sect. 10.9).

Epiphytic orchids have a multilayered rhizodermis called the **velamen** (◘ Fig. 10.5d). A typical velamen has an outer layer of cells and an inner layer (or layers) of heavily sclerified cells, the



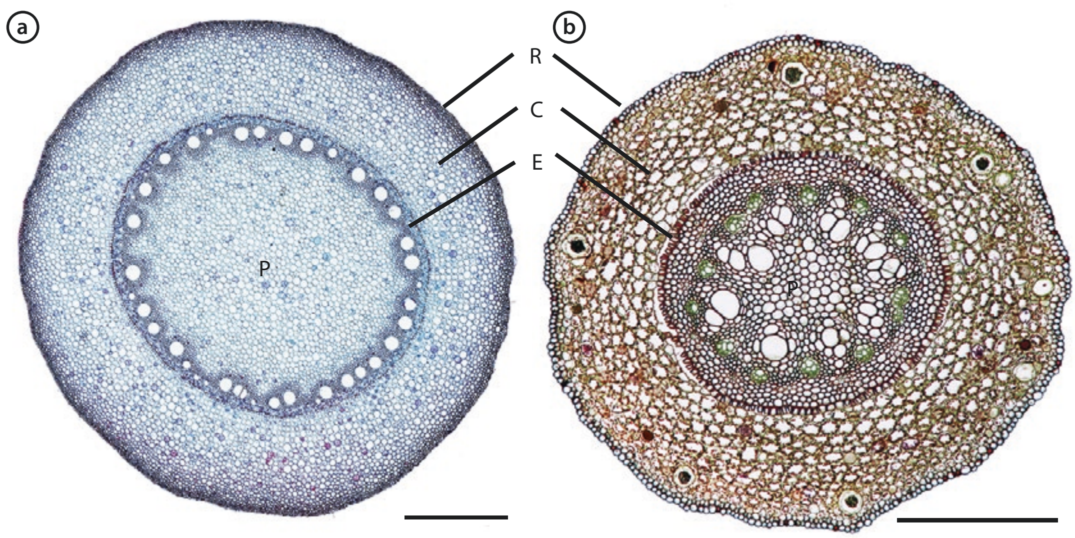
◘ **Fig. 10.5** **c** Iris (*Iris domestica*) roots have a multiple-layered rhizodermis, indicated as the region between the white and black arrows. **d** Aerial roots of orchids (unidentified species) have a velamen (layers of cells between the two black arrows). Note the lignified (stained red) cell walls of the inner layers of the exodermis. Scale bars = 50 µm in **c** and 100 µm in **d**. (**c**, **d** RR Wise)

exodermis (◘ Fig. 10.1c). The velamen serves to protect the root from transpirational loss as well as binding the root to the underlying substrate. In addition, it also absorbs atmospheric moisture and ions (Zotz and Winkler 2013) as well as providing a protection from harmful sunlight UV-B irradiation (Chomicki et al. 2014). The velamen arises from the root apex through a series of divisions that leave most of the cells dead upon maturity.

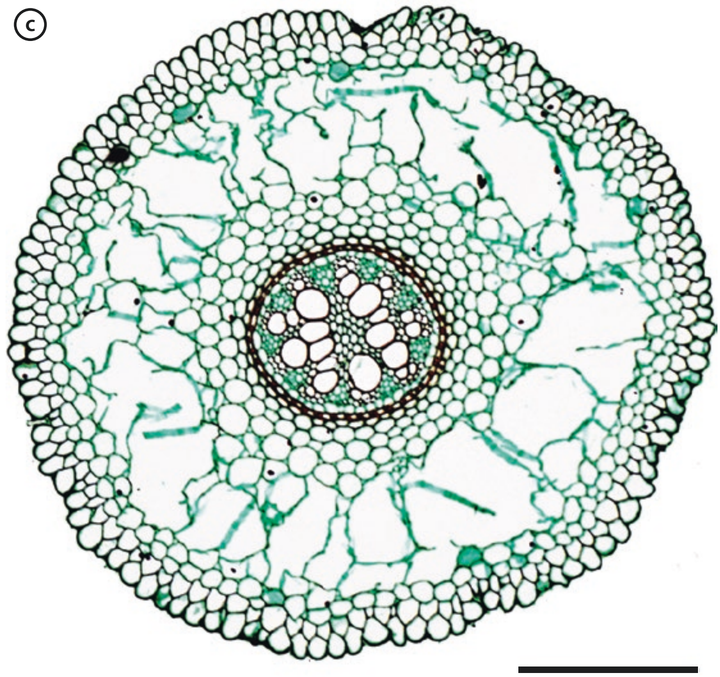
Monocot roots do not show secondary growth and therefore are incapable of periderm development. The outer layers of persistent roots may become thicken and become cutinized and lignified. Eudicot roots do show secondary growth (refer to ► Sect. 10.9) with perennial eudicots such as willow (*Salix* sp.) and pear (*Pyrus* sp.) generating a de novo phellogen that produces a bona fide periderm (refer to ► Chap. 16—Periderm).

10.6 The Root Cortex, Limited by the Endodermis, Is a Site of Storage and Oxygen Transport

The root cortex is parenchymatous tissue derived from the ground meristem. The root cortex, in keeping with its role in storage, is often much larger than the stem cortex. The cortex may become heavily sclerified in older monocot roots. It is bounded by rhizodermis or exodermis to the exterior and endodermis to the interior (◘ Fig. 10.6a, b). For many roots, it is the main site of starch storage, as can be seen in the *Ranunculus* roots shown in ◘ Fig. 10.7b, c. It may contain resin ducts, crystals, or other inclusions. Also, the cortex is the site of aerenchyma (◘ Fig. 10.6c) in those roots that function in gas exchange (◘ Fig. 10.1d).



◘ **Fig. 10.6** **a**, **b** Cross-sections of **a** maize (*Zea mays*) root and **b** greenbrier (*Smilax* sp.) root. R, rhizodermis; C, cortex; E, endodermis; P, pith. Scale bars = 500 µm. (**a**, **b** RR Wise)



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◼ **Fig. 10.6** **c** Aerenchyma in the cortex of lily (*Lilium michiganense*) root. Scale bar = 250 µm. (RR Wise)

The cortex is limited to the interior by the **endodermis**, a structure found in almost all roots, but much less so in stems (► Sect. 11.6). As described in ► Sect. 10.1, the endodermis is a single layer of cells that does not permit the free flow of water and ions between the individual cells but rather forces such materials to cross a cell membrane. This is due to presence of a Casparian strip (named for Johann Robert Caspary, a German botanist who lived from 1818–1887), which is a band of suberized lignin and proteins that covers the radial and transverse (anticlinal) walls of the endodermis. It is a component of the primary cell wall. Its presence forces the water and solutes to pass from the apoplast through the plasma membrane via a symplastic route to cross the endodermis. In monocots, the entire cell may develop thick deposits of suberin as the root matures. After entering the endodermal cells, the water can then move freely to the xylem where it is swept upward to the leaves in a stream of transpirational flow (refer to ► Sect. 10.1). **Passage cells** (sometimes called transfusion cells) lack the heavy suberization and provide for a diffusional pathway with less resistance. They tend to be located at the ends of the xylem poles (◼ Fig. 10.6d).

In most instances, xylem water is under tension (the opposite of pressure); water is pulled through a plant from the soil to the leaves by the evaporation or water from the leaves (transpiration is explained in ► Sect. 7.2). The root endodermis allows for the development of xylem pressure—called **root pressure**—the only instance in which xylem water is not under tension. Root pressure develops because the ions that are moved across the endodermis and loaded into the stele are osmolytes. That is, they bind water. This lowers the water potential of the xylem water and draws additional water into

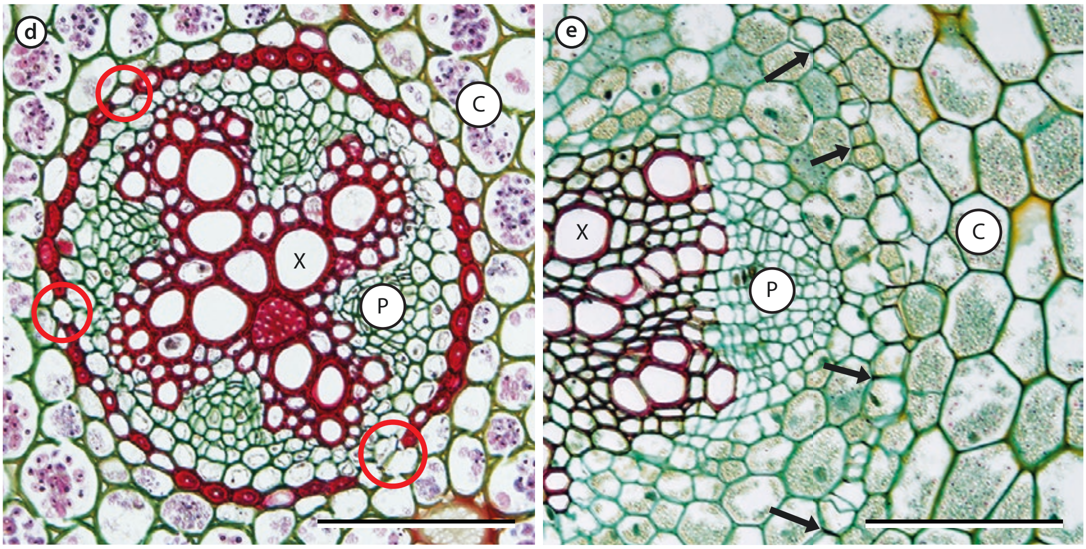


Fig. 10.6 **d** The entire endodermis in buttercup (*Ranunculus acris*) is seen in this view as a dark red circle separating the cortex (C) to the outside from the phloem (P) and xylem (X) on the inside of the stele. The endodermis has heavily suberized cell walls. A Casparian strip is present but obscured by the lignin (stained red) in the thick cell walls. Three passage cells are indicated by the red circles at 5:00, 9:00, and 11:00. **e** A portion of the endodermis in baneberry (*Actaea spicata*) is shown at a higher magnification. The endodermal cell walls are not suberized, and the Casparian strip appears as dark bands on the anticlinal cell walls (arrows). The phloem (P) is to the outside of the xylem (X) indicating that it is a product of the vascular cambium (refer to ▶ Sect. 10.9). *Ranunculus* and *Actaea* are both in the Ranunculaceae. Scale bars = 50 µm in **d** and 100 µm in **e**. (**d**, **e** RR Wise)

the stele, generating a slight pressure. Root pressure is insufficient to push water more than a few centimeters up a stem; whereas xylem tension is capable of pulling water to the top of a 100-meter tree. As such, it plays little to no role in whole plant transpiration, unless the plant is very short. Root pressure is responsible for the phenomenon of **guttation**, the forcing of water out of leaf hydathodes (▶ Sect. 13.1.5). Guttation is most often seen early in the morning, before stomata have opened, and transpiration has the opportunity to develop a tension in the xylem.

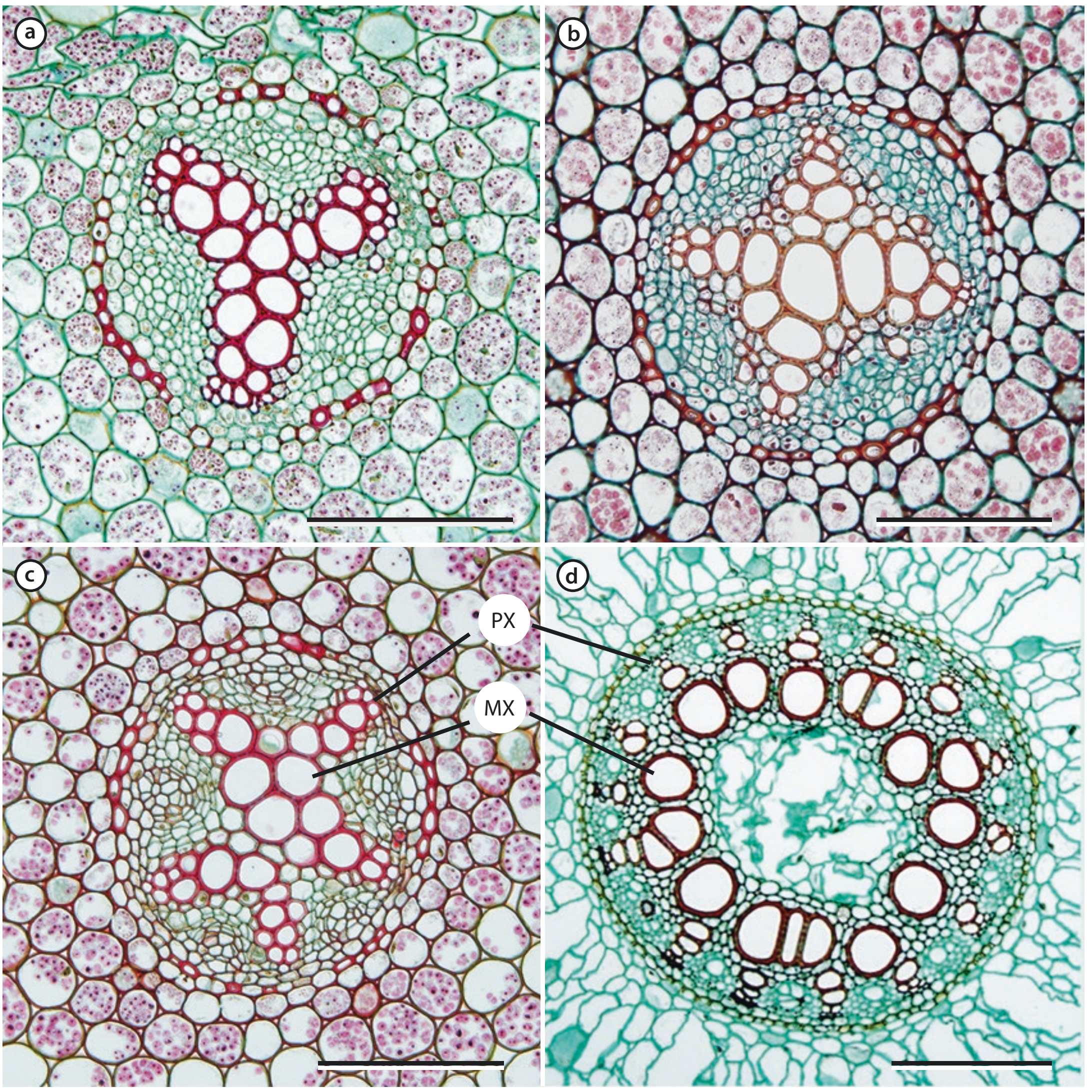
The exodermis lies between the rhizodermis and cortex. Not all roots have an exodermis; an example is shown in the orchid root in ◘ Fig. 10.5d. The exodermis is a functional equivalent of the endodermis. It may be suberized, cutinized, and contain Casparian strips on the anticlinal walls. Like with the endodermis, water and ions must pass into the symplast of the exodermis cells to enter the root cortex (◘ Fig. 10.6e).

10.7 The Stele Contains the Pericycle and the Xylem and Phloem of the Vasculature

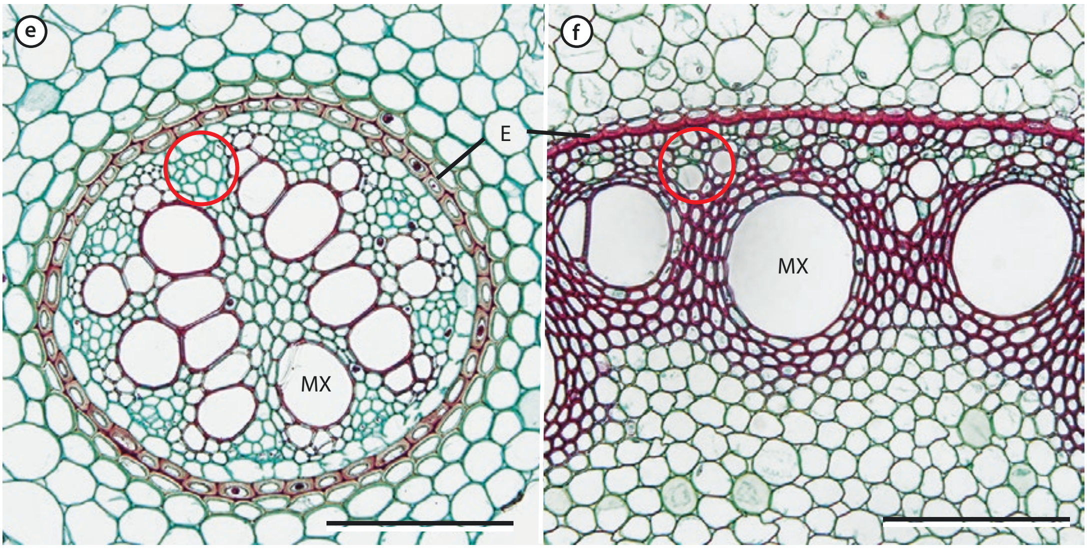
The central vascular cylinder of the root is called the stele, similar in concept to the stele found in many stems (refer to ▶ Chap. 11). The root stele is bound by the endodermis to the exterior and contains xylem, phloem, parenchyma (in some but not all cases), and a meristematic layer, the pericycle, which is the source of lateral roots.

Unlike stems in which the vascular tissues are arranged in discrete bundles of xylem and phloem and spread throughout the stem, all of the root vasculature is a more or less solid cylinder of xylem in the middle with phloem to the exterior. Thus, most eudicot and monocot steles are protosteles. Pith is rare in eudicots as it gets crushed early on in root development but somewhat common in monocots (refer back to ◘ Fig. 10.6a, b).

Root xylem is arranged in a spoke-like pattern with the number of spokes, or "xylem poles," being characteristic of the taxon. Eudicots typically have discrete xylem poles. A two-arm pattern is called **diarch**, followed by **triarch**, *tetrarch*, **pentarch**, and up to as many as eight poles (◘ Fig. 10.7a–c). Monocots are typically **polyarch** with numerous xylem poles arranged in a more or less ring



◘ **Fig. 10.7** **a**–**d** Images of **a** a triarch stele in a buttercup (*Ranunculus acris*) root, **b** tetrarch buttercup stele, **c** pentarch buttercup stele, and **d** polyarch asparagus (*Asparagus officinalis*) stele with multiple individual groupings of xylem. PX, protoxylem; MX, metaxylem. Scale bars = 100 µm in all panels. (**a**–**d** RR Wise)



◘ **Fig. 10.7** **e** Stele in a lily (*Lilium michiganense*) with nine patches of phloem (one is circled) in between metaxylem (MX) groupings. **f** Edge of the stele in a maize (*Zea mays*) root showing the scattered nature of the phloem to the exterior of the metaxylem (MX). Scale bars = 100 µm in both panels. (**e**, **f** RR Wise)

shape at the periphery of the stele and a central pith (◘ Fig. 10.7d). Larger monocot roots have a polyarch with so many xylem poles that they may be called an atactostele (for "scattered" xylem).

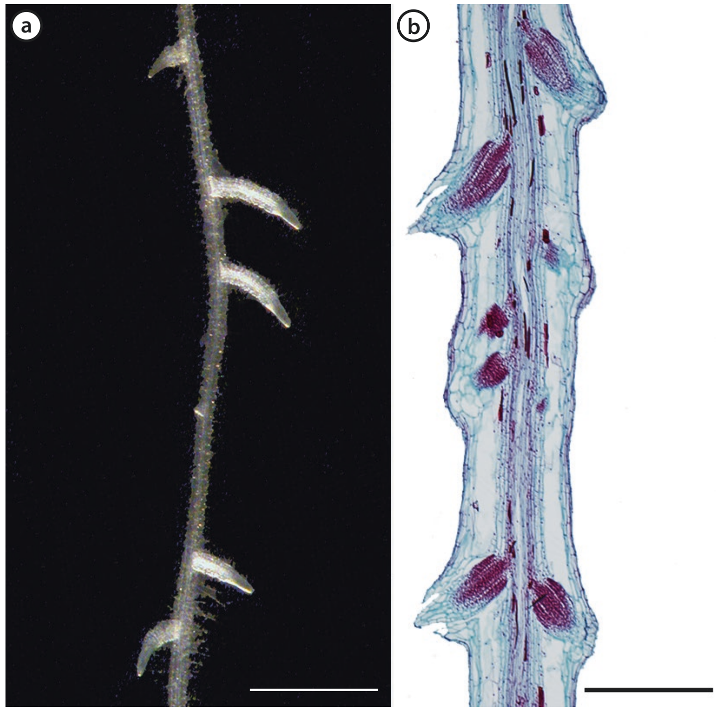
Monocot and eudicot roots both have an exarch pattern of vascular development with protoxylem to the exterior and metaxylem to the interior (◘ Fig. 10.7c, d). [Note that stem vascular development is endarch, ► Chap. 11].

In terms of phloem distribution, primary phloem in eudicot roots is positioned between the xylem arms, as seen in *Ranunculus* (refer back to ◘ Fig. 10.6d). Monocot distribution is similar but the polystelic nature of monocot roots results in individual groupings of xylem with phloem arranged in patches in between the groupings or scattered to the outside of the xylem (◘ Fig. 10.7e, f).

The pericycle is a single layer of parenchyma cells lying just inside the endodermis in all roots. They are prominent and can be seen in most of the figures in this section. Pericycle cells are meristematic and the source of all lateral roots (refer to ► Sect. 10.8). They also contribute to the vascular cambium and cork cambium in those roots that exhibit secondary growth (► Sect. 10.9).

10.8 Lateral Roots Originate in the Pericycle and Push Through the Cortex

Lateral (or **branch**) roots develop off of an existing root, starting just behind the zone where root hairs senesce (◘ Fig. 10.8a, b). In terms of length, quantity, and volume, they represent the vast majority of roots in a root system. Primary laterals arise from a taproot, secondary laterals arise from primary, tertiary from a secondary, and so on. In contrast to the shoot where branches originate

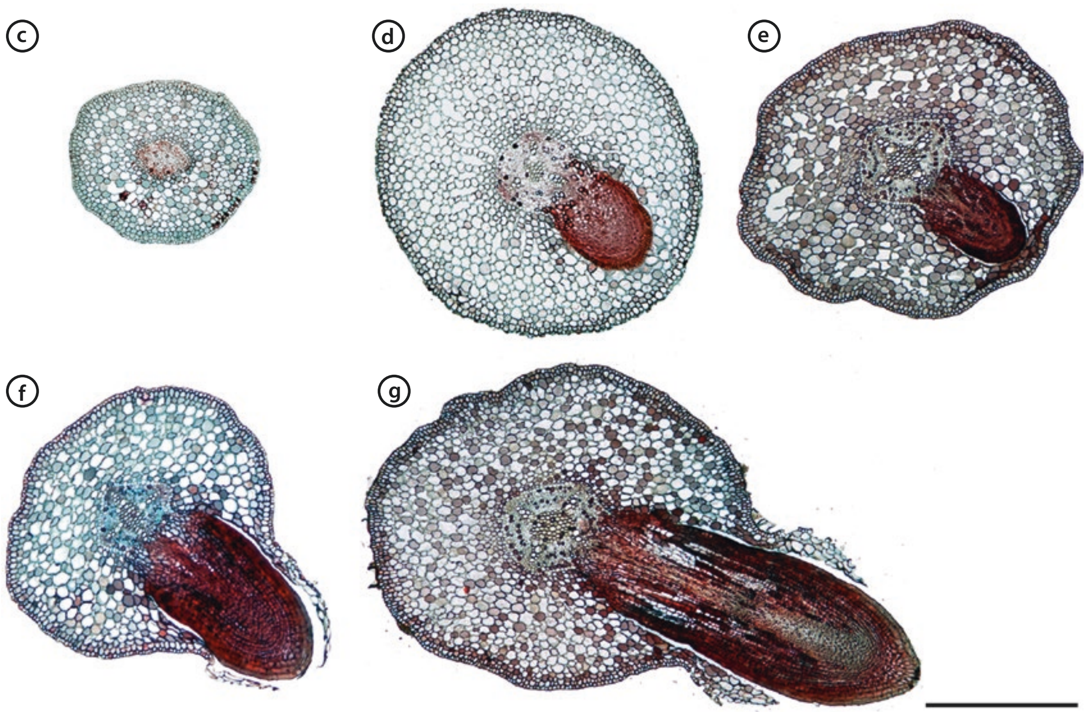


◘ **Fig. 10.8** **a** Lateral roots arising from the primary root of a lyre-leaved cress (*Arabidopsis lyrata*) seedling. Although the root caps cannot be seen at this magnification, the root tips are bending down, indicating that functional root caps are present on all of the developing lateral roots. **b** Longitudinal section of a black willow (*Salix nigra*) root. Each of the red protrusions is a developing lateral root. Scale bars = 2 mm in **a** and 250 µm in **b**. (**a**, **b** RR Wise)

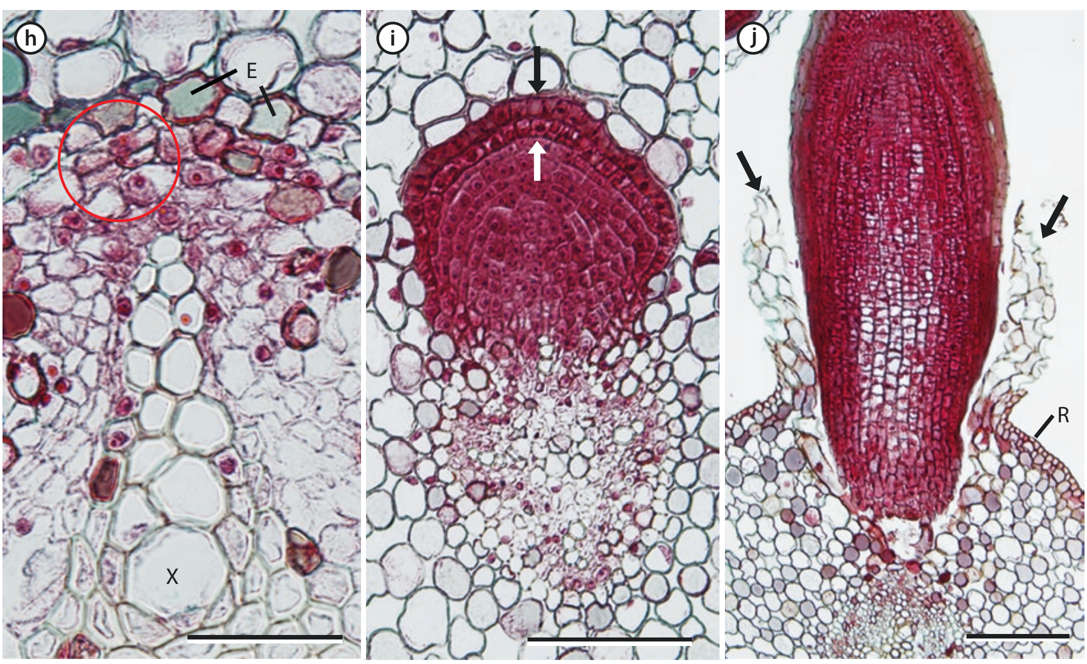
exogenously from the apical meristem, lateral (or branch) roots are initiated **endogenously** in the pericycle without any relation to the apical meristem (◘ Fig. 10.8c–g).

Typically, the point of origin of a lateral root is opposite to the xylem in eudicots and opposite to the phloem in monocots. Here, the pericyclic cells become densely cytoplasmic and resume meristematic activity. This growth occurs through repeated periclinal cell divisions from a few cells designated as founder cells (◘ Fig. 10.8h). The lateral root primordial growth must penetrate the endodermis, cortex, exodermis, and the rhizodermis in order to appear on the surface of parental root. These tissues are stretched and finally ruptured (◘ Fig. 10.8d–f). A root cap meristem develops when root tip is about halfway through the cortex (◘ Fig. 10.8i) and is well defined by the time the root emerges. The exit hole causes damage that is sealed off with a special corky layer surrounding the new lateral root (◘ Fig. 10.8j). Cells of the emerging lateral root develop into xylem and phloem and connect to the vasculature in the stele of the parent root.

The reason for the inability of the root apical meristem to produce lateral roots, and for that function to occur further back in the root via the pericycle, no doubt has to do with the nature of the substrate through which roots grow. Shoots can generate both primary growth and new organs at the shoot tip because they grow through air. There is no resistance to growth. Root tips, on the other



■ **Fig. 10.8** **c**–**g** A sequence of light micrographs of willow (*Salix* sp.) lateral roots arising from the central vascular stele. Scale bar = 0.5 mm. (**c**–**g** RR Wise)

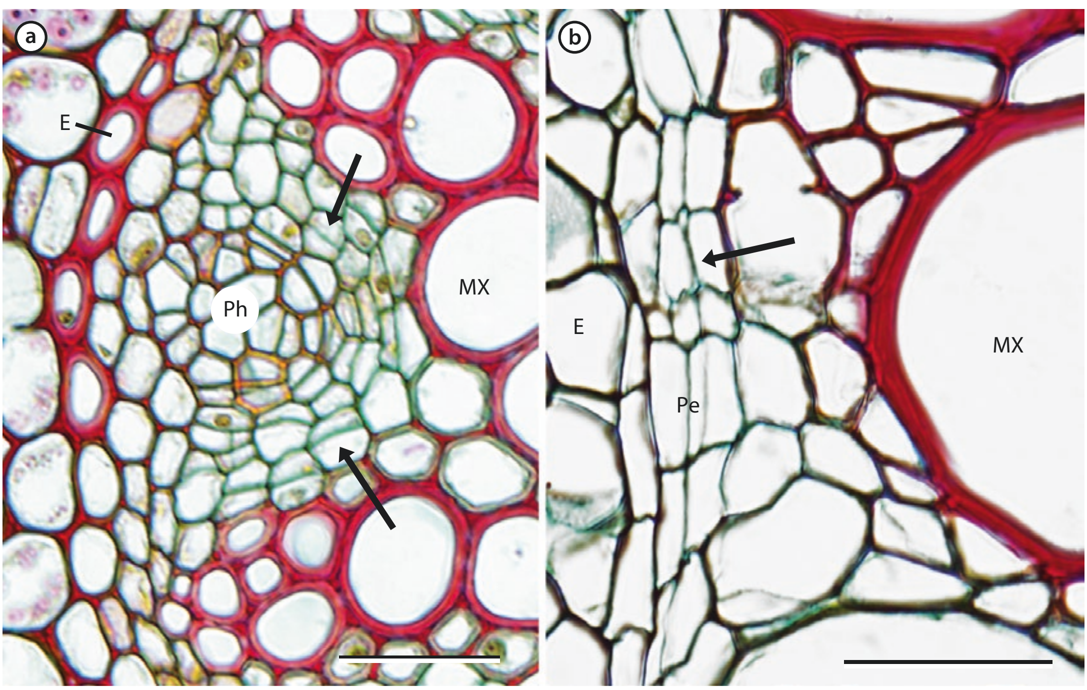


■ **Fig. 10.8** **h**–**j** Root development in black willow (*Salix nigra*). **h** Very early stage in lateral root development. Two pericycle cells (in red circle) opposite the xylem (X) arm are dividing in a periclinal plane. The endodermis (E) lies to the outside of the pericycle. **i** At a later stage, the root tip is about halfway through the cortex and has developed a root cap two cell layers thick (between arrows). **j** After pushing through the rhizodermis (R), the hole in the parent root is sealed by a collar of corky cells (arrows). Scale bars = 25 µm in **h**, 50 µm in **i**, and 100 µm in **j**. (**h**–**j** RR Wise) hand, have to push through soil as they engage in primary growth (i.e., elongate). If lateral roots were produced at the root apex, they would be torn off as the tip pushed through the soil. Lateral roots are initiated further back on the developing root, in a region that is no longer undergoing elongation.

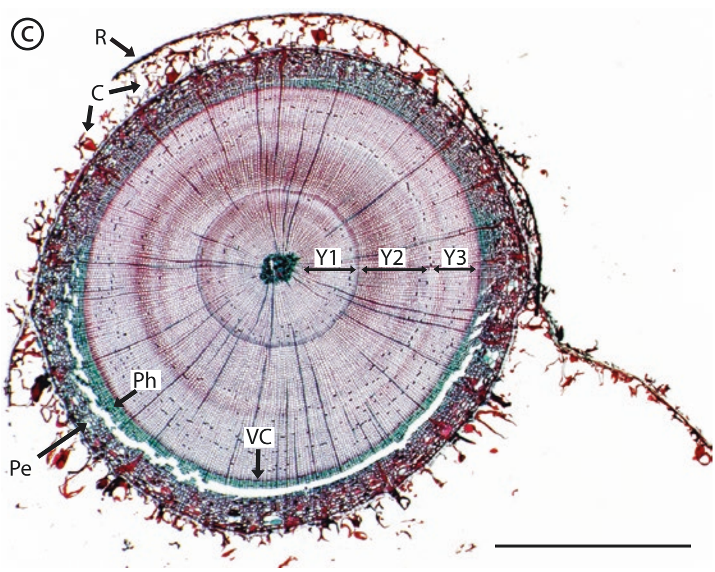
10.9 The Transition from Primary to Secondary Growth in Roots Involves the Development of Two New Meristems

The roots of gymnosperms and woody eudicots exhibit secondary growth. Doing so requires the development of two meristems—a vascular cambium (to produce secondary xylem and phloem) and a phellogen (to replace the rhizodermis with a corky periderm)—both of which must form a continuous cylinder or meristematic tissue. The phloem and the pericycle play roles in the origin of these secondary meristems.

The first step is the differentiation of phloem cells at the inner edge of the protophloem strands into **cambial initials** capable of generating xylem to the inside and phloem to the outside (◘ Fig. 10.9a). Subsequently, pericycle cells to the exterior of the protoxylem poles also divide to produce more new cells of the vascular cambium (◘ Fig. 10.9b). Eventually, the two groups of dividing cells will merge to form a circular meristem and complete an encompassment of the primary xylem.



◘ **Fig. 10.9** **a** Phloem (Ph) cells in a buttercup (*Ranunculus acris*) root exhibiting meristematic activity by dividing in a periclinal plane (arrows). The phloem sits between two metaxylem (MX) arms and is bounded by the endodermis (E) to the exterior. **b** Pericycle (Pe) cells dividing in a periclinal plane (arrow) and contributing to the vascular cambium in a potato (*Solanum tuberosum*) root. Endodermis (E) is to the exterior and metaxylem (MX) to the interior. The cortex is to the left in both images. Scale bars = 25 µm in both panels. (**a**, **b** RR Wise)



◘ **Fig. 10.9** **c** A cross-section of a woody gymnosperm (*Metasequoia glyptostroboides*) root showing a central decomposed pith region of the primary growth and 3 years of secondary growth (Y1, Y2, Y3) with wood rays extending in all directions. Just outside a layer of vascular cambium (VC) is the living secondary phloem (Ph, stained green), and to the outside there is a well-developed periderm (Pe). The original cortex (C) and rhizodermis (R) are in the process of shedding. Scale bar = 1 mm. (RR Wise)

The vascular cambium arises from the inner cells of this new meristem, while the phellogen arises from the outer cells. A periderm consisting of cork toward the outer surface and phellogen (cork cambium) toward the inner surface develops. Both the vascular cambium and the phellogen divide periclinally (as a new wall is formed parallel to the root surface) and anticlinally (with a new wall developing perpendicular to the root surface) which together produce cells that form the thickened root. Note that as in the case of stems (refer to ► Chap. 11), secondary growth is not found in monocots or herbaceous eudicots.

All of the tissues outside of the pericycle, which include the rhizodermis, exodermis, cortex, and endodermis, eventually die and are shed (◘ Fig. 10.9c). The pericycle-derived phellogen generates the periderm for the remaining life of the root. As the vascular cambium becomes active at the start of each growing season, the production of new xylem and phloem increases the girth of the root. With multiple layers of xylem, the root may also become woody and reveal growth rings as in stem wood.

10.10 Symbioses Between Roots/Bacteria and Roots/Fungi Greatly Enhance Nutrient Acquisition

Nitrogen is one of the most essential elements for life as it is a component of nucleic acids, proteins, amines, and a variety of other compounds. Many of these are not only required for the plant, but for other forms of life, as well as in commercial products. While nitrogen makes up 80% our atmosphere, it is not readily available for uptake and use by most organisms since it exists as an essentially inert gas (N_2) due to a triple covalent bond between two nitrogen atoms. In order for N_2 to be made available to organisms, it must be chemically reduced and combined in the form of ammonium (NH_4) in a process called nitrogen fixation.

The electrical energy of lightning produces a small amount of nitrogen fixation in the atmosphere via physical nitrogen fixation (PNF). Biological nitrogen fixation (BNF) is carried out by living organisms, all of them prokaryotic. A few of the BNF bacterial taxa are free-living; however, the largest flux of bioavailable nitrogen into the ecosystem comes from bacteria that form a symbiotic association with plants. In brief, the following reaction represents a summary of the process:

$$N_2 + 8H^+ + 8e^- + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP + 16Pi$$

where N_2 = nitrogen gas, H^+ = hydrogen ions, e^- = electron, ATP = adenosine triphosphate, NH_3 = ammonia, H_2 = hydrogen gas, ADP = adenosine diphosphate, and Pi = inorganic phosphate. Nitrogenase is the enzyme responsible for catalyzing this reaction.

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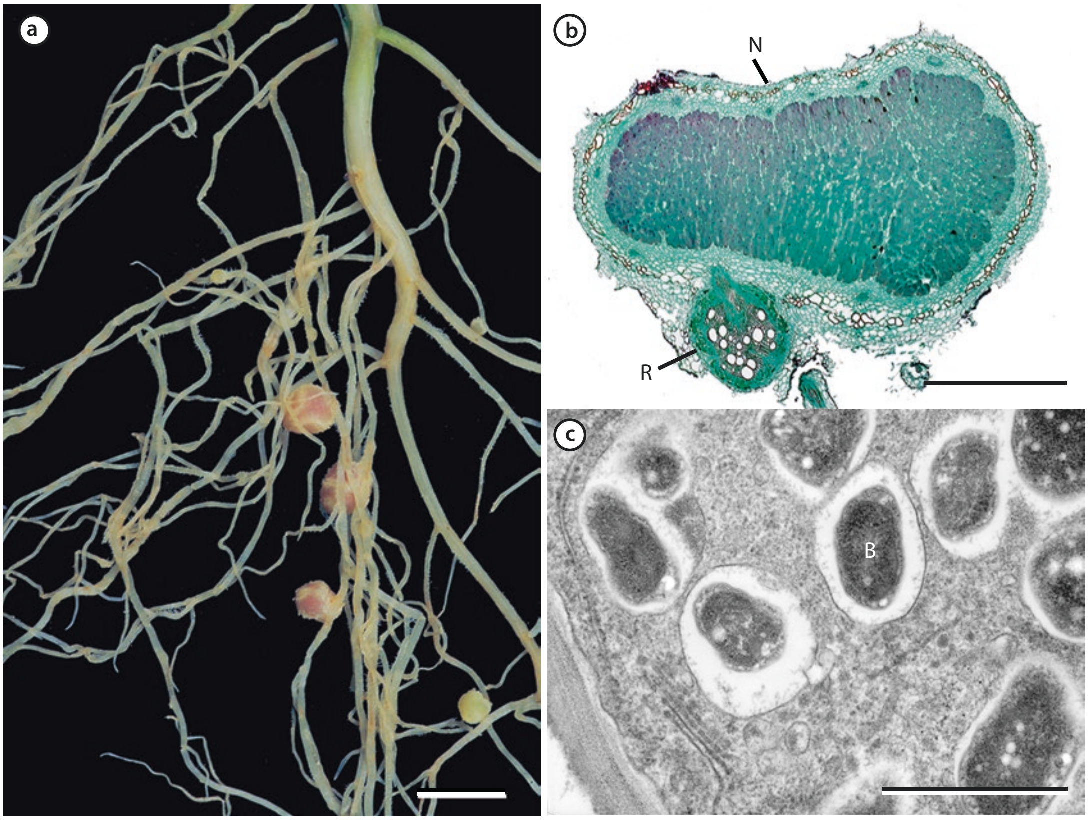
Although BNF symbioses can be found across the kingdom Plantae, including some tropical grasses (*Azosprillium*) and the aquatic fern *Azolla*, the majority, and the best studied, are in association with members of the family Leguminosae and involve species of *Rhizobium* bacteria. The bacterium receives carbohydrates from the plant, and the host plant obtains nitrogen in a bioavailable form from the bacteria.

Rhizobium bacteria are found free-living in the soil, but they must infect a plant root to be capable of nitrogen fixation. Roots release molecules into the rhizosphere that attract the bacteria (homoserine, in the case of *Pisum sativum*). Bacteria are attracted to the signal and move toward the root (positive chemotaxis). Bacteria accumulate in the rhizosphere and multiply. Bacteria release "nod factors" (small polymers of chitin derivatives) that stimulate root hair production. The bacteria release mitogenic signals that stimulate cytokinin production and initiate the formation of a meristem in the cortex of the root, called the primary nodule meristem. The root pericycle becomes active and grows outward, eventually fusing the root vasculature with that of the nodule. Bacteria penetrate the wall of the root hair by secreting pectinase, cellulases, and hemicellulases and grow an "infection thread" through the root hair toward the developing nodule in the root cortex. Growth of the primary nodule meristem pushes the entire mass out of the root to form a large nodule (◘ Fig. 10.10a) filled with bacteria (◘ Fig. 10.10b). The bacteria are "released" into the symplast of the plant cortical cells by budding off of infection thread but never technically enter the cytoplasm. The cells are surrounded by a bit of the infection thread membrane that further thickens by the inclusion of polysaccharides from the host plant into a "peribacteroid membrane" (◘ Fig. 10.10c). The vasculature of the host plant grows to and supplies the nodule with xylem and phloem.



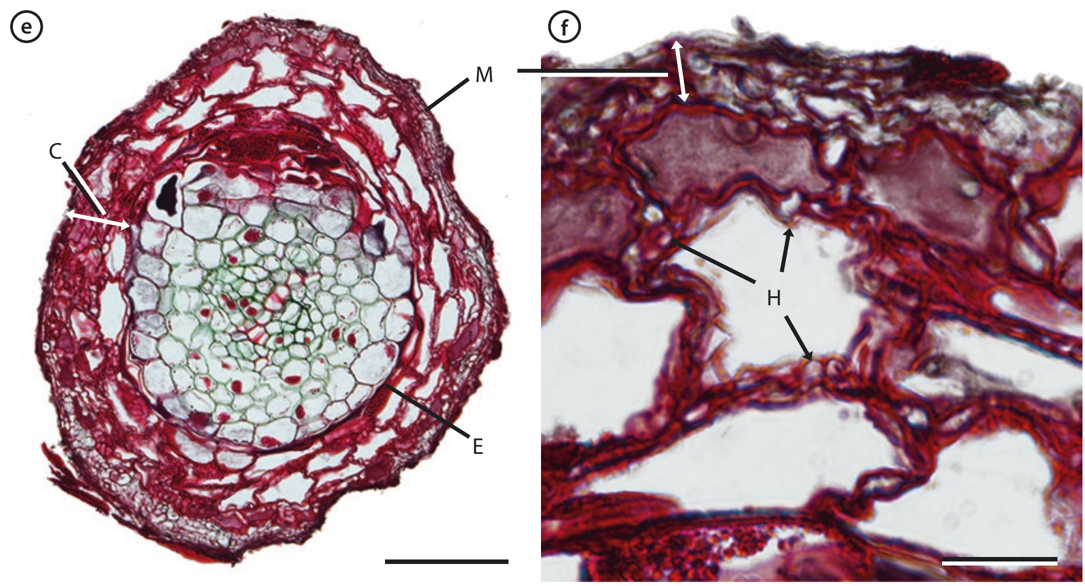
■ **Fig. 10.10** **a**–**c** Root nodules. **a** *Robinia pseudoacacia*. Note red leghemoglobin in the nodules. **b** Soybean (*Glycine max*) root nodule. R, root; N, nodule. **c** TEM of bacteroides (B) in a soybean nodule. Scale bars = 1 cm in **a**, 500 μm in **b**, and 1 μm in **c**. (**a**, **b** RR Wise; **c** L Howard, Dartmouth Electron Microscope Facility, public domain)

Nitrogen fixation usually begins around 10–14 days after the nodules have formed and is mediated by a multienzyme complex called nitrogenase. The energy (in the form of 16 ATP per N_2 fixed) is supplied by plant mitochondria using carbohydrates supplied by the phloem. Nitrogenase is exquisitely sensitive to oxygen. Therefore, the plant synthesizes a red, heme-containing, oxygen-binding protein called leghemoglobin. It is responsible for the pinkish color of the nodules seen in ■ Fig. 10.10a and reduces the oxygen levels within the nodule. Mitochondria can operate at O_2 levels too low to inhibit nitrogenase, so the respiratory supply of ATP is maintained. The NH_3 (ammonia) formed by nitrogenase is toxic. It is converted to amine groups which are used immediately in the synthesis of glutamate, glutamine, or a variety of transportable amino acids (this takes place in the nodule proplastids, refer to ► Sect. 3.5.1). The amino acids are loaded into the xylem and transported throughout the plant via the transpiration stream.

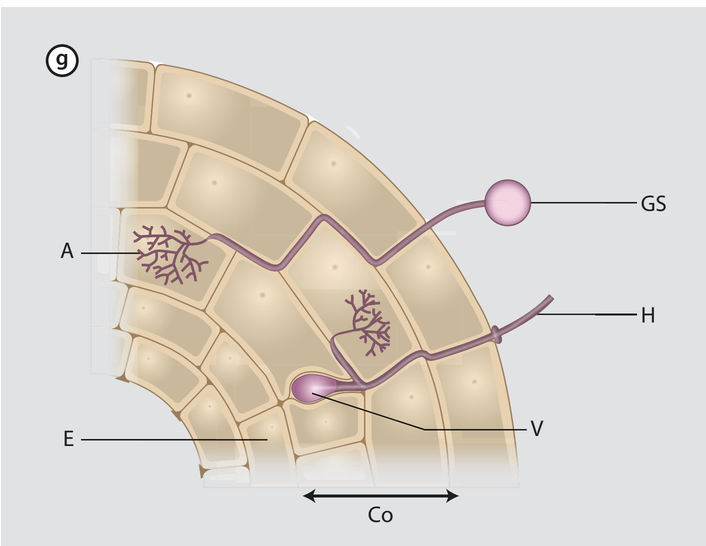
A second form of symbiotic relationship exists between plant roots and fungi. The vast majority of plants—perhaps up to 80%—form symbiotic associations with fungi that provide them with better access to soil nutrients while also providing a defense of diseases and toxic substances (Ercolin and Reinhardt 2011). Such an association is termed mycorrhization (myco, fungus; rhiza, root). It is of benefit to both partners because the plant obtains phosphates and other minerals while simultaneously providing the fungus with sugars and other organic foods. Plants that benefit the most from mycorrhizal associations are those which grow on nutrient-poor soils. The fungi indirectly increase the active surface and absorbent area of the root since the symbiotic fungi effectively spread further through the soil. Additionally, many of the mycorrhizal fungi not only form a physical barrier to the presence of pathogens but also may provide antibiotic compounds against them.

There are two basic forms of mycorrhizae: ectomycorrhizae and endomycorrhizae. Ectomycorrhizal fungi ("outside" root fungus, EMF) infection initiates the formation of short roots that are specialized in nutrient uptake (◘ Fig. 10.10d, Martin et al. 2016) and form a covering of hyphae on the outside of those roots called a mantle (◘ Fig. 10.10e). They also penetrate the root tissue and grow through the apoplastic (cell wall) spaces inside the cortex, forming a structure called the **Hartig net** (◘ Fig. 10.10f). While the fungus is indeed inside the root, it only grows in the cell wall space and does not penetrate into the cells (◘ Fig. 10.8d, e). Thus, the "ecto" (outside) prefix technically applies, even though the fungus is inside the root.

◘ **Fig. 10.10** **d** Ectomycorrhizae on the surface of a blue spruce (*Picea pungens*) root. Note the cluster of short lateral roots (arrow) covered by a thick mantle of light-brown fungus. The lateral root to the top is not heavily infected. Scale bar = 1 mm. (RR Wise)



■ **Fig. 10.10** **e**, **f** Mantle and Hartig net in a pine (*Pinus* sp.) root. **e** The mantle (M) is a thin layer on the root surface. Then entire root cortex (C) is infected with the fungal hyphae of the Hartig net (stained red), but the fungus does not cross the endodermis (E) and enter the stele. **f** The individual hyphal cells (H) of the Hartig net can be seen occupying the apoplast of the cortical parenchyma cells. Scale bars =50 µm in **e** and 10 µm in **f**. (**e**, **f** RR Wise)



■ **Fig. 10.10** **g** Drawing of an endomycorrhizal infection. A = arbuscule, Co = cortex, E = endodermis, GS = germinating spore, H = hypha, V = vesicle. (Modified from M. Piepenbring, CC BY-SA)

Endomycorrhizal fungi, on the other hand, grow into and penetrate individual root cells (■ Fig. 10.10g). Once there, the hyphae form hyphal vesicles or a branched structure called an arbuscule (from “arbor” or tree); therefore, endomycorrhizal fungi of this type are also called arbuscular mycorrhizal fungi (AMF). AMF are far more widespread than EMF. It should be recognized that although the VA hyphae penetrate the interior space of the cells, they do not penetrate the plasma membrane and enter the symplast. The "endo" prefix was applied by light microscopists because the arbuscules occupy the cell interior. The advent of electron microscopy allowed plant scientists to see that the fungus does not truly enter the cell protoplast, but the "endo" (inside) prefix prevails. Mineral ions, primarily phosphate, are concentrated in the arbuscule, which only is present for a short time, perhaps 3–8 days. The arbuscule develops, matures, accumulates minerals, and is then absorbed by the host. Subsequent arbuscules may form in the same cell.

Box 10.2 An Ancient Symbiosis Within a Symbiosis Involving Transkingdom Gene Transfer

Arbuscular mycorrhizal fungi (AMF) infect the roots of host plants in a symbiotic relationship. The fungal partner (a member of the Kingdom Fungi) receives photosynthate from the host plant (Kingdom Plantae), and the host receives soil nutrients from the fungus. Curiously, there are numerous reports of a symbiotic bacterium (*Mollicutes*-related endobacteria or MRE—Kingdom Eubacteria) being hosted within the cytoplasm of some endomycorrhizal fungi, making for a three-partner, three-kingdom symbiosis. Torres-Cortés et al. (2015) further investigated this relationship by performing a genome analysis of an MRE hosted by *Dentiscutata heterogama*, a common AMF. The bacterial partner has a greatly reduced metabolic activity, as evidenced by a paucity of genes for energy production and conversion, carbohydrate transport and metabolism, and inorganic ion transport and metabolism. Several bacterial genes show similarity to genes found in a known AMF genome, and a very large group of bacterial genes have eukaryotic-like domains that are likely to serve regulatory functions within the eukaryotic host. Both observations strongly suggest horizontal gene transfer from the fungus to the bacterium and the ability of the bacterium to directly influence fungal physiology. This fungal/bacterial symbiotic relationship, and its somewhat novel transkingdom gene transfer, is an ancient partnership, perhaps as much as 400 million years old.

Reference: Torres-Cortés et al. (2015).

10

10.11 Chapter Review

■ Concept Review

10.1. *Roots and root systems serve multiple purposes.* Roots function in water and mineral ion uptake, anchorage, storage, and as the source of hormones that play key roles in root-to-shoot communication. The pathway for water and ions can take an apoplastic or a symplastic route to the stele. The endodermis directs the movement of ions from the apoplast into the symplast.

10.2. *Root system morphology is diverse and adapts to soil conditions* via *compensatory growth.* Eudicots have a taproot system, while gymnosperms and monocots have a fibrous root system. Lateral roots arise from the primary taproot. The primary root system of monocots is replaced by a secondary root system of adventitious, proper roots. Root growth responds to local soil conditions via compensatory growth to maximize access to water and minerals and avoid salinity, drought, and flooding.

10.3. *Primary growth of roots involves formation of tissues and their organization.* The root tip is covered by a protective root cap. The slimy mucigel it secretes and the cells it sheds lubricate and ease the passage of the root through the abrasive soil. The zone of division is the source of new cells. The zone of elongation pushes the root forward. Cells differentiate into their mature state in the zone of maturation.

10.4. *The root tip and root cap control the rate and direction of root growth.* The columella of the root cap senses gravity by the action of amyloplasts (statoliths) that settle in response to the gravitational field. This movement initiates growth responses that direct to elongate in a specific direction, usually, but not always, down.

10.5. *The root rhizodermis interacts directly with the soil.* The rhizodermis must be permeable to water and ions, resist microbial infection and help anchor the root in the soil. Root hairs are transient extensions of rhizodermal cells that greatly increase the surface area for water and ion uptake. Aerial roots produce a velamen to protect the root tip from desiccation and take up water and minerals.

10.6. *The root cortex, limited by the endodermis, is the site of storage and oxygen transport.* The root cortex lies between the rhizodermis and the endodermis and is used for storage and for providing a route for oxygen diffusion in flooded roots. The endodermis is an apoplastic barrier to the movement of water and ions from the cortex into the stele and is characterized by the presence of a Casparian strip in the radial cell walls. Root pressure develops inside the endodermis as a consequence of ion (and water) uptake by the xylem. The stele may be defined at the outer boundary by an exodermis, which lies just underneath the external rhizodermis. Some roots develop a polyderm, a multilayer of cells that develops internal to the endodermis and ultimately replaces the rhizodermis.

10.7. *The stele contains the xylem and phloem of the vasculature and the pericycle.* The eudicot stele has a star-shaped central core of xylem surrounded to the exterior by phloem in discrete patches. The xylem core may have two to eight arms or poles with the patterns named after the number of poles (diarch, triarch, tetrarch, pentarch). Monocots have numerous xylem poles and are termed polyarch. Patches of phloem are positioned between, and to the outside of, the xylem arms. The pericycle is the outer layer of the stele and is responsible for lateral root formation.

10.8. *Lateral roots originate in the pericycle and push through the cortex.* Lateral roots develop from existing roots. Lateral root development starts with meristematic divisions of pericycle cells and proceeds by pushing the developing root through the endodermis, cortex, and rhizodermis. The emergent lateral root has a fully developed root cap and is connected to the vasculature of the parent root.

10.9. *The transition from primary to secondary growth in roots involves the development of two new meristems.* In the transition from primary to secondary growth, cells to the interior of the phloem strands and exterior to the xylem poles become meristematic and produce a circular ring of diving cells in the root. Those cells to the interior of that ring mature into a vascular cambium which produces xylem and phloem. Those cells to the exterior of that ring mature into a phellogen, which produces the periderm. The original cortex and rhizodermis, which sit outside the new periderm, are shed.

10.10. *Symbioses between roots/bacteria and roots/fungi greatly enhance nutrient acquisition.* Plant roots have two major symbiotic relationships that greatly increase their ability of their root systems to access mineral resources—nitrogen-fixing bacteria and mycorrhizal fungi. In biological nitrogen fixation (BNF), bacteria capable of reducing gaseous nitrogen to the level of ammonia infect the roots of host plants, via root hairs. The host responds by initiating meristematic growth in the pericycle and the cortex. The large nodule that is produced is colonized by thousands of bacterial cells that engage in BNF. The host plant provides the carbohydrates needed by the bacteria, and the bacteria provide the host with reduced (bioavailable) nitrogen. Mycorrhizal fungi also infect plant roots. Ectomycorrhizal fungi cover the outside of the root and grow between the cells of the cortex. Endomycorrhizal hyphae penetrate the root cortical cells and develop tree-shaped arbuscules in which they accumulate minerals, mostly phosphorous. The arbuscules are short-lived, and the minerals they contain are absorbed by the host plant.

Concept Connections

1. On the figure below, label the root cap, three zones of differentiation, four meristems, and six mature tissues. Which of the mature tissues do each of the meristems give rise to?

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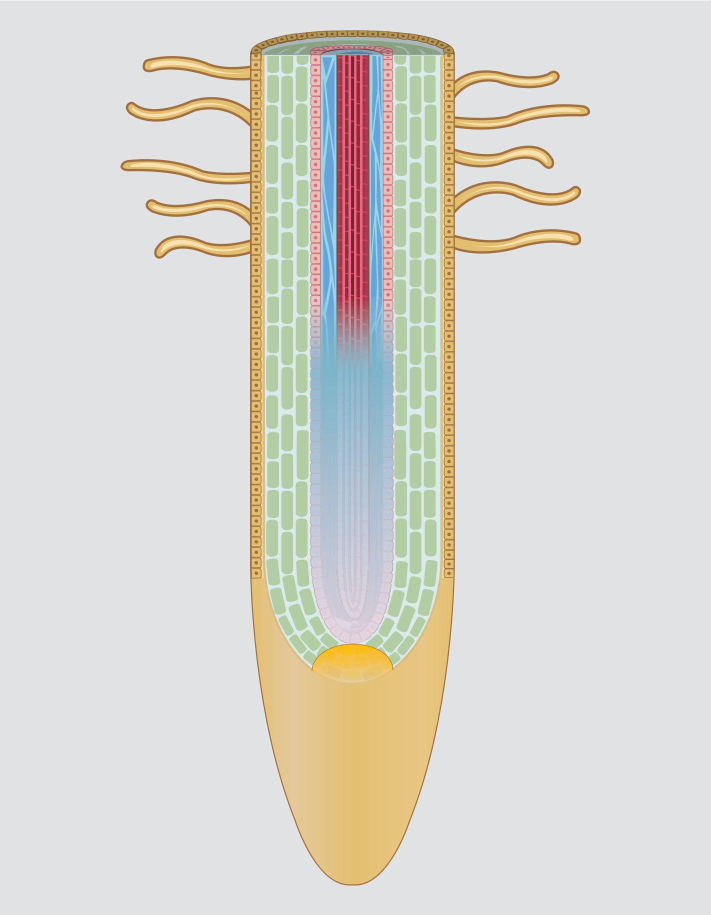

Concept Assessment

2. The exodermis is derived from cells of the
   a. rhizodermis.
   b. cortex.
   c. endodermis.
   d. pericycle.
   e. cambium.

3. The ability of roots to adjust growth to local soil conditions is called
   a. positive gravitropism.
   b. directional growth.
   c. trichoblast formation.
   d. compensatory growth.
   e. meristematic adjustment.

4. Dicot roots typically do not possess
   a. cortex.
   b. rhizodermis.
   c. pith.
   d. endodermis.
   e. pericycle.

5. Passage cells are found in which tissue?
   a. metaxylem.
   b. rhizodermis.
   c. endodermis.
   d. cortex.
   e. pericycle.

6. In eudicots, lateral roots typically initiate from the pericycle
   a. at sites of starch accumulation.
   b. at the protoxylem poles.
   c. between metaxylem cells.
   d. directly from the phloem.
   e. near endodermal passage cells.

7. The development of lateral roots is said to be
   a. endogenous.
   b. exogenous.

8. Cells of the columella
   a. are derived from procambium.
   b. are meristematic.
   c. are adapted for absorption.
   d. possess statoliths.
   e. are derived from ground meristem.

9. The root vascular cambium arises from the
   a. endodermis.
   b. exodermis.
   c. phellogen.
   d. pith.
   e. pericycle.

10. In biological nitrogen fixation and mycorrhizal associations, the microbe receives ___________ and the plant receives ___________.
   a. minerals … water.
   b. ions … carbohydrates.
   c. photosynthate … nitrogen or phosphate.
   d. nitrogen … phosphate.
   e. carbohydrate … ions.

11. A velamen is
    a. formed inside of an exodermis.
    b. a multiple rhizodermis.
    c. characterized by containing a Casparian strip.
    d. found in underground storage roots.
    e. composed of densely cytoplasmic cells upon maturity.

■ **Concept Applications**

12. It is very common in the horticultural trade to propagate plants via stem cuttings. Explain how a piece of stem can be used to regenerate an entire plant—stems, roots, and leaves. Why couldn't root cuttings be used in a similar fashion?

13. Growing tomato plants upside down in hanging buckets is quite the rage. Research and write a minute paper on the role root gravitropism plays in plants growing upside down.

References and Additional Readings

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Stems

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Introduction

Stems are typically aboveground organs that grow toward light (positive phototropism) and away from the ground (negative gravitropism). They provide support for the aerial portions of plants and serve multiple other functions in a plant. Stems play an important role as the conduits of the vascular tissues (xylem and phloem) needed for long-distance transport of water, minerals, photosynthetically derived sugars, and hormones. Indeed, the evolution of vasculature was one of the major advancements needed for plants to colonize the land. Accordingly, the evolution and design of the stem vascular system (a.k.a. **stele**) is of great interest to plant anatomists. This chapter will take an in-depth look at stem diversity and structure and introduce the basics of the plant vascular system.

11.1 Stems Have a Variety of Forms and Functions

One of the primary functions of a stem is the production of leaves and the proper arrangement of those leaves in space. Stems are also the organ from which flowers are generated and are held in the proper position for pollinators. Stems have tissues that provide a means to increase length (apical meristems), girth (lateral meristems), and additional branching (axillary buds). Roots can develop directly from a stem; such roots are called adventitious. By generating xylem and phloem, stems are a conduit for the long-distance transport of water, nutrients, and photosynthate and allow the leaves and the roots to engage in whole-plant communication (◘ Fig. 11.1a–c).

The stem is typically thought of as a long, thin projection from which leaves or flowers emerge. Indeed, that form is found on many extant plants and is the form to have evolved first. However, over time, natural selection produced several other forms and functions (◘ Fig. 11.1d–g). Flattened stems that lack leaves and perform photosynthesis are called **cladodes**; cactus "pads" are a common form. Cladodes that resemble leaves, such as those found on *Acacia* (Dong and He 2017), are also referred to as **cladophylls phyllodes** and **phylloclades**. **Rhizomes** are underground stems that can play the role of a root (anchorage and water uptake), allow for asexual reproduction, or serve as a storage organ as seen in the common potato tuber. **Stolons** differ from rhizomes in that rhizomes grow beneath the soil surface, while stolons grow across the soil surface. Stolons allow for plant dispersal and asexual reproduction. Stems may also serve as perennating organs. **Tendrils** may be modified leaves or stems that aid in attachment of viney plants. Stems may also serve as perennating organs. **Perennation** is the process of survival from one growing season to another as a perennial species. Rhizomes (or tubers) and **corms** (or bulbs) may also serve as perennating organs.

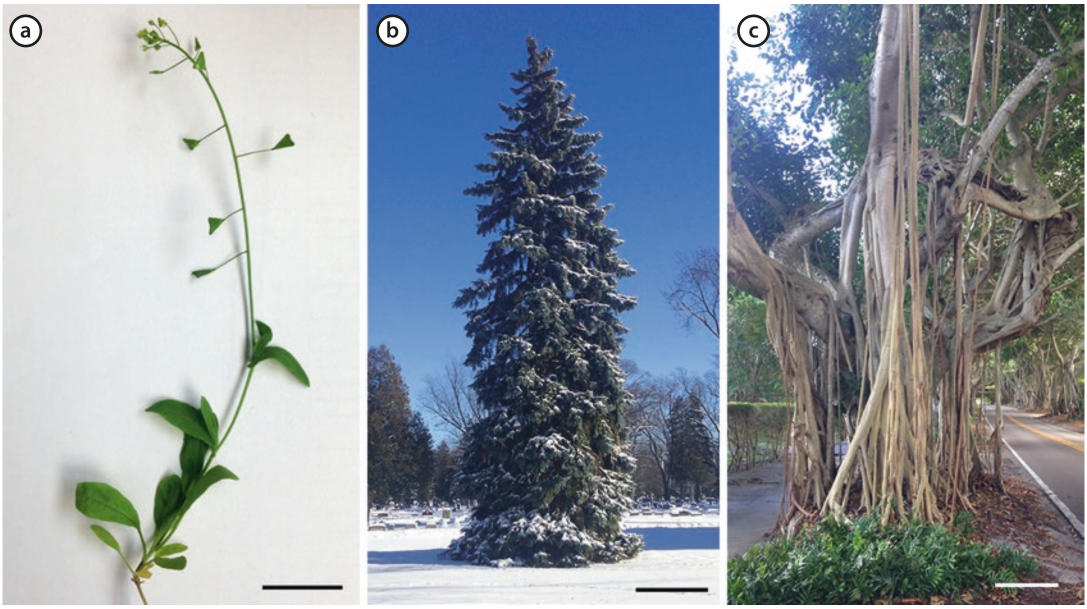


Fig. 11.1 Stems may serve multiple functions. **a** Shepard's purse (*Capsella bursa*) stems give rise to the leaves (L), flowers (Fl), and the fruit (Fr) that develop from flowers. **b** Tree stems provide the mechanisms for increase in girth as a tree develops over the course of time and provide the means to produce additional branching stem growth, as in white spruce (*Picea glauca*). **c** The banyan tree (*Ficus benghalensis*) starts as an epiphyte when an animal deposits a sticky seed on the limb of another tree. The plant develops roots that eventually reach the ground and send shoots up the host trunk. Subsequently, roots are initiated from the limbs, and growth extends outward from the original trunk. Scale bars = 2 cm in **a**, 2 m in **b**, and 1 m in **c**. (**a**–**c** RR Wise)

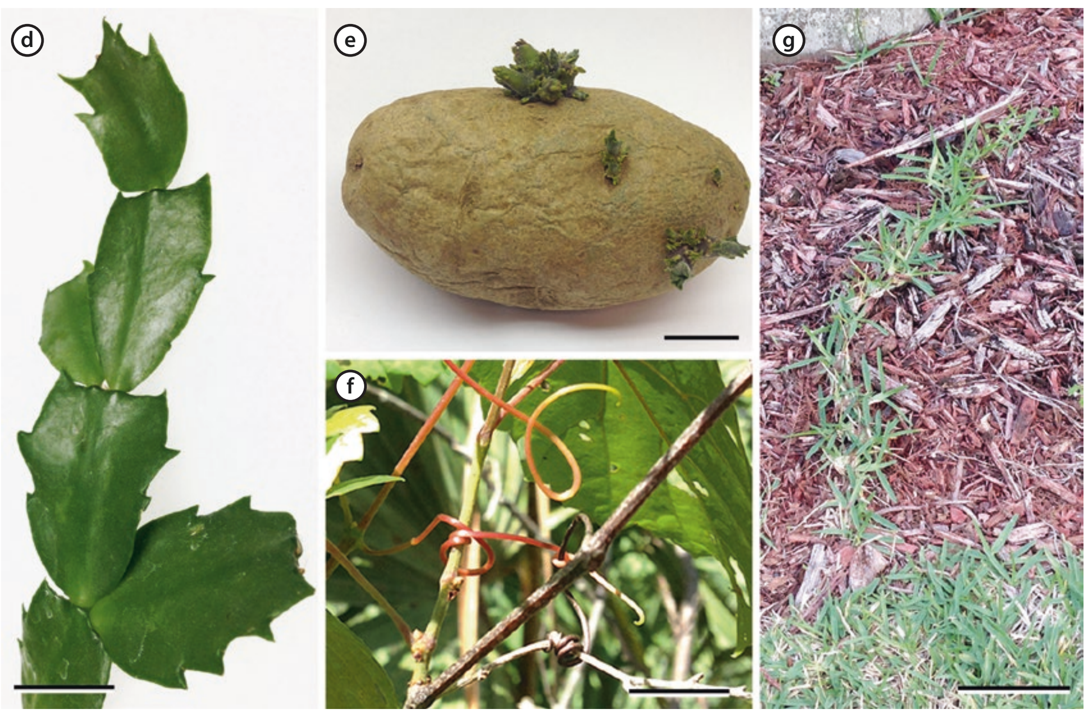
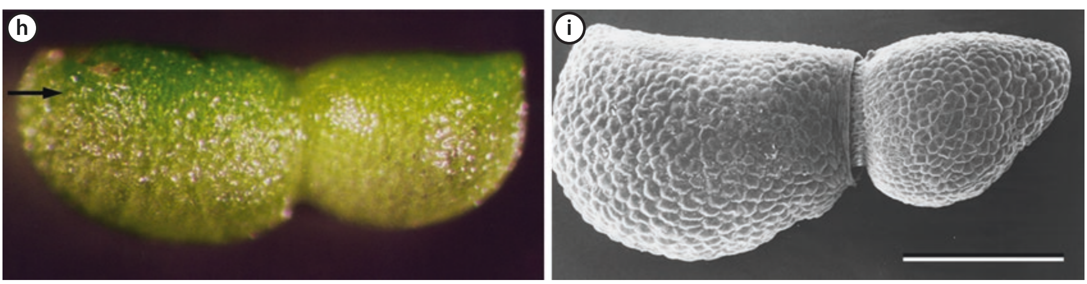


Fig. 11.1 **d** Cladodes of a Christmas cactus (*Schlumbergera* sp.) are clearly photosynthetic. **e** Rhizomes, such as potato (*Solanum tuberosum*) tubers, are underground stems that often function in starch storage. **f** Tendrils are modified stems that help passionflower (*Passiflora* sp.) vines climb up and cling to surfaces. **g** Stolons of St. Augustine grass (*Stenotaphrum secundatum*) grow across the soil surface and are a form of both plant dispersal and asexual reproduction. Scale bars = 2 cm in **d**, **e**, and **f** and 10 cm in **g**. (**d**–**g** RR Wise)

Not all plants possess a stem. For instance, the much-reduced members of the duckweed family (Lemnaceae) are monocots that have adapted an aquatic habitat. The true duckweeds (*Lemna* sp.) are composed of small leaf-like fronds and one to a few roots. Watermeal plants (*Wolffia* sp.) are even more reduced and consist of two connected individuals—a mother frond that asexually produces multiple daughter fronds from a pouch at one end (◘ Fig. 11.1h, i).

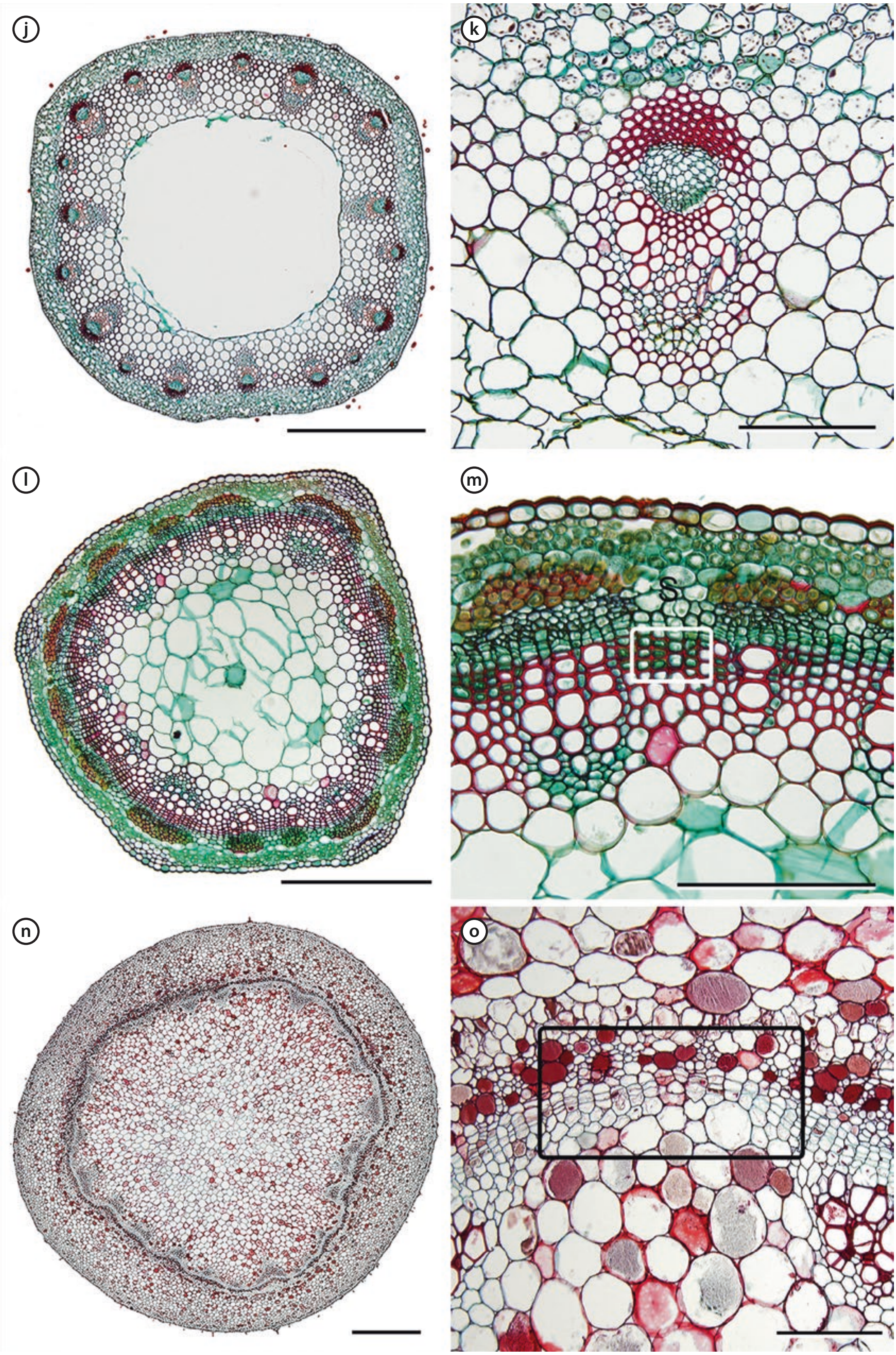
Several basic stem types are apparent based on (a) the presence or absence of secondary growth and (b) on the plant group. Stems with only primary growth are said to be herbaceous, a characteristic found in most annuals (one-year life cycle) and biennials (two-year life cycle). Stems with true secondary growth are commonly called woody stems. The secondary growth arises from a vascular cambium which, in some plants, may remain active for decades, centuries, or even millennia (refer to ◘ Fig. 11.8a), leading to accumulations of xylem and a very large stem diameter.

Eudicot stems may be either herbaceous or woody although a range of intermediate types may be identified (◘ Fig. 11.1j–o) and anomalous versions abound (► Sect. 14.5). Monocot stems lack true secondary growth. However, a primary thickening meristem and diffuse secondary growth (► Sect. 11.9) combined with heavy sclerification can produce large, perennial monocots (refer to the palm tree in ► Fig. 1.19). Woody eudicots will be discussed in more detail in ► Chap. 15—Wood.



◘ **Fig. 11.1** Northern watermeal (*Wolffia borealis*) imaged with light microscopy **h** and scanning electron microscopy **i**. Watermeal plants float on the water surface. These two specimens are laying on their sides, and the waterline is indicated by the arrow in **h**. The mother frond is to the left and the daughter frond to the right in both images. Watermeal is a monocot in the family Lemnaceae. Scale bar in **i** = 250 µm and applies to both panels. (**h, i** RR Wise)

◘ **Fig. 11.1** Examples of herbaceous stems. **j** The buttercup (*Ranunculus* sp.) stem is completely herbaceous with the xylem conducting elements and phloem fibers being the only sclerified tissues. The *Ranunculus* vascular bundles are in a ring and stay separated due to the absence of an **interfascicular cambium**. **k** No vascular cambium is present within the *Ranunculus* bundles, meaning the bundles are closed. **l** Alfalfa (*Medicago sativa*) vascular bundles are separated. **m** An interfascicular cambium is present in alfalfa, but it produces mostly sclerenchyma (cells in boxed area), not xylem conducting elements so the vasculature does not form a ring. **n** In the geranium (*Pelargonium* sp.) stem, the vascular bundles are close together. **o** An active interfascicular cambium (cells in boxed area) produces a cylinder of vasculature. Scale bars = 500 µm in **j** and **n**, 250 µm in **l**, and 100 µm in **k, m,** and **o**. (**j–o** RR Wise)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Box 11.1 Commercial Value of Edible Stems

From an economic standpoint, stems are very important plant parts. We use many plants stems as a food source. Here is a partial list of plants with edible stems or where the stems are important to obtain an edible product:

- Asparagus (*Asparagus officinalis*): entire stem consumed.
- Broccoli (*Brassica oleracea* var. *italica*): the stem and floral tissue are consumed in this species. Often uneaten in favor of broccoli florets, stalks are a good source of antioxidants including ascorbic acid, carotene, and phenols.
- Ginger (*Zingiber officinale*): the rhizome is a modified stem that is typically used to season foods.
- Kohlrabi (*Brassica oleracea* var. *gongylodes*): the same species as cabbage, broccoli, and cauliflower, in kohlrabi, the swollen stem is consumed.
- Maple trees (*Acer* sp.): tree trunks tapped for xylem sap from several tree species including sugar maple (*Acer saccharum*), red maple (*A. rubrum*), silver maple (*A. saccharinum*), and black maple (*A. nigrum*).
- Potato (*Solanum tuberosum*): stem tuber, which is an underground stem is consumed.
- Sugarcane (*Saccharum* sp.): sap of stem used to produce cane sugar.
- Taro (*Colocasia esculenta*): the corm, an underground stem, is made into flour and used in such products as bread and pancake mix.

Reference Wolf (1989)

11

11.2 External Stem Morphology Varies Among Monocots and Herbaceous Eudicots

Stems are divided along their length into nodes and internodes (◘ Fig. 11.2a). Nodes are the points along a stem where lateral organs originate—leaves, flowers, and branches. Internodes are the portions of the stem between nodes, and they develop by intercalary growth. **Intercalary growth** means there is no organized meristem, and the mitotic activity (cell division) occurs between nodes. Internodes vary greatly in length. In rosette plants and bulbs, the internodes are so short that these plants are said to lack internodes entirely (◘ Fig. 11.2b).

Eudicot stems that show secondary growth retain marks of the previous year's growth (◘ Fig. 11.2c–g). The terminal bud represents a separate node at the tip of a short internode that separates it from a pair of subtending lateral (or **axillary**) buds. In the overwintering stage, the terminal bud is covered by several layers of bud scales, which are modified leaves. Leaf scars remain from abscised leaves and show the pattern of leaf traces in the vascular node as indicated by the site(s) of such scars that encircle the stem, with internodes in between the sets of bud scale scars.

Monocot stems may have obvious nodes, such as those seen in bamboo (◘ Fig. 11.2h). The nodes along much of the bamboo stem lack leaves, and an intercalary meristem at each node is responsible for

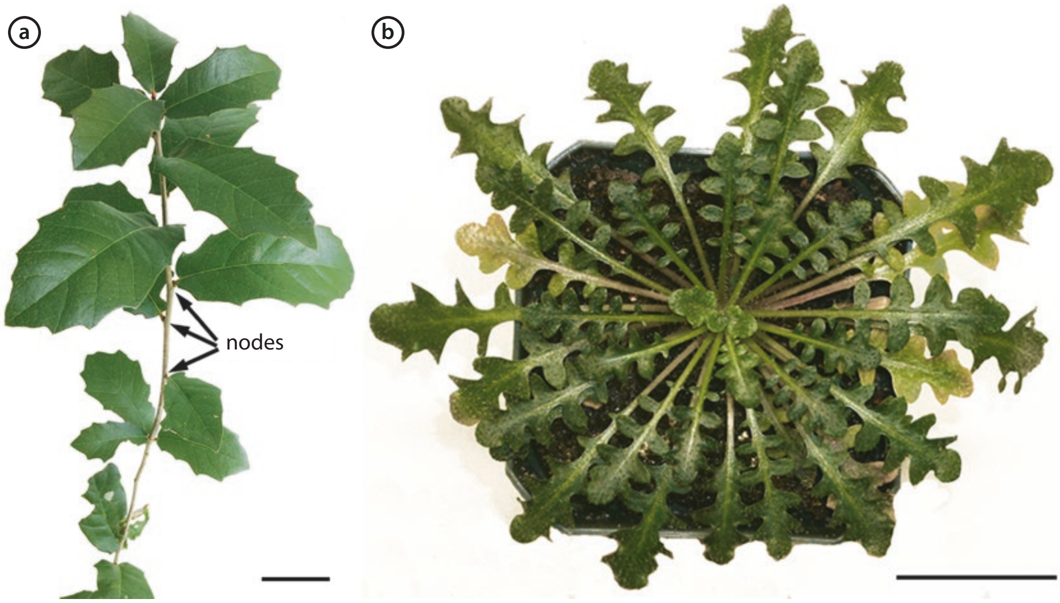


Fig. 11.2 Eudicot stems. **a** Photograph of a stem with node and internode labeled. **b** Picture of a rosette plant (*Arabidopsis lyrata*) showing no stem. Scale bars = 2 cm in both panels. (**a**, **b** RR Wise)

the increase in the length of the stem. A secondary thickening meristem also contributes to the stem growth (refer to ► Sect. 11.9). Many grasses have a stem in which most of the supportive tissue is actually a combination of multiple **leaf sheaths** arranged in concentric rings around a small pith. The leaf is initiated at a node (which is concealed by the subtending leaf sheath) and elongates for some distance as a leaf sheath before the leaf blade extends away from the stem (■ Fig. 11.2i).

Phyllotaxis is the pattern of leaf distribution on the stem. It is an easily identifiable and genetically controlled trait and thus of considerable value to plant systematics in the characterization and identification of plant species. There are three common patterns with numerous variations on the theme: alternate, opposite, and whorled (■ Fig. 11.2j–l). In an alternate pattern, a node produces a single leaf, while the nodes above and below produce leaves on the opposite side of the stem. An opposite phyllotaxis produces two leaves on the same node that are directly opposite each other. In a whorled pattern, multiple leaves arise from a single node.

If successive leaf pairs in an opposite pattern are at right angles to each other, the pattern is called **decussate** (■ Fig. 11.2m). Leaves in a **distichous** phyllotaxis pattern may be either opposite or alternate and lie in vertical rows to either side of the stem, resulting in a fan-shaped plant (■ Fig. 11.2n). Many cacti and succulent plants have a spiral pattern that produces a striking plant form (■ Fig. 11.2o).

Box 11.2 Colonization of Land and the Monocot/Eudicot Split

As the stem evolved, it became important for adaptation to land dwelling as well as aquatic. Aquatic plants did not need the type of support that stems give to aerial portions of the plant. Some of the developmental changes involved the generation of lignin for support, cuticular waxes that prevented water loss, and vascular tissue for long-distance transport of a variety of internal substances in the course of evolution. For larger plants (i.e., those capable of experiencing secondary growth), the tissues that give rise to the vasculature (vascular cambium) do double duty as the tissues that give rise to the supportive tissues (wood). Air (and the more directional light that an atmosphere provides) was a new three-dimensional resource to access, leading to stems and phyllotaxy.

Monocotyledonous plants (monocots) and eudicotyledonous plants (eudicots) have shoot systems with very different architectures. Using molecular and genomic data sets, it has been estimated that the monocots diverged from the established eudicots some 140 million years ago (mya; in the late Jurassic period) and that core eudicots diverged approximately 110 mya. Keep in mind that conifers are not flowering plants and that only monocots and eudicots are descended from flower-producing plants.
Reference Wolf (1989)

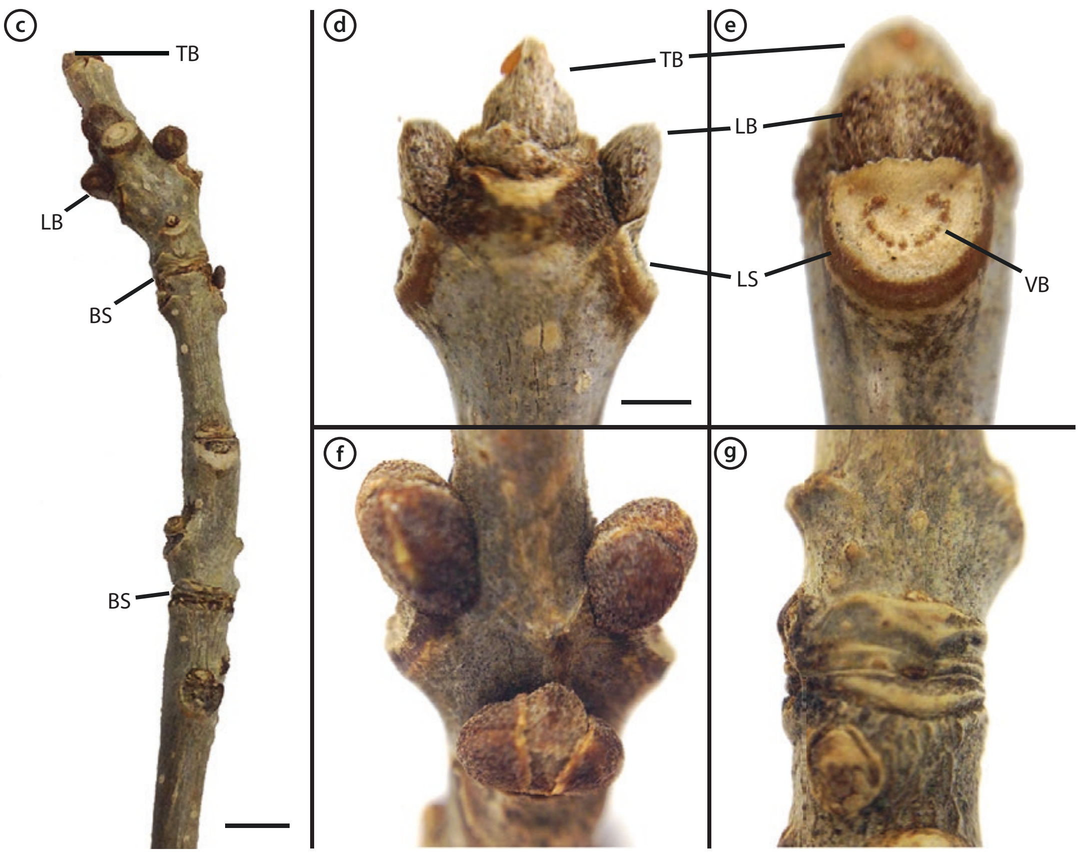


Fig. 11.2 **c** Stem tip of an overwintering green ash (*Fraxinus pennsylvanica*) showing a single terminal bud (TB), multiple lateral buds (LB), and two sets of bud scale scars (BS). The bud scale scars mark the nodes. The other four panels are higher magnification views of **d** a terminal bud with a pair of subtending lateral buds and a pair of leaf scars (LS), **e** a leaf scar seen face-on with a semicircle pattern of vascular bundle (VB) scars, **f** three lateral buds near the stem tip (two above and one below a short internode), and **g** bud scale scars from a previous year's terminal bud. Scale bars = 1 cm in **c** and 5 mm in **d**. The scale bar in **d** also applies to panels **e**, **f**, and **g**. (**c**–**g** RR Wise)

Fig. 11.2 Monocot stems. **h** A forest of moso bamboo (*Phyllostachys edulis*) stems in the Arashiyama Bamboo Grove, Japan, clearly showing nodes and internodes. **i** Zebra grass (*Miscanthus sinensis*) stem with multiple leaf sheaths visible. Scale bars = 1 m in **h** and 5 cm in **i**. (Image **h** courtesy of N.E. Wise; **i** RR Wise)

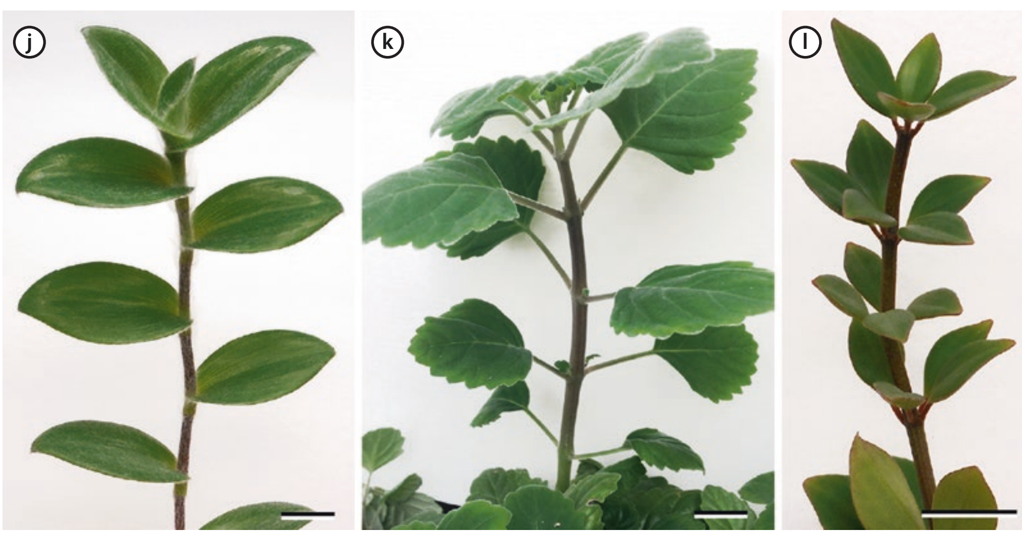


Fig. 11.2 **j** Common phyllotaxis patterns of alternate (*Tradescantia sillamontana*), **k** opposite (*Plectranthus ernstii*), and **l** whorled (*Peperomia pereskiifolia*) leaf arrangements. Scales bars = 2 cm in all three panels. (**j–l** RR Wise)

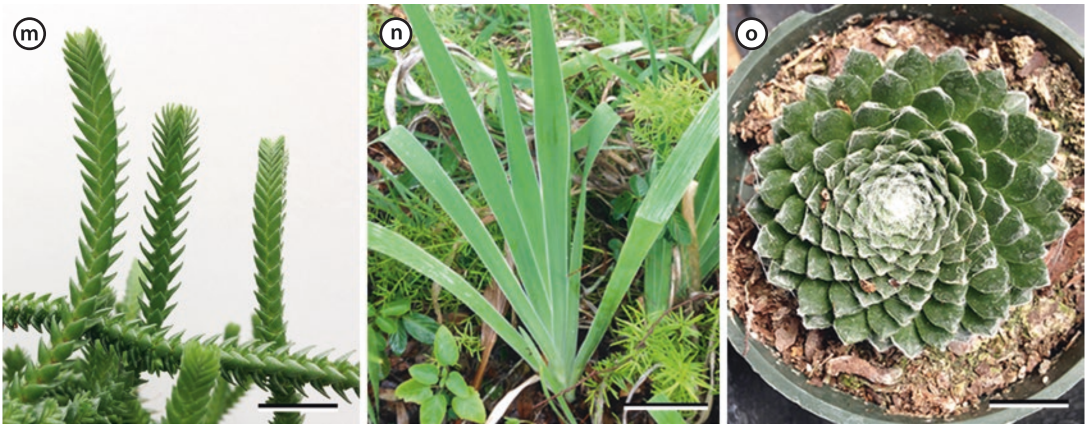


Fig. 11.2 Patterns of leaf initiation. **m** Decussate pattern in rattail crassula (*Crassula muscosa*). **n** Distichous pattern in blackberry lily (*Iris domestica*). **o** Spiral pattern in a cobweb houseleek (*Sempervivum arachnoideum*). Scale bars = 1 cm in **m**, 5 cm in **n,** and 1 cm in **o**. (**m**–**o** RR Wise)

11.3 The Stem Is Composed of Three Tissues: Dermal, Ground, and Vascular

Stem dermal, ground, and vascular tissues are so categorized based on their developmental origins and their final function. **Dermal tissues** originate at the shoot apex, are derived from the protoderm, and function largely in protection. The ground meristem produces the ground tissues of cortex, pith, and conjunctive tissues that provide bulk to the stem as well as possible organic storage. The procambium gives rise to the vascular tissues of xylem and phloem.

Monocot and eudicot stems in the primary state of growth differ slightly in their arrangement of dermal tissue, ground tissue, and vascular tissue (Figs. 11.3a–c and 11.3d–f). Both have an outer epidermis and inner vascular bundles. However, the circular arrangement of the eudicot vascular bundles divides the ground tissue into two zones. The region between the epidermis and the vasculature is called the **cortex**, while the ground tissue in the center of the stem is termed **pith** (a.k.a. **medulla**). The vascular bundles of the monocot stem are intermixed with the ground tissues and termed **medullary bundles**. In case of monocots, all of the ground tissue, regardless of where found in the stem, is called **conjunctive tissue** because there is no clear delimitation between the cortex and the pith as in the eudicot stem.

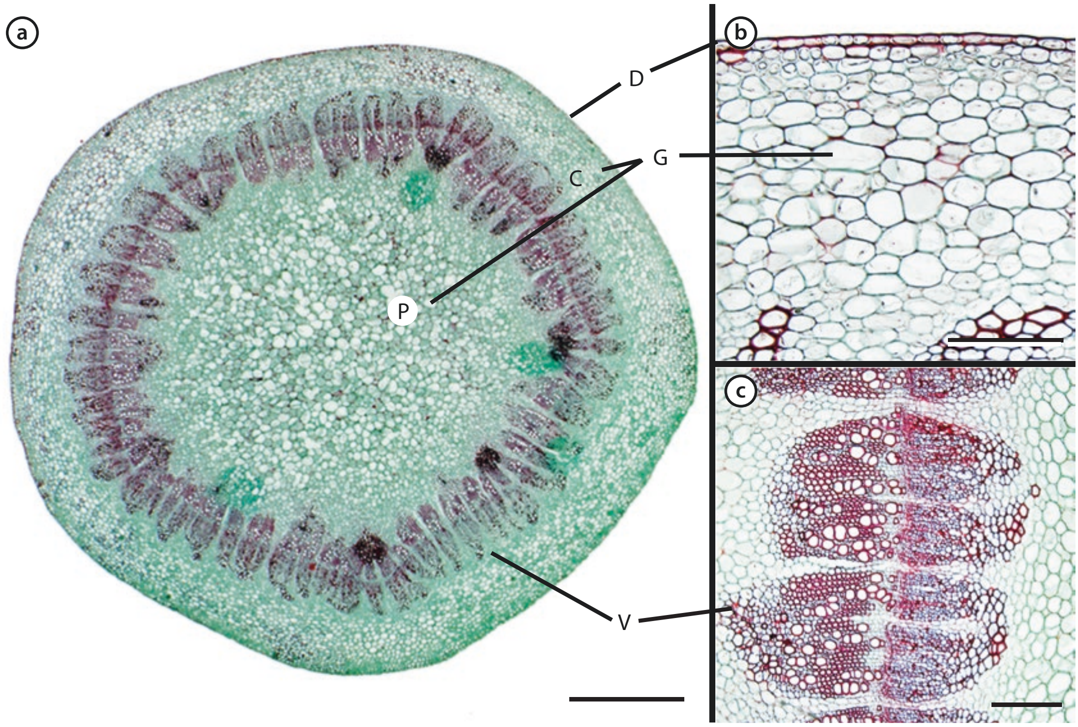


Fig. 11.3 **a**–**c** Cross-section of a eudicot stem (wild cabbage, *Brassica oleracea*) showing dermal tissue (D), ground tissues (G) consisting of cortex (C) and pith (P), and a ring of vascular tissue (V). Scale bars = 500 µm in **a** and 100 µm in **b** and **c**. (**a**–**c** RR Wise)

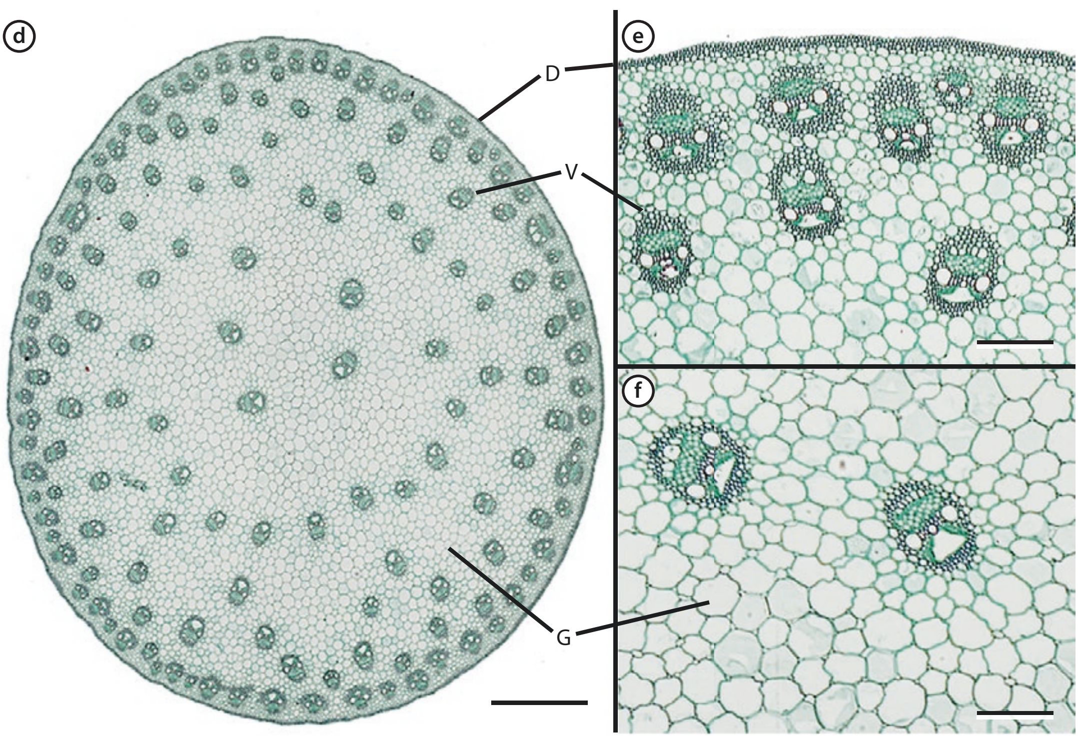
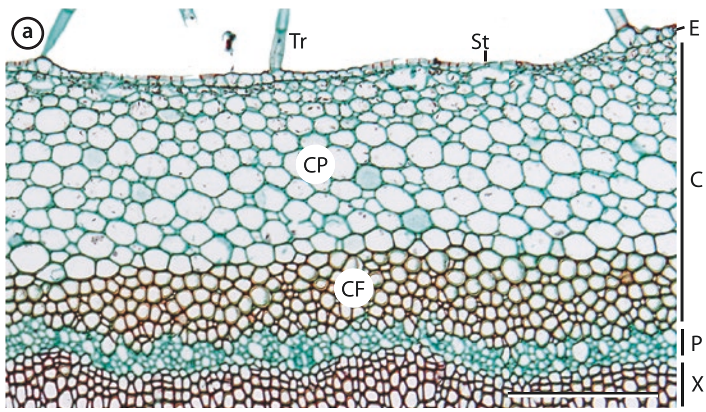


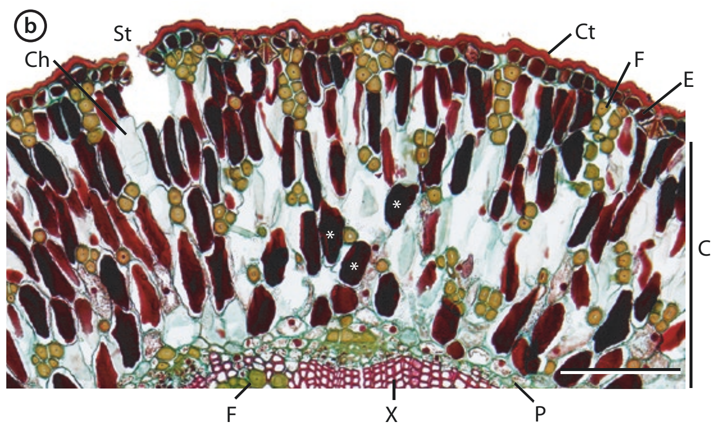
Fig. 11.3 **d**–**f** Cross-section of a monocot stem (maize, *Zea mays*) showing dermal tissue (D), ground tissue (G, a.k.a. conjunctive tissue), and vascular bundles (V). Scale bars = 500 µm in **d** and 100 µm in **e** and **f**. (**d**–**f** RR Wise)

11.4 Dermal Tissues Cover the Stem Exterior

In young stems or those experiencing primary growth, the dermal layer consists in most instances of a single-layered epidermis covered with a waxy cuticle (◘ Fig. 11.4a, b). Epidermal cells are frequently smaller than the underlying cortical parenchyma, and the cuticle varies in thickness depending on age of stem and habitat. Note that the mesophytic *Digitalis* stem and the hydrophytic *Myriophyllum* stem shown in ◘ Fig. 11.5a have a thin cuticle (too thin to be seen in the image), while the xerophytic *Ephedra* stem has a thick cuticle (◘ Fig. 11.4b). The stem epidermis may also have trichomes and stomata, common features of most plant epidermises (refer to ► Chap. 9). In plants with prolonged secondary growth, the epidermis is replaced by a complex tissue called the periderm (► Chap. 16).



◘ **Fig. 11.4** **a** A portion of purple foxglove (*Digitalis purpurea*) stem epidermis and cortex showing trichomes (Tr), one stoma (St), the single-cell epidermal layer (E), and a thick cortex (C) containing cortical parenchyma (CP) and cortical fibers (CF). Phloem (P) and xylem (X) lie to the interior. Scale bar = 50 μm. (RR Wise)



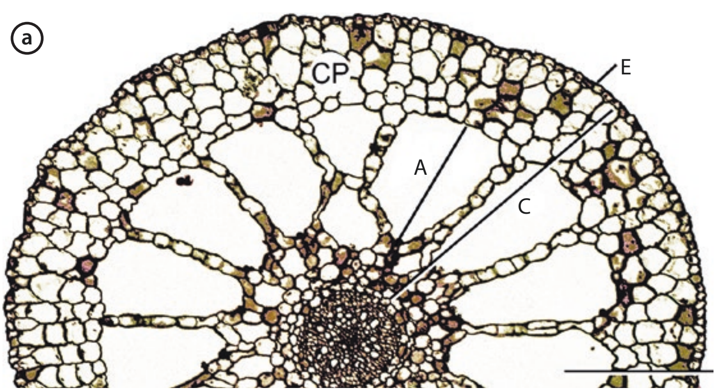
◘ **Fig. 11.4** **b** California jointfir (*Ephedra californica*) stem in cross-section showing a thick, red-stained cuticle (Ct), a single layer of tannin-filled epidermal cells (E), one stoma (St), and a cortex (C) containing a mixture of light-blue chlorenchyma (Ch) and tannin-filled cortical parenchyma (three in the middle of the image are marked with *). Fibers (F), stained tan, are seen scattered throughout the cortex, phloem (P), and xylem (X). Scale bar = 50 μm. (RR Wise)

11.5 Ground Tissues Compose the Cortex, Pith, and Conjunctive Tissue

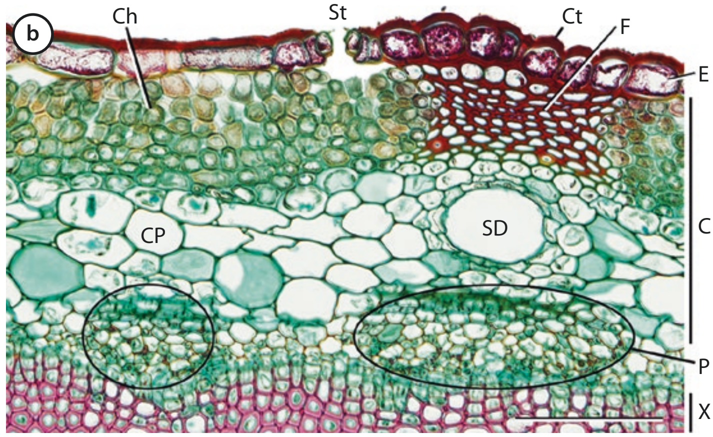
Ground tissues include the cortex and pith in eudicots and conjunctive tissue in monocots. For example, conjunctive tissue in monocots is often represented as parenchyma surrounding the vascular bundles, or it may consist of fibers whose walls can become very thick. Such is the case with corn stem, gingers, lilies, and bulbs like onion. Those fibers surrounding, but not derived from, the vascular bundle are called **perivascular fibers**.

The eudicot stem cortex can be quite varied in thickness, components, and function. The *Digitalis* cortex shown in ◘ Fig. 11.4a consists of parenchyma cells surrounding a ring of cortical fibers for stem support. *Digitalis* is a mesophytic, annual plant with limited secondary growth. *Ephedra* is a desert perennial with a photosynthetic stem, as is evidenced by the stoma and chlorenchyma seen in ◘ Fig. 11.4b. Fibers and tannin-filled cells in the cortex aid in herbivory deterrence. The cortex in milfoil, an aquatic eudicot, consists exclusively of a non-photosynthetic parenchyma and aerenchyma (◘ Fig. 11.5a). The gas-filled aerenchyma tissue provides buoyancy for support and a diffusional pathway for the exchange of carbon dioxide and oxygen between the roots and leaves. Stem aerenchyma often forms as an adaptive response in plants such as sedges (Cyperaceae) that are exposed to transient water logging events (Nawaz et al. 2014). Some stems engage in significant levels of photosynthesis and contain multiple layers of cortical chlorenchyma, as shown in the *Daucus* stem in ◘ Fig. 11.5b. That stem also has a cortical secretory duct, a common feature in other plant stems as well. The cortex may also contain crystals or other idioblasts (◘ Fig. 11.5c, d).

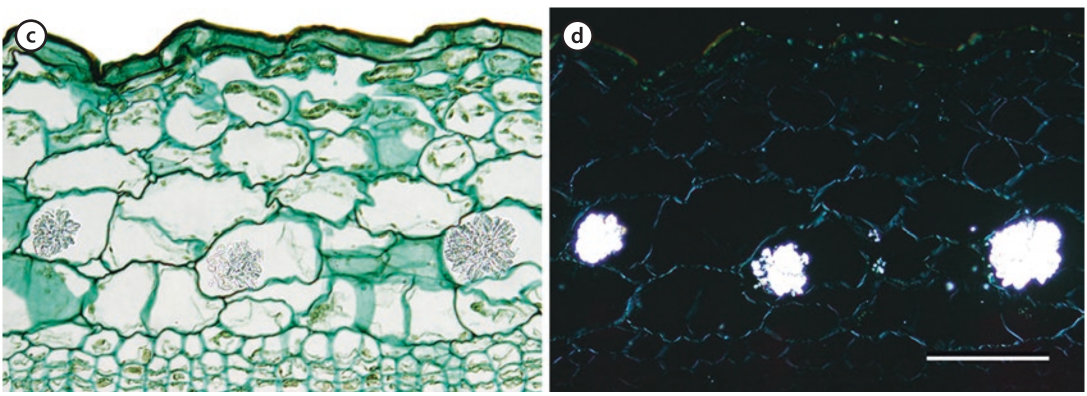
The hypodermis is a region of the cortex consisting of one or more layers of cells lying under the epidermis of some stems. It is



◘ **Fig. 11.5** **a** Water milfoil (*Myriophyllum* sp.) is an aquatic eudicot. Its stem has a single layer of epidermal cells (E) and a wide cortex consisting of an outer layer of parenchyma cells (CP) and an inner zone of aerenchyma (A). The cortical zone (C) extends from inside the epidermis to the inner vascular tissues. Milfoil gains its support from the water and thus has no cortical fibers. Phloem and xylem occupy the center of the stem, and there is no pith. Scale bar = 250 µm. (RR Wise)



◘ Fig. 11.5 **b** This wild carrot (*Daucus carota*) stem cross-section shows one stoma (St), a thick cuticle (Ct), a single layer of epidermal cells (E), and a thick cortex (C). The cortex has multiple layers of chlorenchyma (Ch), a region of cortical parenchyma (CP), a dense patch of fibers (F), and a secretory duct (SD). Phloem (P) exists in discrete patches (circled), and xylem (X) is to the interior. Note the crushed protophloem to the exterior of the phloem patches. Scale bar = 50 µm. (RR Wise)



◘ Fig. 11.5 Two views of the stem of sowbane (*Chenopodium murale*) in **c** brightfield, and **d** polarized light showing crystals in cortex. Scale bar = 50 µm. (**c**, **d** RR Wise)

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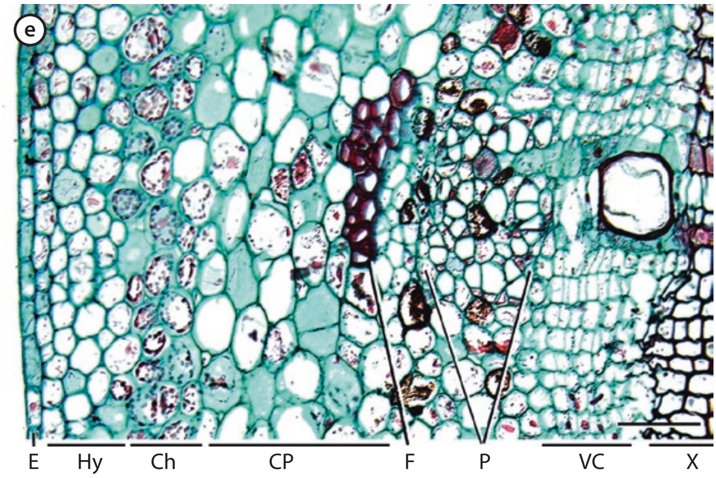
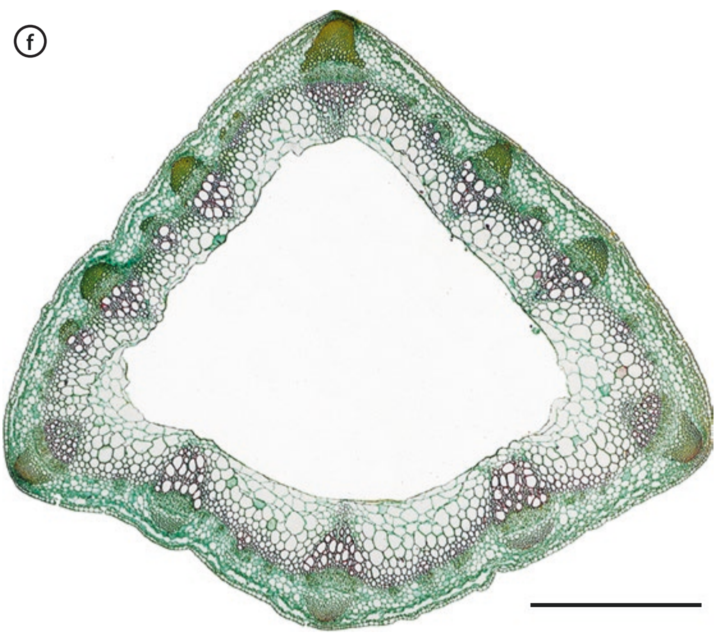
more common in roots than in stems. In xerophytes and succulents (◘ Fig. 11.5e), the hypodermis serves as a water storage tissue. In other stems, hypodermal cells often have thickened walls and may serve as a supportive tissue.

Like the cortex, the pith is part of the ground tissue. It occupies the central region of the typical eudicot stem and is usually pure parenchyma (◘ Fig. 11.3a). Pith develops early in the life of a stem and may play a role in the development of the other tissues that it surrounds, such as the maturing vasculature. Because it is laid down early, and made of weak parenchyma cells, the pith may be destroyed during stem elongation and expansion as shown in the pea stem in ◘ Fig. 11.5f.

The pith can function for storage in a variety of species. Potato tubers, which are rhizomes (◘ Fig. 11.1e), are almost completely



■ **Fig. 11.5** **e** Cross-section of the outer portion of a euphorbia (*Euphorbia* sp.) stem. The epidermis (E) is a single layer of cells. The cortex consists of a hypodermis (Hy), two to three cell layers of chlorenchyma (Ch), cortical parenchyma (CP), and cortical fibers (F). Phloem (P), a wide vascular cambium (VC), and xylem (X) lie to the interior. Scale bar = 50 µm. (RR Wise)



■ **Fig. 11.5** **f** LM of a torn pith in a pea (*Pisum sativum*) stem. Even at this low magnification, the thin cortex, the ring of individual vascular bundles at the periphery of the stem, and the minor pith remnants are apparent. Scale bar = 500 µm. (RR Wise)

filled with pith which functions entirely in starch storage. There is no free starch in a plant cell. All starch is manufactured in plastids and specifically amyloplasts in the case of storage organs. The pith of woody stems, as well, can be a site of starch storage (■ Fig. 11.5g).

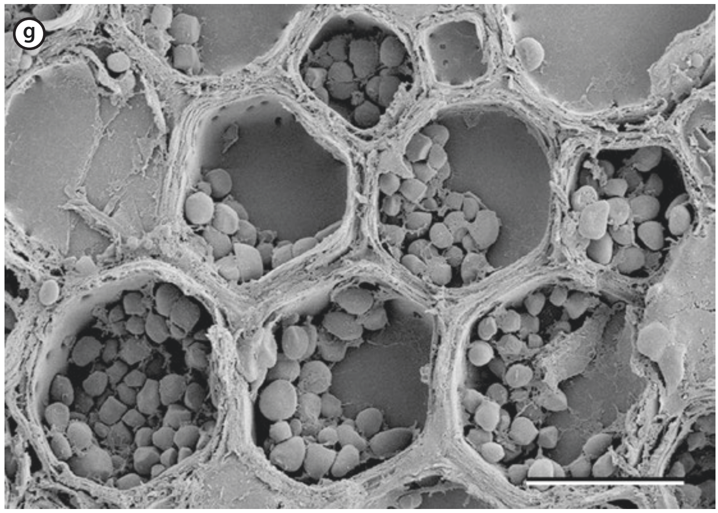


Fig. 11.5 **g** Pith cells observed with SEM of an overwintering Katsura (*Cercidiphyllum japonicum*) stem containing numerous amyloplasts, as seen in the scanning electron microscope. Scale bar = 25 µm. (RR Wise)

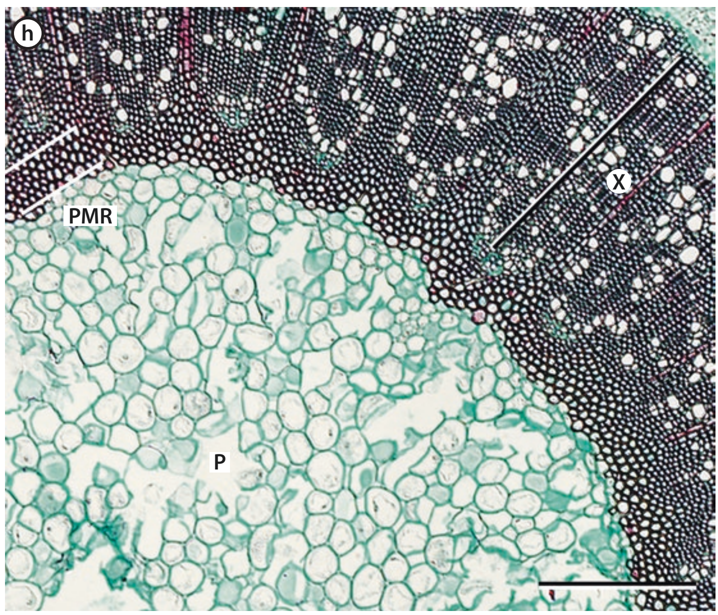
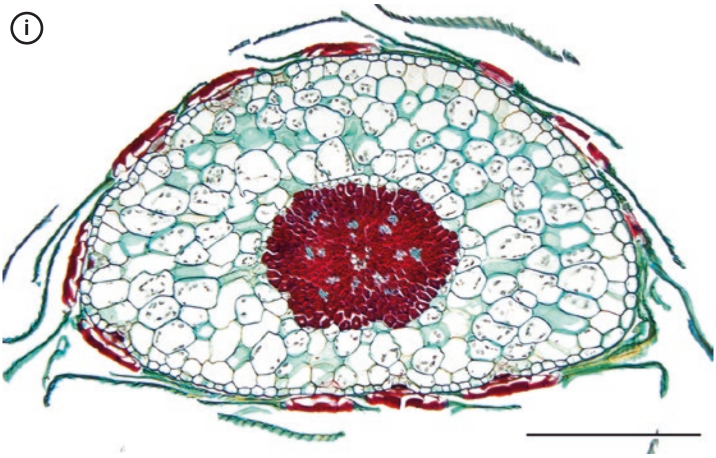


Fig. 11.5 **h** The perimedullary region (PMR, between the two white lines) in this English ivy (*Hedera helix*) stem is a zone of sclerified cells that lies between the xylem (X) to the exterior and pith (P) to the interior. Scale bar = 100 µm. (RR Wise)

In some viney stems, portions of the pith may sclerify to provide support. In *Hedera helix*, the outer cells of the pith sclerify and develop into a zone of supportive tissue called the **perimedullary region** (Fig. 11.5h). The cells of the perimedullary region are derived from pith cells and are therefore part of the ground tissues, not the vascular tissues, in spite of their close association



◘ **Fig. 11.5** **i** Cross-section of a Spanish moss (*Tillandsia usneoides*) stem with a cortex of chlorenchyma cells and a central core of sclerenchyma. The small, blue-stained regions in the sclerenchyma core are isolated vascular bundles. Note the peltate trichomes on the stem surface and compare to ◘ Fig. 9.6r, s. Scale bar = 100 µm. (RR Wise)

◘ **Fig. 11.5** **j** Chambered pith of black walnut (*Juglans nigra*). The pith is made at the onset of the first year's primary growth and is soon surrounded by woody xylem of secondary growth origin. Scale bar = 1 cm. (RR Wise)

with the vasculature. In contrast, in Spanish moss stems, it is the inner pith cells that sclerify and are the main supporting tissue of the stem (◘ Fig. 11.5i). Spanish moss is an epiphyte in the bromeliad family that hangs in large masses from tree limbs and requires a small and very flexible stem. In this plant, the stem cortex is composed of chlorenchyma, and the pith contains a dense collection of fibers that provide support. In other plants, tannins, crystals, or laticifers may occupy the pith. The chambered pith of walnut (◘ Fig. 11.5j) is an important taxonomic trait in that taxon. In some stems, medullary rays connect pith parenchyma with cortical parenchyma. The *Aristolochia* stem in ◘ Fig. 14.5b is a good example.

Like the epidermis (refer to ► Chap. 9), the endodermis is a layer of cells that provides a barrier between two regions or zones (Geldner 2013). Such tissues are sometimes called "limiting layers." The epidermis is the limiting layer between the atmosphere (or water in the case of an aquatic plant) and the interior of the organ,

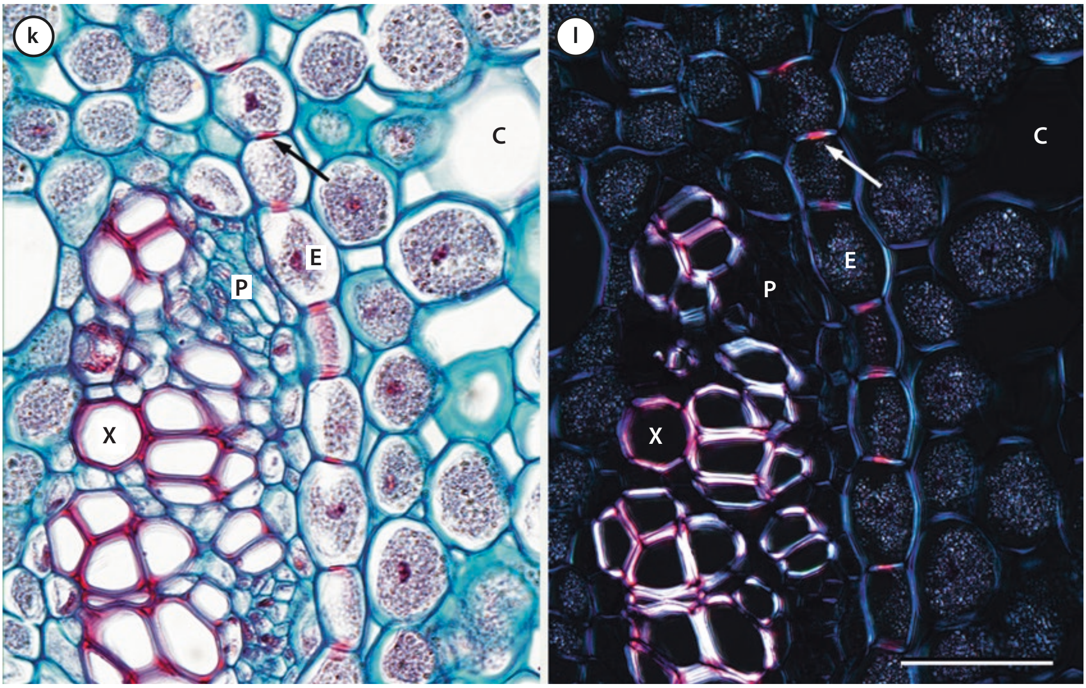


Fig. 11.5 **k**, **l** The endodermis (E) in a sweet flag (*Acorus* sp.) rhizome as seen in (k) brightfield and (l) polarized microscopies. Cortex (C) is to the right, and xylem (X) and phloem (P) are to the left in both images. The Casparian strips (*arrows*) appear red under LM brightfield illumination **k** and show birefringence when viewed through cross-polarizers **l**. Scale bar = 25 µm. (**k**, **l** RR Wise)

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whereas the endodermis is a limiting layer between the cortex and the stele or **vascular cylinder** (Fig. 11.5k, l). In terms of origin, the endodermis is considered to be the inner layer of the cortex.

The degree of separation provided by an endodermis varies between and among plant habitat, species, and organ. A prominent endodermis is relatively rare in aerial stems (Lersten 1997) probably because the pattern of vascular bundles in a eustele (refer to ► Sect. 11.8) is too large to be bound by a single-layer endodermis. However, in roots (► Chap. 10), and some rhizomes, the endodermis is anatomically distinct with thick cell walls and a conspicuous Casparian strip (or band). The Casparian strip (named after Robert Caspary, a nineteenth century German botanist) is a band of cell wall material impregnated with suberin, and sometimes lignin, in the radial and transverse walls of the endodermal cells. It presents an apoplastic barrier to water and solute flow.

The function of the stem endodermis appears to be associated with those organs that might develop a positive pressure in the stele. Under most conditions, the water in the stele is under tension, not pressure, because transpiration from the leaves "pulls" water up the stem. However, the lower part of aerial stems and rhizomes (Fig. 11.5k, l) are subject to the development of root pressure, a process seen when the water potential of the xylem water is higher than that of the soil. Root pressure would force water out of the stele and waterlog the cortex were it not for the barrier to water flow presented by the endodermis. In another

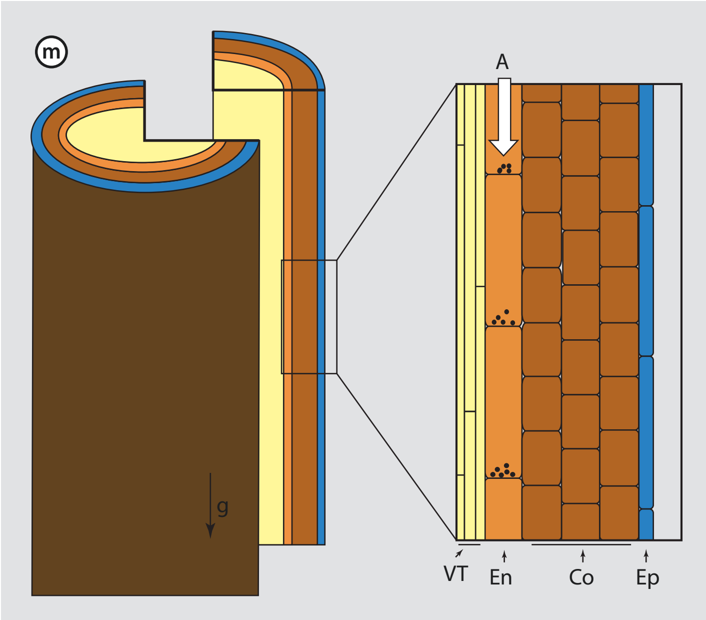


Fig. 11.5 **m** Schematic of the role of endodermal amyloplasts in gravisensing. The endodermis (En) lies between the vascular tissue (VT) to the inside and the cortex (Co) and epidermis (Ep) to the outside. In the presence of a gravitational vector (g), the amyloplasts (A) sediment to the bottom of the endodermal cells. (Redrawn from Palmieri and Kiss 2006)

example, some **halophytes** (plants growing in saline water) such as pickleweed (*Salicornia* sp.) possess an endodermis, presumably to allow salt exchange between the cortex and surrounding water while restricting the loss of water from the stele to the cortex via osmosis.

In addition to the role that the shoot endodermis plays in the water relations of some stems and rhizomes, it may also function in gravisensing, much like the columella of the root cap (► Sect. 10.4). Shoots are negatively gravitropic (grow away from the gravitational field), while roots are positively gravitropic (growing downward). Amyloplasts, which are heavy, starch-containing plastids, are concentrated in the stem endodermal cells (Fig. 11.5m). They settle to the bottom of the endodermal cells and signal directionality via the mechanism described in ► Sect. 3.5.4. The stem tissues respond by redistributing auxin, a plant hormone that induces cell wall loosening and cell elongation, to the lower side of the stem. Those cells elongate, and the stem points upward and away from the gravitational vector.

11.6 Stem Vascular Tissues Are Arranged in Bundles

The vascular system runs throughout the plant—from the roots, through the stem, and out to the leaves and flowers. Many of the concepts and structural motifs discussed in this section on the vasculature of the stem also apply to the xylem and phloem in the other plant organs. In particular, the developmental transitions from protophloem to metaphloem and protoxylem to metaxylem, as described for stems, are similar in other organs as well.

11.6.1 Relationship of Xylem to Phloem in Vascular Bundles

The relationship of xylem to phloem in an individual vascular bundle varies. In an **amphivasal bundle**, the phloem is surrounded by xylem as seen in the stem of *Acorus*, a primitive monocot (◘ Fig. 11.6a). An **amphicribral bundle** has the opposite arrangement, with phloem surrounding the xylem (◘ Fig. 11.6b). Amphicribral and amphivasal bundles are more common in ferns and primitive monocots than gymnosperms and advanced angiosperms. In a **collateral bundle**, the most common type found in angiosperms, phloem is to the outside (abaxial to) the xylem (◘ Fig. 11.6c). However, in some eudicots only, the primary phloem may be found on both the inner and outer sides of the xylem, and this arrangement is called **bicollateral** (◘ Fig. 11.6d). In this case, one area of phloem is adjacent to the cortex, and the other is adjacent to the pith.

Vascular bundles that have a vascular cambium are said to be open because the cambium can continue to generate new xylem and phloem tissues for the life of the bundle. Those that lack a vascular cambium are called closed, meaning all the cells of the vascular bundle fully differentiate to xylem or phloem tissues and none remain in the meristematic state. Beet (◘ Fig. 11.6c) and squash (◘ Fig. 11.6d) are examples of stems with open vascular bundles. Examples of closed vascular bundles are found in *Ranunculus* (◘ Fig. 11.1k) and *Zea* (◘ Fig. 11.6f). Stems with primary growth may have either open or closed vascular bundles.

Differentiation of primary vascular tissues from the procambium is asynchronous. Protoxylem and protophloem are first to mature, followed by metaxylem and metaphloem. Protoxylem and protophloem originate at the stem apical meristem as a consequence of divisions of the procambium. Protoxylem tracheary elements are dead at maturity and may continue to serve as conduits for water flow for some time. They typically are small in diameter and have annular or spiral wall thickenings (◘ Fig. 11.6e), a characteristic that is of advantage in a tissue undergoing elongation. However, protophloem sieve tube elements are often small in both length and diameter and may lack sieve plates and companion cells. They are easily stretched and typically destroyed by stem elongation. Protoxylem, as well, may be torn during stem expansion. The result is a protoxylem lacuna or hole (◘ Fig. 11.6f).

After internode elongation has ceased, parenchyma cells further down the stem and, adjacent to the protoxylem and

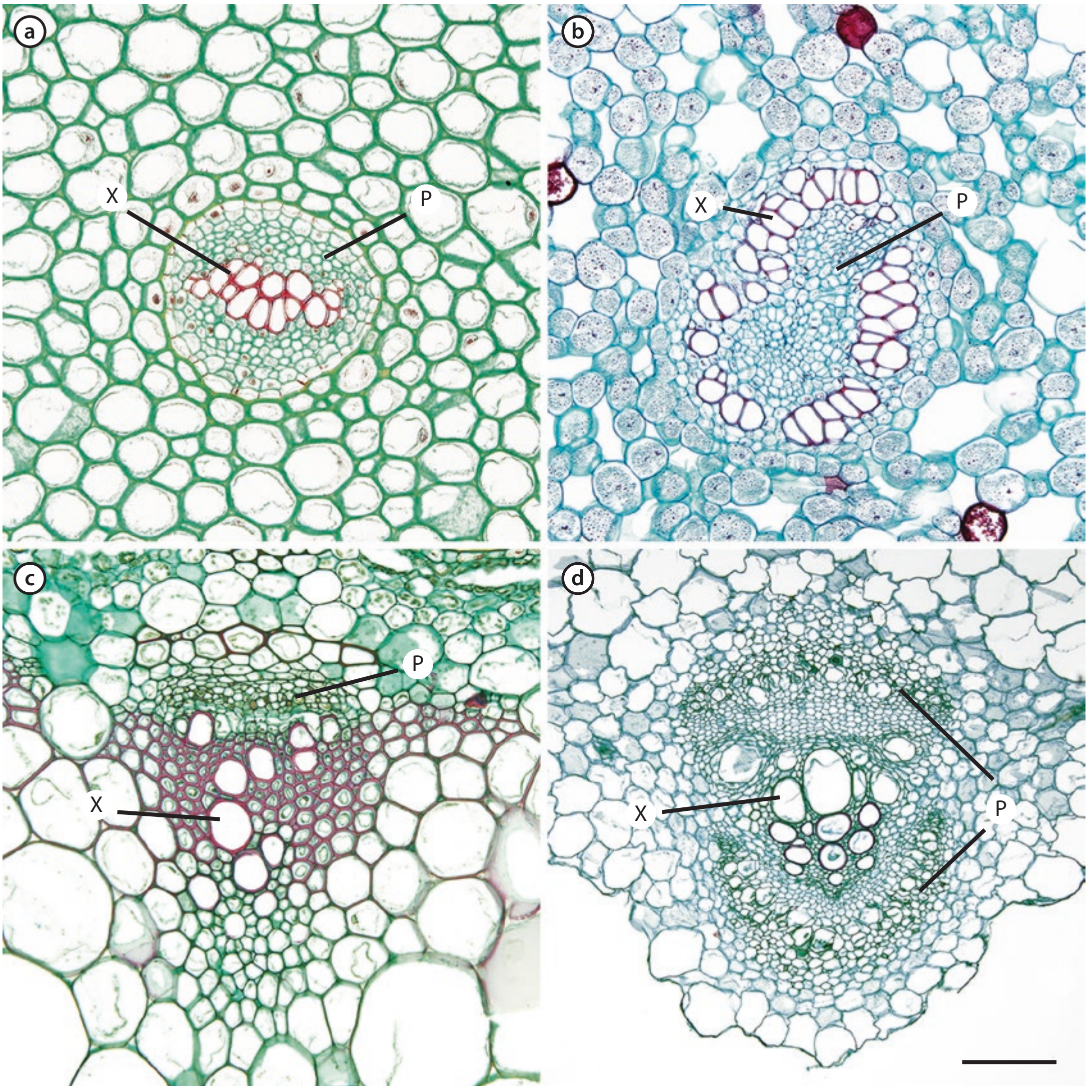


Fig. 11.6 **a-d** Examples of vascular bundle types with different xylem-phloem arrangements: **a** amphicribral bundle from a fern (*Polypodium* sp.) rhizome, **b** amphivasal from a sweet flag (*Acorus* sp.) rhizome, **c** a collateral bundle from a beet (*Beta vulgaris*) stem, and **d** a bicollateral bundle from a squash (*Cucurbita pepo* sp.) stem. Beet and squash have open vascular bundles. Scale bar in **d** = 50 µm and applies to the other panels. (**a**–**d** RR Wise)

protophloem, differentiate into the second type of primary vasculature, **metaxylem** and metaphloem. Note that protoxylem, protophloem, metaxylem, and metaphloem are all primary tissues (Fig. 11.6g). There is no sharp demarcation between protoxylem and metaxylem, and the two forms grade from one to the other during development. However, the latter are usually larger in length and diameter than the former. In plants with true secondary growth, **secondary xylem** and secondary phloem later develop from the vascular cambium (▶ Chap. 14). In those plants lacking secondary growth, the metaxylem and metaphloem are the functional vascular tissues for the life of the plant.

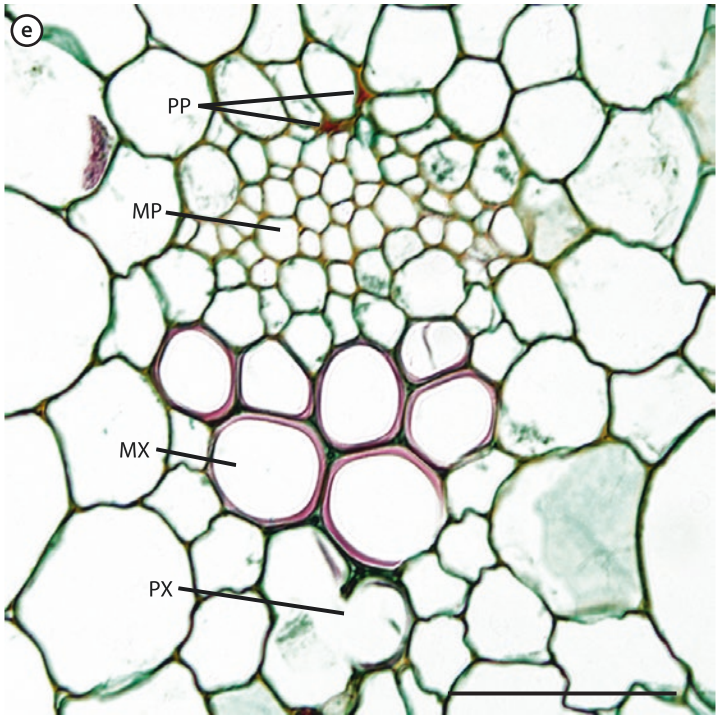


Fig. 11.6 **e** In this cross-section of a young castor bean (*Ricinus communis*) stem, protophloem (PP) and protoxylem (PX) developed first. The protophloem was crushed by expansion and elongation of the stem, while the protoxylem was ripped. Metaxylem (MX) and metaphloem (MT) subsequently developed in an exarch pattern. The stem surface (the adaxial direction) is to the top of the image. This bundle will develop a vascular cambium and, ultimately, be connected in a ring with adjacent bundles via the activity of an interfascicular cambium. The result of that secondary growth will be similar to the example shown in Fig. 11.1n. Scale bar = 50 µm. (RR Wise)

11.6.2 Patterns of Xylem Development in the Stem

With their thick secondary wells, which are not easily ripped or torn, the development of metaxylem vessel elements within vascular bundles is easier to visualize and study than metaphloem development. As a result, four patterns of metaxylem maturation are recognized (Fig. 11.6h–k). Plants with a **centrarch** pattern of maturation possess a single vascular cylinder with protoxylem in the center, surrounded by metaxylem. A **mesarch** stem is similar to centrarch with protoxylem surrounded by metaxylem, but mesarch stems have multiple vascular strands with this maturation pattern. Centrarch and mesarch developmental patterns are characteristic of extinct and living fern taxa. In the **endarch** developmental pattern, metaxylem development is to the exterior (adaxial) of protoxylem. This is the most common form found in the stems of angiosperms. An **exarch** pattern is one in which metaxylem development is to the interior (abaxial) of the protoxylem, as is seen in most angiosperm roots (► Chap. 10—Roots).

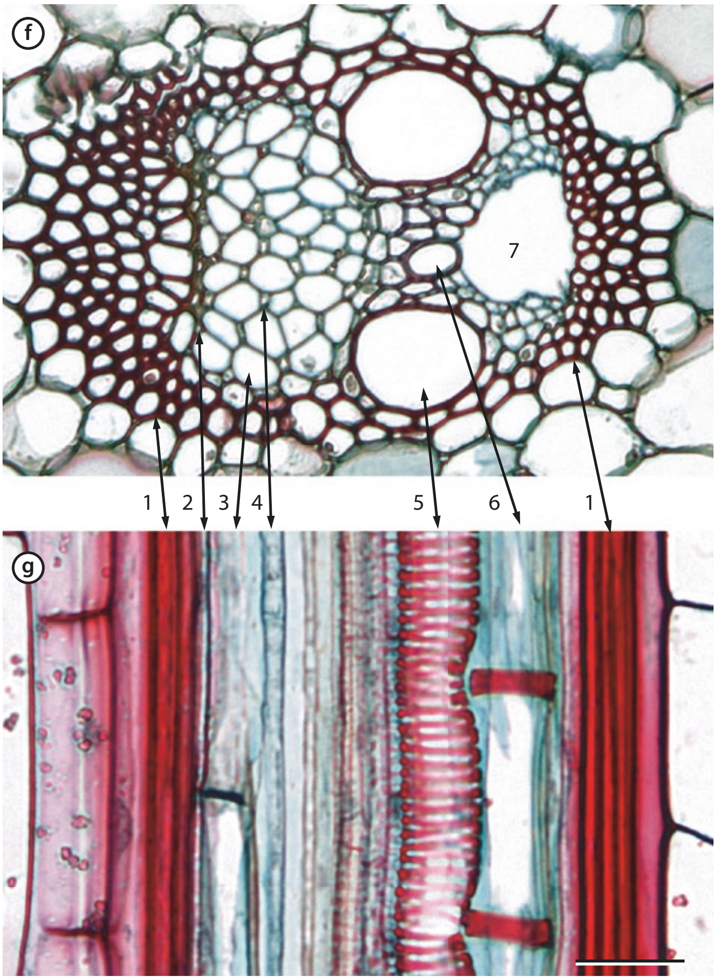
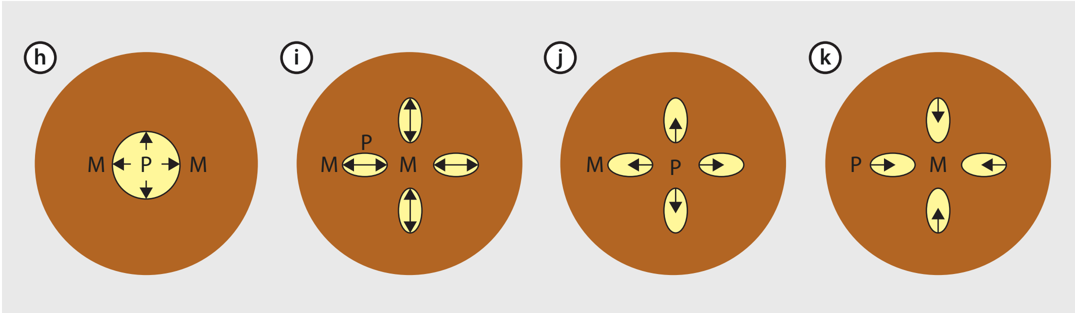


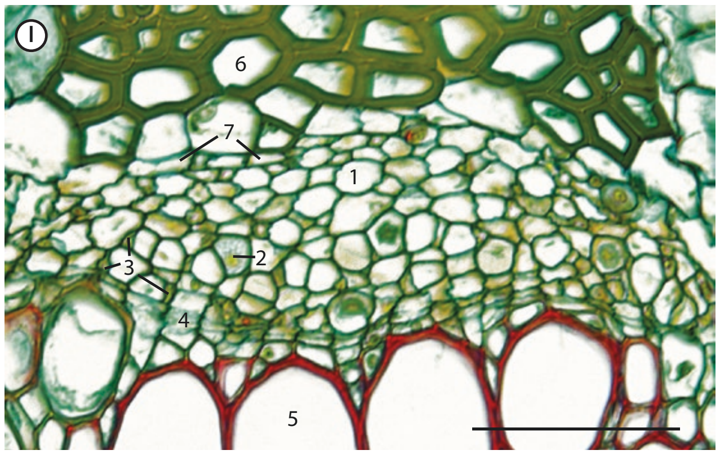
Fig. 11.6 Closed vascular bundles from a mature maize *(Zea mays)* stem. **f** A bundle seen in cross-section is composed of xylem and phloem. A bundle sheath of sclerenchyma fibers (stained dark red due to lignification) surrounds the vascular bundle and separates it from the ground parenchyma or conjunctive tissues. **g** A corresponding longitudinal section shows cell types labeled as 1 = perivascular fibers of the bundle sheath; 2 = crushed protophloem; 3 = metaphloem sieve tube element; 4 = metaphloem companion cell; 5 = metaxylem vessel element; 6 = protoxylem vessel element; 7 = protoxylem lacuna. Given that xylem vessel elements are dead at maturity, water can move through the protoxylem lacuna during transpiration. The metaxylem vessel elements and the internal fibers serve to keep the lacuna from collapsing. Scale bar in **g** = 50 µm and applies to both panels. (**f**, **g** RR Wise)

11.6.3 Patterns of Phloem Development in the Stem

As with xylem, two sequential states of phloem development are identified in gymnosperms and eudicots: primary phloem and secondary phloem (refer to Sect. 1.19.2). The primary phloem develops from the procambium, whereas secondary phloem is produced



◘ **Fig. 11.6** **h–k** Patterns of metaxylem development. The locations of protoxylem (P) and metaxylem (M) are indicated. Phloem development is not considered. (Drawing modified from Wikipedia)



◘ **Fig. 11.6** **l** Cross-section of an open vascular bundle in a pea (*Pisum sativum*) stem. All functional phloem shown here is secondary, i.e., produced by the vascular cambium (#4). The primary phloem (7) is being crushed by growth and expansion of the secondary phloem. Phloem parenchyma cells are present but difficult to identify except in longitudinal section. Examples of the various cell types are labeled as 1 = sieve tube element, 2 = sieve plate, 3 = companion cells, 4 = vascular cambium, 5 = secondary xylem, 6 = phloem fibers. Scale bar = 50 µm. (RR Wise)

by vascular cambium. In stems and roots of plants with secondary growth, primary phloem is very short-lived, and, except in leaves, it is replaced by secondary phloem.

Monocots lack true secondary growth and thus, only have primary phloem. Primary phloem is axial only; there is no radial primary vasculature in gymnosperms, monocots, or eudicots. Developing roots, stems, and leaves may all possess protophloem. It is different from metaphloem in that it has sieve tube cells only—there are no companion cells in protophloem and rarely phloem parenchyma or fibers. The sieve tube elements (STEs) are typically short-lived and are crushed at an early stage by expansion of the organ and subsequent metaphloem development. ◘ Figure 11.6f shows a thin layer of crushed protophloem STEs between the sclerenchymatous bundle sheath and the metaphloem in maize.

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Metaphloem development initiates after the organ ceases growth in length, and this tissue must last for the life of the organ because, by definition, there is no vascular cambium to produce additional secondary phloem. Metaphloem sieve tube elements are larger than those found in protophloem, no doubt in keeping with the increased demand for translocation as the growing plant increases in size. Companion cells are present, and in maize, metaphloem sieve tube elements alternate with narrow companion cells in an orderly fashion resulting in a "checkerboard" pattern when seen in cross-section (refer to ◘ Fig. 11.6f). Metaphloem in woody dicots (which display secondary growth) is crushed by growth of secondary phloem (◘ Fig. 11.6l), much like protophloem is crushed by metaphloem in monocots. Herbaceous eudicots, which lack secondary growth, have a metaphloem that is somewhat similar to that found in monocots in terms of cell sizes.

11.7 Evolutionary Advances Led to Variations in Stem Architecture

Plants colonized the land approximately 480 million years ago. The first land plants were small and leafless and lacked a vascular system, similar to their aquatic ancestors. Life on land required the development of a number of unique structures, mainly lignin to provide support, a cuticle to limit water loss, stomata to allow for gas exchange, leaves to increase the photosynthetic surface area, and vasculature to move water, minerals, and photosynthate throughout the plant.

Stems evolved first, and the first stem vascular systems, like the first land plants, were simple. As plants increased in size and complexity, so did the vasculature of their stems. The subsequent evolution of the leaf, in particular, had a large impact on stem vasculature because the leaf vasculature has to be directly connected to the stem vasculature via a strand of xylem and phloem called a **leaf trace**. The various patterns of stem vasculature are discussed below.

The stele is the cylinder of vascular tissue in the center of a root or stem, and there is significant variation in the arrangement of xylem and phloem in the tracheophyte stele. A number of classification systems have been proposed to define and categorize the different arrangements. The treatment used herein describes two basic types of steles: **protosteles** (no central pith) and **siphonosteles** (central pith) with several variants of each (◘ Table 11.1).

Protosteles (*proto* = first, *stele* = column) have xylem located as a solid mass in the center with no pith. Phloem surrounds the xylem with an endodermis to the exterior of the phloem. Protosteles occur before the siphonostele in the fossil record and are currently found in the seedless vascular plants (ferns and fern allies). Because the types of plants that have protosteles typically have no leaves or, at the most, microphylls, protosteles lack **leaf gaps**, i.e., gaps in the stele where leaf vasculature branches off. In fact, the definition of a microphyll is an appendage that emerges from the protostele without leaving a leaf gap (refer to ► Chap. 12—Leaves).

Table 11.1 Organization of stele types

Protosteles	Haplostele	Cylindrical core of xylem surrounded by phloem	
	Actinostele	Lobed core of xylem surrounded by phloem	
	Plectostele	Interconnected plate-like regions of xylem surrounded by and immersed in phloem tissue	
Siphonosteles	Solenostele	Ectophloic	Phloem to the exterior of xylem
		Amphiphloic	Phloem to both sides of xylem
	Dictyostele	Multiple leaf gaps result in a net-like arrangement	
	Eustele	Discrete vascular bundles are arranged in a field of pith; eudicots have a eustele with a ring of bundles	
		An atactostele is subtype of eustele in which vascular bundles are apparently scattered throughout the pith; found in monocots	

There are three types of protosteles—haplostele, actinostele, and plectostele. The **haplostele** (*haplo* = simple) is the most basic of protosteles, with a cylindrical core of xylem surrounded by phloem and then an endodermis. This type of stele is the most common in roots and, as is shown in Fig. 11.7a, b, the rhizome of *Lygodium* (fern). An **actinostele** (*actino* = star) is a protostele in which the core of xylem is lobed but the entire stele is surrounded by an endodermis. This type of stele is found in stems of the whisk fern, *Psilotum* sp. (Fig. 11.7c, d) and is common in the roots of seed plants. A **plectostele** (*plecto* = folded or pleated, sometimes called a polystele) is a protostele in which interconnected plate-like regions of xylem are surrounded and immersed in phloem tissue, all in turn surrounded by an endodermis. Many modern club mosses (Lycopodiopsida) have this type of stele within their stems (Fig. 11.7e, f). Given that protosteles are defined as having a central core of xylem, it follows that all protosteles are **ectophloic**, meaning the phloem is to the exterior (*ecto*) of the xylem.

The evolution of the leaf drove advancements in stele design producing more complex patterns resulting in the siphonostele (*siphono* = tube or pipe). Siphonosteles have a pith in the center of their stems, surrounded by a cylinder of various designs containing the vascular tissue. There are two types of siphonosteles, solenostele (amphiphloic or ectophloic), and dictyostele. The **solenostele** (*soleno* = cylinder) is the most basic of siphonosteles, with a central core of pith enclosed in a cylinder of vascular tissue. The cylinder

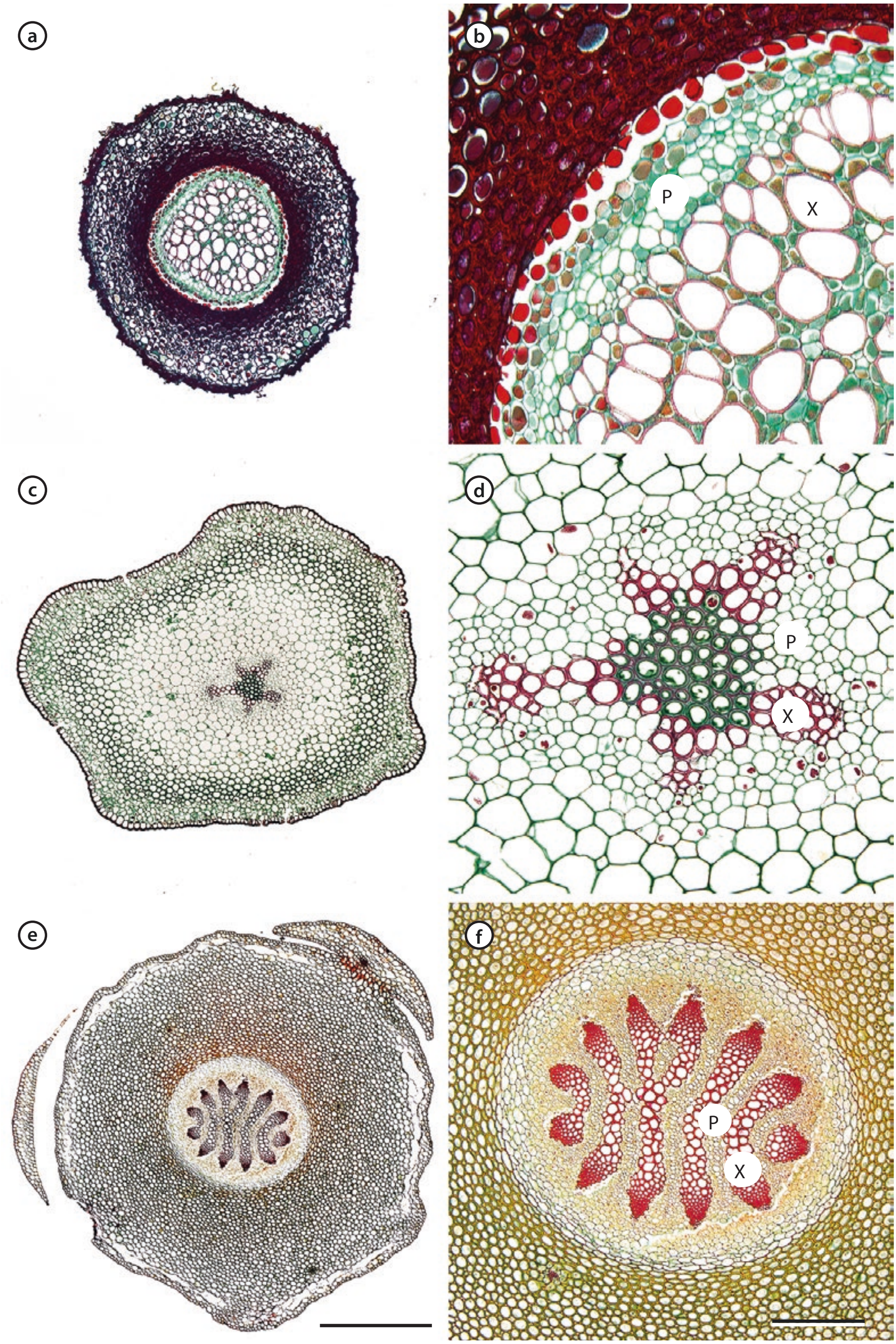


Fig. 11.7 **a**–**f** Examples of the three types of protosteles: **a** and **b**, haplostele from a climbing fern (*Lygodium* sp.) rhizome; **c** and **d**, actinostele from a whisk fern (*Psilotum* sp.) rhizome. **e** and **f**, Plectostele from a ground pine (*Lycopodium* sp.) rhizome. Scale bars = 250 μm for **a**, **c,** and **e** and 100 μm for **b**, **d**, and **f**. (**a**–**f** RR Wise)

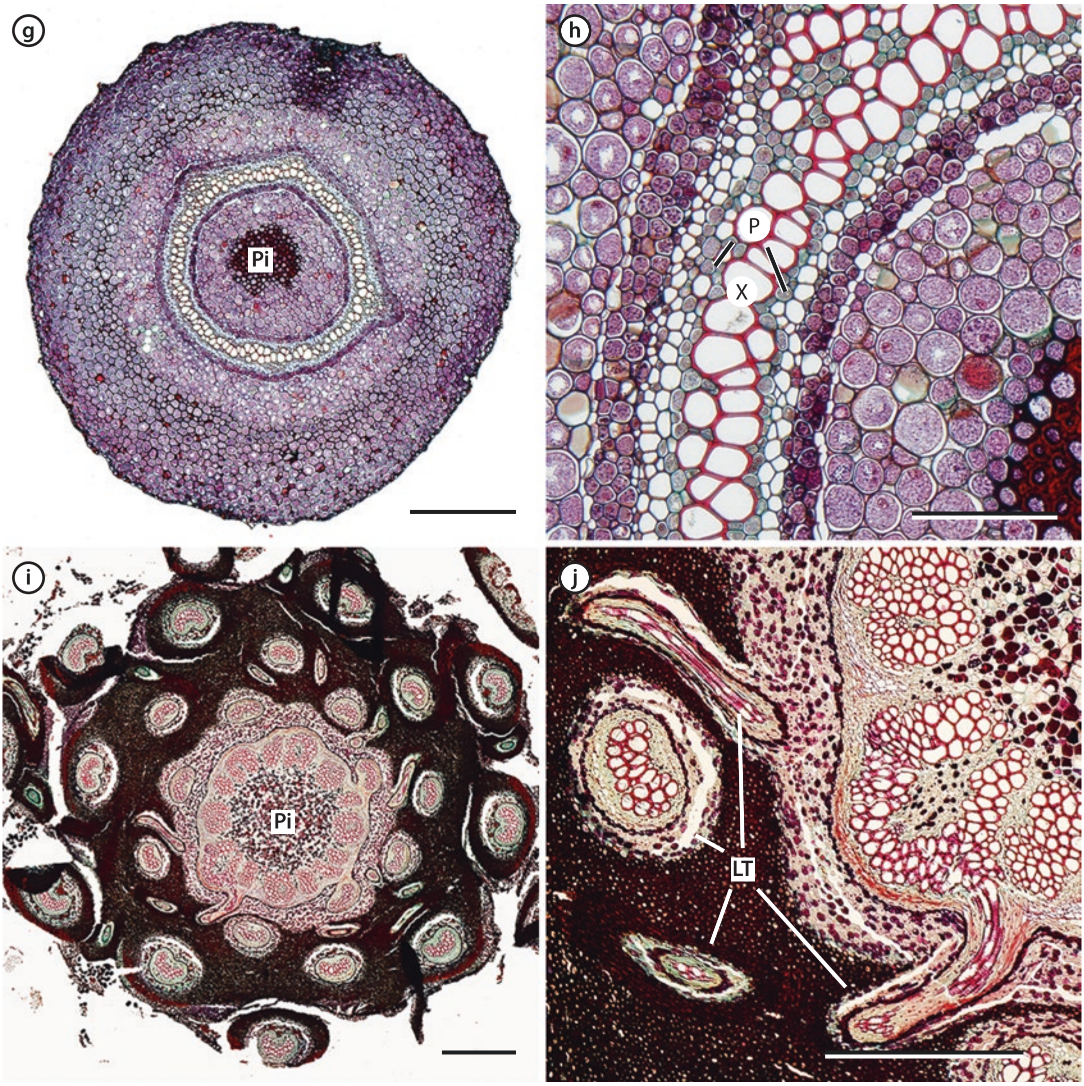
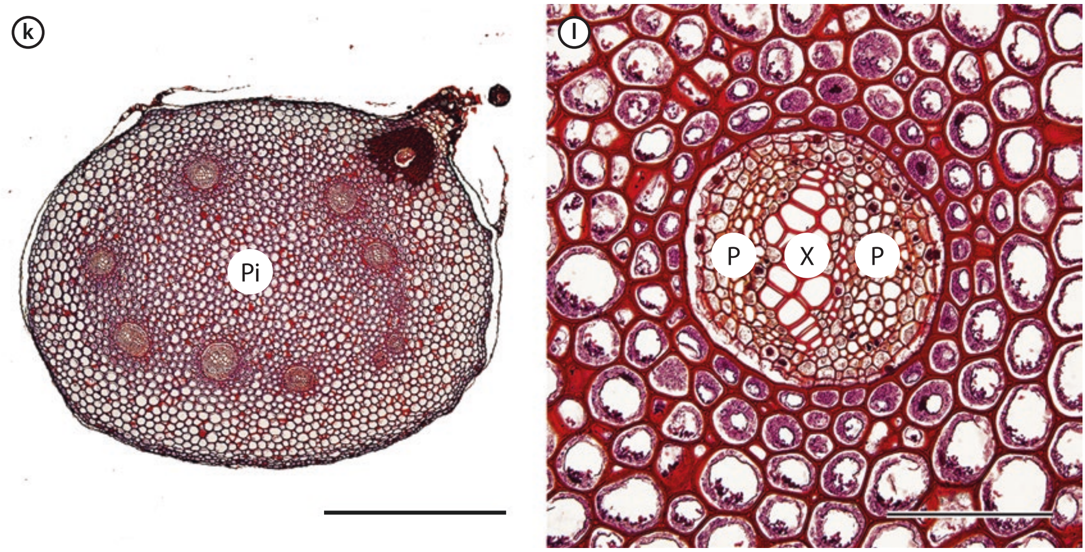


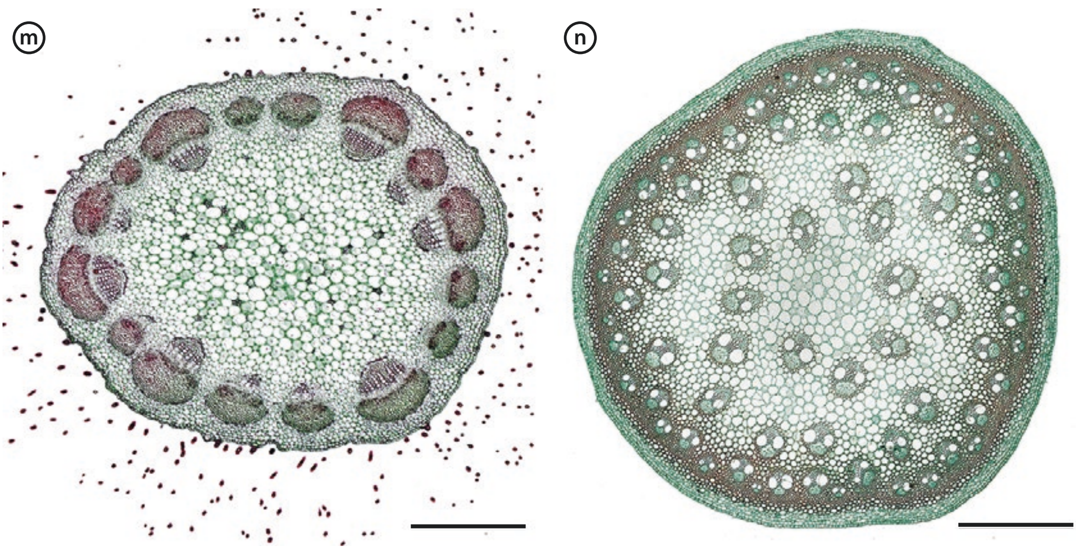
Fig. 11.7 **g**–**j** Examples of the two types of solenosteles. **g** and **h**, Ectophloic solenostele from a royal fern (*Osmunda* sp.) rhizome. **i** and **j**, Amphiphloic solenostele from a maidenhair fern (*Adiantum pedatum*) rhizome. Leaf traces (LT) are indicated. Scale bars = 500 µm in **g** and **i** and 100 µm in **h** and **j**. (**g**–**j** RR Wise)

only shows breaks at the leaf gaps. This type of stele is found only in fern stems today. An **amphiphloic** solenostele (*amphi* = both) has phloem both interior and exterior to the xylem (Fig. 11.7g, h), while an ectophloic solenostele only has phloem to the exterior (Fig. 11.7i, j). [Note: an amphiphloic stele has a continuous layer of phloem to both sides of the xylem in the siphonostele (Fig. 11.7g), an amphicribral vascular bundle has phloem completely surrounding the xylem in a single bundle (Fig. 11.7l), and a bicollateral vascular bundle has a patch of phloem to both sides of the xylem in a single bundle (Fig. 11.6d)].

The **dictyostele** (*dictyo* = net) is actually a variation of the solenostele caused by multiple leaves and short internodes



■ **Fig. 11.7** **k** A dictyostele from a fern (*Polypodium* sp.) rhizome with a central core of pith (Pi) and several vascular bundles. The individual bundles interconnect either above or below the level of the section, which is characteristic of a highly dissected siphonostele, as opposed to a eustele. **l** The individual bundles have a central core of xylem (X) surrounded by phloem (P) making this an amphicribral bundle. Scale bars = 500 µm in (k) and 100 µm in **l**. (**k**, **l** RR Wise)



■ **Fig. 11.7** **m** Cross-section of a red clover (*Trifolium pratense*) eustele stem showing a ring of vascular bundles at the periphery surrounding a central pith. The dots surrounding the stem are trichomes. **n** A greenbrier (*Smilax* sp.) stem in cross-section displaying the atactostele architecture that is characteristic of monocots. Scale bars = 500 µm in both panels. (**m**, **n** RR Wise)

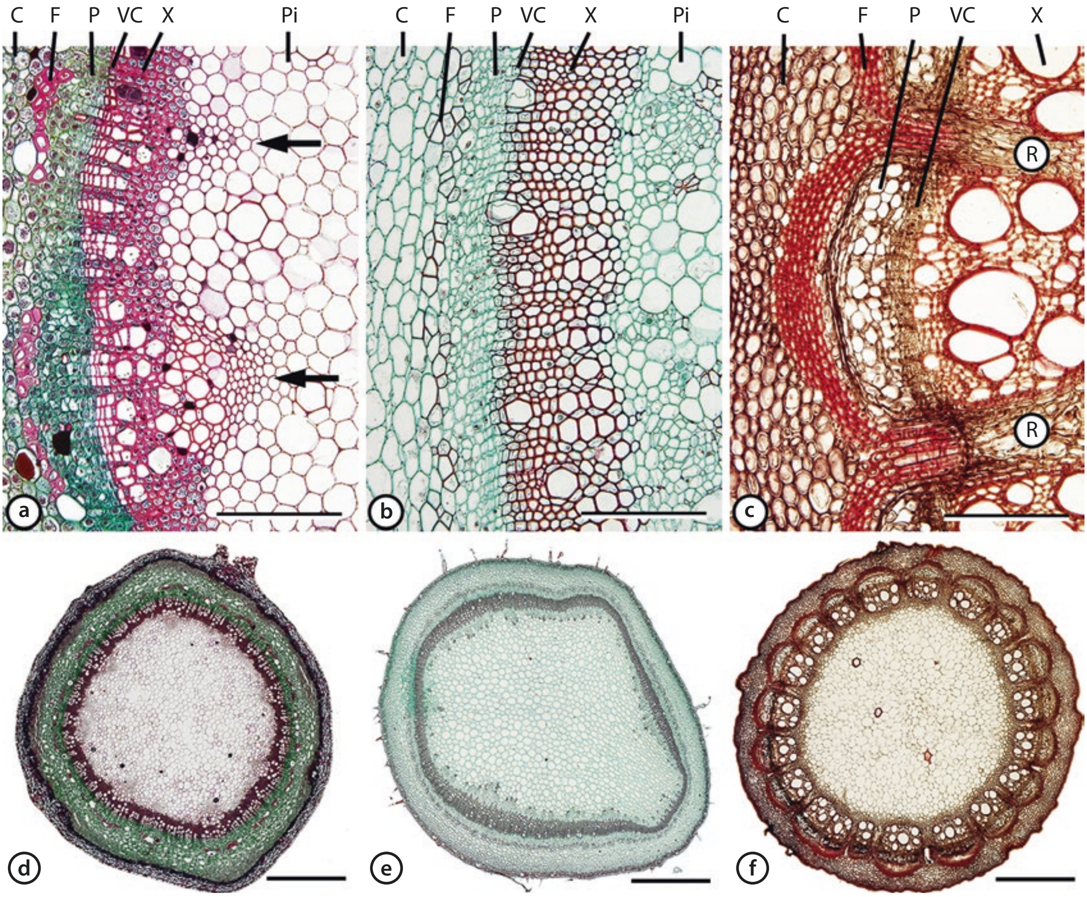
(■ Fig. 11.7k, l). In portions of the stem, the vasculature is still in a tube-like arrangement (a true siphonostele), but the presence of closely arranged leaves along the stem axis creates multiple gaps in the stelar core creating the impression in a single cross-section of a network of vasculature, similar to a eustele, which it is not. Among living plants, dictyosteles are found only in the stems or rhizomes of ferns. They are sometimes called a **dissected siphonostele**, because that is an apt descriptor of their origin and structure.

The **eustele** is the most common stelar arrangement in stems of seed plants. Here, the vascular tissue is arranged in discrete vascular bundles, usually in one or two rings around the central pith, and the endodermis, in eudicot stems at least, is missing (◘ Fig. 11.7m). In addition to being found in stems, the eustele appears in the roots of monocots where an endodermis is present. Monocot stems have a variation on the eustele called an **atactostele** (*atacto* = scattered; Brebner 1902) in which numerous bundles are apparently scattered throughout the stem (◘ Fig. 11.7n). While that notion of "scattered vascular bundles" persists in the literature and texts, and is consistent with what one can see in a single stem cross-section, recent studies have been able to resolve a level of order to the arrangement of bundles (Korn 2016). If viewed in a three-dimensional organization, they are actually distributed in an ordered fashion and interconnected in a complex format as they approach a node. Typically, only two protoxylem and two metaxylem vessels are present in each vascular bundle.

This basic difference in stem architectures between eudicots and monocots arises from the pattern of vascular origination. In eudicots, the procambium arises near the **leaf buttresses**, which bud off the outside of the shoot apical meristem (▶ Sect. 4.7). Thus, the resulting vascular bundles are near the outer edge of the stem, and the interior of the stem is filled with pith parenchyma produced by the ground meristem. Conversely, in the monocot leaf and stem, procambium initiation is scattered within the intercalary meristem, resulting in the apparent scattered distribution of vascular bundles in the mature stem.

11.8 Secondary Growth in Eudicots Initiates in Three Basic Patterns

Secondary growth of the eustele vascular system in eudicot stems can be seen as following three different patterns. In the first, primary growth proceeds as described above with the formation of discrete vascular bundles. Subsequently, an interfascicular cambium forms, and the resulting secondary growth produces xylem and phloem which connect the bundles and form a continuous cylinder, as in elderberry stems (◘ Fig. 11.8a, d). In stems displaying a second form, primary growth produces a continuous ring of vasculature, which is then mirrored with the secondary growth. The tobacco stem is an example (◘ Fig. 11.8b, e). Eudicot stems displaying the second form of secondary growth develop an interfascicular cambium, but it produces only parenchyma, resulting in pith rays. This form is seen most often in vines that need to retain some flexibility such as moonseed (◘ Fig. 11.8c, f) as well as Dutchman's pipe (◘ Fig. 14.5b, c). Repeated annual cycles of secondary growth generates wood and will be discussed in ▶ Chap. 15—Wood.



■ **Fig. 11.8** **a**–**f** Stem cross-sections displaying different secondary growth patterns. **a**, **d** In elderberry (*Sambucus* sp.) the primary vascular system is in strands (*arrows*) which later connect into a ring by the action of an interfascicular cambium. **b**, **e** Both the primary and secondary vascular systems are ring shaped in a tobacco (*Nicotiana tabacum*) stem. **c**, **f**) In the moonseed (*Menispermum* sp.) stem, primary and secondary vascular systems form discrete bundles, and the interfascicular cambium forms parenchyma, resulting in pith rays (R). Cortex (C), fibers (F), phloem (P), vascular cambium (VC), xylem (X), and pith (Pi) are labeled. Scale bars = 100 µm in **a**, **b**, and **c** and 500 µm in **d**, **e**, and **f**. (**a**–**f** RR Wise)

11.9 Monocot Stems Show a Different Form of Secondary Growth than Eudicots

One of the products of eudicot secondary growth is the accumulation of significant supportive tissue in the form of wood, a form of sclerenchyma. Although lacking wood, many monocots stems gain significant support from sclerenchyma tissues and fibrous strands. *Juncus* sp. (■ Fig. 11.9a, b) is a common wetland monocot with an aerenchyma-filled stem and small, peripheral fiber bundles for support. Its stems may reach a meter in length, but unlike other monocots, *Juncus* does not typically have sclerified bundle sheaths. The stem is photosynthetic, with a thick layer of cortical chlorenchyma.

The stem of the three-square bulrush (*Schoenoplectus americanus*) gains support from its angular shape and multiple, large bun-

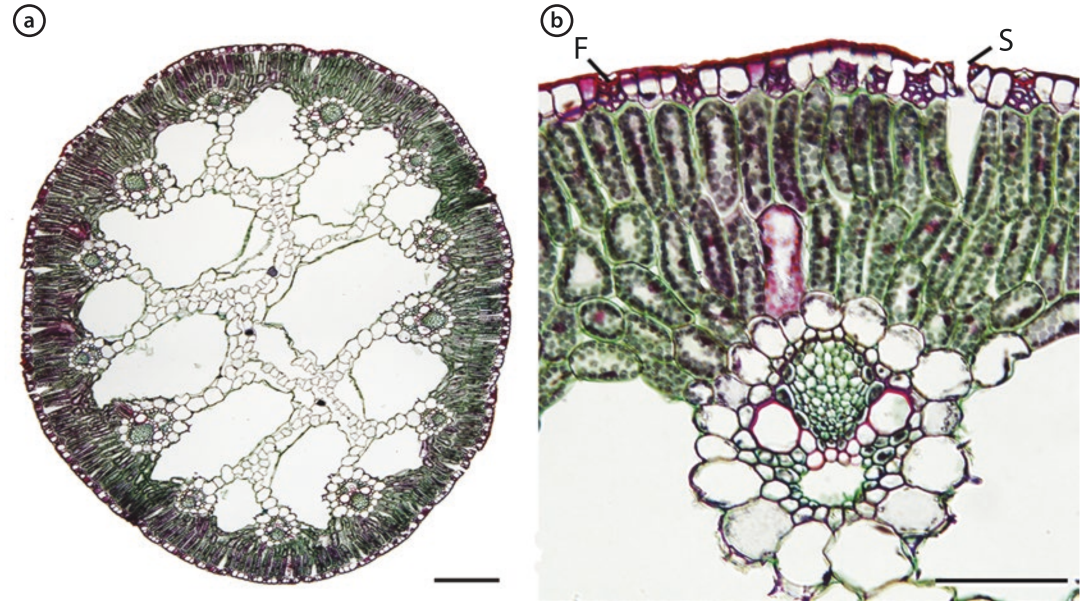


Fig. 11.9 Cross-sections of a Baltic rush (*Juncus balticus*) stem. **a** Uncharacteristic of monocots, the vascular bundles in this stem are arranged in a ring because the center of the stem is filled with aerenchyma tissue that facilitates shoot to root gas exchange. The interior aerenchyma is often torn during growth, but not in this stem. **b** A higher magnification image reveals small bundles of fibers (F) adjacent to the epidermis and no fibers surrounding the vascular bundle (center of image). The cortical chlorenchyma cells assume a palisade-like appearance and are highly photosynthetic. Individual chloroplasts can be observed in the periphery of the cortical chlorenchyma cells. Note the stomatal complex (S). Scale bars = 100 µm in **a** and 50 µm in **b**. (**a**, **b** RR Wise)

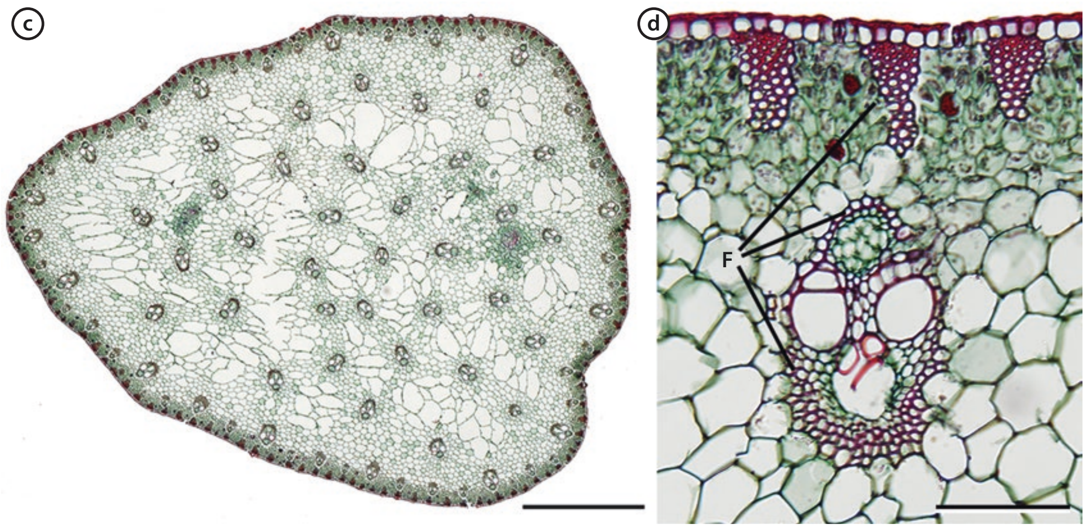
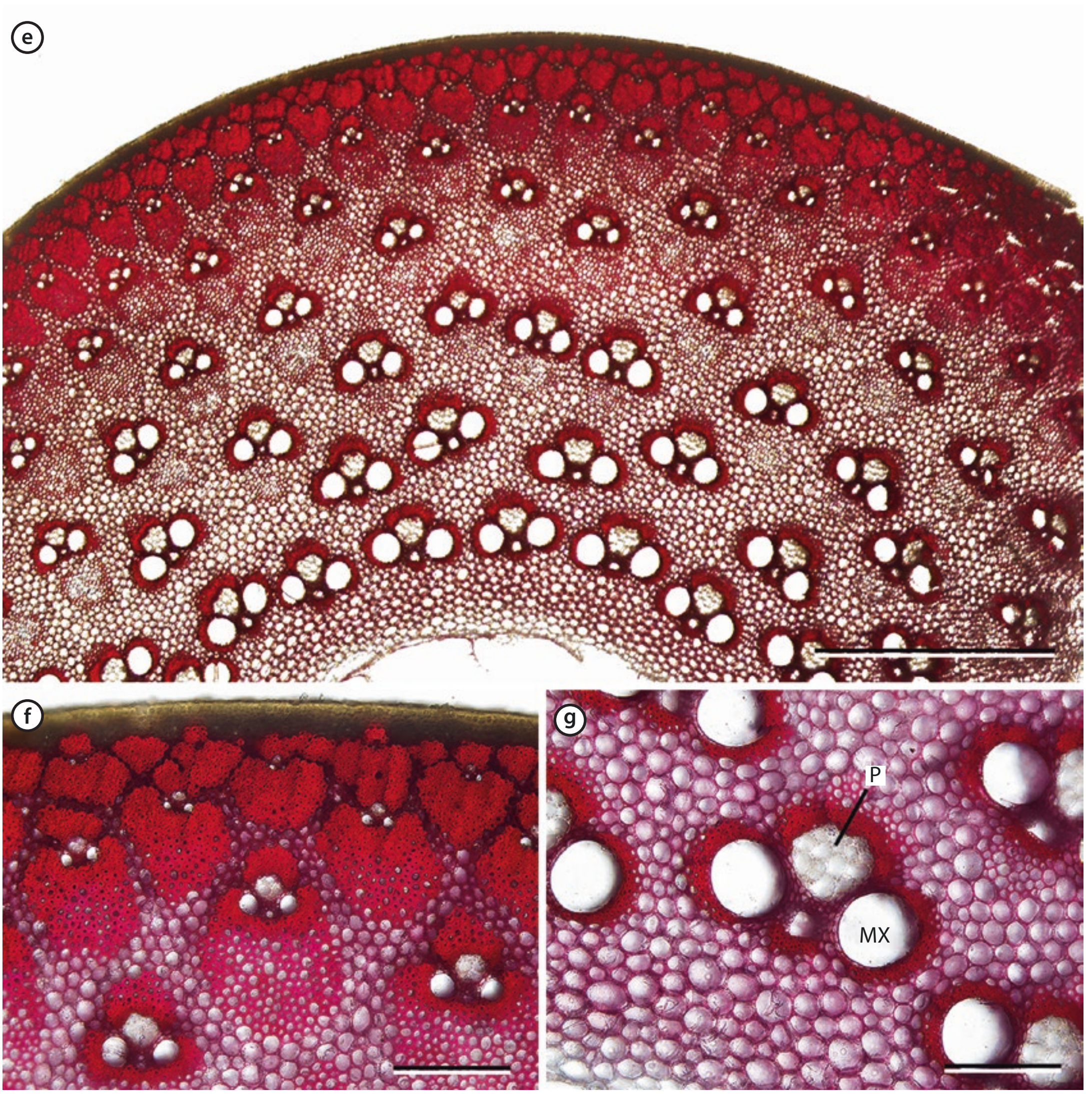


Fig. 11.9 Cross-section of a three-square bulrush (*Schoenoplectus americanus*) stem. **c** The stem interior is intact and filled with vascular bundles ordered throughout the conjunctive tissue in the stem. **d** A thick cuticle covers the stem surface, and large bundles of fibers (F) lie in the green chlorenchyma tissue, just inside the epidermis. Additional fibers are seen surrounding the vascular bundle in the middle of the image. Scale bars = 500 µm in **c** and 50 µm in **d**. (**c**, **d** RR Wise)

dles of fibers at the stem periphery (◘ Fig. 11.9c). The vascular bundle sheaths are also heavily sclerified (◘ Fig. 11.9d). Like *Juncus*, *Schoenoplectus* is a wetland plant with a spongy, aerenchyma-filled stem interior well suited for gas exchange.

Bamboo stems (◘ Fig. 11.2h and 11.9e–g) are extremely strong and have numerous uses such as scaffolding and construction material, especially in Asia. Their strength comes from a tight packing of heavily sclerified vascular bundles (◘ Fig. 11.9e–g).

Even in the absence of true secondary growth (as defined for eudicots), monocot stems such as screw pines (Pandanaceae) and palms



◘ **Fig. 11.9** **e**–**g** Sclerification of vascular bundles in a seabreeze bamboo (*Bambusa malingensis*) stem; phloroglucinol was used to stain the lignin red. **g** A low magnification view showing the heavy sclerification of the outer layers and sclerified bundles to the interior. **f** The outer vascular bundles are almost entirely sclerified. They serve mainly for support, with little role in water movement. **g** The inner vascular bundles provide support and also serve as conduits for transpiration via the metaxylem (MX) and translocation via the phloem (P). Compare the sizes of the metaxylem and phloem in **f** and **g**. The two micrographs are at the same magnification. Scale bars = 500 µm in **g** and 100 µm in **f** and **g**. (**e**–**g** RR Wise)

(Araceae) can be quite large. Monocots have three mechanisms to increase stem diameter and strength: primary thickening meristems, secondary thickening meristems, and intercalary meristems (intercalary meristems were described above).

The **primary thickening meristem** (PMT) is found at the stem apex, and its cells divide in a periclinal plane (parallel to the organ surface), generating anticlinal (perpendicular to the cell surface) files of derivatives (◘ Fig. 11.9h). At the apex, the PMT forms a disc of meristematic cells. The PMT generates a wide crown and contributes to the increase in stem thickness. In some species, PMT activity at the shoulders creates large bulges that extend beyond the shoot apex, leaving it in a recess at the stem tip. As the stem elongates and leaves behind the PMT, its orientation gradually changes to become parallel with the stem axis, while remaining parallel to the stem surface. The PMT also becomes thinner and less active further down the stem. Thus, in most plants with a PMT, the stem diameter is set by the PMT, and further increases in diameter are not possible.

Many monocots have the ability to thicken and strengthen the stem by the activity of a **secondary thickening meristem** (STM). *Cordyline* is a monocot genus of tropical plants that possesses a STM and several other unusual features (◘ Fig. 11.9i–l). First, primary growth produces the stem proper with a pith full of primary vascular bundles surrounded by parenchyma cells (the conjunctive tissue). These primary vascular bundles are collateral, with xylem to the interior and phloem to the exterior (◘ Fig. 11.9l). A primary cortex, sclerified hypodermis, and epidermis develop to

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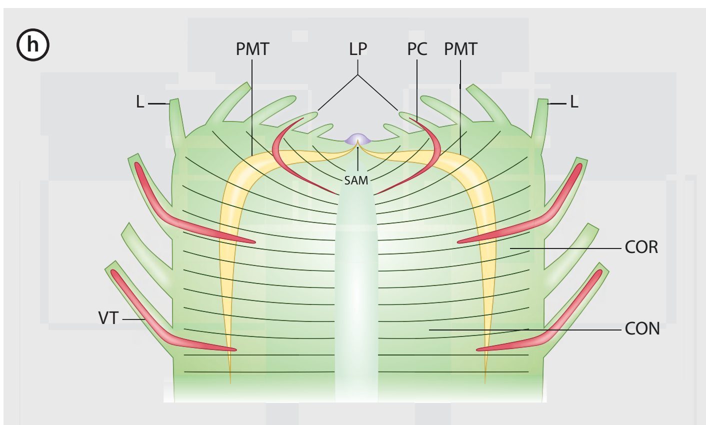

◘ **Fig. 11.9** **h** Diagrammatic representation of a monocot stem tip with a primary thickening meristem. The shoot apical meristem (SAM) generates leaf primordia (LP) in an exogenous manner, as in all stems. A procambium (PC) develops for each leaf primordium and eventually supplies each leaf (L) with a vascular trace (VT). The procambium also generates the axial vascular bundles. The activity of the PMT at the "shoulders" of the stem tilts the leaf bases outward so they point forward and become aligned parallel to the stem axis. PMT derivatives contribute to the cortex (COR) and conjunctive tissues (CON). (Figure modified from DeMason (1983)) (RR Wise)

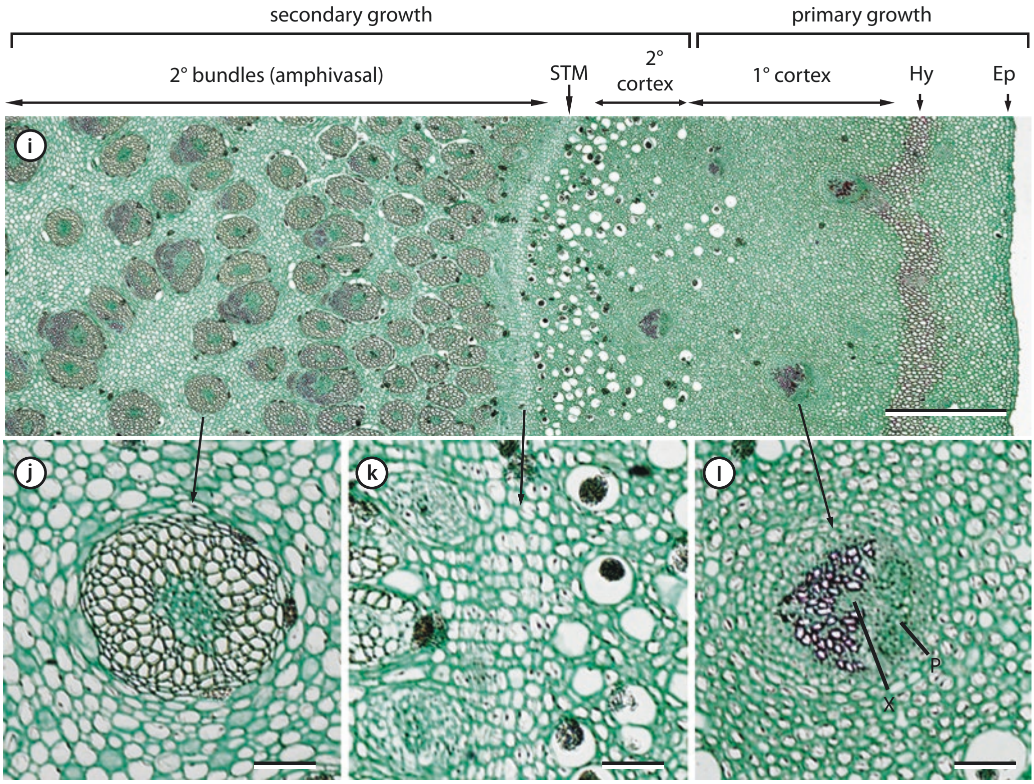

Fig. 11.9 **i** Cordyline (*Cordyline* sp.) stem in cross-section. The secondary thickening meristem (STM) is in the center of the image and shown enlarged in **k**. It has produced a small amount of secondary cortex to the right (exterior) that merges with the primary cortex. **j** The numerous secondary vascular bundles are amphivasal, while **l** the bundles produced by primary growth are collateral. Ep epidermis, Hy hypodermis, P phloem, STM secondary thickening meristem, X xylem. Scale bars = 250 µm in **i** and 25 µm in **j**–**l**. (**i**–**l** RR Wise)

the outside. Subsequently, parenchyma cells near to periphery of the stem become meristematic and generate a ring of vascular cambium called the secondary thickening meristem (STM, Fig. 11.9i, k).

Alternatively, in yucca, the STM has been shown to be a continuum of the PTM (DeMason and Diggle 1984). The STM generates secondary vascular bundles (not a ring but bundles) and additional parenchyma to the inside and a small amount of secondary cortex to the outside. The secondary bundles thus produced are in a pattern sometimes called **diffuse secondary growth** with isolated bundles in a field of ground parenchyma cells. In another unusual twist, the secondary vascular bundles are amphivasal, with a central core of phloem surrounded by xylem as seen in Fig. 11.9j for cordyline.

In a special case of monocot stem thickening, the increased stem thickness seen at the base of many palms (Fig. 11.9m) is due to the development of adventitious roots. They are initiated in the stem interior, and, as they grow outward, they cause the stem to bulge.

Fig. 11.9 **m** Thickening at the base of a queen palm (*Syagrus romanzoffiana*) caused by the development of adventitious roots deep within the stem. Scale bar = 0.5 m. (RR Wise)

11.10 Chapter Review

Concept Review

11.1 *Stems have a variety of forms and functions.* The typical stem produces and supports leaves and flowers. Other stem functions include photosynthesis (cladodes), attachment (tendrils), underground storage (rhizomes), and asexual reproduction (rhizomes and stolons).

11.2 *External stem morphology varies among monocots and herbaceous eudicots.* Stems are divided into nodes, the region where leaves and flowers originate, and internodes, the regions between the nodes. Perennial eudicot stems show evidence of previous year's growth in the form of leaf and bud scale scars. Monocot stems may be quite substantial, as in bamboo, or made of overlapping leaf sheaths as in the grasses. Phyllotaxy is the arrangement of leaves on a stem.

11.3 *The stem is composed of three tissues—dermal, ground, and vascular.* The dermis covers the stem exterior, the vascular tissue contains xylem and phloem, and the ground tissue is represented by the cortex, pith, and conjunctive tissue. The basic arrangement of the three tissues differs between monocots and eudicots.

11.4 *Dermal tissues cover the stem exterior.* The dermal tissue that covers the exterior of the stem has an outer, waxy cuticle and may contain stomata and trichomes.

11.5 *Ground tissues fill the stem interior.* Ground tissue may contain parenchyma, fibers, tannins, starches, and secretory ducts. Ground tissue makes up the cortex, pith, and conjunctive tissue of the stem. An endodermis may separate the cortex from the vascular tissue (stele).

11.6 *Stem vascular tissues are arranged in bundles.* Vascular bundles are arranged in a ring in most eudicot stems and scattered throughout the monocot stem. Depending on the species, xylem may be positioned to the interior, exterior, surround by, or on both sides of the phloem. Protoxylem and protophloem are derived from the procambium; metaxylem and metaphloem are derived from the vascular cambium. Open vascular bundles have a vascular cambium (they possess metaxylem/phloem), closed vascular bundles do not (only have protoxylem/phloem).

11.7 *The stem vascular system shows several forms.* The stele is the vascular cylinder in a stem or root. Protosteles have a solid center of xylem; there are three types. The xylem is cylindrical in a haplostele, lobed in an actinostele, and plate-like in a plectostele. Siphonosteles have pith in the center; there are three types, with subtypes. Solenosteles have either phloem exterior to the xylem (ectophloic) or on both sides of the xylem (amphiphloic). A dictyostele has multiple leaf gaps. A eustele has discrete vascular bundles in a field of pith. Eudicots have a eustele with the bundles arranged in a ring. Monocots have an atactostele—a eustele with the appearance of scattered vascular bundles.

11.8 *Secondary growth in eudicots has three basic patterns.* The ring of vascular bundles in a eudicot eustele showing secondary growth may develop as a) individual vascular bundles that become connected via the activity of an interfascicular cambium, b) a single ring of vascular cambium that produces concentric rings of xylem and phloem, or c) individual bundles that stay separated because the interfascicular cambium produces parenchyma. In the latter case, the tissue between the bundles is called a pith ray.

11.9 *Monocot stems show a different form of secondary growth than eudicots.* Monocot stems lack true secondary growth but can become quite "woody" via the development of sclerified bundle sheaths, the activity of a primary thickening meristem, or the activity of a secondary thickening meristem.

Concept Connections

1. Match the structure in the left column to the function in the right column. Some structures may have more than one function.

a. Rhizome	i. Storage
b. Corm	ii. Attachment
c. Stolon	iii. Perennation
d. Cladode	iv. Asexual reproduction
e. Tendril	v. Photosynthesis

Concept Assessment

2. Primary and secondary thickening meristems are mostly found in
   a. ferns.
   b. gymnosperms.
   c. dicots.
   d. monocots.
   e. uniformly found in all of the above.

3. Herbaceous stems differ from woody stems in that
   a. herbaceous stems only show secondary growth.
   b. herbaceous stems are only found in monocots.
   c. herbaceous refers to monocots. woody refers to eudicots.
   d. herbaceous stems rarely show secondary growth.
   e. herbaceous stems are characteristic of a perennial growth habit.

4. Phyllotaxis is
   a. the generation of roots from a stem.
   b. the ability to undergo secondary growth.
   c. a leaf pattern in which successive leaves are at right angles to each other.
   d. a meristem that contributes to both primary and secondary growth.
   e. the pattern of leaf initiation on the stem.

5. The outer layer of the stem apical meristem is covered by the
   a. dermal layer.
   b. cortex.
   c. endodermis.
   d. ground tissues.
   e. aerenchyma.

6. Lateral organs of stems (leaves, branches, and floral organs) are produced in what manner?
   a. endogenous.
   b. exogenous.

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c. intercalary.
d. from pericycle.
e. from endodermis.

7. The hypodermis is relatively rare in stems.
a. true.
b. false.

8. A leaf gap is found in the ______
a. vascular system of a leaf.
b. apical meristem of a shoot.
c. ground tissue of a leaf.
d. ground tissue of a stem.
e. vascular system of a stem.

9. Support is provided in Spanish moss (*Tillandsia usneoides*) stems by a
a. vascular cambium.
b. sclerified epidermis.
c. sclerified pith.
d. strands of collenchyma.
e. a cortex of chlorenchyma.

10. Protosteles have a simple anatomy with
a. a central core of xylem surrounded by phloem.
b. a central core of pith surrounded by xylem and phloem.
c. a hollow core surrounded by pith, xylem and phloem, in that order.
d. a solid core of sclereids surrounded by chlorenchyma.
e. a tube of xylem and phloem lying just underneath the epidermis.

11. The primary source of stem thickening in squash is
a. sub-epidermal collenchyma.
b. xylem.
c. internal phloem.
d. vascular cambium.
e. perivascular fibers.

Concept Applications

12. Monocot stems lack true vascular cambium, yet some monocots, like palm and bamboo, can make a very strong stem. How do monocots do this?

13. Explain how the monocot primary thickening meristem can contribute to both the length and girth of the stem.

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Leaves

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R. Crang et al., *Plant Anatomy*, https://doi.org/10.1007/978-3-319-77315-5_12

Introduction

Leaves, the lateral organs of the shoot, serve multiple functions in plants. Their primary task is photosynthesis: harvesting light energy and combining it, in the form of high-energy electrons, with carbon dioxide gas taken from the atmosphere. The carbon is reduced and the high-energy electrons in the resulting sugars are the source of the vast majority of chemical energy used by the biosphere. Photosynthesis requires that leaves be able to effectively harvest light and CO_2. Light passes directly through the epidermis and can penetrate effectively into the leaf interior. Indeed, internal leaf morphology serves to maximize the penetration and harvesting of light. CO_2, however, enters the leaf by diffusing through stomatal pores (refer to ► Chap. 9, Epidermis), and stomatal opening is also the cause of water loss from the leaf via transpiration. The competing demands of maximizing carbon uptake while minimizing water usage, combined with a plant's habitat, have provided strong selective pressures during terrestrial plant evolution. The result of 480 million years of land plant evolution has been an extremely wide range of leaf anatomical forms and adaptations.

12.1 Leaves Have a Variety of Shapes and Functions

While leaves can take on many different forms and functions (see below), a typical foliage leaf has a more or less flattened form with two obvious surfaces, which is to say it is **bifacial**. The upper (adaxial or toward the shoot axis) and lower (abaxial or away from the shoot axis) surfaces of the leaf are easily distinguished (◘ Fig. 12.1a, b). In most plants, leaves are dorsiventral in their internal structure, meaning there is a different internal tissue morphology between the adaxial direction and the abaxial direction (◘ Fig. 12.1c). This contrasts with organs with a cylindrical axis such as stems and roots which are radially symmetrical. The main part of the leaf is its **lamina** (or leaf blade) to which the above characteristics belong. In addition, leaves often have a **petiole** and a pair of **stipules**. A petiole attaches the lamina to the stem. Stipules are usually paired flaps or projections of tissue found beneath the petiole, if present at all.

In terms of leaf variants, a **frond** is a large, usually compound, deeply divided leaf with individual leaflets. The name is commonly applied to the leaves of ferns (◘ Fig. 12.1d) and palms, although much reduced monocots in the family Lemnaceae (duckweeds, watermeal, and mud midgets) are also said to have (actually be almost entirely composed of) fronds (refer to ◘ Fig. 11.1h, i). Conifers have flattened and elongated leaves: scalelike in the junipers and cedars and needlelike in the spruces and pines (◘ Fig. 12.1e). Many grasses have a leaf with a long and stiff leaf sheath that connects the base of the plant to the leaves. Lacking a true stem, the individual **leaf sheaths** wrap around and form the stalk. A leaf blade extends from the top of the sheath (◘ Fig. 11.2i). The "trunk" of a 10-meter tall banana (*Musa*) "tree" is a **pseudostem** composed entirely of leaf sheaths that originate at the soil surface and terminate in the leaf blade proper.

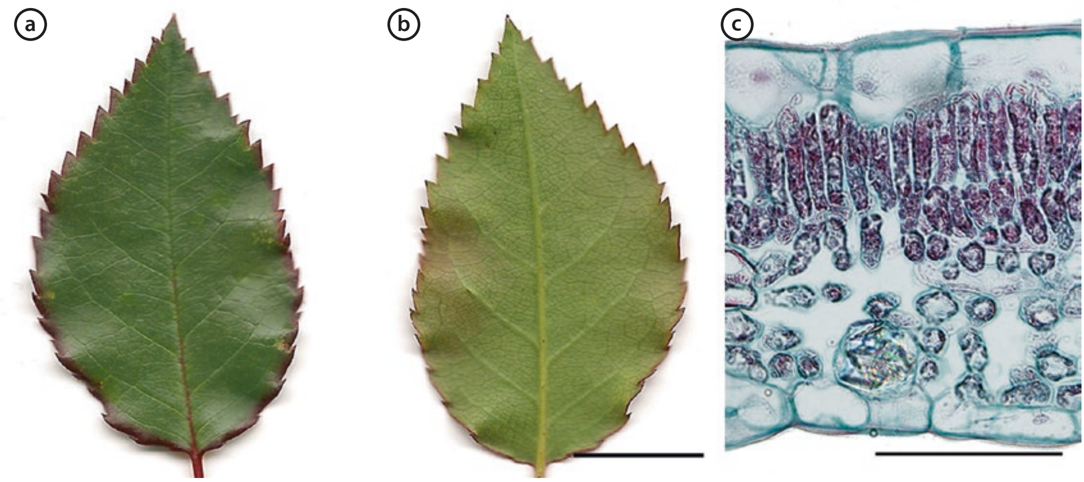


Fig. 12.1 A typical foliage leaf, i.e., macrophyll, from a rose plant (*Rosa* sp.) showing **a** the adaxial surface, **b** the abaxial surface with ridges formed by the major veins, and **c** a cross-section with the adaxis toward the top. A portion of the leaf petiole is visible at the bottoms of **a** and **b**. Scale bar = 1 cm in **a** and **b**, 50 µm in **c** (**a**–**c** RR Wise)

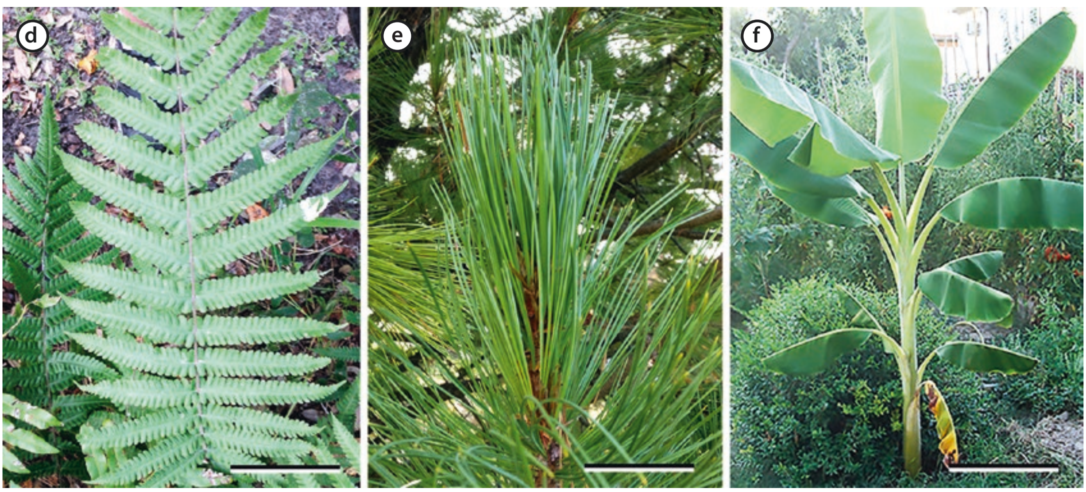


Fig. 12.1 Leaves of **d** southern wood fern (*Dryopteris ludoviciana*), **e** Swiss pine (*Pinus cembra*), and **f** banana (*Musa* sp.)*. The entire "trunk" of the banana "tree" is composed of tightly wrapped leaf sheaths. Scale bars = 10 cm in **d**, 5 cm in **e**, and 1 m in **f** (**d**, **e** RR Wise; **f** I Lorenzini, CC BY-SA 3.0)

Box 12.1 Modern Plant Science Research Relies on Plant Anatomical Studies

Rice (*Oryza sativa*) is one of the most heavily cultivated crop plants in the world. Achieving maximum production and yield relies on a host of conditions that serve to increase water efficiency, nutrient uptake, carbon partitioning, and light interception. Leaf angle plays a large role in the latter. Rice leaves have a long leaf sheath that encircles the stem and leads to a leaf blade that extends free of the stem. The greater the angle between the leaf blade and the stem, the more the leaf blade extends away from the stem, increasing light absorption but shading neighboring plants. The lesser the leaf angle, the more erect the leaf blade, the less light is absorbed, and the more light is available to neighboring plants. The leaf blade attaches to the leaf sheath at the lamina joint, the shape of which dictates the leaf angle. Therefore, understanding the anatomy and developmental control of the lamina joint can yield insights into leaf erectness, photosynthesis efficiency, and grain yield. Zhou et al. (2017) investigated the anatomical development of the rice lamina joint. They found that leaf angle was determined by the patterns and location of cell divisions and expansions, cell wall thickenings, and programmed cell death at the abaxial or adaxial sides of the joint. A wide range of genes involved in cell division, cell growth, hormone signaling, transcription factors, and signaling protein kinases were expressed in distinct spatial patterns. Their detailed study of the rice lamina joint, as it relates to crop-level productivity, combined anatomical observations with molecular studies and highlights the intersection of traditional plant anatomy approaches with cutting-edge molecular techniques.

Reference: Zhou et al. (2017).

Modified leaves have a variety of functions. **Cataphylls** are modified leaves that serve a function other than photosynthesis. **Cotyledons** which store food reserves in the eudicotyledon seed and the **scutellum** of grass seeds are also considered to be a form of a cataphyll. The functions of both are discussed in ► Chap. 19. Bud scales protect overwintering buds (◘ Fig. 12.1g) and are a form of cataphyll as well. Clematis (*Clematis* sp.) has compound leaves with each leaflet attached to a central rachis. The rachis acts as a tendril (◘ Fig. 12.1h) that wraps around any available substrate to achieve effective climbing. The traps on the carnivorous pitcher plant are also modified tubular leaves (◘ Fig. 12.1i). Cacti have thick photosynthetic stems and modified leaves called spines that serve as effective antiherbivory defenses (◘ Fig. 12.1j). Onion bulb scales (◘ Fig. 12.1k) are modified leaves that store food reserves.

Finally, it should be pointed out that some plants lack leaves entirely. Parasitic plants such as dodder (*Cuscuta* sp., ◘ Fig. 14.7a) and love vine (*Cassytha filiformis*, ◘ Fig. 14.7b) derive all their nutrition from their host plant and have no need for photosynthesis, not even in their stems, which lack chlorophyll and are yellow.

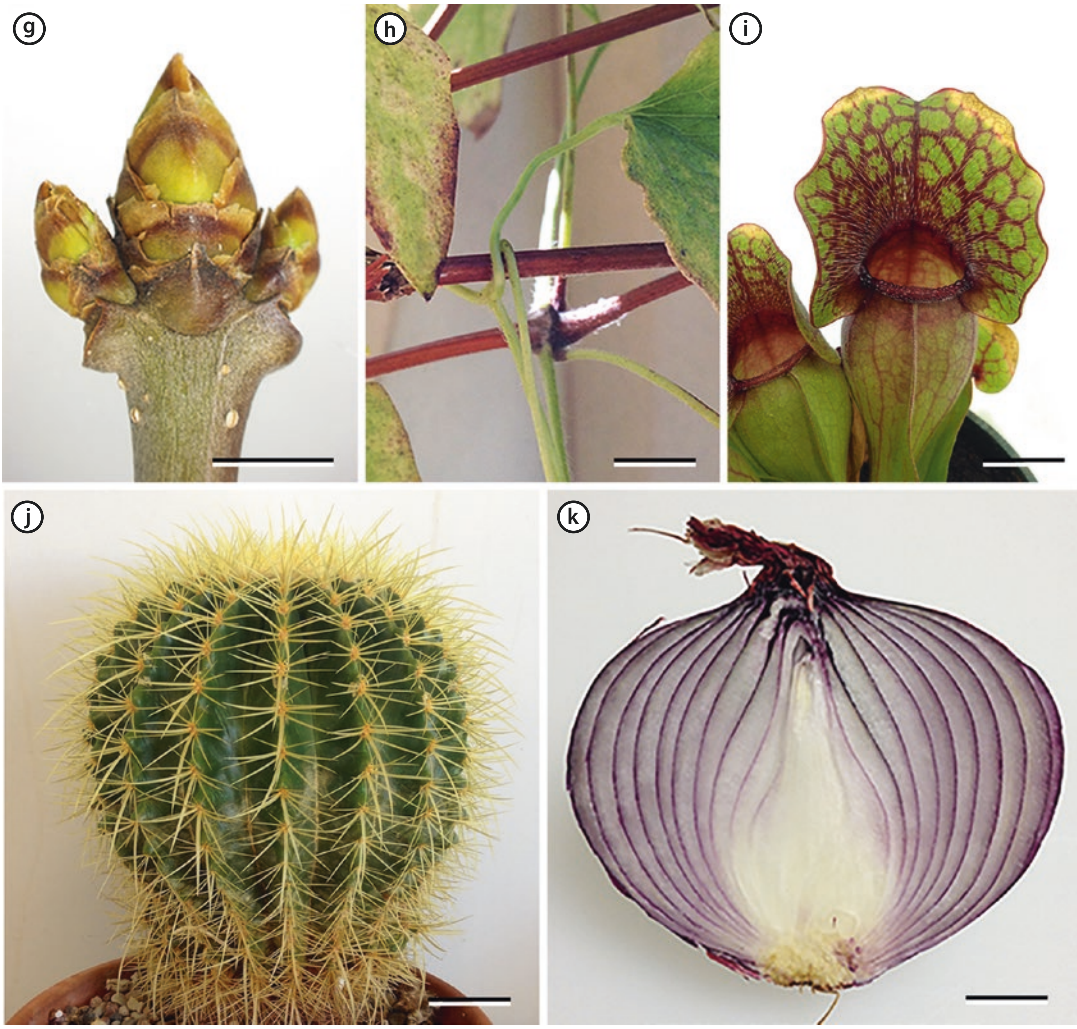


Fig. 12.1 Modified leaves. **g** Cataphylls (bud scales) surrounding three terminal buds on a lilac (*Syringa* sp.) stem, **h** clematis (*Clematis* sp.) tendrils, **i** an insect-trapping pitcher on *Sarracenia* sp., **j** golden barrel cactus (*Echinocactus grusonii*) stem covered with spines, **k** an onion (*Allium* sp.) bulb (stem and leaves) cut in radial section to show individual bulb scales. Scale bars = 1 cm in **g**, 0.5 cm in **h**, 1 cm in **i**, 3 cm in **j**, and 2 cm in **k** (**g**–**k** RR Wise)

12.2 The Vascular System Spreads Throughout the Leaf

Leaf evolution reflects increased complexity of venation, the arrangement of **veins** in a leaf. One hypothesis on the origin of leaves with considerable, but not unanimous, support poses that the progenitors to leaves were small, planar outgrowths of a photosynthetic stem called **enations**. Enations lack a vascular connection to the stem and may be found on stems of the extant, primitive fern *Psilotum nudum* (Fig. 12.2a). Subsequently, a vascular strand emerged from the stele and entered the enation resulting in a microphyll, a leaf with a single, unbranched vascular strand as may

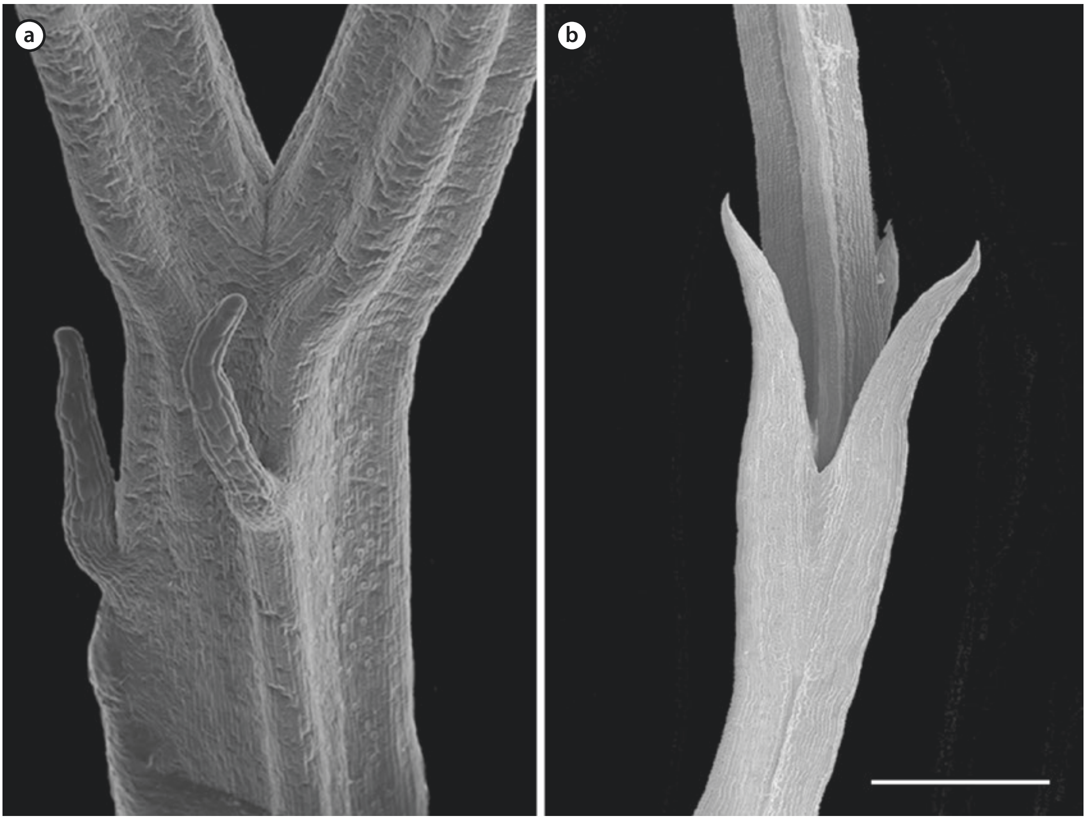
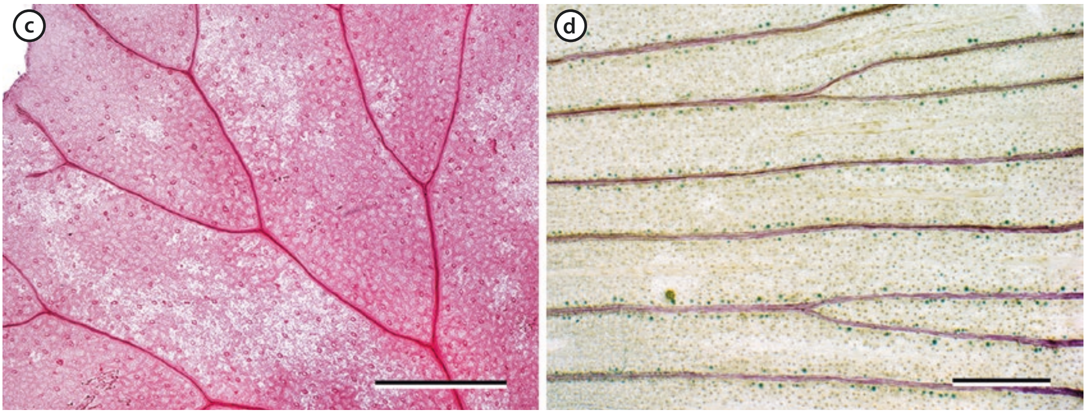


Fig. 12.2 **a**, **b** Leaf evolution. **a** Two enations on a skeleton fork fern (*Psilotum nudum*) stem, **b** two microphylls on a horsetail (*Equisetum* sp.) vegetative stem. Although it cannot be seen in these scanning electron micrographs, the *Psilotum* enations lack vasculature, and the *Equisetum* microphylls have a single, unbranched vascular strand. Scale bar = 1 mm and applies to both panels (**a**, **b** RR Wise)

be seen in many modern-day ferns (Fig. 12.2b). Finally, over the course of time, the vascular system branched out forming the complex pattern of vascular angiosperm leaf blades or megaphylls (Fig. 12.1c–g).

The vascular system of leaves consists of veins which branch and form a continuous network extending throughout the leaf and passing into the stem. Each vein contains both xylem and phloem tissue; the two tissues are always found together. There are several types of venation, but the most common patterns are the **dichotomous venation** pattern in ferns and ginkgo, **parallel venation** found in the monocots, and the **reticulate venation** of most eudicot leaves.

Leaves of many pteridophytes and the maidenhair tree (*Ginkgo biloba*) have dichotomous venation (Fig. 12.2c, d). From an evolutionary perspective, such venation pattern is considered to be ancestral. Each vein branches dichotomously into two others of equal size, and they in turn divide in the same way resulting in a dense venation pattern, all of the same size order. Veins lack anastomoses and end blindly in the mesophyll or approach the leaf margin.



◘ **Fig. 12.2** Clearings showing dichotomous leaf venation in **c** the sensitive fern (*Onoclea sensibilis*) and **d** ginkgo (*Ginkgo biloba*). The leaves were treated with bleach to remove pigments and then stained with safranin to reveal the vasculature. The mesophyll tissue is intact. Scale bars = 0.5 mm in **c** and 1 mm in **d**. (**c**, **d** RR Wise; specimens prepared by J.D. Curtis)

Ginkgo is a primitive gymnosperm that is now widely cultivated (◘ Fig. 1.16c), but virtually unknown in the wild state. The leaves are deciduous and can be highly variable—even on the same tree. The order, Ginkgoales, was most abundant during the Jurassic period (approx. 200 million years ago) when it was found almost worldwide. *Ginkgo biloba* is believed to be the oldest existing tree specimen. It became nearly extinct with few specimens left in western China until it was rediscovered in China and Japan during the late seventeenth century and subsequently became cultivated worldwide. The leaves are distinctive due to their lobed appearance and dichotomous branching parallel venation.

Monocot leaves have parallel venation (◘ Fig. 12.2e, f). While some veins are larger, most are of similar size. Careful observation of such leaf lamina shows that veins may indeed branch and converge in places, especially near the base and apex of the blade. It is also noteworthy that, at the microscopic level, a reticulate arrangement may exist with the vascular bundles. The small veins that interconnect the larger parallel veins in grasses are called **commissural veins**. It is believed that an intercellular signal induces the ground meristem cells into progenitor cells which subsequently form the commissural veins.

In the reticulate venation pattern (◘ Fig. 12.2g), the major veins spread out in a somewhat palmate pattern across the leaf. From these, minor veins branch off to join with other minor veins, thus forming a conspicuous network as shown in the inset of ◘ Fig. 12.2g. The network that is formed by minor veins varies in size and shape. Accordingly, the veins subdivide the lamina surface into small areas called **areoles** (sing. = areole) delineated by the thinnest veins. Areoles may contain one or more blind terminal veins (◘ Fig. 12.2h) in which the terminal vessel element lacks a perforation plate.

Two main types of veins are recognized according to their size and function, major veins and minor veins. Major veins conduct water and photosynthates and provide mechanical support to the delicate mesophyll. Major veins are typically composed of vascular

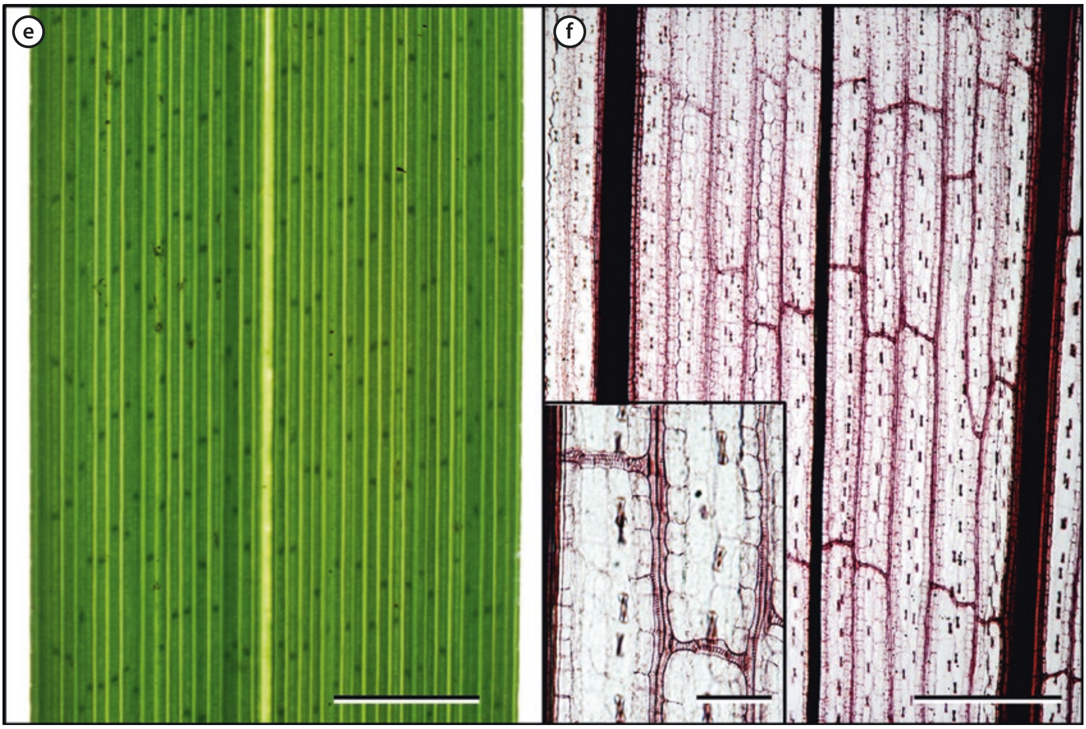


Fig. 12.2 **e**, **f** Parallel venation in monocot leaves. **e** Lemon grass (*Cymbopogon citratus*) seen in macrophotography, **f** a leaf clearing of maize (*Zea mays*). The inset in **f** shows commissural veins connecting the main veins. The rows of red dots are stomata. Scale bars = 5 mm in **e**, 500 µm in **f**, and 100 µm in inset to **f** (**e**, **f** RR Wise)

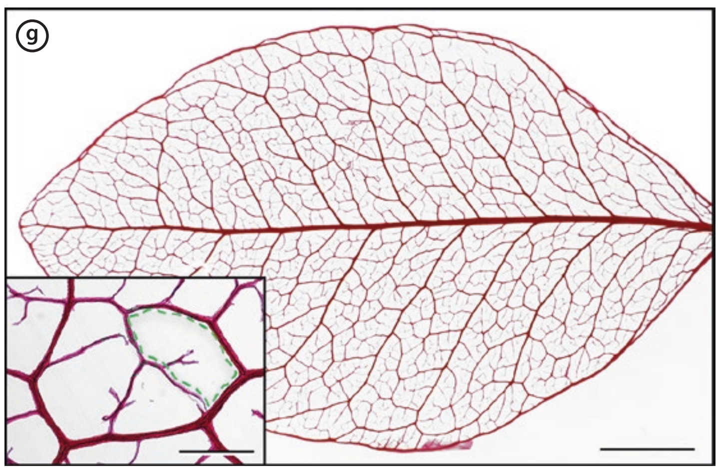


Fig. 12.2 **g** Reticulate venation in a skeletonized leaf of heavenly bamboo (*Nandina domestica*) as shown in a low magnification view with a medium magnification insert. The area in the inset bounded by a green dashed line is a single areole. Note the blind terminal minor veins inside the areoles. The leaf was processed by treating in hot sodium carbonate and using a soft brush to remove the epidermal and mesophyll tissues, leaving only the vasculature. The leaf was then stained in safranin. Scale bar = 1 mm in main figure, 250 µm in inset. (RR Wise; specimen prepared by J.D. Curtis)

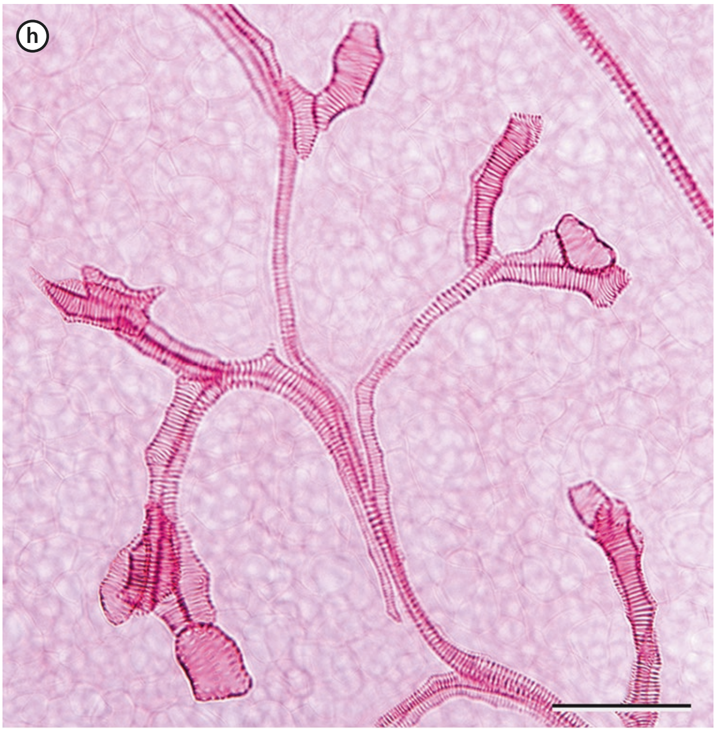


Fig. 12.2 **h** Blind terminal minor veins as shown in a cleared leaf of crown of thorns (*Euphorbia milii*). Scale bar = 50 µm. (RR Wise; specimen prepared by J.D. Curtis)

bundles, **bundle sheaths**, undifferentiated parenchyma, sclerenchyma, and collenchyma. Most major veins in eudicots usually appear as ribs on the abaxial side of the lamina, and it is the major veins that determine the venation pattern of a leaf (Fig. 12.1b). The major vein in the center of the leaf is called the midrib. By contrast, minor veins are completely enclosed in the mesophyll and not visible from the leaf surface.

The xylem and phloem in the major and minor leaf veins are not in direct contact with mesophyll cells or intercellular air spaces. The vascular tissues are delimited from them by a bundle sheath composed of specialized parenchyma cells. Major leaf veins serve as the main conduit for water and photosynthate. The functions of the minor veins are to distribute the transpiration stream throughout the mesophyll and to load the phloem with photosynthates produced by the chlorenchyma cells in the leaf mesophyll. Accordingly, no mesophyll cell is more than a few cells away from a minor vein. A minor vein consists of a small vascular bundle containing a few phloem sieve tube elements and a few xylem tracheary elements enclosed in a bundle sheath. Accordingly, all photosynthate produced in the mesophyll chlorenchyma must pass through the minor vein bundle sheath to be loaded into a phloem sieve tube element.

Two main types of minor veins are distinguished based on the method by which they take up photosynthate from the mesophyll into the bundle sheath cells. [Note: Phloem loading is a separate process. The photosynthate in the bundle sheath travels to the phloem companion cells and is loaded into the sieve tube elements either symplastically or apoplastically [Refer to ▶ Chap. 8 – Phloem]. **Open veins** have symplastic connections with the leaf mesophyll cells as evidenced by large fields of plasmodesmata in their shared walls (◘ Fig. 12.2i–k). Sugars pass directly from a mesophyll cell to an adjacent bundle sheath cell via the plasmodesmata. Plasmodesmata also connect the bundle sheath cell to the phloem sieve tube member. In contrast, **closed veins** lack plasmodesmatal connections and take up photosynthate apoplastically. In this case, the sugars are exported from the mesophyll cell to the apoplast and then taken up from the apoplast by the bundle sheath cell. A similar process occurs at the bundle sheath cell—phloem sieve tube element boundary. Extensive cell wall ingrowths increase the surface area for uptake and accompany the apoplastic uptake pathway in the bundle sheaths of closed veins (◘ Fig. 12.2l–n).

In eudicot leaves, veins may effectively divide the leaf into areas with separate air spaces. In some instances, the bundle sheath is limited to a single layer of cells surrounding the vascular bundle (◘ Fig. 12.2p, q). This architecture allows for lateral flow of air and water vapor within the leaf, primarily in the spongy mesophyll where most of the air space is found. Leaves with this style of bundle sheath are said to be **homobaric** (homo = the same, baric = atmosphere). Vascular bundle sheaths in the leaves of other plants, however, have vertical rows of clear parenchyma cells extending from the vascular bundle to both leaf surfaces (◘ Fig. 12.2o, q). These **bundle sheath extensions** (BSEs) effectively seal off individual areas of the leaf and result in a **heterobaric** leaf (different atmosphere). In forest foliar strata, heterobaric leaves are typically found in higher strata and homobaric leaves in lower strata. In terms of advantage, heterobaric leaves in the highest part of the canopy have higher light intensity and temperature, whereas homobaric leaves are more common in the lower strata with less light but higher humidity. The bundle sheath also plays specialized roles in C_4 photosynthesis as detailed in ▶ Sect. 12.5, Kranz anatomy.

In leaf cross-sections, veins occupy the middle of the leaf. Leaf vascular bundles are typically closed (meaning no secondary growth). However, an active vascular cambium capable of producing up to 45 years of growth has been reported in long-lived leaves of bristlecone pine (Ewers and Schmid 1981). In all vascular bundles—root, shoot, or leaf—the xylem is oriented facing the adaxial direction and the phloem toward the abaxis. That arrangement is indicated in ◘ Fig. 12.2q and may be seen in numerous other images in this text.

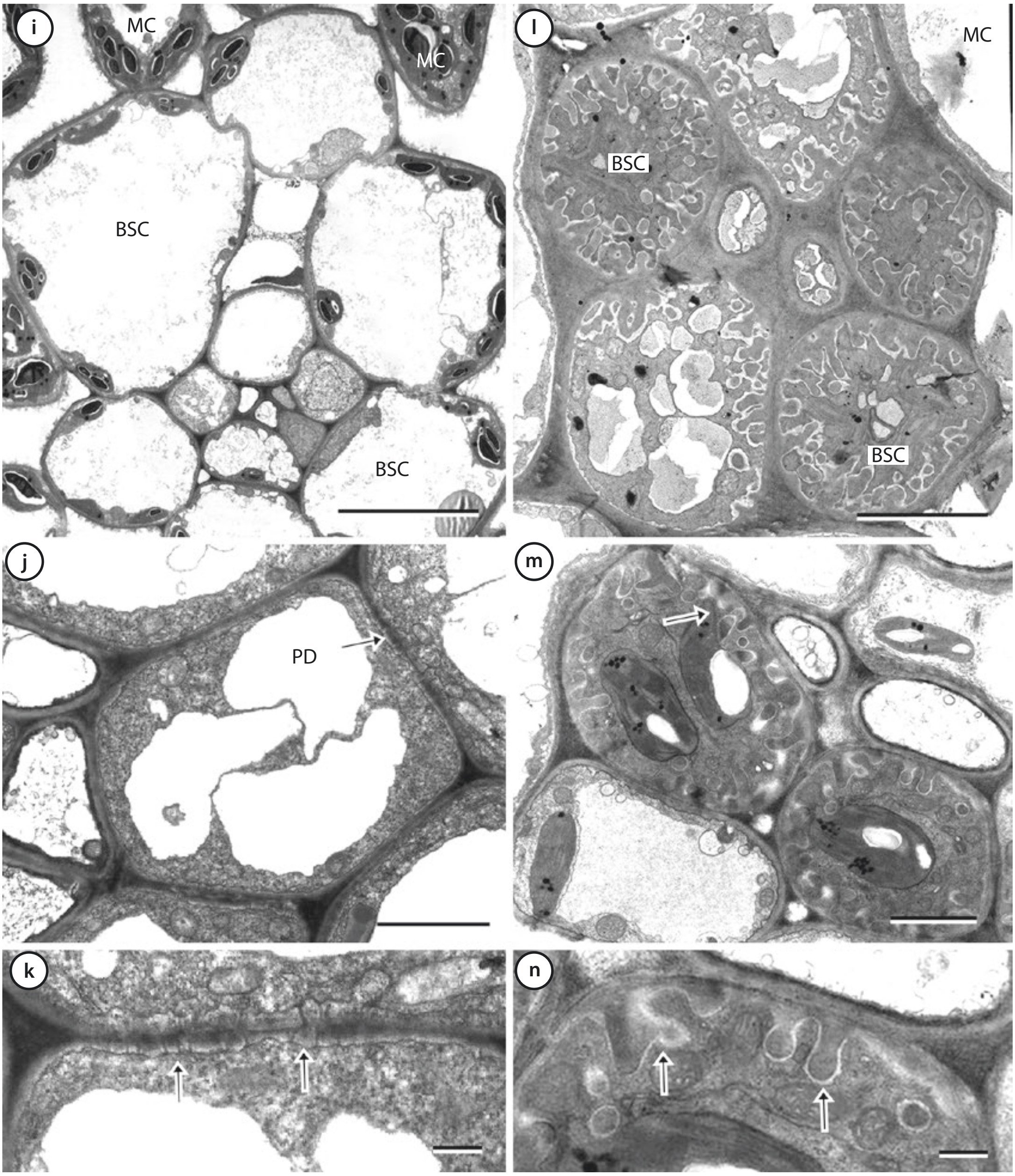


Fig. 12.2 Transmission electron micrographs of **i**, **j**, and **k** open and **l**, **m**, and **n** closed minor leaf veins. **i** A low magnification view of an open bundle sheath showing the relationship between the mesophyll cells (MC), bundle sheath cells (BSC), and the few cells of the minor vein in a leaf of *Paederia scandens* (Rubiaceae). **j** A single bundle sheath cell from *Hamelia patens* (Rubiaceae) with the plasmodesmata-containing wall indicated (PD). **k** A higher magnification view of **j** showing an area of cell wall with numerous plasmodesmata (*arrows*). **l** The bundle sheath cells (BSC) surrounding a closed vascular bundle in *Onosma gmelinii* (Boraginaceae) contain numerous cell wall ingrowths. **m** Two bundle sheath cells in a *Asperula kryloviana* (Rubiaceae) leaf. **n** A higher magnification view of **m** showing the cell wall ingrowths (*arrows*). Scale bars = 20 μm in **i** and **l**, 5 μm in **j** and **m**, and 1 μm in **k** and **n** (**i**–**n** Denis Batashev and Olga V Voitsekhovskaja, Komarov Botanical Institute, St. Petersburg, Russia)

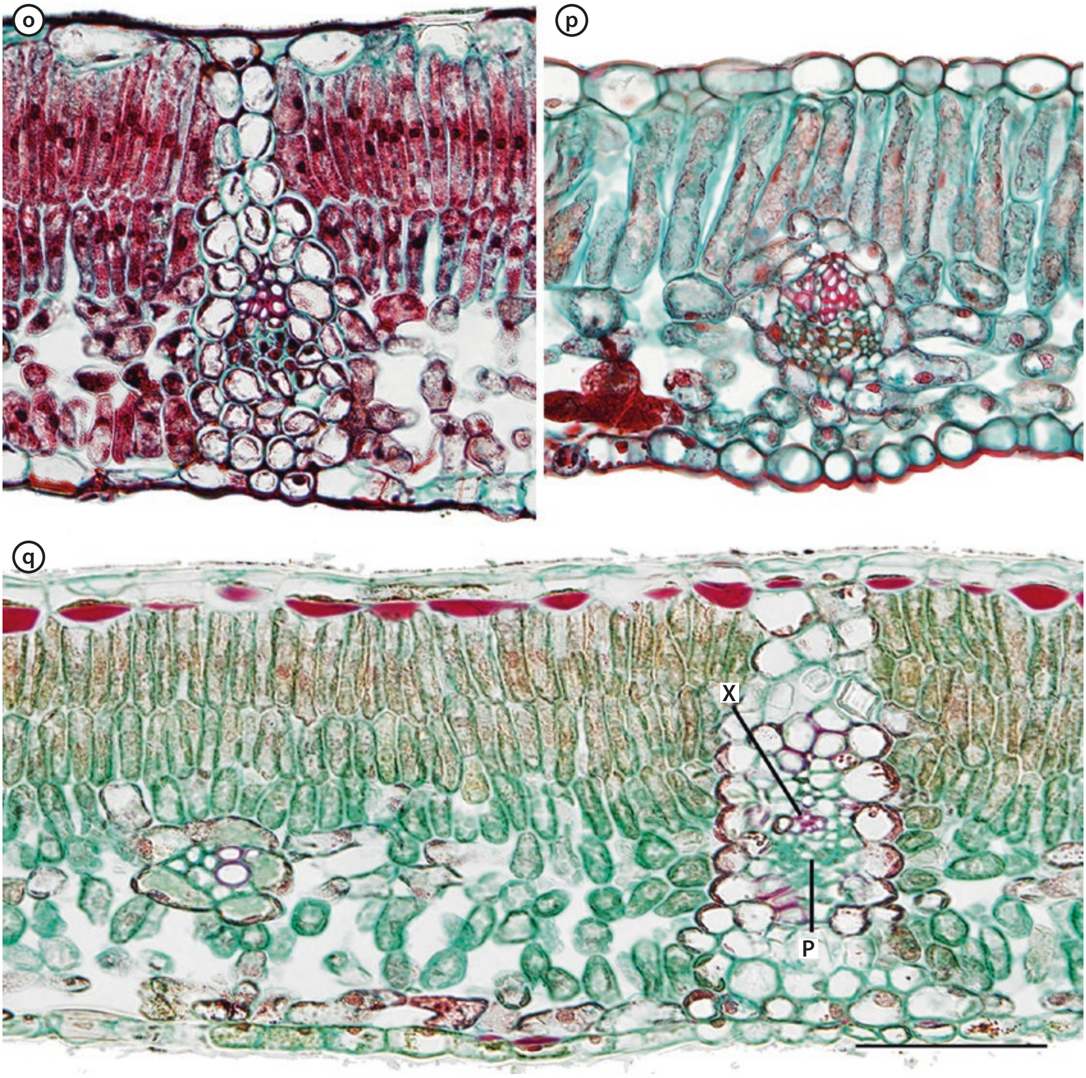
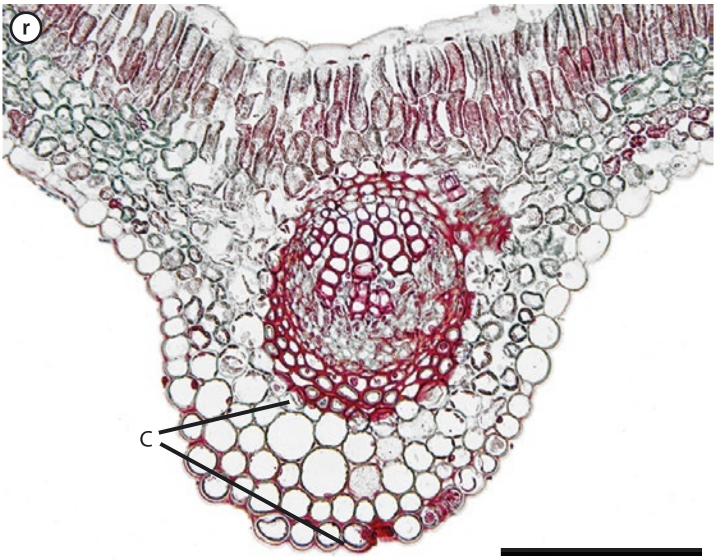


Fig. 12.2 **o**–**q** Heterobaric and homobaric leaves seen in cross-section. **o** Bundle sheath extensions in a heterobaric Osage orange (*Maclura pomifera*) leaf. **p** Homobaric leaf of privet (*Ligustrum* sp.) which lacks bundle sheath extensions. **q** Bundles with and without sheath extensions in a cherry (*Prunus* sp.) leaf. Note the xylem (X) is toward the adaxis and the phloem (P) is toward the abaxis. Also note the single palisade layer in **p**, double in **o**, and triple in **q**. Scale bar in **q** = 50 µm and applies to all panels (**o**–**q** RR Wise)

The vascular system may play a role of providing support to leaves via the development of collenchyma, sclerenchyma fibers, or individual sclereids. If the leaf bundle has collenchyma, that tissue may protrude below the abaxial surface of the lamina in the form of a prominent rib (Fig. 12.2r). Fibers are most often associated with large veins, either surrounding them completely or forming abaxial or (to a lesser extent) adaxial caps. Collenchyma is also often found at the periphery of the major veins and on the leaf margin where it helps to prevent tearing of the leaf.



◘ **Fig. 12.2** **r** Cross-section of an alfalfa (*Medicago sativa*) leaf midrib. Collenchyma (C) forms a bulge at the abaxial side of the midrib. Scale bar = 100 µm (RR Wise)

12.3 Leaf Morphology Is Optimized for Light Absorption, Gas Exchange, and Water Conservation

While many leaf modifications may be found in the kingdom Plantae (refer to ◘ Fig. 12.1g–k), leaves on most plants are engaged primarily, if not exclusively, in photosynthesis. In such leaves, called foliage leaves, the leaf epidermis consists of a single (or occasionally multiple) layer of cells covering the entire leaf surface and is continuous with the surface of the stem. In addition, the epidermis contains a variety of cells including guard cells, pavement cells, trichomes (glandular and nonglandular), and idioblasts, whose descriptions have been given in the chapters on the epidermis (► Chap. 9) and secretory structures (► Chap. 13).

12.3.1 Typical Dorsiventral Eudicot Leaves

The anatomy of the leaf lamina is normally best shown in cross-sectional view. A typical mature, C_3, eudicot leaf (◘ Fig. 12.3a) has an adaxial (upper) epidermis, an abaxial epidermis, and a zone of photosynthetic tissue in between called the mesophyll. In the epidermis, only guard cells have chloroplasts, which are used to drive stomatal opening and closing (► Sect. 3.5.10).

Comparing a cross-section with an accompanying paradermal section reveals the leaf structure in three dimensions (◘ Fig. 12.3b, c). Mesophyll is, as a rule, a multilayered parenchyma (also classified as

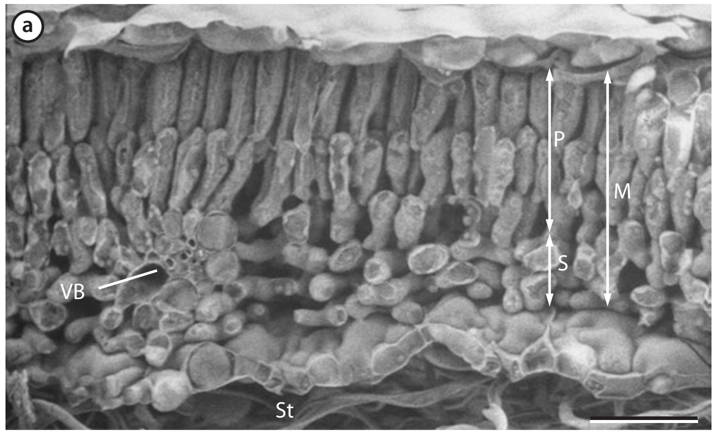


Fig. 12.3 **a** Colorado cinquefoil (*Potentilla subjuga*). M mesophyll, P palisade mesophyll, S spongy mesophyll, St stoma, VB vascular bundle. Scale bar = 50 µm (RR Wise)

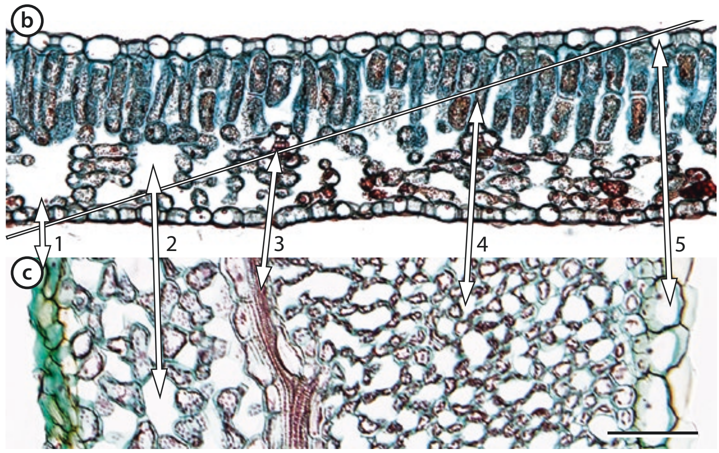


Fig. 12.3 Comparison of **b** cross and **c** paradermal sections in privet (*Ligustrum* sp.), a C_3, eudicot species with homobaric leaves. **b** In cross-section, the internal structure of palisade and spongy mesophyll layers is easily seen. The diagonal line in **b** indicates the plane of the paradermal section. **c** The paradermal section cuts through the different levels of tissue semi-parallel to the leaf surface. 1 abaxial epidermis, 2 spongy mesophyll with intercellular spaces (at *arrow heads*), 3 minor vein, 4 palisade mesophyll with vacuoles (at *arrow heads*), 5 adaxial epidermis. Scale bar = 100 µm (**b**, **c** RR Wise)

chlorenchyma) consisting of cells which are similar in their structure and functional specialization for photosynthesis. Their most important specific feature is the extraordinary development of chloroplasts. There is no other tissue where there are so many chloroplasts or such a high level of organization. The presence of a highly developed anastomosing system of intercellular air spaces in which more than half of the cell surfaces are in contact with the gas phase is a characteristic of mesophyll. The remaining surfaces are in cell-to-cell contact and have numerous plasmodesmata that allow for symplastic continuity among mesophyll cells and the vascular system.

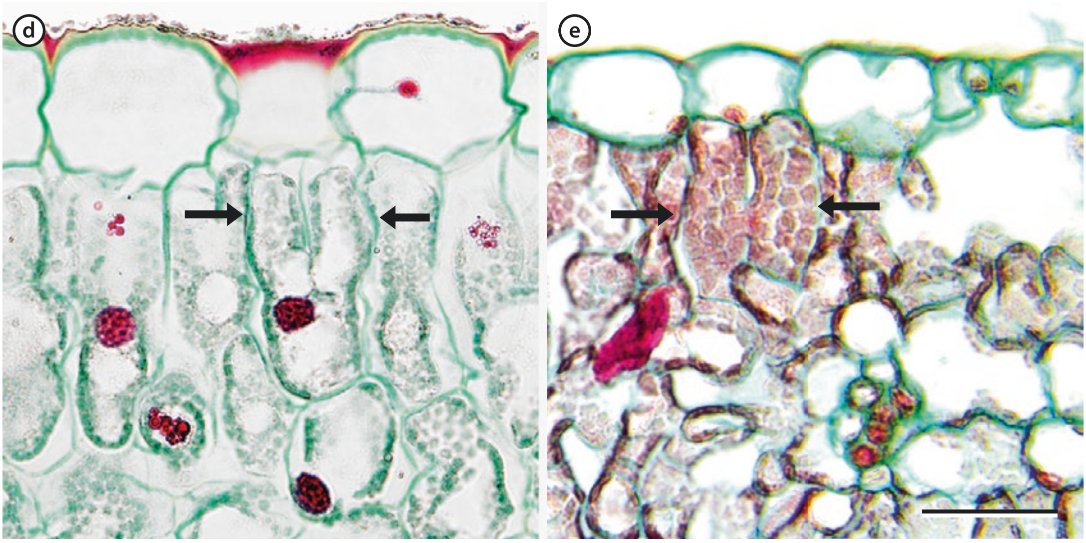
In the eudicot leaf, the mesophyll is typically divided into two layers of chlorenchyma (▪ Fig. 12.3a, b). The layer toward the adaxis, called the **palisade mesophyll**, is composed of long, columnar, tightly packed cells with little intercellular air space. Palisade cells have a large vacuole and numerous chloroplasts, because those cells are exposed to the highest irradiance level and photosynthesize at a high rate. The **spongy mesophyll** toward the abaxis has mostly isodiametric cells and a large amount of intercellular air space. Spongy mesophyll cells are smaller than palisade mesophyll cells, with fewer chloroplasts, in accordance with the lower light level toward the abaxis. This style of leaf morphology is common in plants that hold their leaves directly from the stem and more or less perpendicular to the sun's rays, exposing the adaxis to incoming light. The form of leaf anatomy is called dorsiventral (or bifacial) to indicate that the leaf has distinctly different internal anatomy in a abaxial/adaxial direction (dorsiventral), and the two layers of the mesophyll are composed of morphologically different tissues (bifacial).

All of these anatomical features of the eudicot leaf relate leaf orientation and to the three competing demands placed on a leaf of 1) light absorption, 2) CO_2 uptake, and 3) water conservation. The light environment inside the leaf is quite heterogeneous; not all chloroplasts receive that same quantity and quality of light. Leaf anatomy is maximized to take advantage of that heterogeneity to maximize photosynthesis during diurnal and seasonal variations in light level (Xiao et al. 2016).

Both the palisade layer and the spongy layer are actively engaged in photosynthesis, which requires constant supplies of light and carbon dioxide. At the adaxial surface, which receives more irradiance than the abaxial surface, the columnar shape of the palisade cells, combined with their large vacuoles, serves to bend and focus light to the leaf interior. Some of the incoming light is absorbed by chloroplasts and used for photosynthesis, but some is focused to the spongy layer. The palisade cells, therefore, are anatomically specialized to not only absorb light but also to facilitate the penetration of light to chloroplasts in the lower, spongy mesophyll layer. The spongy mesophyll layer, with its fewer chloroplasts and larger exposure to internal air spaces, is specialized in CO_2 absorption, which enters the leaf via the numerous abaxial stomata. Some consider the spongy mesophyll to be a form of aerenchyma. Placing the stomata on the abaxial surface has another advantage in that the atmospheric humidity is lower in the shaded, underside of the leaf. A higher external humidity reduces transpirational water loss.

12.3.2 Variations in Palisade Parenchyma

The palisade mesophyll is typically a single layer of long and tubular cells at the leaf adaxis (▪ Fig. 12.3a, b); however other shapes and arrangements exist. Individual palisade parenchyma may be Y-shaped as in *Lilium* or X-shaped as in *Lactuca* (▪ Fig. 12.3d, e). The arrangement and numbers of palisade layers in a leaf vary as



■ **Fig. 12.3** **d**, **e** Cross section of **d** lily (*Lilium* sp.) leaf showing a Y-shaped palisade cell and **e** a lettuce (*Lactuca* sp.) leaf with an X-shaped palisade cell (between arrows). Scale bar in **e** = 25 µm and applies to both panels (**d**, **e** RR Wise)

■ **Fig. 12.3** **f** Cross-section of a willow (*Salix* sp.) leaf composed entirely of palisade parenchyma mesophyll cells. Note also the vascular bundle extension in this heterobaric leaf. Scale bar = 50 µm (RR Wise)

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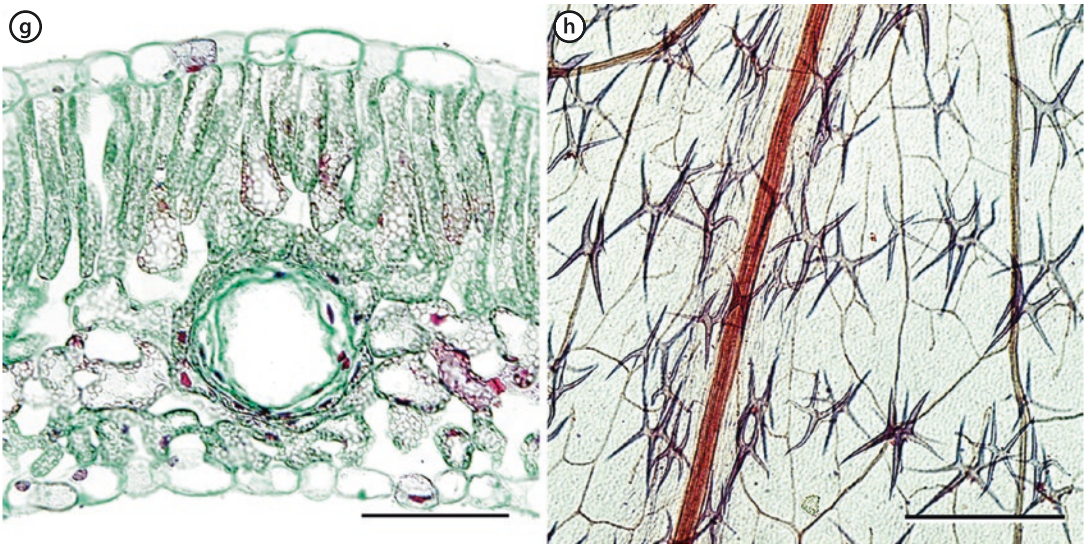
well. A bifacial/dorsiventral eudicot leaf may have one, two, or three palisade layers, as can be seen in ■ Fig. 12.2o, p, and q. **Isobilateral** or **isolateral** (meaning "same both sides") leaves are strictly defined as having the same "face" at both sides of the leaf. There are three different anatomical arrangements that qualify as isobilateral. (1) Leaves may lack a spongy layer and be composed of only a palisade mesophyll layer; *Salix* is an example of a palisade-only, isobilateral leaf (■ Fig. 12.3f). (2) Leaves may lack a palisade layer and be composed of only a spongy mesophyll; grasses (▶ Sect. 12.3.3) and hydrophytes (▶ Sect. 12.8) commonly have spongy-only, isobilateral leaves. (3) Isobilateral leaves may have two palisade layers, one at each surface, with a spongy layer in between; this arrangement is common in water-storing xerophytic plants (▶ Sect. 12.6).



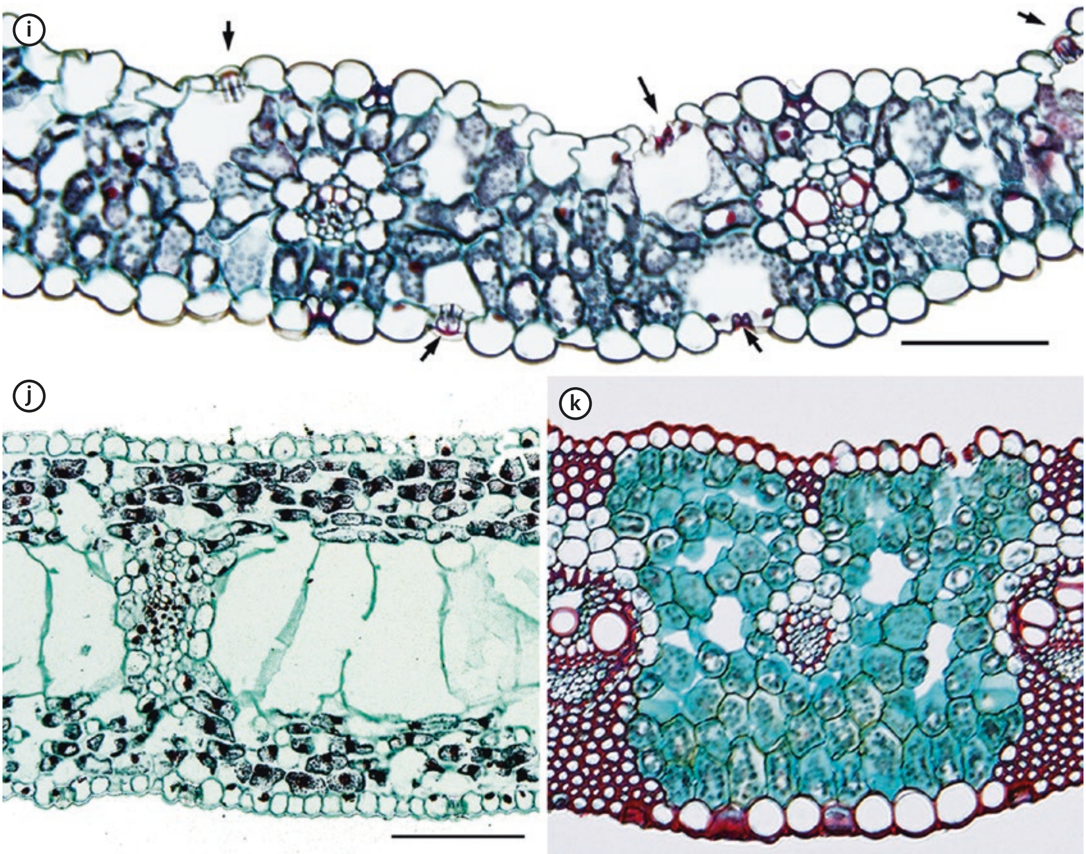
◘ **Fig. 12.3** **g** A resin canal in a cotton (*Gossypium hirsutum*) leaf cross-section. The canal is lined with an epithelium of secretory parenchyma cells. **h** Astrosclereids as seen in a clearing of a shepherd's purse (*Capsella bursa-pastoris*) leaf. Scale bars = 50 µm in **g** and 250 µm in **h**. (**g** RR Wise; specimen in **h** prepared by J.D. Curtis)

In addition to the chlorenchyma of the palisade and spongy layers, non-photosynthetic cells in the mesophyll may include oil cells, crystal-containing idioblasts, and mucilage cells. Resin canals and sclereids may be interspersed among the mesophyll cells (◘ Fig. 12.3g, h).

Adaxial and abaxial epidermises in eudicot leaves often differ from each other in the size and shape of ground epidermal cells and in the frequency of trichomes and stomata. In leaves which are oriented with the adaxial epidermis toward the light (as described above for the typical eudicot leaf), stomata mostly occur within the abaxial epidermis (i.e., designated as hypostomatous leaves). Such a location allows for the reduction of water loss during transpiration. In vertical or upright leaves without a preferable orientation with respect to light, the stomata may be found in both epidermises (**amphistomatous leaves**). Many grass leaves, with upright positioning, are amphistomatous, as is wheat (◘ Fig. 12.3i). In other cases, such as leaves of **xeromorphic** grasses (◘ Fig. 12.6a) or floating leaves of water plants (◘ Fig. 12.8b), the stomata are confined to the upper epidermis (i.e., designated as epistomatic leaves). Leaf anatomical adaptations to various environmental conditions are discussed in more detail in ► Sects. 12.6–12.9.

12.3.3 Isobilateral and Unifacial Monocot Leaves

The leaves of most monocot species are more or less upright and crowded to either side by neighboring leaves. In this orientation, a single light-focusing palisade layer and the dorsiventral/bifacial



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◘ **Fig. 12.3** **i**–**k** Isobilateral monocot leaves with identical abaxial and adaxial surfaces and a homogeneous mesophyll of isodiametric loosely arranged cells. **i** Wheat (*Triticum aestivum*) (arrows indicate stomata), **j** Amaryllis (*Amaryllis belladonna*) and **k** Kentucky bluegrass (*Poa pratensis*). The abaxis is to the bottom of all three images. Scale bars = 100 µm in all three panels. (**i**–**k** RR Wise)

tissue arrangement described above for eudicots would not be adaptive. In general, therefore, the majority of monocots, such as grasses, lilies, and irises, have parallel-veined isobilateral leaves. Therefore, an isobilateral, mesophyll-only arrangement can be seen in monocots such as wheat, amaryllis, and *Poa* (◘ Fig. 12.3i–k).

A **unifacial** leaf has an unusual anatomy. Leaf development at the apical meristem usually starts as a leaf buttress growing off of one side of the apex as shown in ◘ Fig. 4.7b for an *Elodea* shoot tip. In this way, the leaf assumes an adaxial (toward the axis) and an abaxial (away from the axis) symmetry very early on in its development, and the two faces develop accordingly. However, in some monocots, only the abaxial side continues development, and an adaxial side never develops. In iris, the leaf is flattened and is oriented along the vertical axis of the plant (◘ Fig. 12.3l). As noted above, vascular bundles are always arranged with their phloem toward the abaxial surface. Therefore, in the iris leaf, vascular bundles on both sides of the leaf are oriented with their phloem facing the outside of the leaf. The middle of the leaf is filled with non-photosynthetic parenchyma (in some iris varieties, mucilaginous cavities may

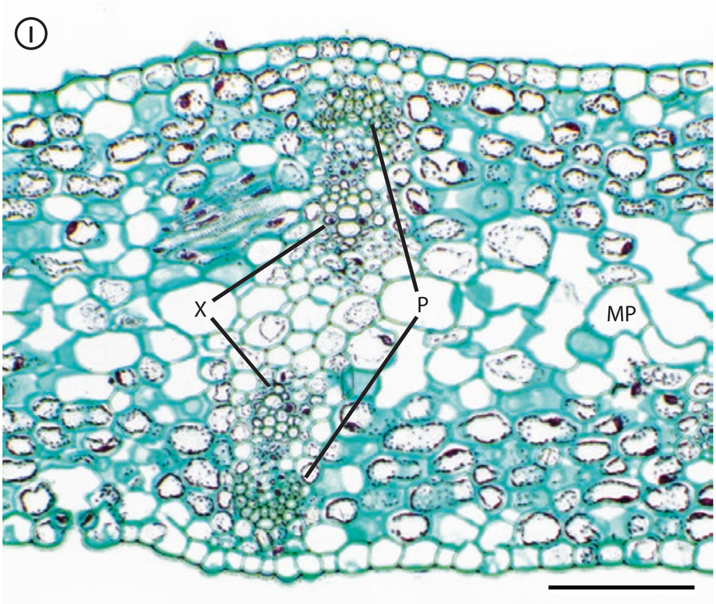

Fig. 12.3 **l** Anatomy of a unifacial monocot leaf of (*Iris domestica*). Note that the abaxial orientation of the vascular bundles as evidenced by the phloem (P) tissues lying outside the xylem (X) tissues. The location of the missing adaxial surface is occupied by mesophyll parenchyma (MP). Scale bar = 100 µm (RR Wise)

occupy the leaf interior). There is only an abaxial side, which is on both sides. This same basic developmental pathway can be seen in the tubular leaves of onion (Fig. 9.1i) or bulrush (Fig. 12.3q, r). The two differences are as follows: (1) the leaves are cylindrical and not flattened and (2) the internal parenchyma breaks down, leaving a hollow, tubular leaf.

12.3.4 Centric Eudicot Leaves

Centric leaves are circular in cross-section, with a solid interior, in which the palisade parenchyma layer forms a continuous ring around the spongy mesophyll. The centric leaf shape minimizes the surface area to volume (SA/V) ratio. Because transpiration occurs at the surface and the water lost comes from the interior, a low SA/V ratio reduces transpiration, and centric leaves are often found on xerophytes or halophytes. In the pincushion tree (*Hakea drupacea*, Fig. 12.3m, n), the palisade forms a double layer surrounding a central core of parenchyma with small vascular bundles scattered throughout. *Hakea* is a drought-resistant evergreen native to southwestern Australia and naturalized elsewhere. Saltwort (*Salsola* sp.) is a C_4 plant with centric leaves and a prominent bundle sheath lying to the interior of a single layer of palisade cells (Fig. 12.3o, p). Saltwort is known to store water in the leaf interior (Carolin et al. 1975).

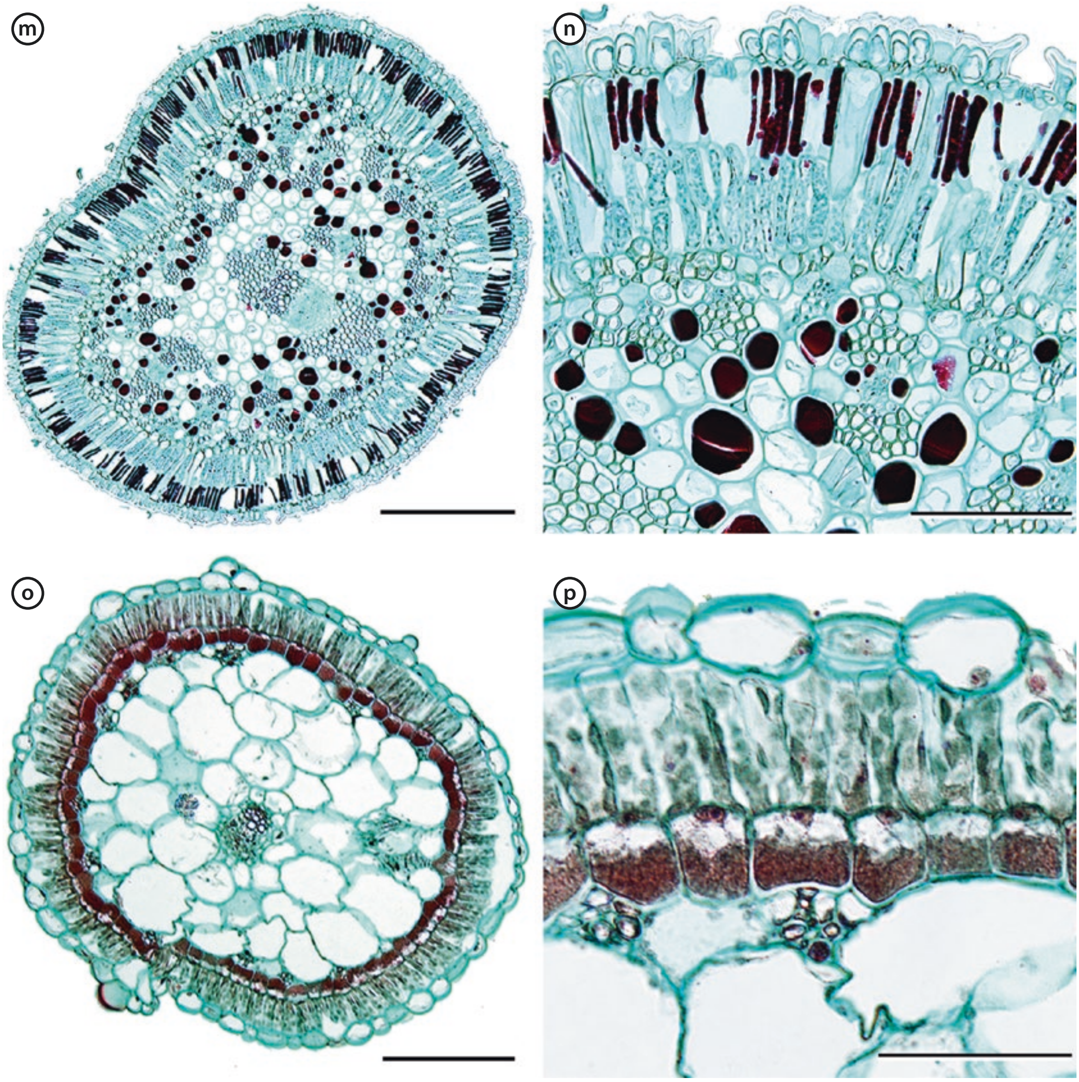

Fig. 12.3 **m**–**p** Eudicot centric leaves. **m**, **n** Sweet hakea (*Hakea drupacea*) has a double layer of palisade parenchyma surrounding a central core of parenchyma with small vascular bundles scattered throughout. **o**, **p** The saltwort (*Salsola* sp.) centric leaf has a single layer of palisade cells to the exterior of a dense bundle sheath. Scattered minor bundles lie just inside the bundle sheath. A larger major bundle sits at the center of the water-storing parenchyma. Scale bars = 250 µm in **m**, 100 µm in **m** and **o**, and 25 µm in **p** (**m**–**p** RR Wise)

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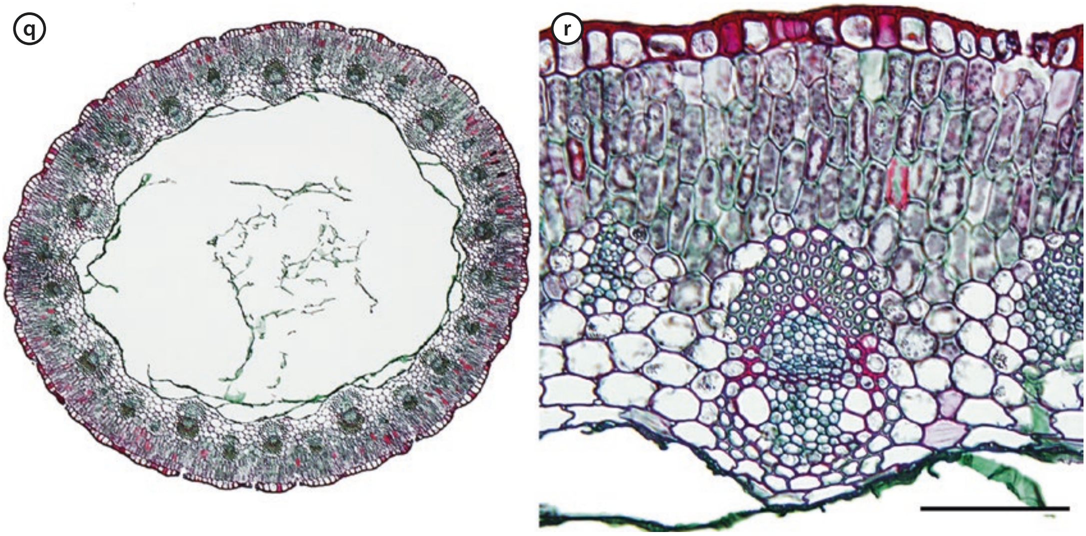
12.3.5 Tubular Leaves

Tubular leaves are round, like centric leaves, but they have a hollow interior. *Juncus* leaf is tubular with multiple palisade layers (Fig. 12.3q, r). The palisade mesophyll appears next to the epidermis around the complete cylinder. Below it is the non-photosynthetic spongy mesophyll in which vascular bundles are found. Note that the phloem of vascular bundles faces the exterior of the leaf, as in the stem. The central part of the leaf, which is hollow, was originally composed of thin-walled parenchyma which was a stable tissue and therefore torn apart as the outer part of the tubular leaf expanded. The



◘ **Fig. 12.3** **q**, **r** Tubular leaf of bulrush (*Juncus* sp.). Scale bars = 250 µm in **q** and 50 µm in **r** (**q**, **r** RR Wise)

adaxial side is to the inside of the leaf. It is unifacial because an adaxial epidermis never developed. *Juncus* is an aquatic plant with emergent leaves, meaning the roots are submerged below the surface, in oxygen poor soil, while the leaves are extended above the surface. The open center of the *Juncus* leaf allows for the diffusion of oxygen, which is photosynthetically generated by the chloroplasts of the leaf, down to the roots. Onion (*Allium cepa)* which is shown in ◘ Fig. 9.1i also has a tubular leaf. In this case, the tubular shape of the onion provides a structural advantage (Schulgasser and Witzum 1992).

Technically speaking, the carnivorous trap of the carnivorous pitcher plant *Sarracenia* sp. (◘ Fig. 12.1i) is a tubular leaf modified to make a trap. It, however, is bifacial (Shreve 1906). In addition, the leaf sheaths which compose much of the support structure of *Miscanthus* sp. grass (◘ Fig. 11.2i) and wheat are tubular leaves.

12.4 The Light Environment During Development Can Modify Leaf Anatomy

Besides availability of water (refer to following sections), light intensity is an especially important ecological factor affecting leaf anatomy. The various placements of the leaf palisade layer(s) discussed above reflect the adaptation of a plant to its light environment. Different light intensities intercepted by a leaf during development can also have an impact on the anatomy of the mature leaf. Where light intensity during leaf development is low, as in the interior of a tree's crown, **shade leaves** are formed. They are usually larger in area than **sun leaves**—leaves that develop at the light-exposed periphery of the crown—but thinner. Shade leaves have a thinner cuticle, less internal air space, and a single palisade layer (compare ◘ Fig. 12.4a, b). The chloroplasts of shade leaves possess larger grana (i.e., more thylakoids; refer to ◘ Fig. 3.5v, w) and contain more

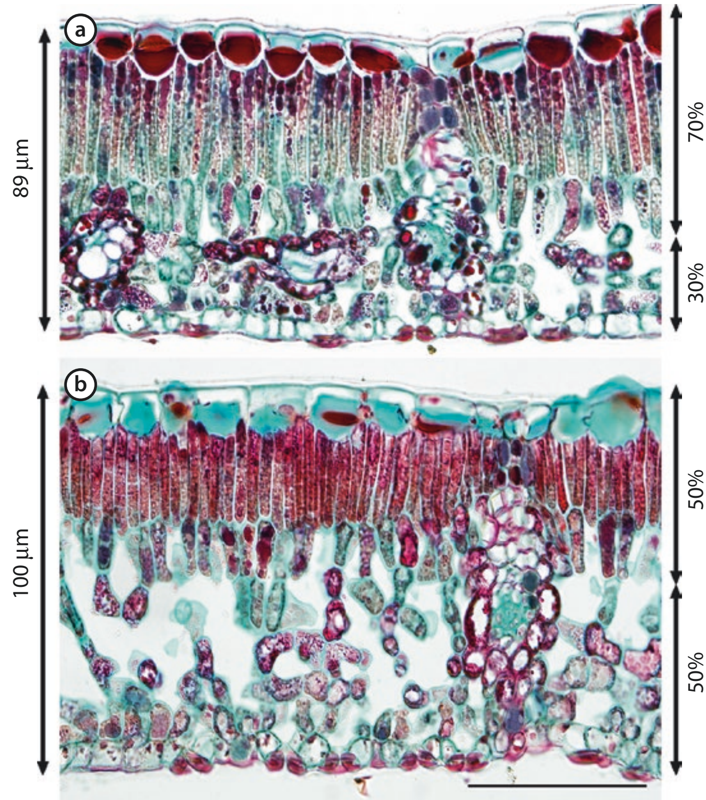
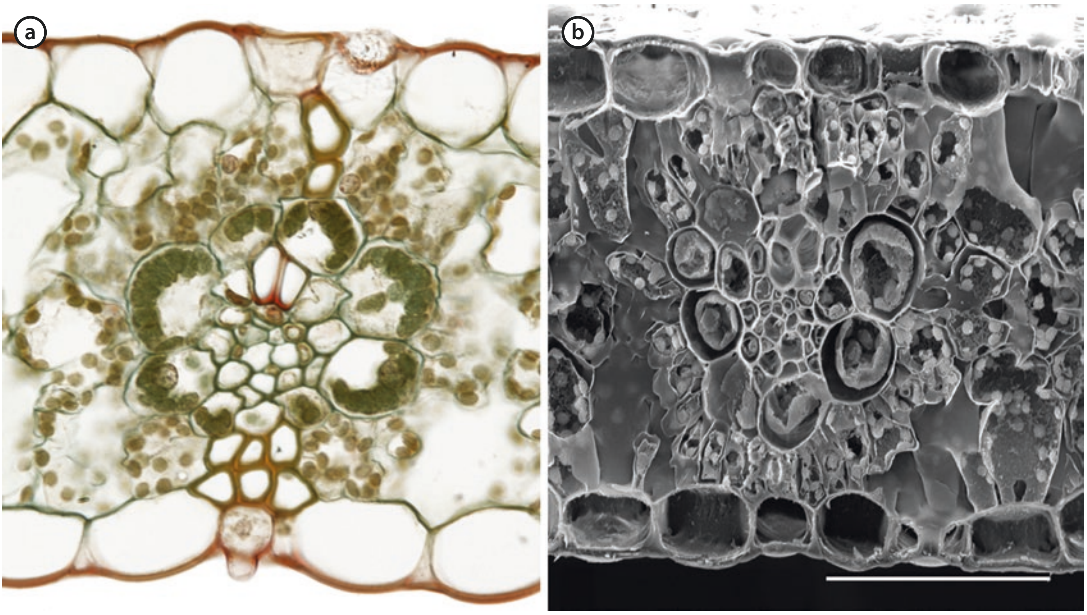


Fig. 12.4 **a** Shade and **b** sun leaves from oak (*Quercus* sp.). Images are labeled to indicate leaf, palisade mesophyll, and spongy mesophyll thicknesses. Scale bar in **b** = 50 µm and applies to both panels (**a**, **b** RR Wise)

chlorophyll. Sun leaves often have two or more palisade layers and considerably more internal air space.

The sun/shade developmental plasticity allows plants to optimize photosynthesis based on the light environment. Photosynthesis requires two substrates—light and carbon dioxide (water is being ignored for this discussion)—and one of them is always limiting. At the periphery of the crown, CO_2 is limiting and light is saturating. That is, the leaf has all the light it can use, and the maximal rate of photosynthesis is limited by the supply of carbon dioxide. Thus, such leaves have a thin light-absorbing layer (the palisade) and a robust, airy CO_2-absorbing layer (spongy mesophyll). Shade leaves develop the opposite anatomy: a thick palisade to capture any available light and a thinner spongy layer because there is less need for CO_2 uptake. The rate of photosynthesis in a sun leaf can be as much as five times that of a shade leaf.

Shade and sun leaves may often be found in different parts of the crown of the same tree, but keep in mind these differences are only expressed during leaf development. Transferring a shade leaf to the sun by trimming back outer crown foliage will not cause a mature leaf to thicken.



■ **Fig. 12.5** Maize (*Zea mays*) leaf in cross-section. **a** Light micrograph showing a single leaf vein surrounded by a ring of large bundle sheath cells. Note the centrifugal orientation of the bundle sheath chloroplasts, placing them closer to the surrounding mesophyll chloroplasts (refer to ■ Fig. 3.5 q, r). **b** Scanning electron micrograph of a similar view. The bundle sheath cell contents are slightly shrunken in this preparation. Scale bar in **b** = 100 µm and applies to both panels (**a**, **b** RR Wise)

12.5 Kranz Leaf Anatomy Is a Specialization of the C_4 Photosynthetic Pathway

As described in ► Sect. 12.3, the bundle sheath cells of C_3 plants are rather inconspicuous. In contrast, C_4 bundle sheath cells are large and bright green due to the presence of numerous chloroplasts. This anatomical variant is called **Kranz anatomy** (German for "halo" or "wreath") and is unique to plants that utilize the C_4 photosynthetic pathway (■ Fig. 12.5a, b).

C_4 photosynthesis and its dimorphic chloroplasts were introduced in ► Chap. 3 (► Sect. 3.5.9). Because the two chloroplasts have such different biochemical roles to play in the leaf, they typically must be kept in different compartments in plants. Therefore, in addition to having two different chloroplast types, C_4 plants also have unique bundle sheath cells that are used to provide the necessary spatial separation of those two organelles (■ Fig. 12.5). No other part of the anatomy is affected in the C_4 syndrome.

C_4 photosynthesis has independently evolved multiple times and is found in both monocots and eudicots, being more common in the former. Kranz leaf anatomy is found in most, but not all, C_4 plants. Indeed, a few members of the Chenopodiaceae engage in single-cell C_4 photosynthesis, in which elements of the cytoskeleton separate the chloroplasts involved in the primary CO_2 fixation and those performing secondary CO_2 fixation into distinct compartments in the leaf cells (Voznesenskaya et al. 2001).

Box 12.2 Single-Cell C4 Photosynthesis Relies on Spatial Separation, No Matter How Small

C_4 photosynthesis is predicated on a spatial separation of the primary carboxylating enzyme, phospho*enol*pyruvate carboxylase (PEPcase), from the secondary carboxylating enzyme, ribulose-*bis*phosphate carboxylase/oxygenase (Rubisco). This is because the former operates well in a low [CO_2] and high [O_2] environment while the latter requires the opposite. In leaves with Kranz anatomy, this spatial separation is achieved with PEPcase being found in the mesophyll cells and Rubisco in the bundle sheath cells. Oddly, some plants, notably members of the genus *Bienertia* (Chenopodiaceae), are capable of single-cell C_4 photosynthesis. In this case, the leaf mesophyll cells are quite large, 80–110 µm in diameter, and a cluster of chloroplasts in the center of the cell is separated by scattered chloroplasts at the cell periphery by a large vacuole. PEPcase and primary carbon fixation are found in the periphery of the cell, while Rubisco and secondary fixation are localized to the chloroplasts in the central cluster (Voznesenskaya et al. 2001). Jurić et al. (2017) subsequently modeled the diffusion of CO_2 and O_2 within *Bienertia* mesophyll cells and demonstrated that a spatial separation of only 10 µm, well within the dimensions of the cells, could provide diffusive resistance necessary to spatially separate the primary carbon fixing reactions catalyzed by PEPcase from the secondary fixation reactions catalyzed by Rubisco.

Reference: Jurić et al. (2017).

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There are two basic variants of bundle sheath anatomy in C_4 plants. The single-layer bundle sheath of maize (◘ Fig. 12.5a, b) is in direct contact with leaf mesophyll cells to the exterior and vascular tissue to the interior, and the individual bundle sheath cells are quite large. Sugar cane (◘ Fig. 12.5c) likewise has a single bundle sheath layer, but its bundle sheath cells are smaller and more numerous than in maize. Single layer bundle sheaths are most common in the subfamily Panicoideae or the “warm season” grasses. Grama grass, a member of the “cool season” grass subfamily Pooideae, has two layers of bundle sheath cells (◘ Fig. 12.5d). The outer layer is parenchymatous, while the inner layer, called the **mestome**, has thickened cell walls. The mestome walls may be suberized and contain numerous plasmodesmatal connections to the vascular tissues to the interior and the outer layer of the sheath to the exterior. The mestome appears to allow the leaf a certain degree of differential control over the opposite movements of water from the xylem to the mesophyll and of photosynthate from the mesophyll to the phloem.

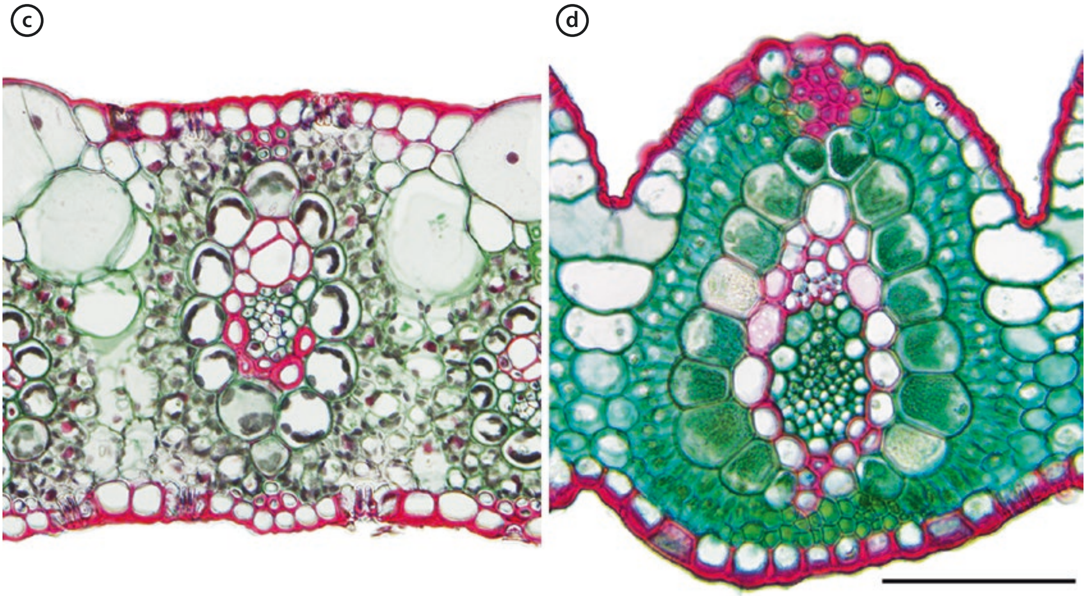

Fig. 12.5 Grass leaves with Kranz anatomy. **c** Sugar cane (*Saccharum officinarum*) has a single layer of photosynthetic bundle sheath cells, **d** while grama grass (*Bouteloua breviseta*) has a double layer of bundle sheath cells; the inner layer (mestome) is sclerified while the outer is parenchymatous. Gama grass is a xerophyte and shows features such as bulliform cells and a thick cuticle which are discussed in the next section. Scale bar in **d** = 50 µm and applies to both panels (**c**, **d** RR Wise)

12.6 Xeromorphic Angiosperm Leaves Conserve Water in Arid Environments

Water is of vital importance to plant survival and has been a strong force driving the evolution of leaf anatomy. Angiosperms may be divided into three basic categories based on their major adaptations to water supply. Leaves are typically the most plastic of organs in their ability to change their structure as an adaptation to a particular ecological factor. Xerophytes ("xeric" = dry, "phyte" = plant) are adapted to habitats with seasonal or permanent restrictions in water supply. Hydrophytes ("water plants") live in or on lakes, ponds, and streams. **Mesophytes** (literally "middle plants") are adapted to more favorable conditions and lack the specialized adaptations to overly dry or wet growing conditions. Mesophytic leaves, while not named as such, have been the subject of the much of the chapter so far. Xerophytic leaves are discussed in this section, in ► Sect. 12.7 (succulent leaves), and in ► Sect. 12.9 (gymnosperm leaves). Hydrophytic leaves are covered in ► Sect. 12.8.

Water loss through transpiration is a necessary evil for plants. Stomata must remain open for the diffusion of carbon dioxide to feed photosynthesis. However, the leaf interior is saturated with water—water that diffuses out through the open stomata as a gas (or vapor). Diffusion is a passive process driven by the difference in concentration between the area of high concentration and the area of low concentration and is dependent on temperature (which is ignored in this discussion) and the mass of the molecules that are diffusing. Because CO_2 (which is diffusing into the leaf) and water vapor (which is diffusing out of the leaf) have different concentration gradients and different molecular masses, any resistance in their shared diffusional pathway (i.e., from the leaf to the atmosphere or vice versa, via the stomata) will have a different impact on the total flux of gases. As a consequence, leaf anatomical adaptations that inhibit diffusion, such as sunken stomata, dense coverings of trichomes, and leaf rolling, have a greater impact on H_2O diffusion than CO_2 diffusion. The diffusion of both gases is inhibited, but the diffusion of H_2O is inhibited more than the diffusion of CO_2, and water use efficiency (the ratio of water lost to carbon gained) is improved. Growth may be slowed, but competitiveness is enhanced. This is the evolutionary bargain xerophytes have struck.

Beach grasses are prototypical xerophytic plants. Sandy beach soil holds little water. Exposure to full sunlight and steady winds places a high transpirational demand on the leaves while requiring a tough, flexible leaf design. In addition to evolutionarily driven anatomical adaptations, short-term water status can actually affect leaf shape. Many grasses are capable of rolling or folding their leaves during drought due to the presence of specialized motor (or **bulliform**) cells in the adaxial epidermis (◘ Fig. 12.6a–c) (Kadioglu and Terzi 2007). If the water supply is sufficient, these cells are turgid and keep the leaf open. In the case of water deficit, the cells lose turgor and shrink. The leaf, like a spring, rolls into a tube with the adaxial surface and stomata oriented to the inside of the tube. The leaf rolling involves not only the obvious changes in the size of the bulliform cells but also takes advantage of the entire leaf surface as

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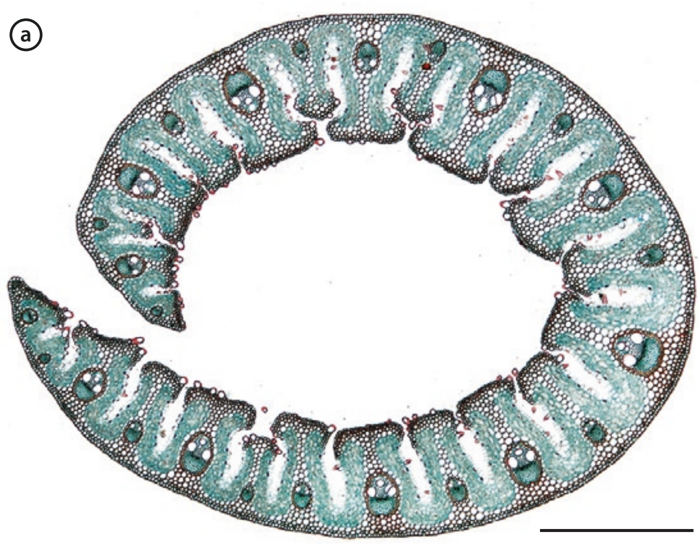
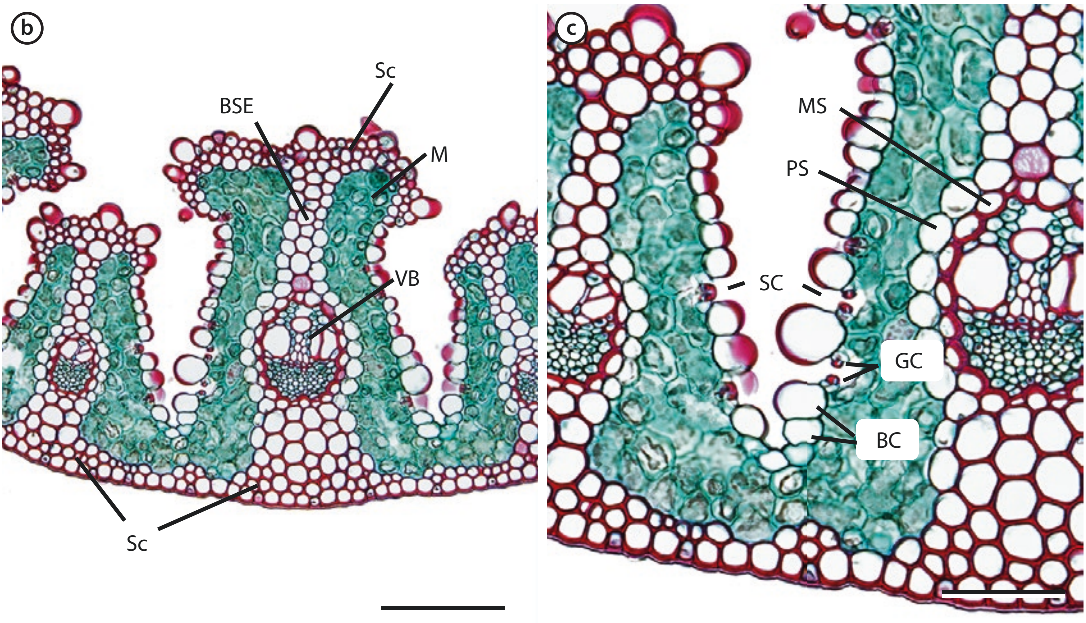


◘ **Fig. 12.6** **a** Typical xeromorphic leaf of European beachgrass (*Ammophila arenaria*) in the rolled-up configuration. Scale bar = 0.5 mm (RR Wise)



◘ **Fig. 12.6** Details of the xeromorphic European beachgrass (*Ammophila arenaria*) leaf. **b** Vascular bundles (VB) have large bundle sheath extensions (BSE) which isolate areas of the compact mesophyll (M) into a heterobaric leaf. Both the outside (abaxial) and inside (adaxial) epidermal cells are heavily sclerified (Sc). **c** Stomatal guard cells (GC) sit below the leaf surface in stomatal crypts (SC). Thin-walled, non-sclerified bulliform cells (BC) occupy the hinge area of the leaf. Note the compact arrangement of mesophyll cells. There are two bundle sheaths in this species, an inner sclerenchymatous sheath designated the mestome sheath (MS) and an outer parenchymatous sheath (PS). The cell walls of the mestome sheath have "U-like" secondary thickenings. Scale bars = 50 µm in **b** 25 µm in **c** (**b**, **c** RR Wise)

a structure (Moulia 2000). Rolling of leaves allows them to reduce transpiration. Bulliform cells in *Poa pratensis* are particularly large (◘ Fig. 12.6d). Like many grasses, *Ammophila and Poa* leaves are epistomatous, with stomata on the upper, or adaxial, surface only. All stomata are found on the adaxial leaf surface and are concentrated in depressions called stomatal crypts that are found on the inner, unexposed side of the rolled leaves. A thick cuticle and heavy sclerification (a condition called **sclerophylly**) of the abaxial surface protect the rolled-up leaf from abrasion by windblown sand particles.

New Zealand hemp has **sclerophyllous leaves** with extensive columns of fibers at each vascular bundle (◘ Fig. 12.6e). These fibers are classified as hard and are highly lignified. Strands of these fibers are commercially used for cordage. Through lysigenous breakdown of the mesophyll, large central air cavities are formed. The photosynthetic mesophyll is concentrated beneath both the adaxial and abaxial epidermal layers. The leaf surfaces are covered with a thick layer of cuticular waxes (◘ Fig. 12.6f, g).

Eudicot leaves, as well, may have several xeromorphic adaptations. The surface of the Russian olive leaf is covered with a dense layer of thin trichomes that obscure the leaf surface (◘ Fig. 12.6h). *Nerium oleander* leaves have several xeromorphic adaptations. First, their stomata are housed in large, abaxial **stomatal crypts**

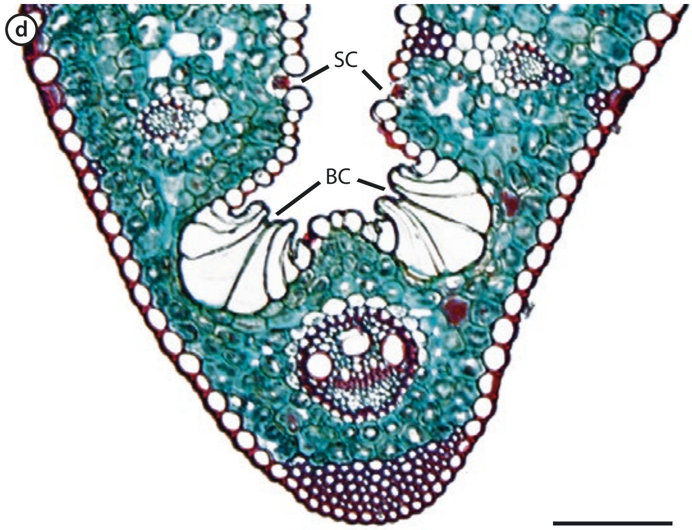


Fig. 12.6 **d** Cross-section of the midrib of an involute Kentucky bluegrass (*Poa pratensis*) leaf showing stomatal crypts (SC) and bulliform cells (BC). Scale bar = 100 µm (RR Wise)

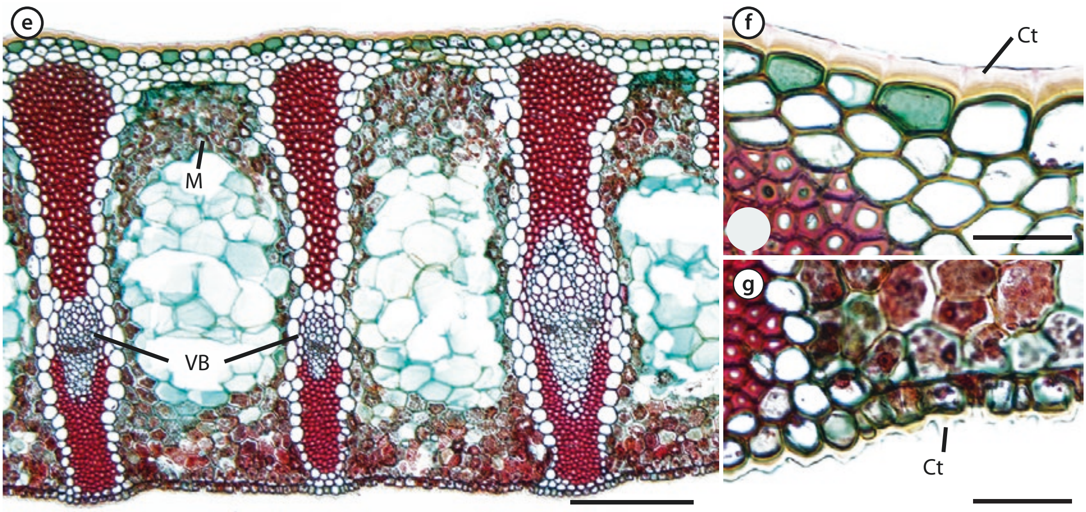


Fig. 12.6 **e**–**g** Xeromorphic leaf of a non-grassy monocot, New Zealand hemp (*Phormium tenax*). **e** Note the massive columns of fibers in the bundle sheath extensions, which provide significant support to this sclerophyllous leaf. Vascular bundles (VB) and the photosynthetic mesophyll (M) are labeled. **f** and **g** Higher magnification views of **f** the adaxial surface and **g** the abaxial surface showing the thick cuticle (Ct). Scale bars = 100 µm in **e** and 20 µm in **f** and **g** (**e**–**g** RR Wise)

(Fig. 12.6i–k); each crypt may have five to ten stomata. The tissue lining the crypt is epidermal (as is obvious from the presence of stomata). Epidermal trichomes grow into the crypts and fill the crypts with a dense forest of trichomes (Fig. 12.6i–k), with the effect of creating a pocket of water vapor, and thus reducing water loss by transpiration, especially in the wind. *Nerium* also has a thick cuticle and multiple layers of adaxial palisade (not shown), which are both xerophytic traits.

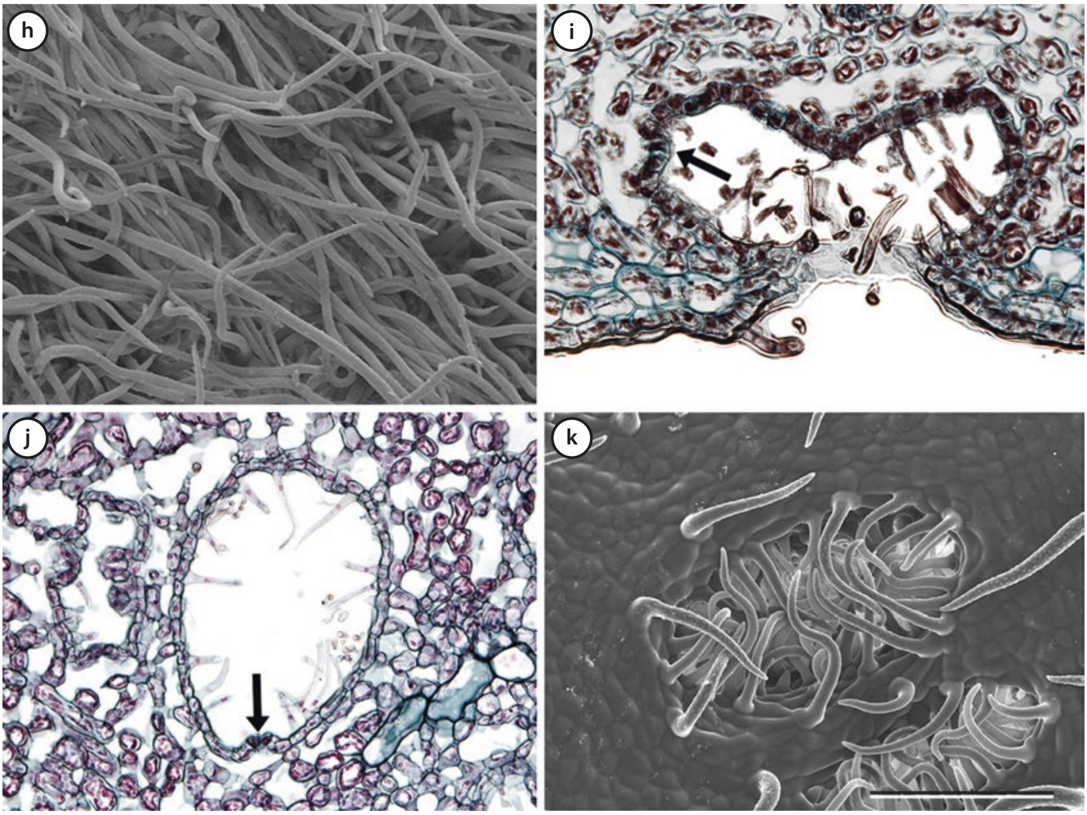


Fig. 12.6 **h**–**k** Xeromorphic leaf surfaces. **h** SEM of the surface of a Russian olive (*Elaeagnus angustifolia*) leaf showing a dense layer of hair-like trichomes, so dense they obscure the underlying stomata. **i** A cross-section of a single stomatal crypt on the abaxial surface of an oleander (*Nerium oleander*) leaf lined with dense epidermal cells. One stoma is indicated by the arrow. All other stomata are out of the plane of section. **j** The same structure as described in **i**, except in paradermal section. Arrow marks a stoma and trichomes are evident. Note the epidermal layer lining the crypt and the surrounding spongy mesophyll. **k** SEM of a *Nerium* leaf abaxial surface. The forest of trichomes filling the crypt is clearly seen. Scale bar in **k** = 100 µm and applies to all panels (**h**–**k** RR Wise)

12.7 Succulent Leaves Are Adapted for Water Storage

The xerophytes discussed above have adapted to dry conditions largely by limiting the amount of water lost via transpiration. A second strategy used by some xerophytes is to store water internally in the leaf or stem, which imparts a character called **succulence**. The cactus shown in ◘ Fig. 12.1j is a stem succulent. The cactus stem has a photosynthetic exterior and a fleshy, water-storing interior while its leaves are non-photosynthetic, spiny, protective structures. Leaf succulence is a second water-storing strategy and will be discussed here.

The desert plants *Yucca*, *Agave*, and *Aloe* are typical, desert-dwelling leaf succulents. The saltwort shown in ◘ Fig. 12.3o–p also has succulent leaves and is found in salt marshes which, from the standpoint of water availability, can mimic desert conditions.

Yucca leaves can be a millimeter or more in thickness (◘ Fig. 12.7a). Compare that to the 100–200 µm mesophytic leaves

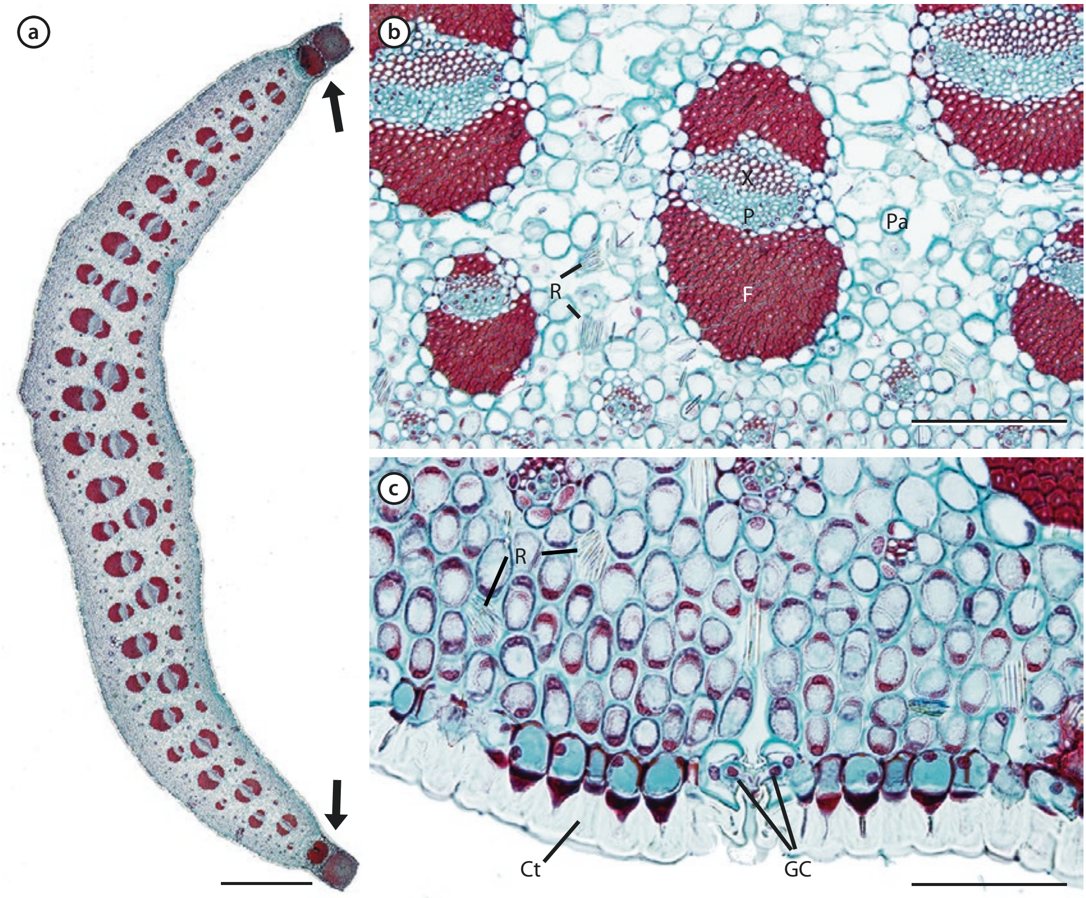
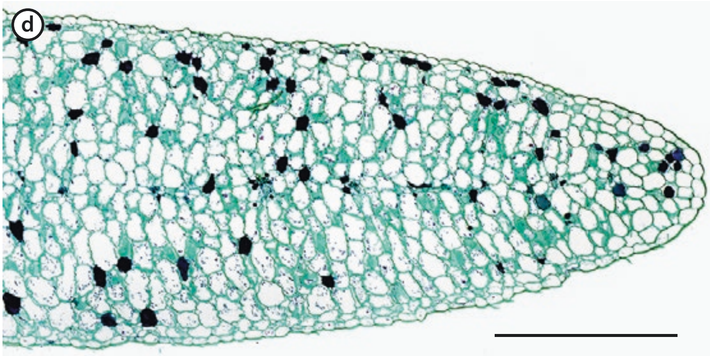


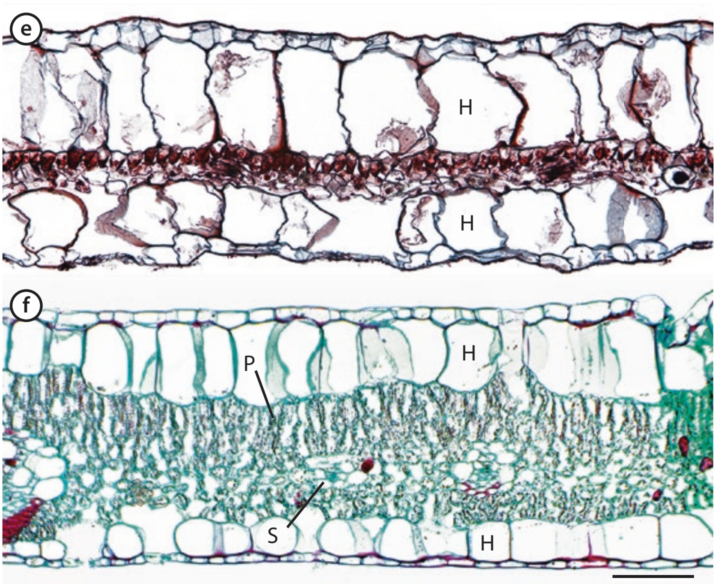
Fig. 12.7 Cross-sections of an isobilateral succulent leaf, yucca (*Yucca* sp.). **a** Large fiber bundles strengthen the leaf margins (*arrows*) and cap the vascular bundles. **b** The interior of the leaf has numerous vascular bundles containing xylem (X) and phloem (P) with large fiber (F) caps to both sides. The water-storing parenchyma (Pa) has few organelles. **c** The mesophyll cells closest to the leaf surface are small with a dense cytoplasm (note the difference in scale between **b** and **c**. A thick waxy cuticle (Ct) covers the leaf, and guard cells (GC) are sunken beneath the epidermis. There is little internal air space, even in the photosynthetic tissue. Scale bars = 500 µm in **a**, 50 µm in **b**, and 100 µm in **c** (**a**–**c** RR Wise)

introduced in ► Sects. 12.3, 12.4, and 12.5. Succulent leaves accumulate water in the vacuoles of large, thin-walled water storage parenchyma cells in the mesophyll (Fig. 12.7b). The photosynthetic mesophyll lies near the leaf surface on both the abaxial and adaxial sides (Fig. 12.7c). Large fiber bundles protect both the leaf margins and the vascular bundles to the interior. Stomata are sunken below the epidermis, which is covered with a thick layer of cuticular wax. *Sedum*, another leaf succulent, has many of the same leaf characteristics (Fig. 12.7d).

Begonia and canna leaves have an enlarged, water-storing hypodermis on both sides of the leaf, lying just underneath the epidermises (Fig. 12.7e, f). Canna is grown as a food crop for its large, starch-filled tubers. Under well-watered conditions, the hypodermal cells are filled with water and turgid. During drought, the stored water is used by the plant, and the hypodermis shrinks significantly (Brück et al. 2001).



■ **Fig. 12.7** **d** Cross-section of an isobilateral *Sedum* sp. leaf filled with large, water-storing parenchyma cells. Scale bar = 500 µm (RR Wise)



■ **Fig. 12.7** **e** Begonia (*Begonia* sp.) **e** and **f** canna (*Canna* sp.) leaves have a hypodermis modified for water storage. The leaves are bifacial in that they have a thin band of distinct palisade (P) and spongy (S) mesophyll sandwiched between an upper and lower hypodermis (H). The layers are not distinct in the *Begonia* leaf. Scale bar in **f** = 100 µm and applies to both panels (**e**, **f** RR Wise)

12.8 Aquatic Angiosperms Have Hydromorphic Leaves

Aquatic plants are found in the ferns, monocots, and eudicots. They may have leaves that are fully submerged, float on the surface, or emerge from the water. As an example, northern wild rice (*Zizania palustris*) has all three forms of leaves. Seeds germinate underwater, and the first leaves to emerge from the embryo remain submerged. Subsequent leaves grow to and float across the water surface. A third set of leaves emerges from the water and extends up to 1 meter above the surface (Sculthorpe 1967). Aquatic leaf shape varies.

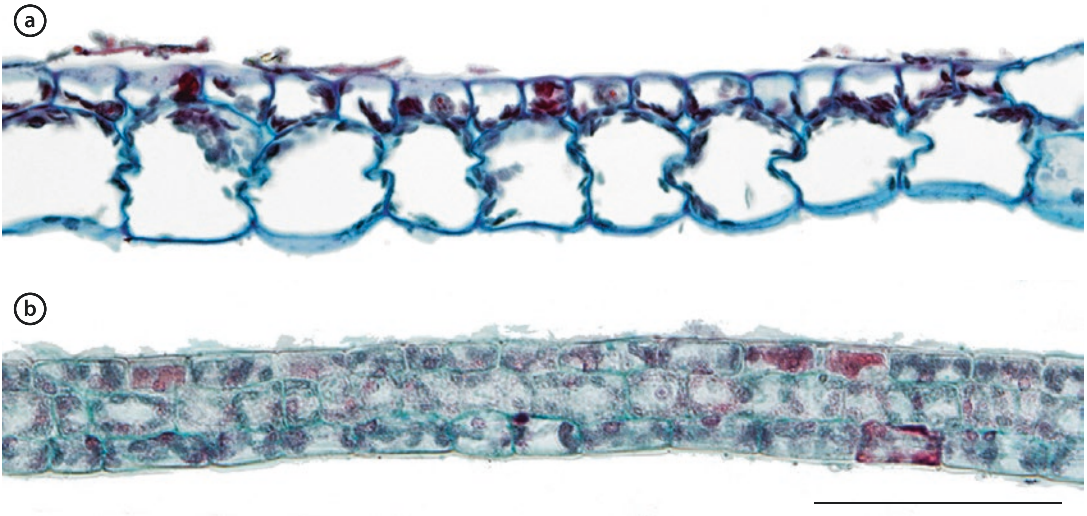


Fig. 12.8 **a** Submerged leaves of Canadian waterweed (*Elodea canadensis*) are only two cell layers thick. Chloroplasts are found in both layers. **b** Submerged leaf of pondweed (*Potamogeton* sp.) has three layers, two epidermal layers, and one mesophyll layer. The leaves of both plants are thin, with a minimal cuticle, no internal gas spaces, and no xylem. Scale bar in **b** = 50 µm and applies to both panels (**a**, **b** RR Wise)

12

Typically, leaves found in or on flowing water such as rivers and streams are long and narrow, while those found in or on quiet waters, ponds and lakes, may be oval or round.

Submerged leaves clearly do not face the same constraints on transpiration and gas exchange as aerial leaves and usually have a thin cuticle and lack stomata and intercellular air spaces (Fig. 12.8a). Light levels under water are reduced, photosynthetic rates are low, and dissolved gasses diffuse into the leaf from the surrounding water. With no need for transpiration and buoyancy provided by the water, xylem and fibers are usually absent. The thin cuticle probably serves as a barrier to bacterial and fungal infection, rather than as a barrier to water loss.

Because diffusion is only effective over short distances, most submerged leaves have a single-layered mesophyll, such as *Potamogeton* (Fig. 12.8b), or lack a mesophyll entirely. *Elodea* leaves are so thin that photosynthesis takes place in the cells of the bilayer leaf, each of which qualifies as an epidermis (Fig. 12.8a).

In other, larger submerged plants such as *Myriophyllum* (Fig. 12.8c), the leaves are finely divided into cylindrical **pinnae**. Such structure improves diffusion of carbon dioxide from water into the leaf for photosynthesis in the absence of gas spaces. The leaves and petioles are centric and unifacial which may allow for a greater and more uniform surface for the diffusion of carbon dioxide from the water into the leaf for photosynthesis. The movement of the surrounding water through the fingerlike leaves also helps circulate dissolved gases.

In floating leaves, stomata are found on upper surface exposed to the air but not on the lower surface in contact with the water

◼ **Fig. 12.8** **c** Cross-section of a pinna of a leaf from the submerged hydrophyte water milfoil (*Myriophyllum* sp.). The plant has pinnately divided leaves which lack cuticle, stomata, sclerenchyma, and air spaces in the mesophyll. The inset shows the centric and unifacial structure of a single leaf. Scale bars = 2 mm in main panel and 200 µm in inset (RR Wise)

(◼ Fig. 12.8d, e). Palisade mesophyll consists of several layers of rather short cells at the adaxial surface. There is little shade on the surface of a pond and little CO_2 uptake from the bottom leaf surface which is floating on the water. Therefore, there is no need for an abaxial spongy mesophyll layer. Air spaces in spongy mesophyll constitute an aerenchyma that provides buoyancy. Structural support is provided by astrosclereids that extend throughout the mesophyll in all three dimensions.

Emergent leaves of aquatic plants face different constraints. Here, aerenchyma does not serve for buoyancy, but as a diffusional pathway for the movement of gases, oxygen primarily, from aerial leaves to the submerged stem and roots which are exposed to low environmental oxygen concentrations. Large galleries, or **lacunae**, run the length of the leaf (◼ Fig. 12.8f, g). While some of the oxygen in the diffusional pathway originates from the air,

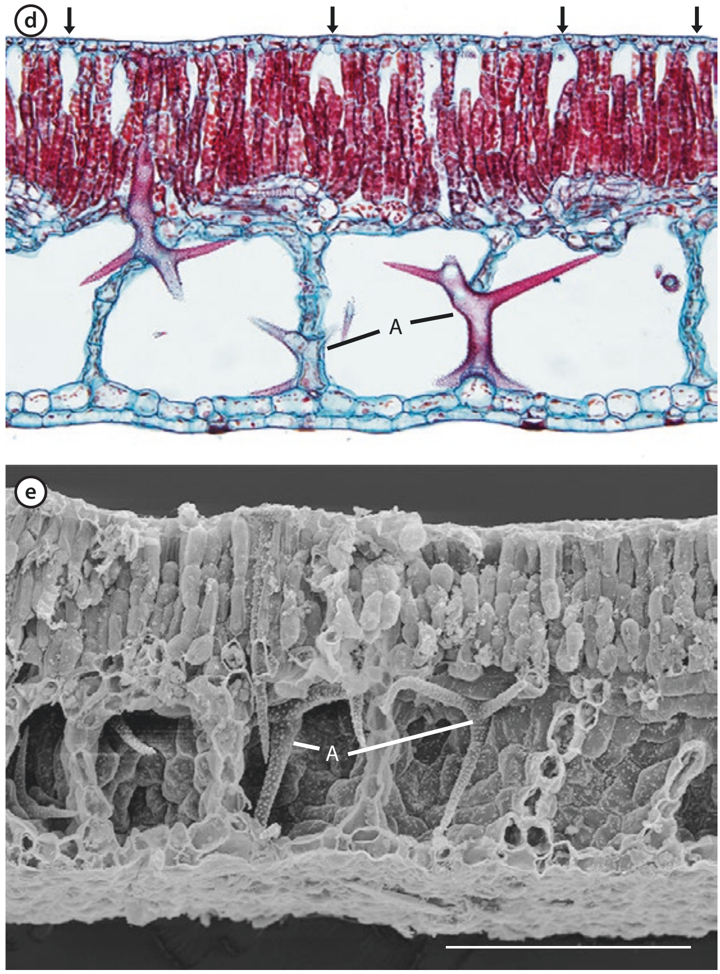
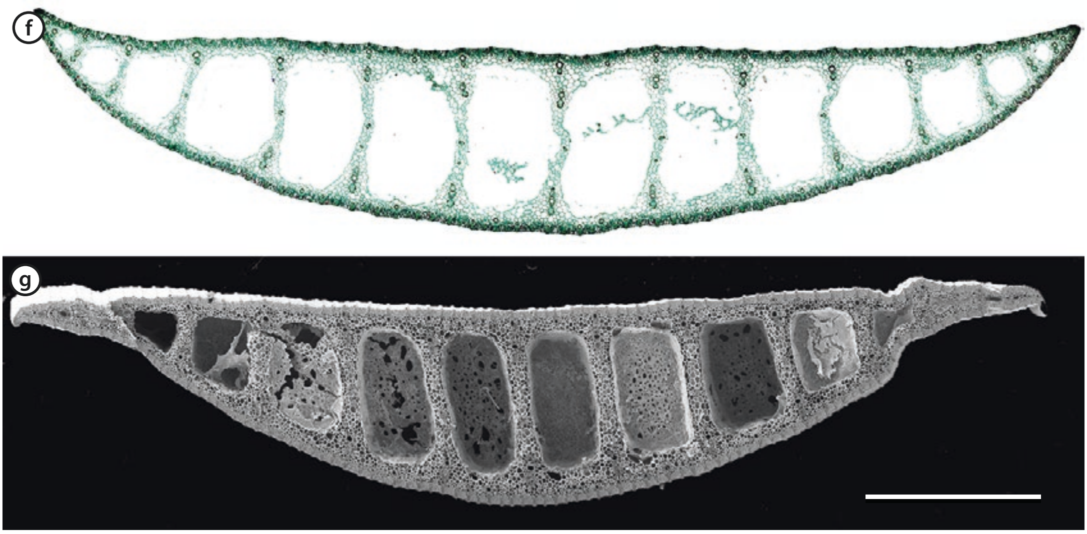


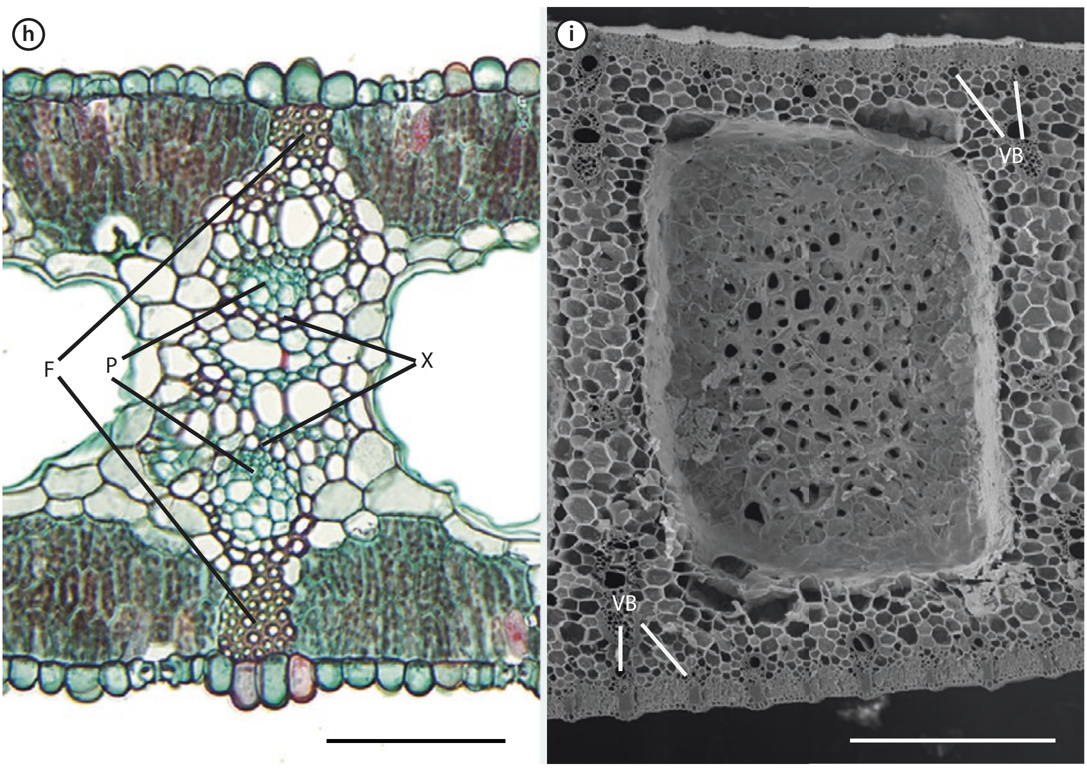
Fig. 12.8 Cross-sections of bifacial floating leaves from the fragrant water lily (*Nymphaea odorata*). **d** Palisade parenchyma lies on the adaxial surface, which has numerous stomata (*arrows*). Note the substomatal cavity underneath each stoma. Astrosclereids (A) provide support to the aerenchyma tissue on the abaxial surface. **e** The air spaces of the aerenchyma can be seen to extend throughout the leaf. Scale bar in **e** = 200 µm and applies to both panels (**d**, **e** RR Wise)

most of it is generated by the chloroplasts in the leaf itself (Sand-Jensen and Prahl 1982). Thus, much of the oxygen consumed by the roots is generated by photosynthesis and recycled from the leaves.

Being aerial, the leaves must have some means of support, usually in the form of bundles of fibers (Fig. 12.8h) in the vascular bundle sheath extensions and structural cross bracing in the leaf lacunae (Fig. 12.8i).



■ **Fig. 12.8** **f**, **g** Cross-sections of cattail (*Typha latifolia*) leaves. Large areas of aerenchyma form lacunae for gas exchange and facilitate the diffusion of oxygen from the atmosphere to the submerged portions in *Typha latifolia* LM and SEM. Scale bar = 2 mm (**f**, **g** RR Wise)



■ **Fig. 12.8** **h** Cross-section of a relatively thin portion of a cattail (*Typha latifolia*) leaf. Fibers (F) cap the xylem (X) and phloem (P) bundles in this isobilateral leaf. **i** In a much thicker cattail leaf, vascular bundles (VB) are arranged near the leaf surface, and a wall of porous aerenchyma provides structural support by cross bracing the leaf lacuna. Scale bars = 50 µm in **h** and 500 µm in **i** (**h**, **i** RR Wise)

12.9 Xeromorphic Conifer Leaves Conserve Water During Winter

Conifers (Coniferophyta) are the cone-bearing gymnosperms (refer to ► Sect. 1.16 for an overview of gymnosperms) and include species of pine, cedar, cypress, juniper, fir, redwood, spruce, and yew. Most of the conifers retain their leaves for multiple growing seasons and are thus termed "evergreens" with individual leaves living for 2–4 years, on average, or as long as 30 years in some species. The deciduous larches and tamaracks (*Larix* sp.) are among the few exceptions to the evergreen habit. Many conifers are native to temperate climate zones where low winter temperatures and heavy snowfall are common. In terms of water availability, winter conditions mimic drought in that there is very little liquid water in the soil. Therefore, xeromorphy—or a leaf with structural adaptations to dry conditions—is a hallmark of the gymnosperms. The epidermis consists of pavement cells with thick lignified secondary walls and a heavy cuticle. Stomata are deeply sunken with overarching subsidiary cells. The **epistomatal cavity** (depression over guard cells of stomata) is usually filled with dense deposits of wax particles which greatly reduce water loss. A sclerenchymatous hypodermis layer underlies the epidermis. It is interrupted only by substomatal cavities (◘ Fig. 12.9a–c).

Conifer leaves may be needle-shaped (pines), scalelike (cedars, cypress), or flattened (spruces and firs), thus reducing the surface-to-volume ratio and likewise transpiration. Pine needles are arranged in bundles of one to five individual leaves called a fascicle. In this case, each leaf assumes a section of the circle (◘ Fig. 12.9d–f). Larger, scalelike leaves are flattened in the dorsiventral direction and may have an adaxial palisade mesophyll and an abaxial spongy mesophyll (◘ Fig. 12.9g). The mesophyll may be homogeneous and compact as in pines or differentiated into palisade and spongy parenchyma as in fir, larch, and cycads. Conspicuous resin ducts are found in all conifer leaves. (◘ Fig. 12.9d–i).

Conifer leaves contain a central cylinder of vascular tissues and fibers called a **fibrovascular bundle** (◘ Fig. 12.9j). The bundle is bounded by an endodermis, which separates and isolates it from the leaf mesophyll. Interior to the endodermis is a layer or two of cells called **transfusion tissue**. Transfusion tissue is composed of living parenchyma cells and dead tracheids, and its presence and role are unique to gymnosperms (Wordsell 1897). The transfusion tissue lies between the xylem and the mesophyll and serves to recover solutes from the transpiration stream before they leave the fibrovascular bundle and return them to the adjacent phloem (Canny 1993).

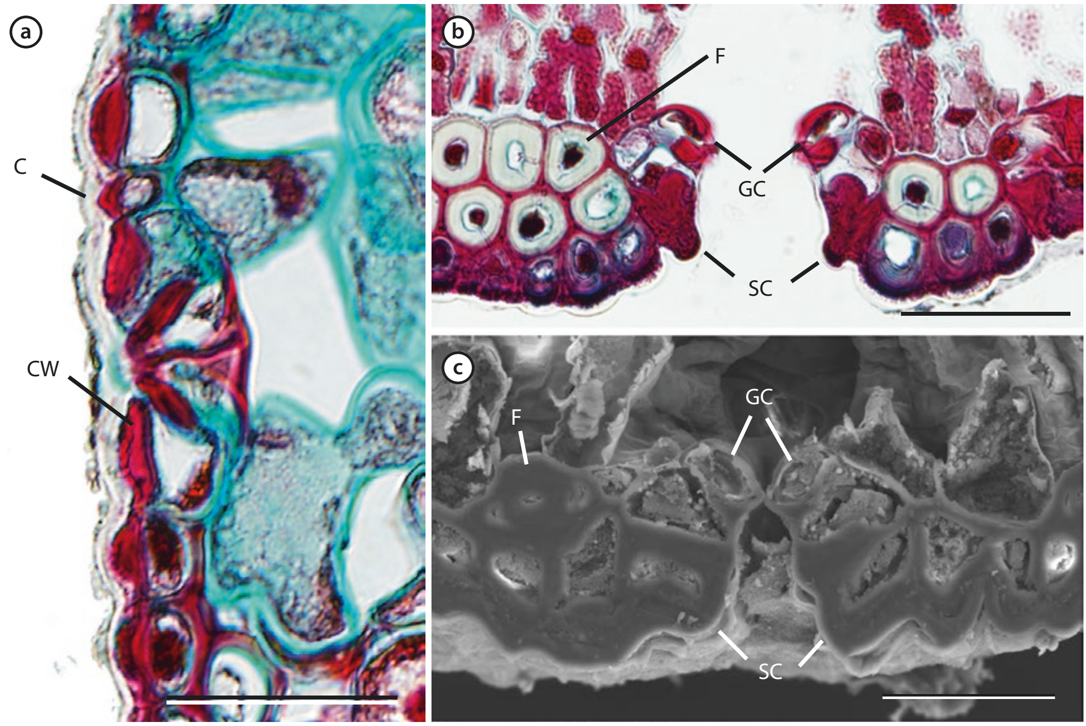


Fig. 12.9 **a**–**c** Xeromorphic characters of gymnosperm leaves. **a** Eastern hemlock (*Tsuga canadensis*) epidermis showing a thick cuticle (C) and thick epidermal cell walls (CW). Mesophyll cells are to the right in the figure. **b** and **c** show hypodermal fibers (F) and sunken guard cells (GC) overarched by subsidiary cells (SC) in **b** single-leaf pinyon (*Pinus monophylla*) and **c** white fir (*Abies concolor*). Scale bars = 20 μm in **d** and 50 μm in **e** and **f** (**a**–**c** RR Wise)

12.10 Leaf Abscission Is a Timed and Genetically Controlled Process

In many plants, the leaf is a temporary organ, designed to take advantage of favorable conditions during the growing season and then discarded as environmental conditions become less favorable. **Drought deciduous** plants, such as *Euphorbia splendens*, drop their leaves at the start of seasonal dry periods whereas winter deciduous plants, such as many temperate, eudicot trees, drop their leaves in the fall, prior to winter, in a process called **autumnal senescence**. The actual shedding of the leaf is called abscission ("ab" = away from and "scise" meaning to cut). Leaf abscission is preceded by multiple physiological and anatomical changes.

The senescence of deciduous leaves is the end result of a detailed and genetically controlled process of resource recovery. Chloroplasts

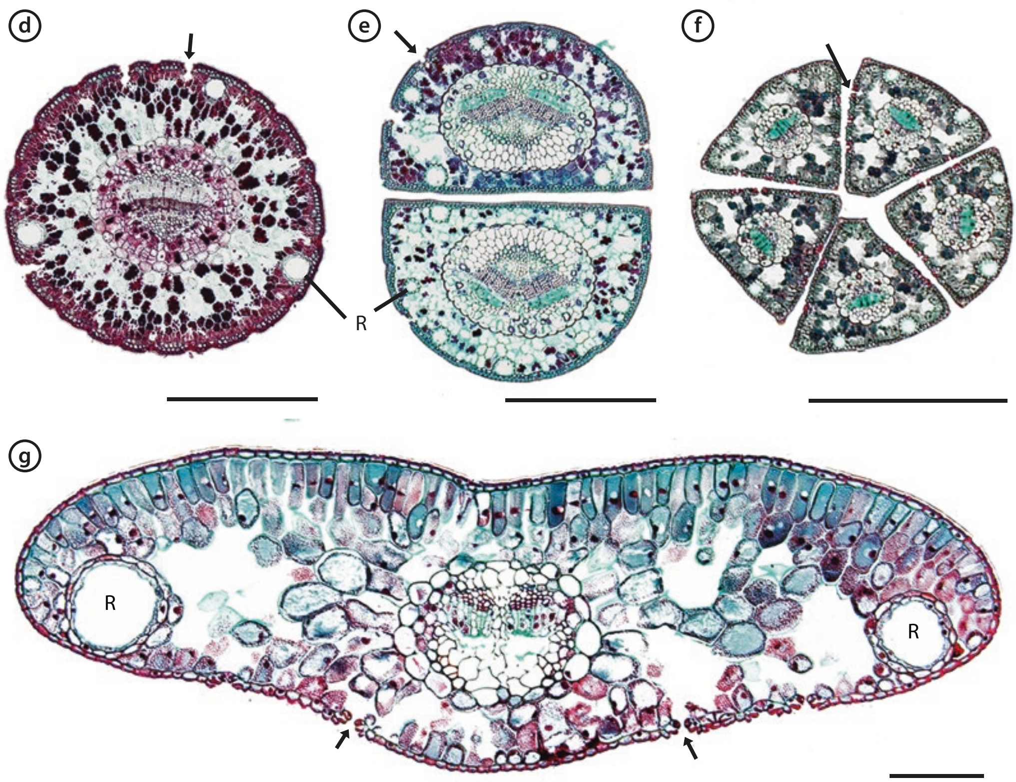


Fig. 12.9 Cross-sections of conifer leaves. **d** One leaf in a fascicle of the single-leaf pinyon (*Pinus monophylla*). **e** Two-leaf fascicle of the Austrian pine (*Pinus nigra*). **f** Five-leaf fascicle of white pine (*Pinus strobus*). **g** This fir (*Abies* sp.) leaf has a flattened shape with a palisade parenchyma to the adaxis and spongy mesophyll to the abaxis. In all images, resin ducts are labeled (R) and arrows indicate stomata. Scale bars = 500 µm in **d** through **f** and 100 µm in **g** (**d**–**g** RR Wise)

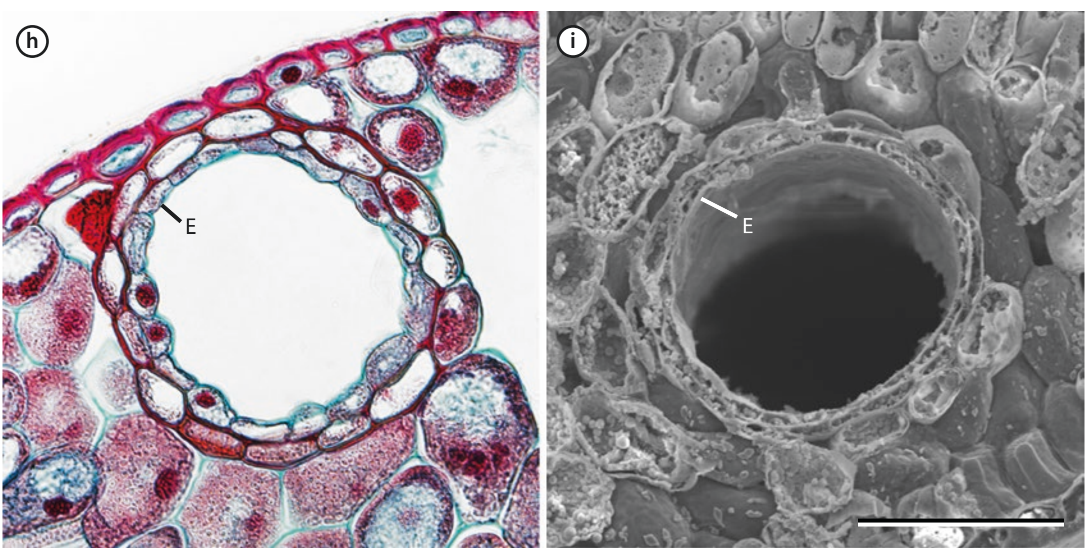
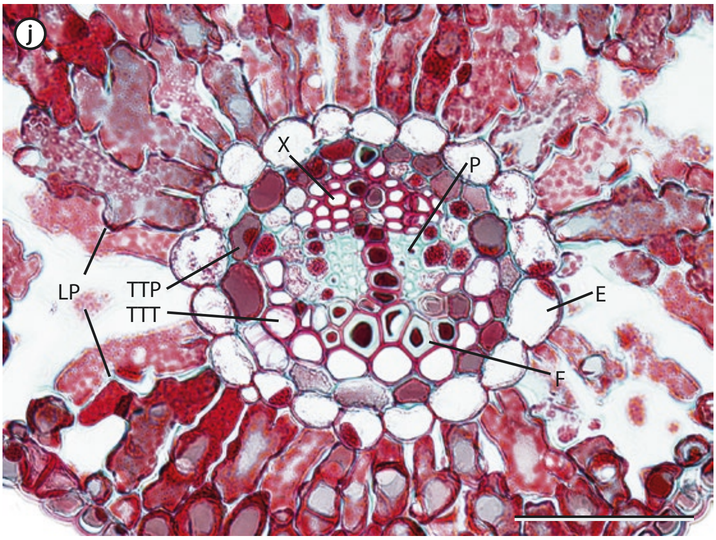


Fig. 12.9 **h**, **i** Resin ducts in leaves of balsam fir (*Abies balsamea*) as seen in the light microscope **h** and the scanning electron microscope **i**. The resin is secreted by the layer of epithelial cells (E). Scale bar in **i** = 100 µm and applies to both panels (**h**, **i** RR Wise)



◘ **Fig. 12.9** **j** Central fibrovascular bundle from a tamarack (*Larix laricina*) leaf. The bundle contains xylem (X), phloem (P), fibers (F), and transfusion tissue (TT) and is bounded by an endodermis (E). The transfusion tissues consist of living parenchyma (TTP) and dead tracheids (TTT). Lobed parenchyma cells (LP) lie in the mesophyll. Scale bar = 100 µm (RR Wise)

contain the vast majority of protein in a leaf, and the valuable amino acids in those proteins must be recovered. Plants undergoing autumnal senescence use the environmental cues of shortening day length and cooler temperatures to initiate chloroplast breakdown, resulting in the conversion of that organelle to a gerontoplast (refer to ► Sect. 3.5.6). At the end of that process, the leaf is shed or abscised. The chloroplast-to-gerontoplast conversion begins prior to and accompanies the process of abscission. If timed correctly (the coordinated processes can be disrupted by a late summer drought, a heavy fall rainstorm, or an early winter freeze), all of the leaf protein will have been removed and recovered before the leaf is ultimately shed.

Leaf abscission starts with the formation of a specialized separation layer of mitotically active cells called an **abscission zone** (◘ Fig. 12.10a, b). Abscission zones are found at the site of connection of petioles with the stem. This layer of cells defines a transverse rupture zone. Similar zones are also found at the sites of connection for flowers and fruits, because they abscise as well. It typically starts with cell divisions that take place perpendicular to the axis of the petiole. The growth of the abscission layer does not extend through the vascular tissues. It is a region that has parenchyma cells with thin walls, tracheids instead of vessels, and a near lack of fibers. Differentiation of this zone may be early, or it may start just before activation. Initiation of the abscission zone involves the action of the plant growth regulator ethylene (a gas), to stimulate degradation of the middle lamella and hydrolysis of the cellulosic walls. Since lignin is not affected, everything at the juncture site is eventually severed except for xylem.

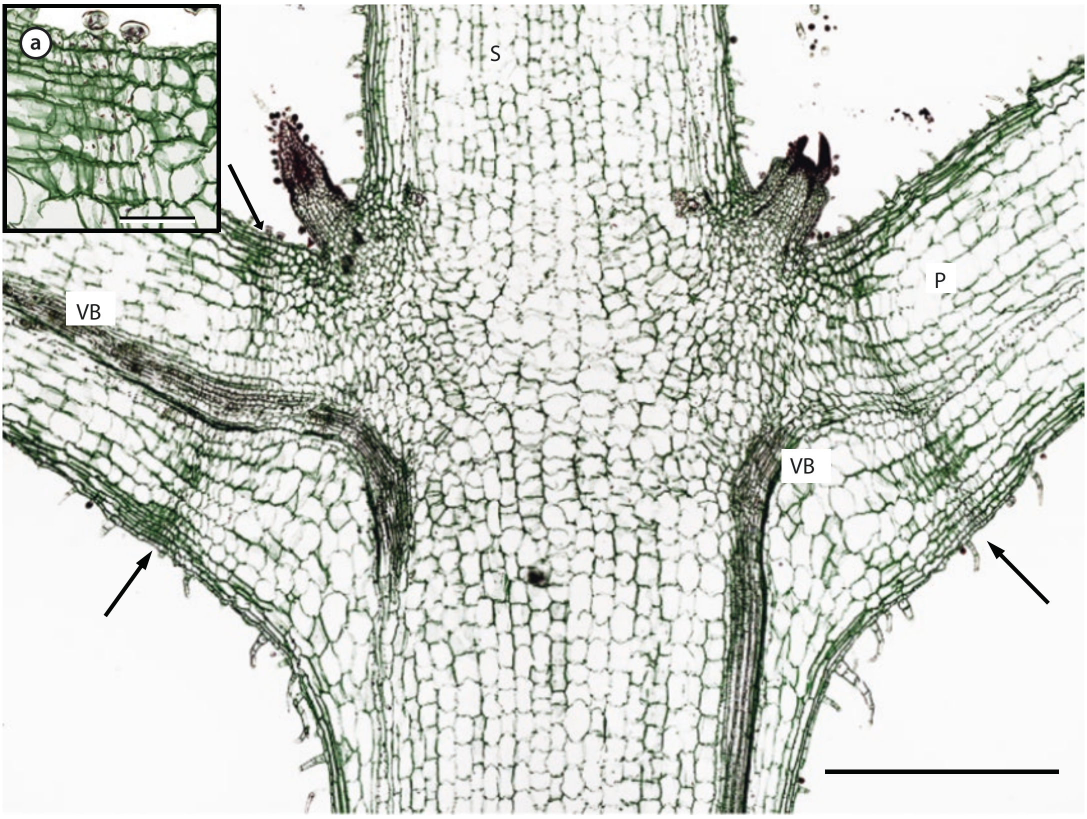


Fig. 12.10 **a** General view of early abscission zones (*arrows*) in coleus (*Plectranthus scutellarioides*) leaves extending off a central stem (S). Vascular bundles (VB) can be seen. The one to the left extends into the petiole (P). A similar connection is not revealed, but exists, to the petiole on the right. Inset at top left shows the *tabular* cell shape of the early abscission zone. Scale bars = 500 µm in main panel and 50 µm in inset (RR Wise)

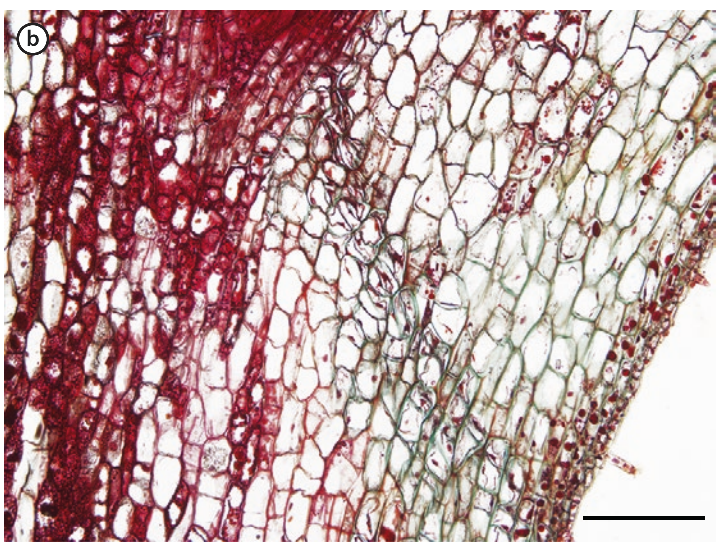
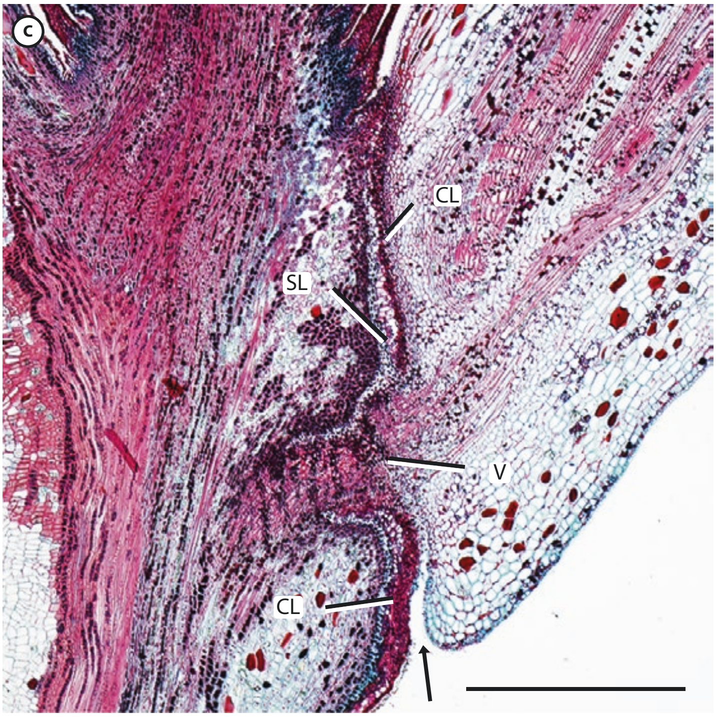


Fig. 12.10 **b** Higher magnification view of an early abscission zone in a black walnut (*Juglans nigra*) petiole. Stem is to the left and petiole to the right. Scale bar = 250 µm (RR Wise)



■ **Fig. 12.10** **c** Mature abscission zone in American elm (*Ulmus americana*). Stem is to the left and petiole is to the right. The separation layer (SL) of thin-walled cells is bordered by protective corky layers (CL) to either side. Note that the vasculature (V) has not fully separated yet and that the corky layer is thicker on the stem side than on the petiole side. Separation has begun at the bottom of the petiole (*arrow*) and will eventually propagate through the zone and result in leaf abscission. Scale bar = 500 µm (RR Wise)

As the abscission process progresses, the abscission zone is subdivided into a **separation layer** of thin-walled empty cells through which the actual break occurs and two **corky layers** at both sides of the separation layer (■ Fig. 12.10c). Corky layers are cork cells that appear dark brown due to the deposition of specific "protective" substances (e.g., suberin) in their cells. Physical force, in time, breaks the xylem. The formation of the weak abscission zone prevents injury to the living tissues in the stem, and the cork layer left behind protects the newly exposed stem surface from desiccation and infection by microorganisms. Abscission of the leaf will leave a **leaf scar** appearing on the side of the stem (■ Fig. 12.10d). The protective layer on the stem side is gradually transformed in each leaf scar with further periderm development beneath the scar.

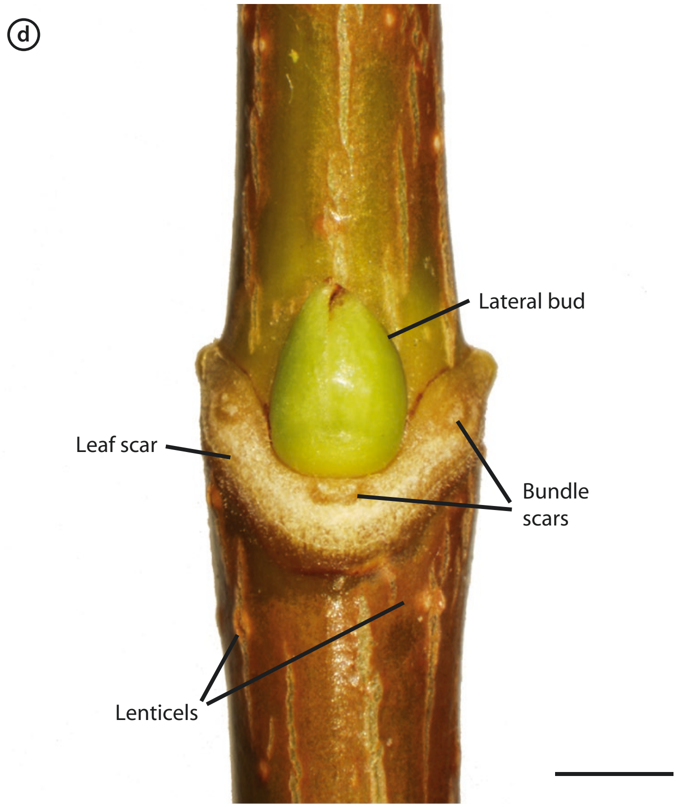


Fig. 12.10 **d** A leaf has recently abscised from this node on a red maple (*Acer rubrum*) stem. A single leaf scar shows where the petiole was attached, and bundle scars mark the location of vascular bundles. The lateral (axillary) bud will be the source of next years' leaf. The stem has multiple lenticels for gas exchange. Scale bar = 2 mm (RR Wise)

12.11 Chapter Review

Concept Review

12.1 *Leaves have a variety of shapes and functions.* Leaves arise from the nodes of the stem, and while most leaves are the plant's green, planar photosynthetic organs, other shapes, and functions have evolved. Gymnosperm leaves are scalelike or needlelike. Some monocot leaves form a large portion of the plant "stem." Other leaves serve as protective spines or coverings, food or water storage organs, tendrils for attachment, or carnivorous traps. Some plants lack leaves entirely.

12.2 *The vas*culature system spreads throughout the leaf. Enations are small outgrowths on the stems of primitive plants that lack a vascular connection to the stele in the stem. Microphylls are likewise small and primitive, but their vasculature is connected to that of the stem. Subsequent evolution led to the macrophyll with a branching system of veins seen in most extant plant species. Ferns and *Ginkgo* have a simple, dichotomously branched vascular system. Monocots have parallel venation and eudicots have reticulate venation.

Vascular bundles have bundle sheaths that control the flux of water and photosynthate between the xylem, phloem, and leaf mesophyll. In heterobaric leaves, bundle sheath extensions extend to the leaf surface and divide the leaf into separate gaseous compartments. Homobaric leaves lack the extensions. Collenchyma and fibers surrounding the vasculature may provide structural support to the leaf.

12.3 *Leaf morphology is optimized for light absorption, gas exchange, and water conservation.* The prototypical eudicot leaf has a double-layer photosynthetic mesophyll divided into the palisade mesophyll and the spongy mesophyll, in an arrangement called bifacial. The leaf surfaces are bounded by two epidermises which contain stomata and trichomes. An isobilateral leaf only has palisade or spongy mesophyll. Unifacial and tubular leaves have one face, typically the adaxial, fused so that both faces are abaxial. Centric leaves are round and solid in the middle; tubular leaves are round and hollow in the middle.

12.4 *The light environment during development can modify leaf anatomy.* In plants with large foliage crowns, such as many trees, leaves that develop inside the canopy do so under shaded conditions and leaves that develop at the periphery of the canopy are exposed to high light during development. This leads to different leaf morphologies that take advantage of the availability of light. "Shade" leaves are thicker overall with a greater proportion of palisade than spongy mesophyll. "Sun" leaves are the opposite, being thinner and a lower ratio of palisade thickness to spongy thickness.

12.5 *Kranz leaf anatomy is a specialization of the C4 photosynthetic pathway.* C4 photosynthesis requires a spatial separation of the initial carbon fixation steps and the final carbon fixation steps. In many C4 plants, the initial fixation is performed in the mesophyll cells and the final in the large, conspicuous bundle sheath cells. This "halo" of large cells surrounding the vascular bundle is the source of the term "Kranz" anatomy. Warm season grasses have a single layer of bundle sheath cells. Cool season grasses have a double layer, the inner layer called the mestome.

12.6 *Xeromorphic angiosperm leaves conserve water in arid environments.* Xerophytes are plants adapted to water-limiting conditions and have a number of anatomical adaptations including a thick cuticle, dense covering of trichomes, sunken stomata, and the ability to roll their leaves via water loss from bulliform cells. The leaves are often sclerophyllous as a consequence of thick bundles of heavily sclerified fibers associated with the vasculature or scattered throughout the leaf.

12.7 *Succulent leaves are adapted for water storage.* Succulence is a morphology characterized by the storage of water in thick, fleshy stems or leaves. Many desert plants use this strategy, in addition to other xerophytic adaptations such as thick cuticle and sunken stomata, to conserve water in extremely arid environments. Succulent leaves typically have their photosynthetic tissues close to the leaf surface and an interior of large, thin-walled, water-storing parenchyma. Other leaves develop one or more water-storing hypodermises lying just underneath the epidermis.

12.8 *Aquatic angiosperms have hydromorphic leaves.* Hydrophyte plants are adapted to an aquatic habitat. Their leaves may be submerged, floating, or emergent. Submerged leaves may be only 2–3 cell layers thick and have a thin cuticle with little to no vasculature. Floating leaves are epistomatous with stomata on the top (adaxial) surface only. A palisade parenchyma underlies the adaxial epidermis while large, air-filled aerenchyma tissue occupies the bottom portion of the leaf. Emergent leaves have both an aerenchyma as well as large open ducts called lacunae that provide a diffusional pathway for oxygen transport to the submerged roots. They may also have sclerenchyma and vasculature.

12.9 *Xeromorphic gymnosperm leaves conserve water during winter.* Evergreen conifer trees experience drought conditions during their overwintering phase. Therefore, their leaves have anatomical adaptations similar to those found on other xerophytes.

12.10 *Leaf abscission is a timed and genetically controlled process.* Plants may shed their leaves upon the imposition of seasonal drought or winter freezing in a process called abscission. The formation of an abscission zone in the leaf petiole is preceded and accompanied by a reallocation of the leaf protein and recovery and export of those products from the leaf to the stem. Cells in the abscission zone form three layers, a middle, thin-walled weak layer called the separation layer which is bounded by two thicker, corky layers, one on either side. Eventually, the separation layer will fail and the leaf will abscise. The scar on the stem left by the leaf will be sealed by the corky layer, which will prevent desiccation and block microbial invasion.

12

■ Concept Connections

1. Match the leaf type to the function and the example given in the text.

Leaf type	Function	Example given in text
a. Foliage	i. Support	a. Eudicotyledon seed
b. Leaf sheath	ii. Photosynthesis	b. Cacti
c. Cataphyll	iii. Antiherbivory	c. Many grasses
d. Frond	iv. Photosynthesis	d. Monocotyledon seed
e. Pseudostem	v. Protection	e. Flowering plants
f. Scutellum	vi. Photosynthesis	f. *Rosa* sp.

Leaf type	Function	Example given in text
g. Needle	vii. Food storage	g. Ferns and duckweeds
h. Spine	viii. Floral structures	h. Bud scales
i. Cotyledon	ix. Support	i. Conifers
j. Hypsophyll	x. Attachment	j. *Clematis* sp.
k. Tendril	xi. Absorption	k. *Musa* sp.

Concept Assessment

2. Hypostomatous leaves have
   a. no stomata.
   b. paracytic stomata.
   c. stomata on abaxial epidermis.
   d. stomata always open as a part of a hydathode.
   e. a lack of stomatal chambers.

3. An areole is
   a. a leaf mesophyll region bounded by vascular tissues.
   b. an air space within the mesophyll of a leaf.
   c. the opening of a stoma.
   d. an enlargement of a petiole.
   e. a leaf separated into different regions by bundle sheath extensions.

4. Mestome sheath cells
   a. possess large chloroplasts with starch.
   b. have thickened walls.
   c. function as bulliform cells.
   d. encircle only the phloem of leaf veins.
   e. are commonly found in C3 plants.

5. Leaf abscission is early recognized by the appearance of
   a. separation of the vascular tissues.
   b. an accumulation of starch at the site of abscission.
   c. meristematic activity of the protoderm.
   d. cell division parallel to the axis of the petiole.
   e. tabular cells in the abscission zone.

6. What plant regulator growth regularly helps promote the formation of leaf abscission?
   a. gibberellin.
   b. abscisic acid.
   c. ethylene.
   d. auxin.
   e. florigen.

7. When the two sides of mesophyll of a leaf are similar in structure, the leaf is said to be
   a. hypostomatous.
   b. mesophytic.
   c. dorsiventral.
   d. unifacial.
   e. tubular.

8. Commissural veins are found
   a. in eudicots.
   b. connecting parallel veins in monocots.
   c. as leaf midveins.
   d. only in petioles.
   e. where there is dichotomous vein branching.

9. "Closed" minor veins lack
   a. secondary walls.
   b. a bundle sheath.
   c. companion cells.
   d. plasmodesmata.
   e. protoplasmic structure.

10. What is missing in leaves with Kranz anatomy?
    a. bundle sheath.
    b. palisade mesophyll.
    c. spongy mesophyll.
    d. stomata.
    e. vascularization.

11. Bulliform cells
    a. enable the leaf to fold.
    b. are found in the endodermis.
    c. are highly photosynthetic.
    d. are characteristic of hydromorphic plants.
    e. are derived from procambium.

Concept Applications

12. Compile and discuss the xeromorphic adaptations found in the *epidermis* of the oleander (*Nerium oleander*) leaf.

13. Few gymnosperms occupy desert or arid ecological niches. However, most gymnosperms have leaves with multiple xeromorphic anatomical adaptations. Why is this so?

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Secretory Structures

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Introduction

A secretory structure is essentially any structure, simple or complex, that produces a secretion within, on, or from a plant. We witness secretion in plants daily from watching butterflies or other animals search for nectar rewards in flowers and experience the scent of the plant or as we encounter the sting of nettle plants during a walk in the woods. Secretory systems may be classified by their location in the plant, but they may also be named according to the product or products that are exuded including ones termed nectaries, hydathodes, glandular hairs/trichomes, salt glands, colleters, crystal-containing idioblasts, tannin cells, internal oil glands and cells, resin ducts, as well as protein and gum-secreting systems. Secretory products may be released externally onto the surface of an organ (as in the case of nectaries, hydathodes, and salt glands), internally from a cell into canals (as in resin ducts), or into subcuticular cavities (as in **glandular trichomes**).

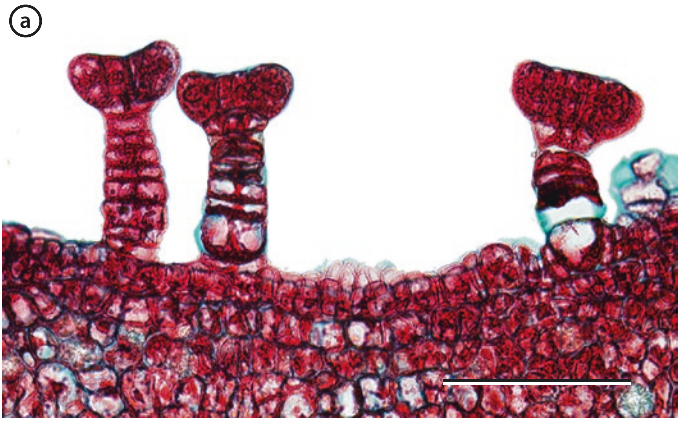
While secretory activities are found in virtually all plant cells at some time during their life, there are isolated individual cells (idioblasts) and cell complexes (glands) whose primary function is to perform secretion on a regular basis. Single-cell secretory structures are called granular cells, in contrast to multicellular structures that are referred to as glands. Secretory structures are important to plants because they reward pollinators by providing nectar, attract prey, excrete dissolved substances, or help in defense of herbivory. They may also accumulate in a vacuole of a cell in the form of crystals (as in crystal-containing idioblasts) or amorphous inclusions (as in tannin and oil cells). Plant secretory products have played important and interesting roles in human history (Stewart 2009).

13.1 External Secretion Involves Moving Substances to the Surface of the Plant

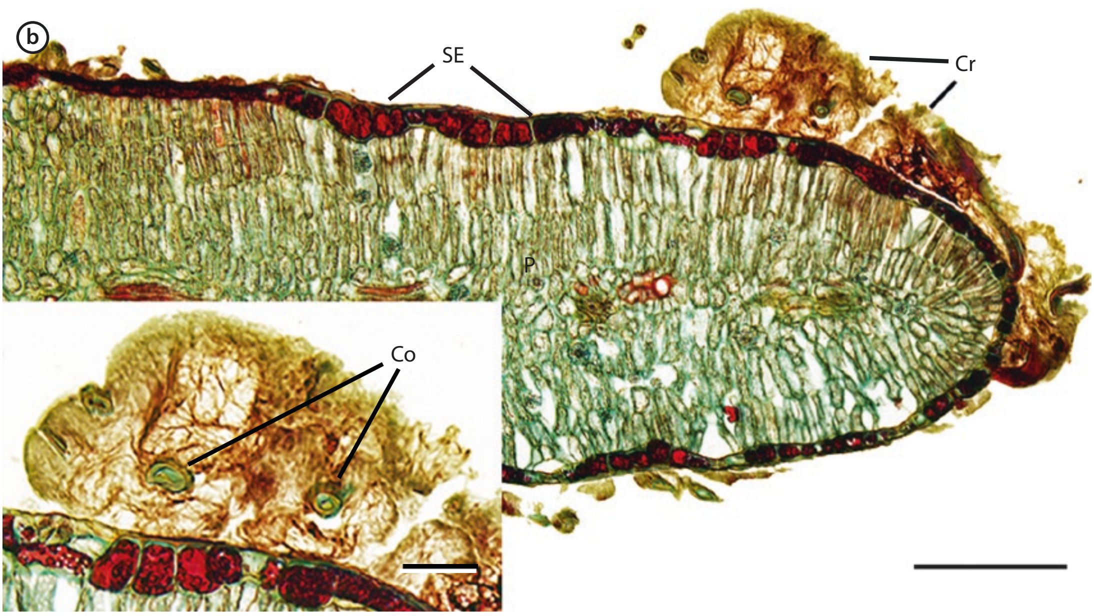
External secretory systems include those systems that are located on, within, or just below the epidermal layer. These systems include glandular trichomes that include, but are not limited to, colleters and stinging trichomes. Other secretory structures include nectaries, hydathodes, and salt glands.

13.1.1 Glandular Trichomes

Glandular trichomes (glandular hairs) of various morphologies are formed on the surface of the aboveground parts of plants, such as stems, leaves, bud scales, and reproductive organs (◘ Fig. 13.1a). These structures are of epidermal origin and secrete substances external to the plant. Given the epidermal location of many glandular trichomes, detailed information on the anatomy of basic trichome structures can be found in ► Chap. 9. However, glandular trichomes are also associated with more specialized structures such as colleters and stinging trichomes, as well as specific types of secretions including essential oils.



◘ **Fig. 13.1** **a** Three stalked, glandular trichomes on the surface (pericarp) of a black walnut (*Juglans nigra*) fruit. Scale bar = 50 µm. (RR Wise)



◘ **Fig. 13.1** **b** Colleters are glandular trichomes producing a sticky hydrophobic secretion known as creosote. Shown here are colleters on the leaf of the creosote bush (*Larrea tridentata*). The leaves have an outer layer of secretory epidermis (SE, stained dark brown or red) covering a parenchymatous mesophyll (P, lightly stained due to vacuolation). Two colleters (Co) are seen in cross-section in the insert. Secreted creosote (Cr) is external to the leaf and appears light brown to reddish due in part to an accumulation of carotenoids. Scale bars = 100 µm for main image and 50 µm for insert. (RR Wise)

13.1.2 Colleters

Colleters are multicellular glandular trichomes of a leaf or bud scale that generate a resinous, hydrophobic secretion (Esau 1953). Colleters often produce **terpenes**, which are lipophilic substances that provide defense against insects and fungi. While colleters in some plants are quite large with several layers of cells, on leaves of the creosote bush, they appear as thin trichomes embedded in a large accumulation of secretion (◘ Fig. 13.1b). The creosote bush inhabits the deserts of western North America. Their leaf secretions reduce transpiration and help the plants survive the very arid conditions. The stomata typically only open during the morning when humidity is high, but close down by midday to prevent water loss. Thus, photosynthesis only occurs in the morning.

Box 13.1 Diversity of Colleter Anatomy and Function in the Rubiaceae

Colleters are plant secretory structures that produce a sticky exudate. The secretions primarily serve to protect leaves from desiccation or a meristem from desiccation, insect attack, or pathogen attack. But not all colleters are the same. Judkevich et al. (2017) recently conducted a thorough study of colleters on both vegetative and reproductive organs in the Spermacoceae, a tribe within the Rubiaceae family known to have a diversity of colleter types. The "standard" colleter type is defined as a multicellular trichome with a central axis made of parenchyma tissue with a secretory palisade layer. The standard type of colleter was found on the stipules, calyx, and bracteoles and on buds found on the underground rhizomes of a few species. Other nonstandard colleters were green, due to the presence of an active chlorenchyma. The fate of the photosynthate produced by that tissue is unknown. It may contribute to the production of the secretion or to the overall photosynthesis of the plant. The colleters of two species had a vascular connection to the vasculature of the stipule or calyx to which they were attached. This study revealed the diversity of colleter types within a single plant taxon and indicates that colleters may serve multiple functions within the angiosperms.

Reference: Judkevich et al. (2017).

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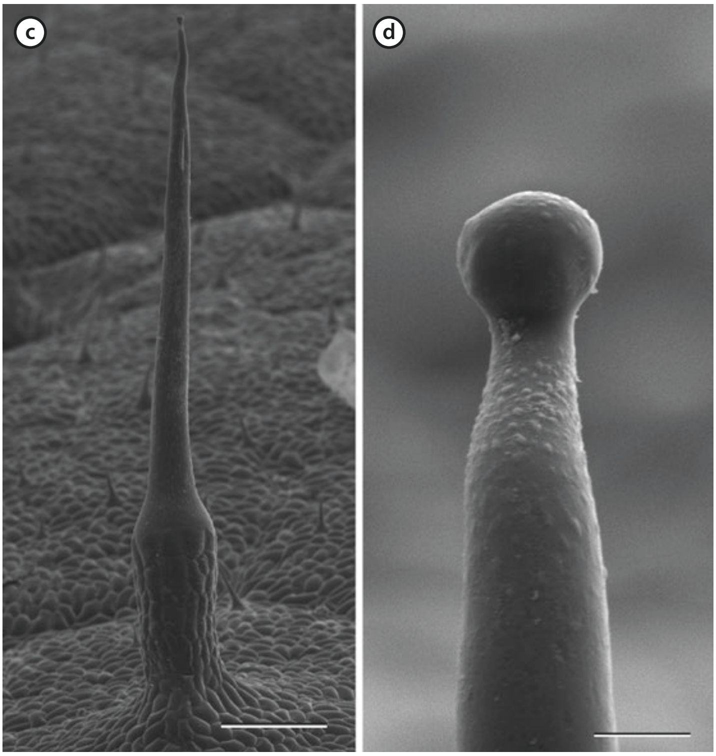
13.1.3 Stinging Hairs

Stinging hairs, which produce toxic substances stored in the cell vacuole, are a special type of glandular trichome. Plants associated with stinging hairs are often found in the Urticaceae and Euphorbiaceae, but also can be found in other families. These structures are used to defend plants from herbivores. In the case of the stinging nettles, *Dendrocnide* and *Urtica*, the stinging hair consists of an elongated tapering, needlelike stinging cell structure up to 1.5 mm long, whose basal part is covered by smaller supporting cells which in combination form a pedestal (◘ Fig. 13.1c). The stinging cell terminates by a small head and neck (◘ Fig. 13.1d) whose thin wall is very fragile due to its impregnation by silica (◘ Fig. 13.1e, f). The wall can be easily broken during contact with skin and may then release a complex mixture of stinging and irritating chemicals into the skin in a manner somewhat similar to a hypodermic needle, thus being an effective retardant to animals that otherwise may have foraged on the plant.

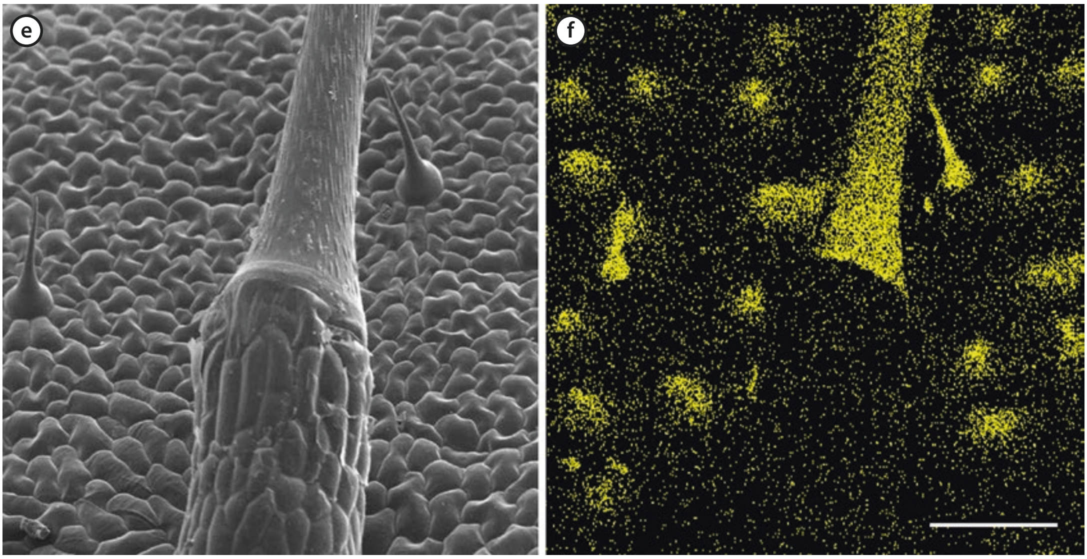


◘ **Fig. 13.1** **c**, **d** Views of a stinging hair of the stinging brush (*Dendrocnide moroides*) as visualized with scanning electron microscopy. Scale bars = 250 µm in **c** and 10 µm in **d**. (**c**, **d** RR Wise)

The scanning electron microscope generates highly detailed electron micrographs by capturing and imaging the electrons emanating from a specimen's surface upon bombardment with source electrons (◘ Fig. 13.1e). In addition, X-ray photons are also emitted as a result of the electron bombardment, and the energies of those X-rays are specific for the element from which they were emitted. In short, an X-ray microanalyzer attached to a scanning electron microscope allows one to "take pictures" of specific elemental sites. Typically, this technique is called "X-ray elemental microanalysis" (XRMA). The walls of the stinging nettle hair as well as other smaller trichomes are clearly visible as containing silicon in ◘ Fig. 13.1f.

13.1.4 Nectaries

Nectaries secrete a sugar solution called nectar. The sugars may be complex but most often are comprised of a mixture of sucrose, glucose, and fructose. Nectaries are most often associated with flowers (**floral nectaries**), but may also develop on leaves and stems (**extrafloral nectaries**). Floral nectaries may be located in many floral parts such as stamens (intrastaminal nectaries) or at the base or on top of the ovary (septal nectaries; refer to ◘ Fig. 18.2g, h). While conspicuous flowers attract floral visitors, nectar typically



■ **Fig. 13.1** **e**, **f** Base of a common nettle (*Urtica dioica*) stinging hair as visualized with **c** scanning electron microscopy SEM and **d** an X-ray elemental map **d**. The location of silicon is indicated as yellow pixels in **d**. Scale bar = 100 µm for both panels. (**e**, **f** RR Wise)

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acts as a reward to pollinators. Extrafloral nectar may also attract animals, such as ants, that defend the plant from other herbivorous insects. Nectaries vary greatly in morphology and anatomy, which is not surprising given the diversity of structures where they may be located.

There are a variety of structural patterns for nectaries (■ Fig. 13.1g), but they are mostly represented by small protuberances where nectar collects in a reservoir (■ Fig. 13.1h). The nectary comprises a single-layered epidermis and three or four layers of small subepidermal cells (■ Fig. 13.1i). Beneath these are found several layers of larger parenchyma cells. Epidermal cells have a thin, permeable, reticulate cuticle with associated swellings that coincide with the middle lamella between adjoining epidermal cells.

Nectar is thought to pass both along the apoplast and symplast and then eventually through the stretched and distended or broken cuticle. The secretory cells are collenchymatous and nucleated and have numerous pits with plasmodesmata, mitochondria, rough endoplasmic reticulum, and plastids with many plastoglobuli but few lamellae. Sub-secretory cells contain fewer plastids than secretory cells. Vasculature supplies the gland with water and carbohydrates for sugar synthesis. The process of nectar secretion may cause the separation of the cuticle from the outer periclinal walls of the palisade-like cells forming the secretory epidermis. In fact, it may be necessary for the cuticle to rupture before insects can access the nectar.

Nectaries outside of floral structure are referred to as extrafloral nectaries and may be located on leaf blades or petioles of the leaf (■ Fig. 13.1j, k). They typically produce sugar complexes along with smaller amounts of amino acids and organic acids. Cells of the nectaries have extensive plasmodesmata that may aid in the transport of sugars to the nectary surface, just below the cuticle, which

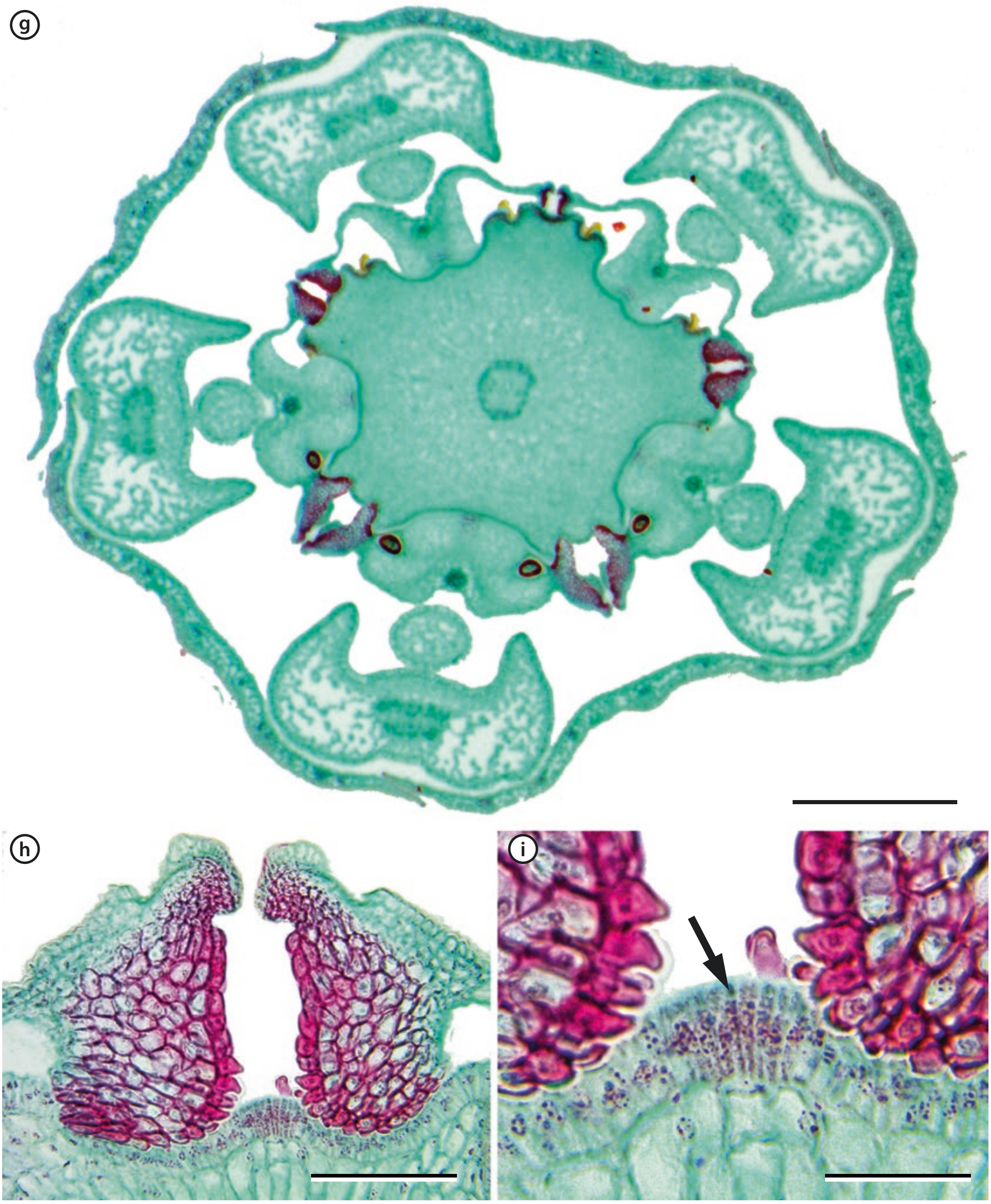
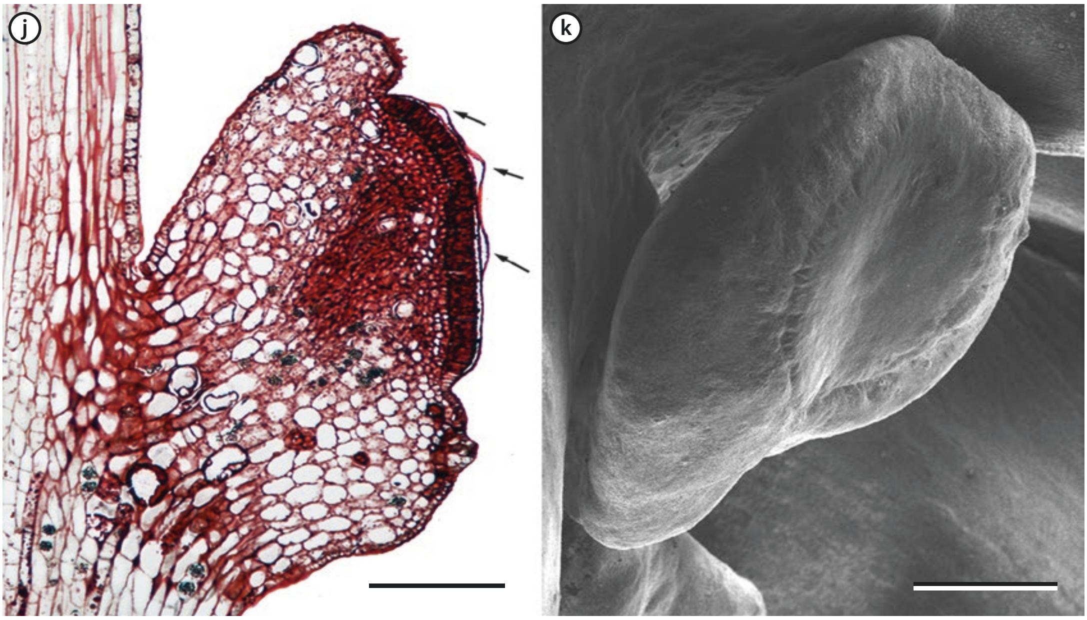


Fig. 13.1 Floral nectaries of milkweed (*Asclepias* sp.). **g** Cross-section of a milkweed flower showing an arrangement of five floral parts and five nectaries. Lignified cells at the margins of the nectary stain red. The lignified hoods covering the nectariferous tissue require some effort on the part of pollinators (bees, wasps, and butterflies) to access the nectar. This insures the pollinator will occupy to flower long enough to pick up a pollen sac for transfer to the next flower. **h** Higher magnification of a single nectary. **i** Detail of the nectariferous tissue, indicated by the arrow. Scale bars = 1 μm in **g**, 25 μm in **h**, and 10 μm in **i**. (**g**–**i** RR Wise)

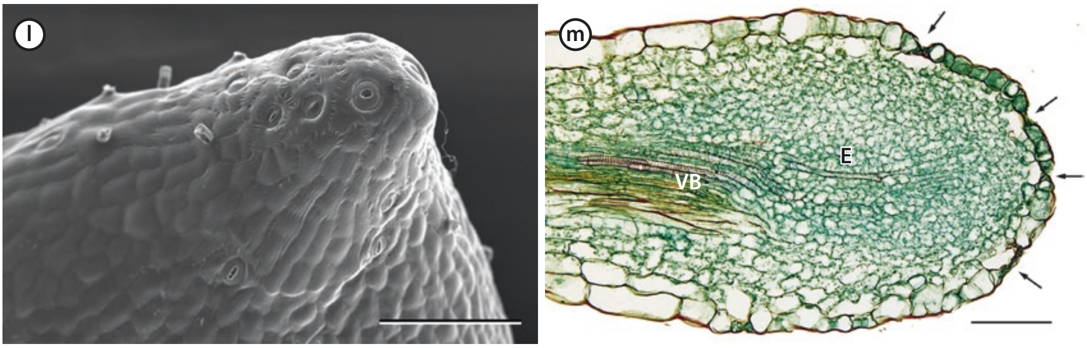


■ **Fig. 13.1** **j**, **k** Light micrograph **d** and scanning electron micrograph **e** of extrafloral nectaries from the leaf petiole of castor bean (*Ricinus communis*). Note the separation of the cuticle from the gland surface in **d** (*arrows*). Scale bars = 250 µm in **j** and 500 µm in **k**. (**j**, **k** RR Wise)

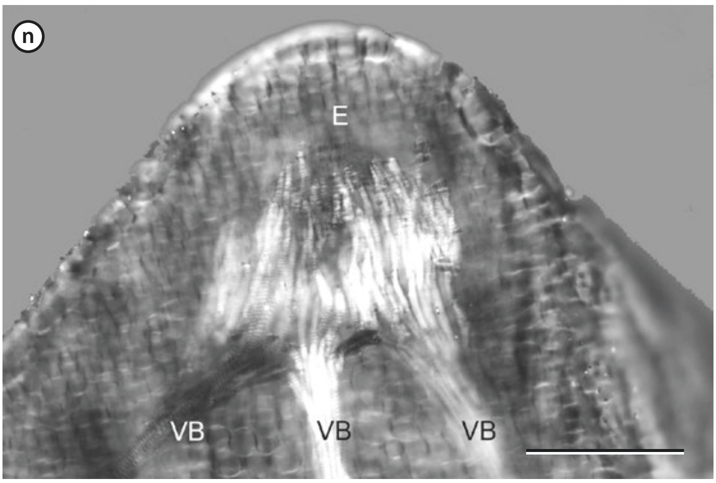
will eventually rupture and release the sugars. Extrafloral nectaries primarily attract ants, which in turn provide significant protection for the plant by attacking and warding off herbivores. About 100 plant genera have evolved this complicated mutualistic relationship; they are aptly named "myrmecophytes" ("ant plants") (Del Val and Dirzo 2004).

13.1.5 Hydathodes

Hydathodes are external secretory structures that exude water with dissolved substances such as amino acids and/or low concentrations of salts. The water excreted by hydathodes appears as droplets on the surface of the organ, in a process called guttation. The process is usually noticed in early morning when there is high humidity. Two types of hydathodes are recognized: (1) *active*, the form of glandular trichomes in which water is actively exuded by secretory cells that are not connected to water-conducting tracheary elements, and (2) *passive*, usually located at leaf margins or tips of leaves (■ Fig. 13.1l, m). In passive hydathodes, water is supplied by vascular bundles (■ Fig. 13.1n) and then passes through intercellular spaces of a tissue called the **epithem** composed of mesophyll cells that represent modified vascular bundle ends. Eventually, water is exuded onto the leaf surface through modified stomata, which are permanently open.



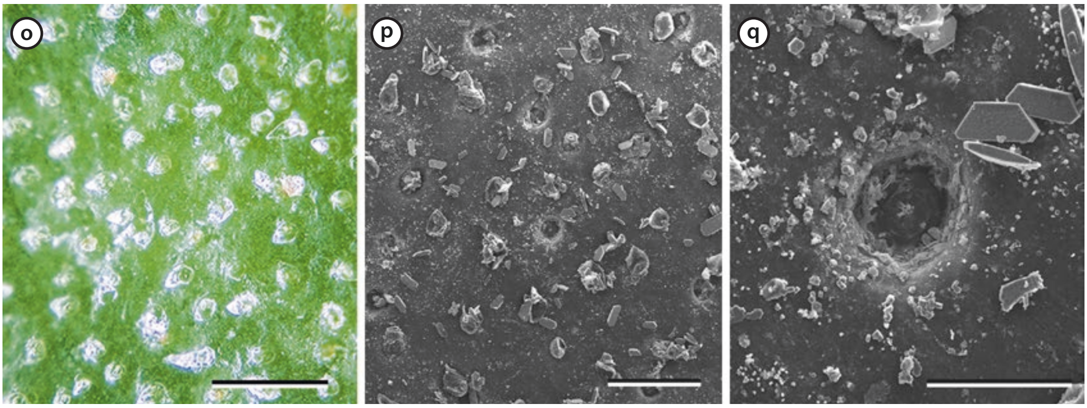
◘ **Fig. 13.1** **l** SEM of a chrysanthemum (*Chrysanthemum* sp.) passive hydathode at a leaf tip showing multiple stomata that are open. **m** Terminal leaf margin of cabbage (*Brassica oleracea*) revealing a passive type of hydathode with a large epithem (E), which fills almost the entire mesophyll and permanent stomatal openings (*arrows*). Water is supplied by the vascular bundles (VB). Scale bars = 200 µm in **l** and 250 µm in **m**. (**l**, **m** RR Wise)



◘ **Fig. 13.1** **n** A single hydathode in the leaf of the lyre-leaved sand cress (*Arabidopsis lyrata*). The image was taken with differential interference contrast (DIC) illumination, which highlights the lignified cell walls of the tracheary elements in the vascular bundles (VB). The epithem (E) is between the vascular bundles and the hydathode tip. Scale bar = 200 µm. (RR Wise)

13.1.6 Salt Glands

Halophytes are plants that grow in salt water or on saline soils. However, salts (sodium chloride being the main, but not only form) are toxic to most plant physiological processes. Halophytes therefore have evolved two different salt management strategies. The first is to retard salt uptake at the root cells to prevent it from entering the water of the transpiration stream. Red mangrove (*Rhizophora mangle*) is a salt excluder, and its roots are effective barriers to salt uptake. Black mangrove (*Avicennia germinans*) uses a second strategy, salt excretion. These plants take up salts, but then excrete the



■ **Fig. 13.1** **o** Salt crystals on surface of a black mangrove (*Avicennia germinans*) leaf. **p** Surface detail showing numerous salt glands and crystals on leaf. **q** A single salt gland showing dried crystals of salt. Scale bars = 400 µm in **o**, 200 µm in **p**, and 50 µm in **q**. (**o**–**q** RR Wise)

salt at the terminus of the transpiration stream (i.e., the leaf), using specialized external secretory structures called **salt glands** on the leaf surface (■ Fig. 13.1o–q).

13.2 Carnivorous Plants Have Evolved External Secretory Structures as a Mechanism for Nutrient Acquisition

Plants species evolve structures that have many different secretory functions. In this section, the focus will introduce some of the ecological anatomy of external secretory structures of carnivorous plants.

Certain plants are capable of growing in nutrient-depleted environments despite also having photosynthetic activity. Among these is a group that derives their essential elements from animal sources and may thereby be called "carnivorous plants" (although Darwin 1875 officially used the term "insectivorous plants"). Almost 600 species and subspecies of carnivorous plants have been identified (Barthlott et al. 2007). Many carnivorous plants have reduced root systems relative to their noncarnivorous plants and are adapted to trapping and digesting insects, arachnids, slugs, worms, caterpillars, and, upon occasion, small animals, such as frogs or mice.

Bog plants, such as those shown in ■ Fig. 13.2a, b, grow in waters with an acidic *p*H, often from 4.0 to 6.0. Under such conditions, elements such as nitrogen, phosphorus, and calcium precipitate out and are not available for uptake. Nitrogen in particular may often be scarce in the environment, but for green plants it is an essential nutrient for proteins and nucleic acids. Thus, without specialized adaptations, plants cannot survive because the building blocks for compounds needed for growth are missing.

Fig. 13.2 **a**, **b** Typical scenes from a bog in northern Wisconsin in which various types of carnivorous plants may be found among the grasses and sphagnum moss. Pitcher plants (*Sarracenia purpurea*) are seen in **a** and sundew (*Drosera intermedia*) in **b**. Scale bar = 5 cm for both panels. (**a**, **b** RR Wise)

Carnivorous plants, such as the Venus flytrap (*Dionaea muscipula*), have developed a unique means of survival in that ecological niche due to extracting key elements from various animal forms of life that can provide a good source of elements and energy-laden compounds which are missing from the soil and water solutes. For such carnivorous plants, this is accomplished by relatively simple means of physical and chemical activities by actively trapping prey with a modified, hinged leaf.

Let us consider the Venus flytrap that has modified leaves with secretory hairs which attract many animal species by exuding mucopolysaccharides and other sugars from glands at the base of rim-mounted hairs (often referred to as cilia). The modified leaves also have terminal lobes that are hinged along the midrib and can snap closed when trigger hairs (modified trichomes) are contacted (Fig. 13.2c). In most cases there are three or four such trigger hairs located on each lobe. When an object contacts two of the three hairs within about 20 s (or even contact with one such hair twice in that period of time), a small electrical signal is activated through the phloem that opens pores in the inside cells of the lobes that are filled with water, and, once opened, the water flows to the outside of the lobes causing the two lobes to collapse and close on the object that caused contact with the trigger hair.

The rims of the lobes have a large number of spikelike trichomes (or cilia), which, like bars in a cell, entrap the organism inside. However, there remains space between the bars large enough for very small organisms to make their way out thus relieving the flytrap plant from wasting a good deal of effort for too small of a reward. In addition to food from animal digestion, flytraps also carry out photosynthesis, in fact direct sunlight is favored, and those flytraps in

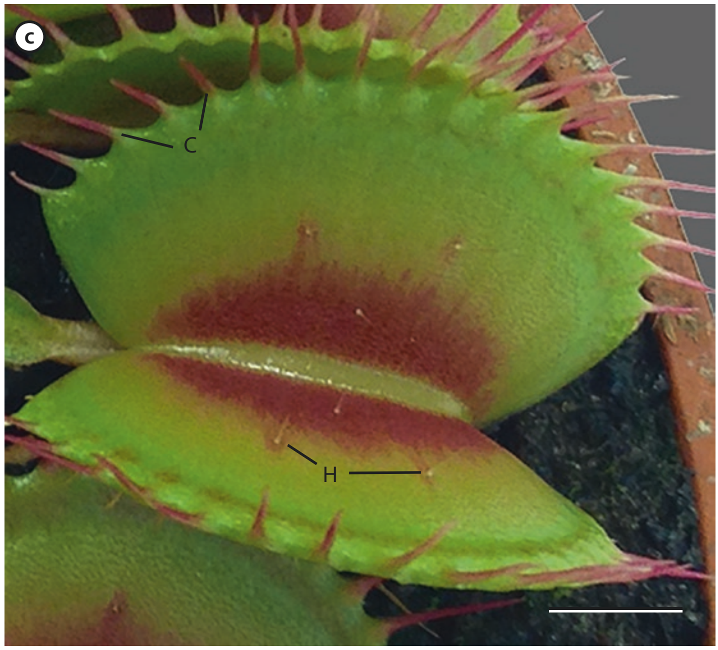


Fig. 13.2 **c** A Venus flytrap (*Dionaea muscipula*) showing the trigger hairs (H), which initiate the closure of the trap, and the marginal modified trichomes (or cilia, C). Scale bar = 1 cm. (RR Wise)

high light levels usually have traps with red anthocyanin pigments, whereas those in lower light levels are more green or yellow-green. The Venus flytrap is native to bogs and swamps of North Carolina, in the southeastern USA.

In review, physical contact creates a small ion flow (modified electrical current), which activates the release of water pressure in parenchymatous cells that cause the leaf lobes to collapse within about one-tenth of a second. Normally, the leaf trap stays closed for 1–5 days before reopening.

This sets the stage for the next event, the release of secreted proteolytic enzymes from glandular trichomes within the trap that envelop the prey and digest it (Fig. 13.2d, e). These also include strong acids like phosphoric, nitric, or hydrochloric acids that kill and degrade the body of the prey. The digestive glands will absorb the released nutrients, which are carried in the phloem, and to some extent through the apoplastic components of the plant cellular structures.

Some carnivorous plants, termed "pitcher plants" (Fig. 13.2a), employ a more passive means of entrapment by virtue of its funnel-like modified leaf that contains trichomes that exude secretory attractants, as well as ones that are angled in a downward direction. When the "pitcher" is dry, insects such as ants may largely keep their grip in moving about the interior of the funnel (actually the adaxial leaf surface). However, when the pitcher is wet due to rain or heavy dew, the trichomes as well as wax crystals over the inner funnel surface become very slick, and the invasive organisms lose hold and slide to the bottom of the funnel where secreted digestive

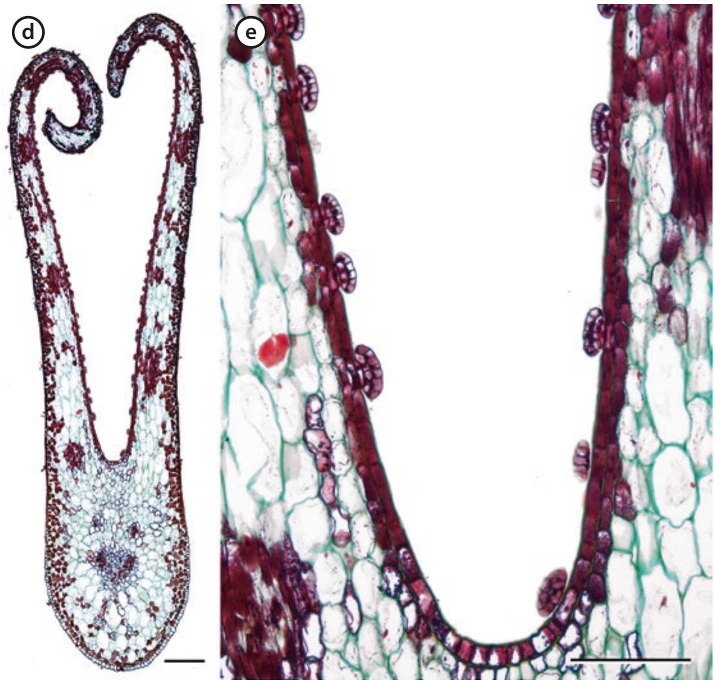


Fig. 13.2 **d**, **e** A closed Venus flytrap (*Dionaea muscipula*) in cross-section. Entire leaf showing that the entire adaxis (inner surface) is lined by numerous peltate digestive glands. **e** Higher magnification view of the trap and glands. Upon closure of the trap, the glands begin secreting digestive fluid, which fills the enclosed space around the prey. The same glands are involved in the absorption of digestive products from the trap interior. Digestive glands consist of a layer of secretory cells, two layers of filling cells, and a basal cell. The dark-stained cells in the mesophyll of the trap wall are tannin-containing cells. Scale bars = 250 µm in **d** and 50 µm in **e**. (**d**, **e** RR Wise)

fluids have accumulated. Escape is unlikely due to the downward pointed trichomes, the wax crystals, and their slippery surface.

Even larger organisms, such as mice, have been found to lose their grip and to fall prey to the digestive system of the pitcher plant. After 2–3 weeks the entire mouse will become digested, including the bones. There are over 100 species of pitcher plants including hybrids and cultivars, but the common names do not imply any evolutionary relationships among the organisms.

While the pitcher plant represents a unique type of carnivorous plant, recent studies have shown an even more amazing adaptation in its coevolution with bats. In the forests of Borneo, a tropical pitcher plant, *Nepenthes hemsleyana*, feeds on bat guano and thus does not need to carry out its own digestive processes. This is accomplished by a mutualistic relationship with bats in which the pitcher plant has a structure called a "reflector" that echoes acoustic signals from the bats to reveal the plant's location. The bats are attracted to the pitcher plant and are rewarded with a stable, spacious, and parasite-free roosting site. The bats in turn reward the pitcher plant with their feces that is digested by the plant secretions within the pitcher (Grafe et al. 2011). While not technically

Fig. 13.2 **f** A general view of the spoonleaf sundew plant (*Drosera intermedia*), one of the multiple species that grow in wet, acidic environments including bog-like regions with poor nutrient soils. This specimen was photographed in east central Florida. Scale bar = 1 cm. (RR Wise)

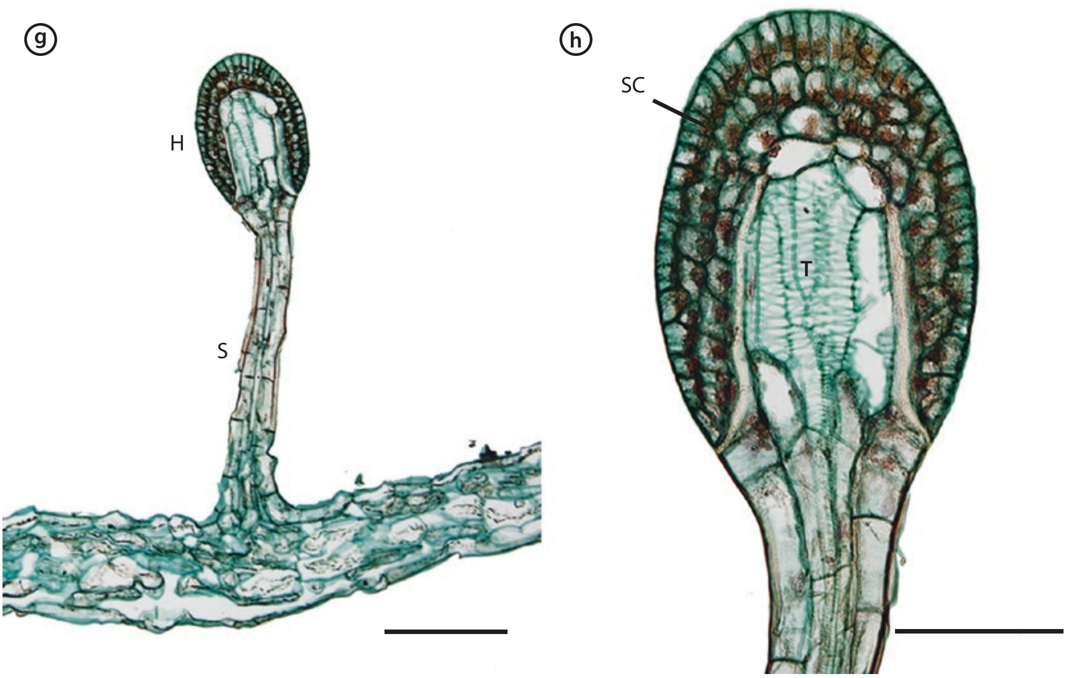
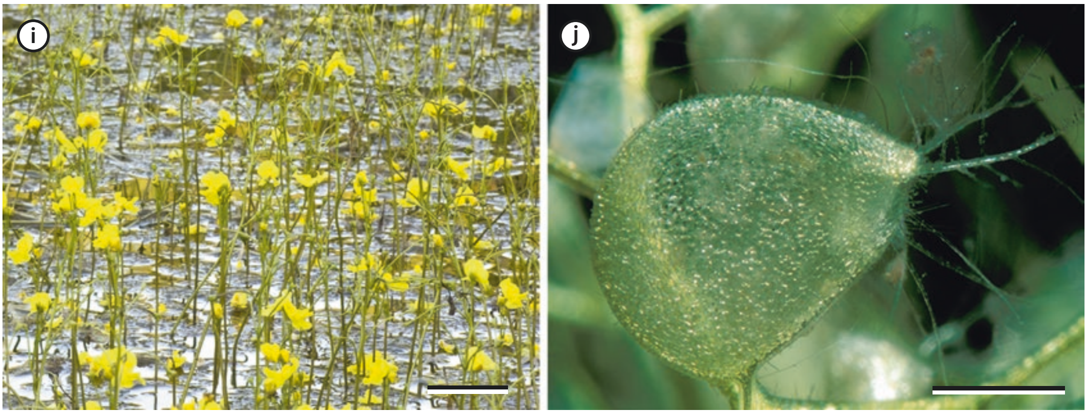


Fig. 13.2 **g** Tentacles (or gland) in sundew (*Drosera* sp.) consist of a stalk (S) of various lengths and a head (H). **h** An outer layer of secretory cells (SC) surrounds a group of tracheids (T). Scale bars = 100 μm in **g** and 50 μm in **h**. (**g**, **h** RR Wise)

carnivory, this relationship uses many of the same features as found in the insect-trapping pitcher plants.

Other carnivorous plants include the sundew plant (Fig. 13.2b and f), which also exhibits passive entrapment by virtue of producing a modified leaf with many secretory trichomes (Fig. 13.2g, h) that



◘ **Fig. 13.2** **i** Flowering and above-water view of the swollen bladderwort (*Utricularia inflata*) carnivorous plant from North Carolina, USA. Flowers are approximately 8–10 cm. **j** Beneath the water, bladderlike pouches trap the prey. Scale bars = 5 cm in **i** and 1 mm in **j**. (**i** ,**j** B Rice, ► sarracenia.com)

generate both attractants and digestive fluids at the surface. Small organisms, usually insects or spiders, are attracted and are trapped by sticky secretions produced by the trichomes, which may infold somewhat and digest the prey in situ.

Not all carnivorous plants are found in bogs. In fact, the great bladderwort (*Utricularia macrorhiza*) plant (◘ Fig. 13.2i, j), a carnivorous species, has been found in the freshwaters of Lake Michigan along the Chicago shoreline by small sandy dunes, which are nutrient depleted. It appears as floating stems with bright yellow flowers above the waterline, but most of the plant is underneath the water where bladderlike pouches are filled with water. On the pouches are protruding hairs that serve as trigger-like mechanisms for catching prey. If aquatic invertebrates hit the hairs, water shoots out of the bladders and creates a vacuum-like effect internally. When the water rushes back into the pouches, it carries the prey (usually water fleas, zooplankton, and other small aquatic insects) along, where they remain until digested.

Box 13.2 Evolutionary Connections Between Plant Carnivory and Defense

Carnivorous plants lack a highly developed root system due to the harsh acidic conditions in which they live, such as in acidic bogs. These plants are known for trapping insects with modified leaves to supplement their nutritive needs. Insects are trapped and subsequently broken down via secretion of digestive enzymes. The plant digestive response occurs within 2 h following detection of insect movements within the trap. By utilizing the mRNA that was expressed within cells, researchers discovered that the movements of the insect within the Venus flytrap lead to the production and secretion of enzymes including chitinases, proteinases, and hydrolases that digest the hard chitin exoskeleton. This induction of hydrolase activity is similar to the plant defensive response to herbivory. Venus flytraps also respond to triggering by an insect, in a similar fashion that noncarnivorous plants respond to stress by producing jasmonic acid. The use of the molecular genetics of mRNA and the analysis of protein expression indicated that genes controlling carnivorous plants such as the Venus flytrap are related to the defense genes of noncarnivorous plants. Reference: Bemm et al. (2016).

13.3 Internal Secretory Structures Include Oil Cavities, Resin Ducts, and Laticifers

In contrast to external structures, internal secretory structures include secretory cavities and canals (ducts), laticifers, and idioblasts. These structures are found in tissues such as xylem, phloem, cortical, and pith parenchyma where they remain within the cytoplasm and may contain oils, latex, crystals, and resin.

13.3.1 Oil Cavities

Oil cavities within leaves, such as in members of the Myrtaceae (i.e., *Eucalyptus* sp.) and Rutaceae, are large, spherical, isolated intercellular spaces that are the sites of internal secretion and storage. They may be found throughout the plant and, in leaves, may be part of the epidermis (◘ Fig. 13.3a) or the mesophyll (◘ Fig. 13.3b). The cavities, which are filled with oils or other secretions, are lined by epithelial cells, the sites of oil synthesis. These secretions are also termed volatile or ethereal oils and are aromatic, oily substances and upon extraction are termed "essential oils" (refer to ► Sect. 13.5). The oils can be present in nearly any portion of a plant depending upon the species. Many oils are produced by plants to serve as important antiherbivory chemicals.

13.3.2 Resin Ducts

In contrast to the isolated nature of secretory cavities, **resin ducts** (or canals) are extended structures that may run the entire length of a leaf or stem. They are filled with secretion and lined by a layer of epithelial (secretory) cells. Such ducts may be found in the cortex, in primary and secondary phloem, in pith, or in the secondary xylem of stems and roots; they may also develop in leaves (◘ Fig. 13.3c) and flower parts. Resin ducts are similar to other plant secretory structures such as colleters and oil glands that produce

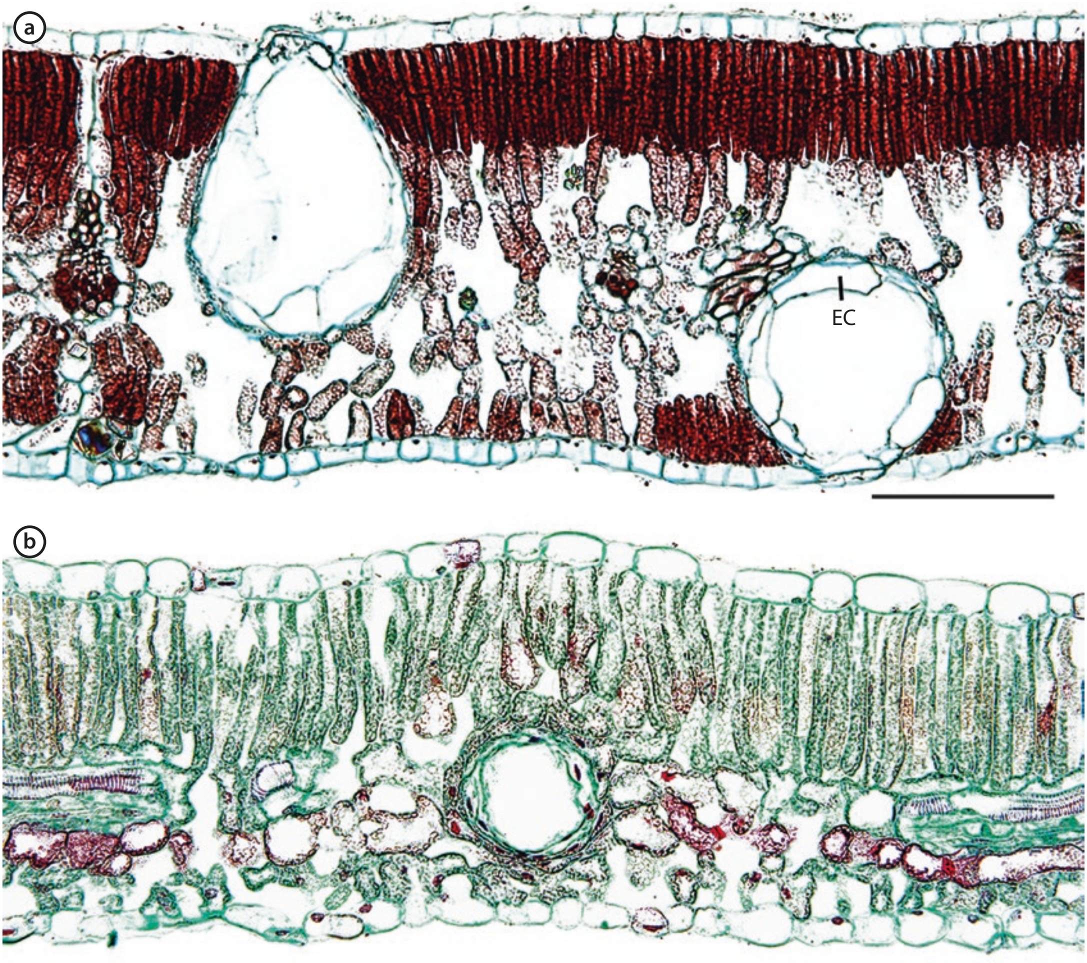


Fig. 13.3 **a** Epidermal oil cavities in a eucalyptus (*Eucalyptus* sp.) leaf. **b** A mesophyll oil gland in a cotton (*Gossypium hirsutum*) leaf. Note the epithelial cells (EC) lining the cavities that would contain oil within a living leaf and the red-stained nuclei in the cotton epithelial cells. The oil was extracted during specimen preparation; thus, the cavities appear empty. Scale bars = 100 µm in both panels. (**a**, **b** RR Wise)

mainly terpenes, i.e., lipophilic substances that provide defense against insects and fungi. Resins are released from cells into canals. They are common in gymnosperm leaves (Fig. 13.3d) and stems (Fig. 13.3e) and in response to injury (Fig. 13.3f). These are the resins that were extracted and used in the production of pine tar (refer to Fig. 15.2).

Essential oils are involved in both external and internal secretion in plants. Some plants, such as many in the mint family (Lamiaceae), often exude essential oils externally from glandular trichomes, but in some cases, the oils are stored in a subcuticular space prior to secretion.

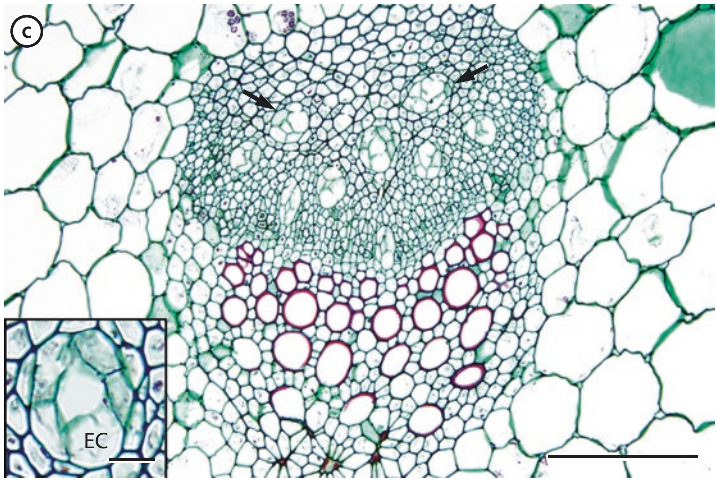


Fig. 13.3 **c** Cross-sectional view of a vascular bundle from celery (*Apium graveolens*) petiole, depicting nine small resin ducts (two are indicated with *arrows*) in the phloem. The resin ducts are rosettes of epithelial cells surrounding the **resin canals** (inset). The elongation of the petiole has ceased, and the secretion completed. When viewed with electron microscopy, the epithelial cells appear to be in a highly vacuolated, inactive state. Scale bar = 100 µm in main panel, 10 µm in inset. (RR Wise)

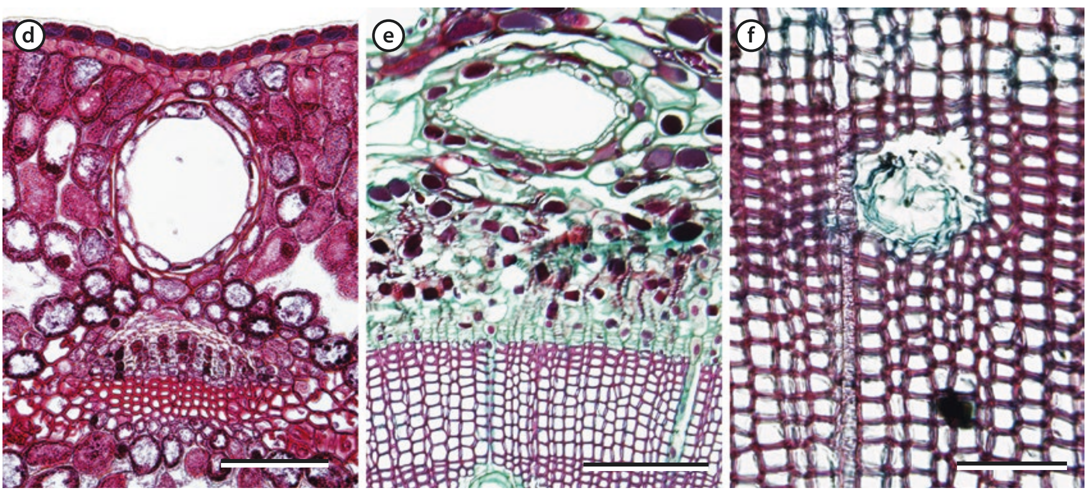


Fig. 13.3 **d**–**f** Resin ducts in **d** red cedar (*Juniperus virginiana*) leaf, **e** red pine (*Pinus resinosa*) stem, and **f** damaged lodgepole pine (*Pinus contorta*) stem. Scale bars = 50 µm in **d**, 100 µm in **e**, and 50 µm in **f**. (**d**–**f** RR Wise)

13.3.3 Laticifers

Laticifers are a special type of internal secretory system. Like resin ducts, they can be quite long, but they are differentiated from ducts in that they produce milky substances, primarily **latex**. Laticifers are either chains of fused cells whose cross-walls are digested in the center or single cells with nearly unlimited growth. The first are termed **articulated laticifers** (a.k.a. **laticiferous vessels**) (Fig. 13.3g); the second are **non-articulated laticifers** (a.k.a. **laticiferous cells**)

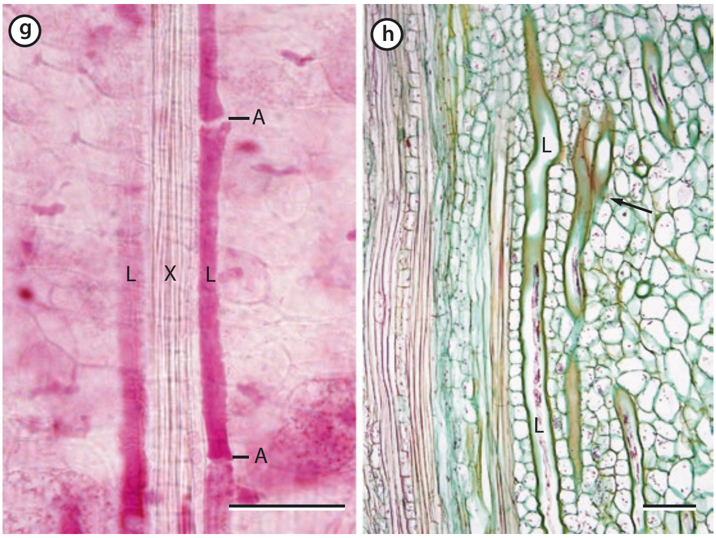


Fig. 13.3 **g** Articulated (A), anastomosing (connected cells) laticifers (L) lying on either side of a xylem strand (X) in a banana leaf (*Musa* sp.). The laticifers are stained red. The term "anastomosing" implies that the adjacent laticifers fuse with each other to form one long secretory structure. **h** A longitudinal section of *Euphorbia* sp. stem laticifers (L) with one showing a branch visible as a "fork" (*arrow*). Non-articulated anastomosing laticifers characterize all of the Euphorbiaceae. Scale bars = 50 µm in **g** and 100 µm in **h**. (**g**, **h** RR Wise)

(Fig. 13.3h). Non-articulated laticifers grow **intrusively** (pushing aside neighboring cells). They undergo mitoses that are not accompanied by cytokinesis. As a result, a multinuclear (coenocytic) cell is formed. Both articulated and non-articulated laticifers may be branched (i.e., anastomosed). Latex is a typically a milky fluid, but it can also be clear, brown, or orange. Latex is composed of both organic (alkaloids, terpenoids such as those in rubber particles, tannins, etc.) and inorganic substances (crystals) in an aqueous phase. The latex is a powerful defense against herbivores. Plants that contain latex are found within the Euphorbiaceae and the Apocynaceae that includes the dogbanes, milkweeds, and other plant families.

Some insects utilize plant defenses for their own benefit. Monarch butterflies (*Danaus plexippus*) are migratory insects within North America. Monarch caterpillars consume milkweed leaves and thus ingest latex that contains cardiac glycosides that are toxic to many other insects. The insect sequesters the toxin within the body, which renders it as distasteful to many potential predators. Predators with previous experience with eating monarchs learn to avoid them by cueing in on the butterfly's distinctive aposematic coloration. Thus, the monarch uses the products of plant defense for its own defense.

Often there is a question about how to distinguish between euphorbia (Euphorbiaceae) and cacti (Cactaceae) that have evolved via convergent evolution. One general distinction between the plant families is the presence or absence of latex. A small cut or prick of the plant will show either a watery fluid (cactus) or a "milky white" latex (euphorbia). While both may have spines, cacti typically have multiple ones that are on raised circular disks called areolas, whereas euphorbs have paired spines but no areolas. Cacti are typically found in arid regions of the Americas; alternatively, euphorbs are found worldwide in multiple environments. Some euphorbs lack succulence and have broad leaves. This includes the poinsettia (*Euphorbia pulcherrima*), castor bean (*Ricinus communis*), and the economically important rubber tree (*Hevea brasiliensis*).

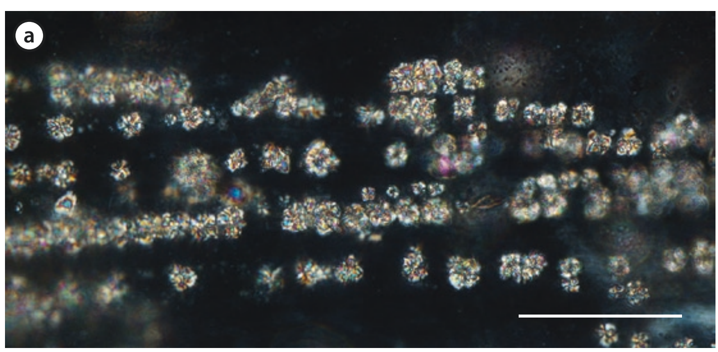
13.4 Idioblasts Are Internal Secretory Cells That Contain Crystals, Cystoliths, or Tannins

Crystals, cystoliths, and tannins are found in unique individual and isolated cells termed idioblasts. "Idio-" is Latin for distinct or separate, and idioblasts are so named because they are uniquely different in structure and function from the surrounding cells or tissues of plants. Idioblasts may be found in any plant organ and in any tissue.

13.4.1 Crystal Idioblasts

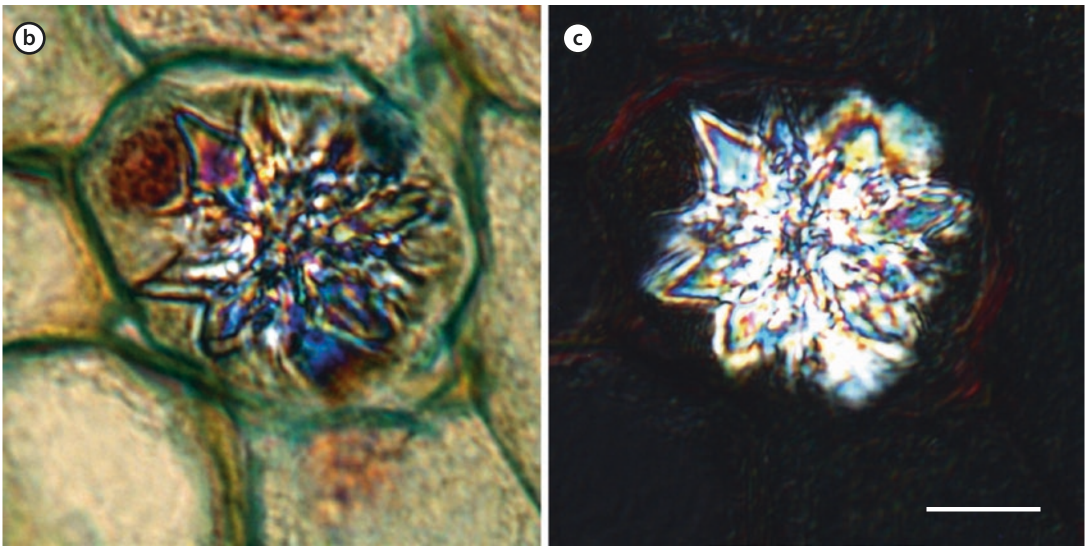
Crystals are common features of many plants and plant organs (◘ Fig. 13.4a). The vast majorities are composed of calcium oxalate, but calcium carbonate, magnesium carbonate, and calcium malate crystals can be found as well (Franceschi and Nakata 2005). When calcium carbonate is found, it is usually in association with cell wall material in a cystolith (refer to ► Sect. 13.4.2).

Although calcium oxalate (CaOx) crystals may appear to be in the cell wall or even the cuticle, their formation is always within the vacuole(s) of the cell. Calcium is an important regulator of many cellular enzymes and functions; therefore its concentration must be tightly controlled. Significant evidence exists to support the hypothesis that crystal formation is a method for the plant to sequester Ca^{+2} into a non-soluble, nonphysiological form and then remobilize it if needed (Franceschi and Nakata 2005). In addition, crystals have well-known antiherbivory effects. The leaves of dumb cane (see below) when eaten release sharp, pointed crystals that can

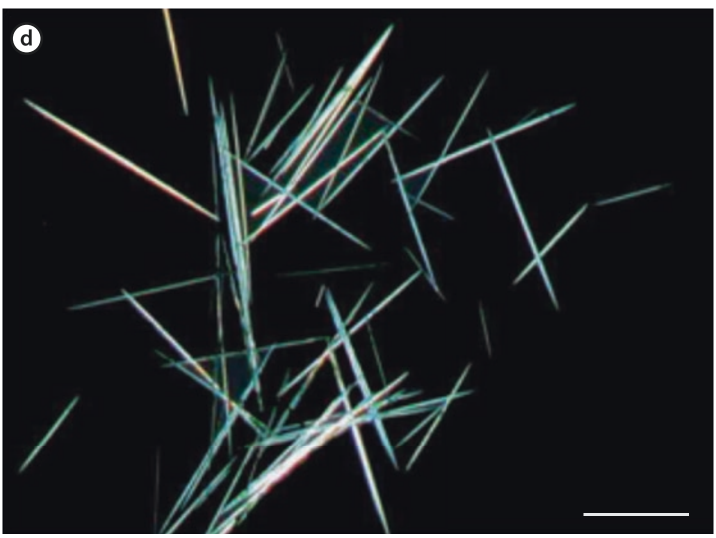


◘ **Fig. 13.4** **a** A paper birch (*Betula papyrifera*) leaf shown using polarized light. Druse crystals are aligned with the vasculature, forming rows of diamond-like jewels. Scale bar = 50 µm. (RR Wise) lead to a severe numbing of the mouth and throat and a temporary loss of speech.

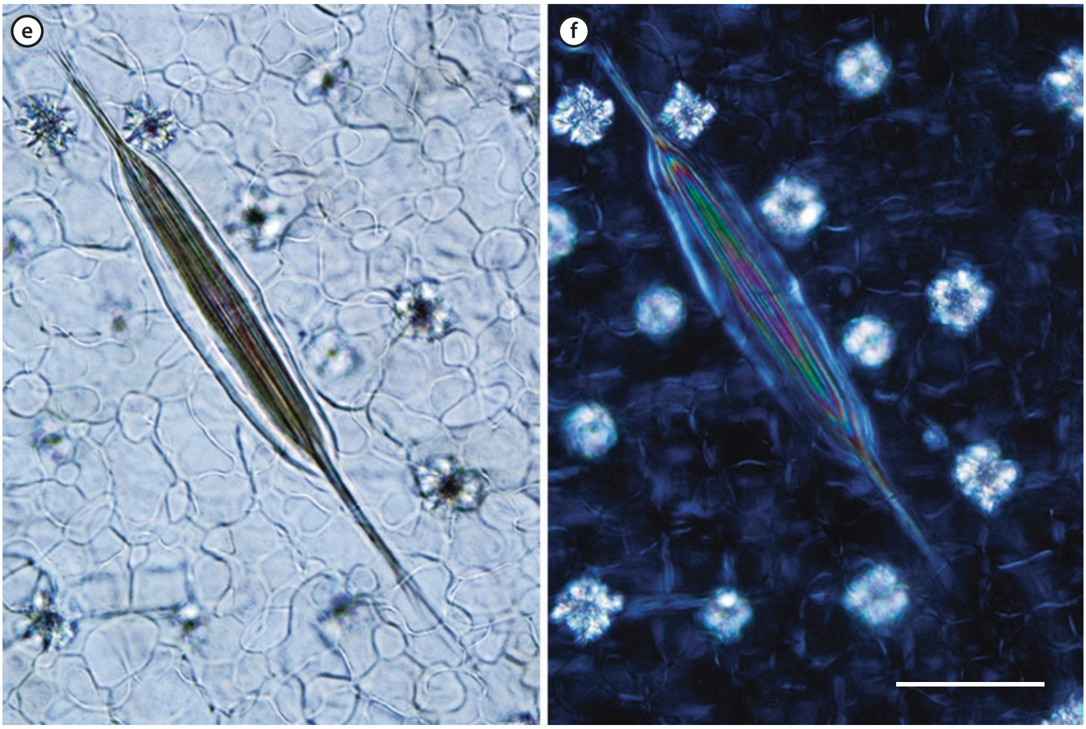
Calcium oxalate crystals can take a variety of forms, and form is used as the most common method of categorizing crystals (tissue location is the other). All crystals are formed in the cell vacuole. **Druse** crystals are isodiametric with many pointed facets (◘ Fig. 13.4b, c). **Raphide** and **styloid** crystals are both **acicular**, meaning needle-shaped (◘ Fig. 13.4d). They differ in that styloids are solitary, while raphides occur in bundles of up to several dozen individual crystals. Raphides are present in specialized cells called



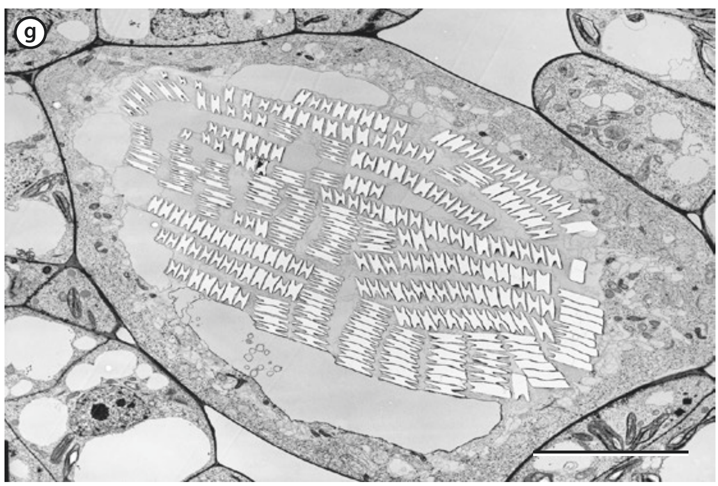
◘ **Fig. 13.4** **b**, **c** Druse crystal in the stem of ginkgo (*Ginkgo biloba*) viewed under brightfield **b** and polarized light **c** illumination. Scale bar = 10 µm for both panels. (**b**, **c** RR Wise)



◘ **Fig. 13.4** **d** Polarized light of isolated acicular crystals designated as raphides from dumb cane (*Dieffenbachia seguine*). Ingestion can cause a very sore throat and temporary speechlessness when swallowed. Scale bar = 25 µm. (RR Wise)



■ **Fig. 13.4** **e** Raphides in a biforine cell from a dumb cane (*Dieffenbachia* sp.) leaf. Styloid crystals are being extruded from both ends of the biforine. Note also the numerous druse crystals in the background. **e** Viewed with bright-field light microscopy. **f** Viewed with polarized light. Scale bar = 50 µm for both panels. (**e**, **f** RR Wise)



■ **Fig. 13.4** **g** Raphides in the vacuole of a water lettuce (*Pistia stratiotes*) leaf. The raphides are lost during sample preparation leaving empty spaces in the tissue section. Scale bar = 10 µm. (Image courtesy of Gayle Volk and Vincent Franceschi)

biforine cells (■ Fig. 13.4e–g) that are capable of ejecting the raphide crystals upon disruption, causing the symptoms that gave dumb cane its name. **Crystal sands** appear as clusters of small, individual cube-like particles scattered throughout the cell cytoplasm

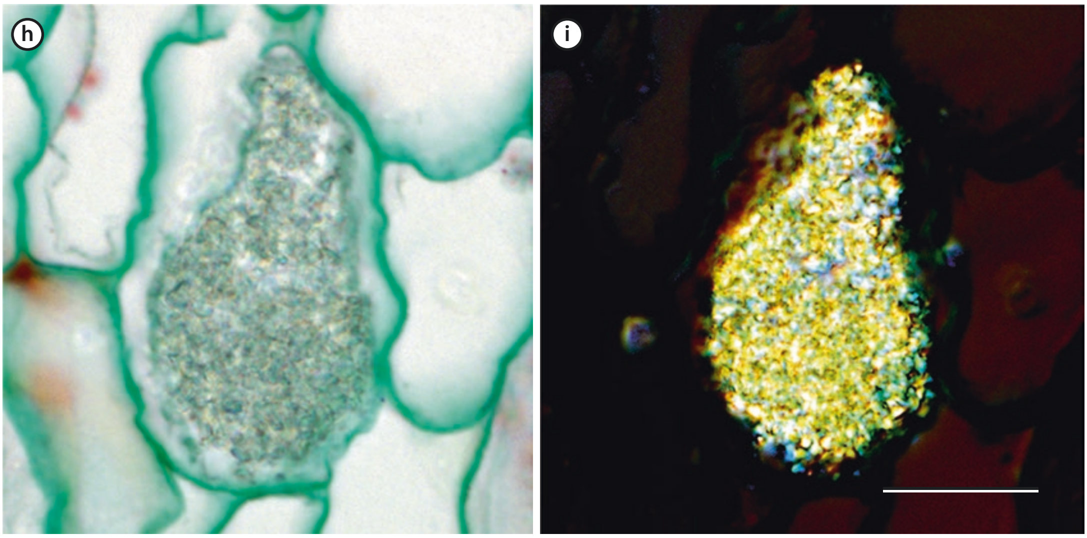


Fig. 13.4 **h**, **i** Brightfield **h** and polarized light **i** images of crystal sand in tobacco (*Nicotiana tabacum*) root. Scale bar = 10 µm for both panels. (**h**, **i** RR Wise)

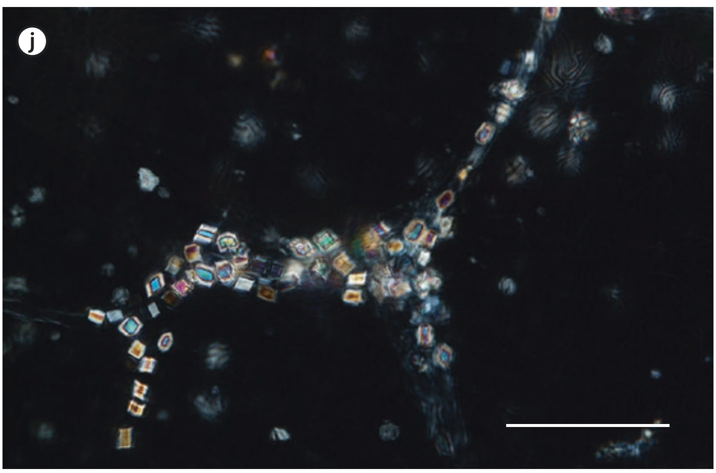


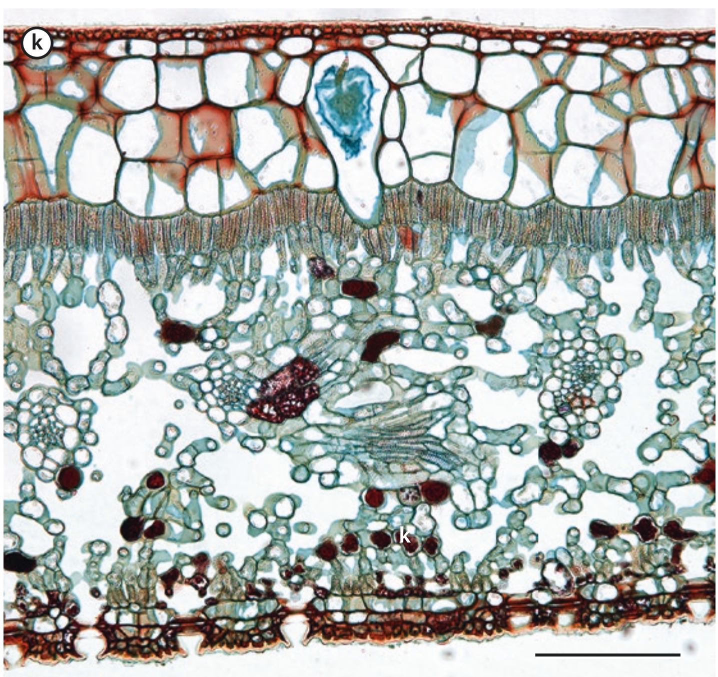
Fig. 13.4 **j** Polarized light image of prismatic crystals from a quaking aspen (*Populus tremuloides*) leaf. The crystals lie along leaf veins, which cannot be seen in polarized light. Scale bar = 50 µm. (RR Wise)

(Fig. 13.4h, i). **Prismatic crystals** are large and sometimes with pointed ends and usually only occur as one to several per cell (Fig. 13.4j). All crystals exhibit birefringence such that light is refracted when illuminated with polarized light in the light microscope, an effect seen in some of the micrographs in this section.

13.4.2 Cystoliths

Lithocysts (literally "rock box") are large epidermal cells containing amorphous calcium carbonate in a cellulose matrix; the cellulose core arises from and remains connected to the primary cell wall (◘ Fig. 13.4k). Lithocysts may extend inward towards the leaf mesophyll and do not project above the surface of the leaf as is the case with trichomes. The calcium carbonate concretion is called a **cystolith** (or “box rock”). Cystoliths are found in less than a dozen of the 620 angiosperm families, and vary in structure (◘ Fig. 13.4l–o). Their function and that of the calcium carbonate inclusions remain cryptic. However, plants are known to sequester calcium in a number of insoluble forms, which may be related to the need to keep intercellular calcium levels low. As evidence of this, experiments using varying soil calcium levels, and therefore the amount of Ca^{+2} available to be taken up by the plant, demonstrate a relationship between Ca^{+2} uptake and lithocyst development. Although they are undoubtedly involved in calcium storage and regulation, cystoliths differ from calcium oxalate crystals in that they store amorphous calcium carbonate as opposed to crystalline CaOx (hence the lack of cystolith birefringence), and they are extracellular (cell wall or apoplastic), while CaOx crystals are intracellular (vacuole or symplastic).

The elemental composition of a cystolith can be imaged using XRMA (◘ Fig. 13.4p). ◘ Figure 13.4q shows that the cystolith has much higher levels of calcium than the surrounding cells and that the cellulose stalk is high in silicon. If the X-ray microanalyzer had been used to image the carbon or oxygen of the carbonate, those elements would not have stood out against the backdrop of the abundant carbon and oxygen in the surrounding leaf tissue; the entire field of view would have been yellow.



◘ **Fig. 13.4** **k** A lithocyst in the adaxial, multiple-layered epidermis of a fig (*Ficus* sp.) leaf. Note how the cystolith is attached to the cell wall by a small stalk composed of cellulose. Scale bar = 125 µm. (RR Wise)

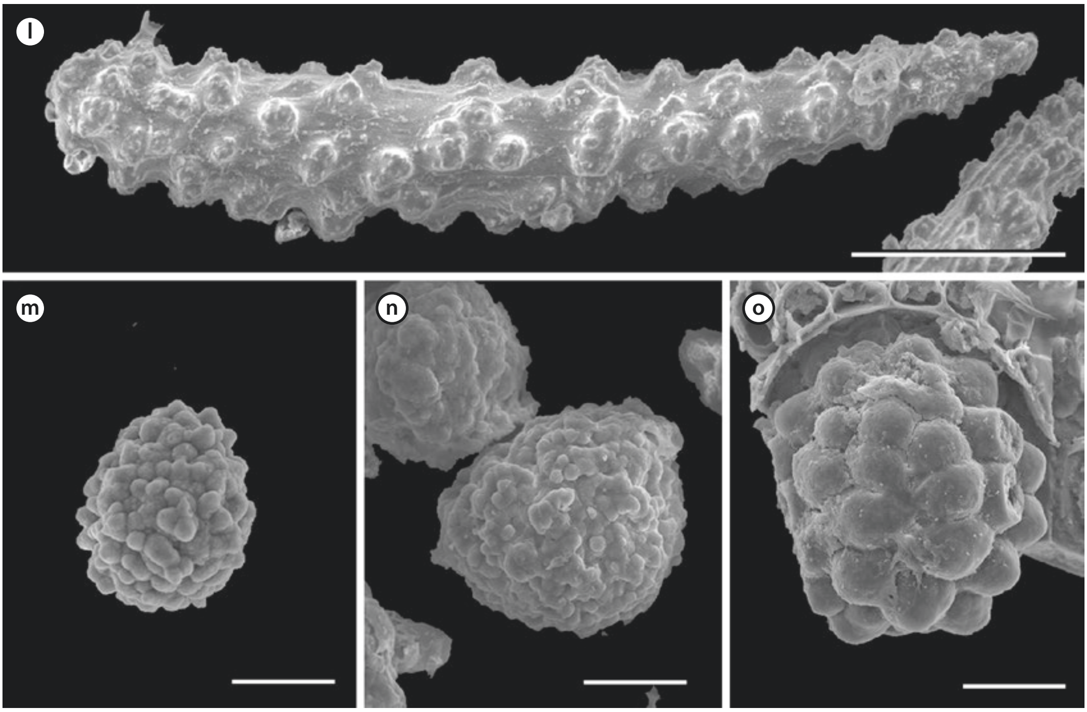


Fig. 13.4 Cystoliths from **l** Mexican petunia (*Ruellia simplex*), **m** creeping fig (*Ficus pumila*), **n** white mulberry (*Morus alba*), **o** hops (*Humulus lupulus*). Scale bars = 50 µm in **l** and 25 µm in **m**–**o**. (**l**–**o** RR Wise)

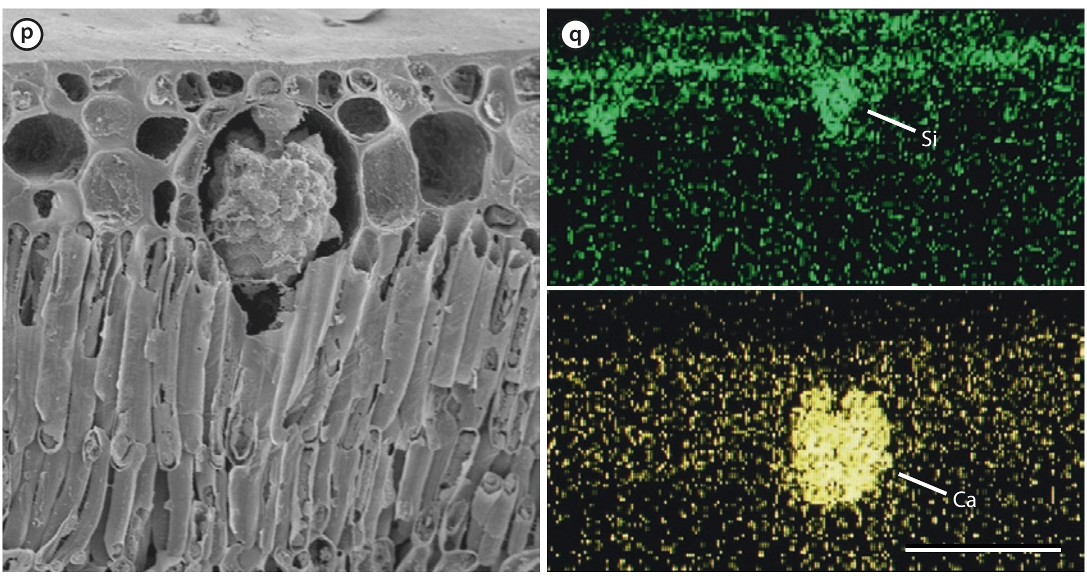
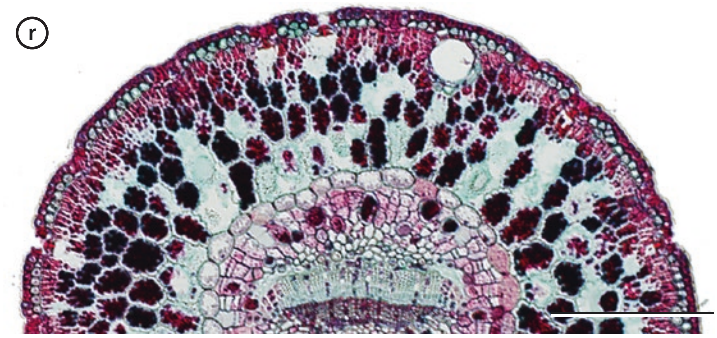


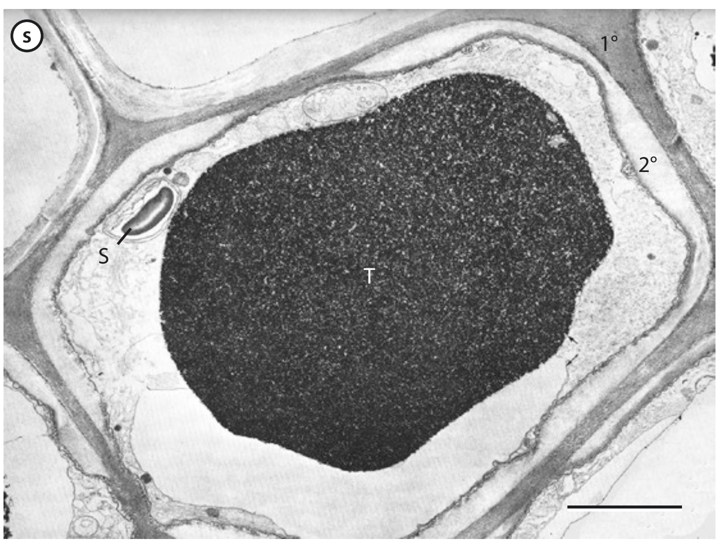
Fig. 13.4 A lithocyst in the epidermis of a fiddle leaf fig (*Ficus lyrata*) leaf. **p** The scanning electron micrograph shows the size and morphology of a cystolith within a lithocyst. **q** X-ray microanalysis images of the same area indicates that the cystolith contains high levels of calcium (*highlighted in yellow*) suspended by a silicon-rich stalk (*green*). Scale bar = 50 µm. (**p**, **q** Nicholas Gabel)

13.4.3 Tannin-Containing Idioblasts

Tannin compounds are widely distributed in many species of plants (Mole 1993), where they play a valuable role in protection from predation, and perhaps also as pesticides, and in plant growth regulation. Tannins are localized within the vacuoles of specialized cells and stained black in both light (■ Fig. 13.4r) and electron microscopy (■ Fig. 13.4s). The astringency from the tannins is what causes the dry and "pucker" feeling in the mouth following the consumption of unripened fruit or red wine. Likewise, the destruction or modification of tannins with time plays an important role in the ripening of fruit and the aging of wine.



■ **Fig. 13.4** **r** A portion of single-leaf piñon (*Pinus monophylla*) leaf with many large tannin-filled cells. A large resin duct can be seen near the epidermis in the 1:00 position. Scale bar = 250 µm. (RR Wise)



■ **Fig. 13.4** **s** Tannin cell in the vascular parenchyma of an eastern white pine (*Pinus strobus*) needle visualized with transmission electron microscopy. The dark inclusion (T) in the vacuole represents a product of tannin (a phenolic compound) reaction with the fixatives used in specimen preparation. Primary (1°) and secondary (2°) walls are indicated. Scale bar = 10 µm. (Image from: Ledbetter and Porter (1970), with permission)

13.5 Essential Oils Are Valuable Plant Extracts

Essential oils (the word "essential" meaning an embodiment of the essence of the plant) are extracts of any plant part that are used in a variety of applications including food additives, perfumes, drugs, and medicines (Burt 2004) (◘ Fig. 13.5a, b). While there are many types of plant extracts (think tea and coffee) and no clear lines between the different types, an essential oil typically contains true oils produced by internal or external secretory structures (Guenther 1948) (◘ Fig. 13.5a). Essential oils and other plant extracts have been used by humans for thousands of years and continue to play important roles today. Essential oils are typically extracted via distillation, organic solvents, supercritical CO_2, or a process called cold pressing which avoids the use of heat and solvents (Soto et al. 2004) (◘ Fig. 13.5b). The legalization of medical and recreational marijuana in many areas of the USA has driven an acceleration of the development of small- to medium-scale tetrahydrocannabinol (THC) extraction technologies, some of which can be quite dangerous in the hands of do-it-yourselfers (Hughes 2015).

13.6 Toxic Oils Often Cause Severe Dermatitis

The bane of countless trekkers throughout many wildlife regions of the USA (exceptions are California, Alaska, and Hawaii) has been plants that produce highly toxic oils. These plants commonly include poison oak, poison ivy, and poison sumac that are members of the genus *Toxicodendron* within the Anacardiaceae. These plants contain toxic oil, primarily urushiol, that is found within secretory canals of the phloem. This compound is found within the sap of most, if not all, plant structures and serves as an allergen that can cause a skin rash in sensitive individuals (also known as urushiol-induced contact dermatitis).

Urushiol is a mixture of several closely related aromatic (ring) organic compounds, which varies in composition by species. Those with longer side chains of unsaturated alkyls tend to produce stronger reactions. Upon absorption in the skin, urushiol becomes recognized by the immune system's dendritic cells and then migrates to lymph nodes where they stimulate the migration of T-lymphocytes into the skin and produce rashes and extreme irritation.

A variety of compounds have been found in the plant *Gelsemium elegans*, commonly known as "heartbreak grass" (◘ Fig. 13.6). The toxic compounds (largely alkaloids) are primarily found in the underground rhizome. Ingesting a solution of extracts of *Gelsemium* and alcohol is fatal, sometimes in a matter of seconds. It acts by paralyzing the respiratory centers, causing tremors, paralysis of extremities, convulsions, urination, defecation, and uncontrolled salivation. Death is brought about by paralysis of the spinal cord, near complete loss of muscular power and brain damage. In very small doses, studies have shown that extracts can wipe out tumor

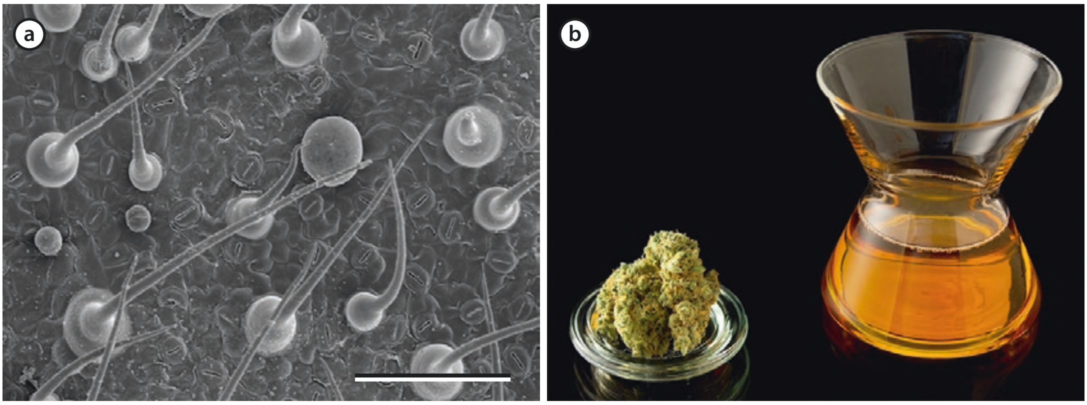


Fig. 13.5 THC-producing glands on the surface of a marijuana (*Cannabis sativa*) leaf. Image **b** shows extraction products. Scale bar in **a** = 15 µm. (**a** RR Wise; **b** AR Wise, Avitas Agriculture, Seattle, WA)

Fig. 13.6 Heartbreak grass (*Gelsemium elegans*) grows as a vine in southeastern and southwestern USA, as well as in southern China near rivers and streambeds. Careful minute administration of extracts provided pain relief in the nineteenth century for some individuals, but that is no longer used for obvious reasons. Scale bar = 2 cm. (RR Wise)

cells linked to leukemia and cancer of the liver, lungs, breast, and colon. Some people who have consumed honey containing traces of *Gelsemium* toxins have died within hours. Table 13.1 provides a partial list of toxic plants and the causes of their toxicity

Table 13.1 A partial listing of toxic and dangerous plants		
Common name	**Scientific name**	**Cause of toxicity**
Castor oil plant	*Ricinus communis*	Ricin from seeds
Suicide tree	*Cerbera odollam*	Cerberin from seeds
Little apple of death	*Hippomane mancinella*	Toxic milky sap
Rosary pea	*Abrus precatorius*	Abrin in seeds
Dumb cane	*Dieffenbachia* sp.	Raphides of calcium oxalate
Angel's trumpet	*Brugmansia* sp.	Atropine and scopolamine
Oleander	*Nerium oleander*	Cardiac glycosides
Hemlock	*Conium maculatum*	Coniline from leaves, seeds, and roots
Wolf's bane	*Aconitum lycoctonum*	Aconitine neurotoxins and cardiotoxins

13.7 Chapter Review

Concept Review

13.1 *External secretion involves moving substances outside of the plant.* Plants secrete to the exterior a large variety of oils, resins, salts, nectars, and toxins from a wide range of specific structures.

13.2 *Carnivorous plants have evolved external secretory structures as a mechanism for nutrient acquisition.* Carnivory in plants is a strategy for acquiring minerals in nutrient-deficient environments by capturing and digesting small animals, usually insects, in leaf traps or with sticky secretions. The prey is then digested, and the nutrients are absorbed by the leaf.

13.3 *Internal secretory structures include oil cavities, laticifers, and resin ducts.* Internal secretory products include oils, latex, and resins. They are diverse in both chemistry and function.

13.4 *Idioblasts are internal secretory cells that contain crystals or tannins.* Idioblasts are cells that appear different or out of place, as compared to surrounding cells. Many contain calcium oxalate (in several different crystal shapes), calcium carbonate (found in cystoliths), or tannins (located in the vacuole).

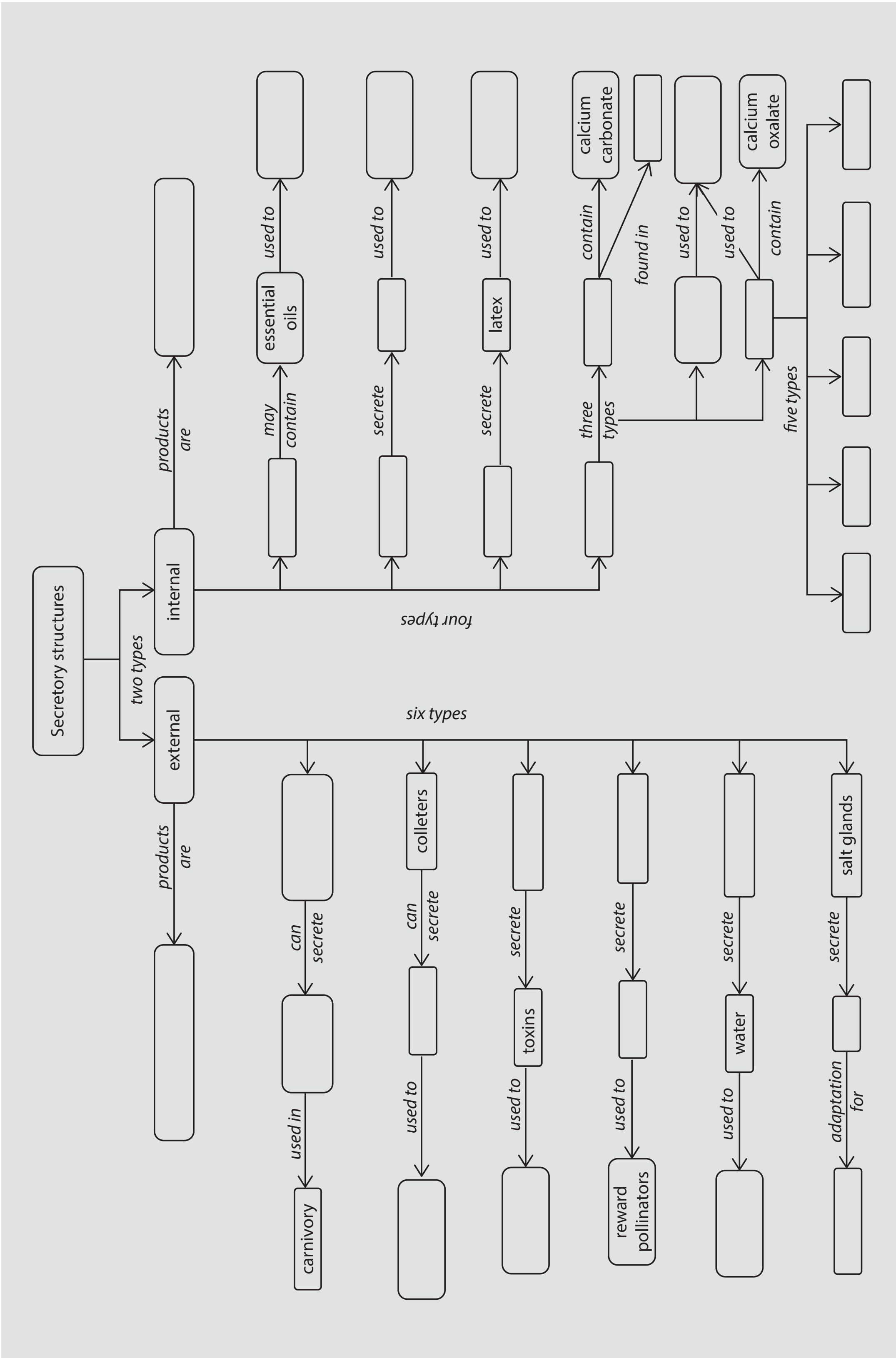
13.5 *Essential oils are valuable plant extracts.* For thousands of years, the products of internal and external secretory structures—typically called essential oils—have been extracted and used by humans for food additives, drugs, and medicines.

13.6 *Toxic oils often cause severe dermatitis.* The secretions of multiple plant species contain a variety of toxic oils that can cause serious allergic reactions and skin irritation.

Concept Connections

1. Insert the terms below into the following concept map. Every term will be used once and only once (except for "deter herbivory" which will be used five times).

Creosote	Idioblasts	Resin ducts
Crystal sand	Laticifers	Salt
Crystals	Lithocysts	Secreted to surface
Cystoliths	Nectar	Stinging hairs
Deter herbivory (use five times)	Nectaries	Stored internally
Digestive enzymes	Oil cavities	Styloid
Druse	Prismatic	Tannin bodies
Glandular trichomes	Raphide	Water
Halophytes	Reduce transpiration	Water balance
	Resin	


Secretory structures
two types
internal
external
products are
four types
six types
essential oils
may contain
used to
secrete
latex
three types
contain
calcium carbonate
found in
five types
calcium oxalate
can secrete
used in
carnivory
colleters
toxins
reward pollinators
water
salt glands
adaptation for

■ Concept Assessment

2. Single-celled laticifers that are branched are said to be
   a. articulated.
   b. non-articulated.
   c. anastomosed.
   d. both articulated and anastomosed.
   e. both non-articulated and anastomosed.

3. Epithelial cells of resin ducts are densely cytoplasmic.
   a. true.
   b. false.

4. Peltate digestive glands are likely to be found in
   a. *dionaea.*
   b. *dracaena.*
   c. *drosera.*
   d. *drosophyllum.*
   e. *pinguicula.*

5. Which secretory structure is most likely derived from the epidermis?
   a. resin duct.
   b. tannin cell.
   c. laticifer.
   d. druse-containing cell.
   e. colleters.

6. Epithem cells are
   a. modified epidermal cells.
   b. modified vascular bundle cells.
   c. a kind of transfer cell.
   d. glandular trichomes.
   e. individual units of laticifers.

7. Trichomes that secrete a sticky substance typically attract
   a. pollinators.
   b. predators.
   c. prey.
   d. people.
   e. water for secretion.

8. Hydathodes have stomata.
   a. true.
   b. false.

9. Raphides develop in
   a. chloroplasts.
   b. nuclei.
   c. endoplasmic reticulum.
   d. vacuoles.
   e. more than one of the above.

10. Lithocysts contain
    a. druses.
    b. raphides.
    c. prismatic crystals.
    d. tannins.
    e. cystoliths.

11. Latex is produced by
    a. glandular trichomes.
    b. laticifers.
    c. vacuoles.
    d. nectaries.
    e. resin ducts.

- **Concept Applications**

12. Plants are often not very nice to their distantly related zoological cousins. Compile a list of the structures plants use to deter herbivory, and explain how each helps to protect the plant. Even when plants offer a sweet reward for the attentions of a bird or insect, it is only to serve their own needs. What secretory structures and secretions do plants use to attract and reward animals? What benefit(s) do the plants gain?

13. Carnivorous plants are found in soils with low-nutrient environments and use carnivory to acquire minerals (mostly nitrogen) that are not available in the soil. Explain the additional observation that carnivorous plants are usually found in high-light environments.

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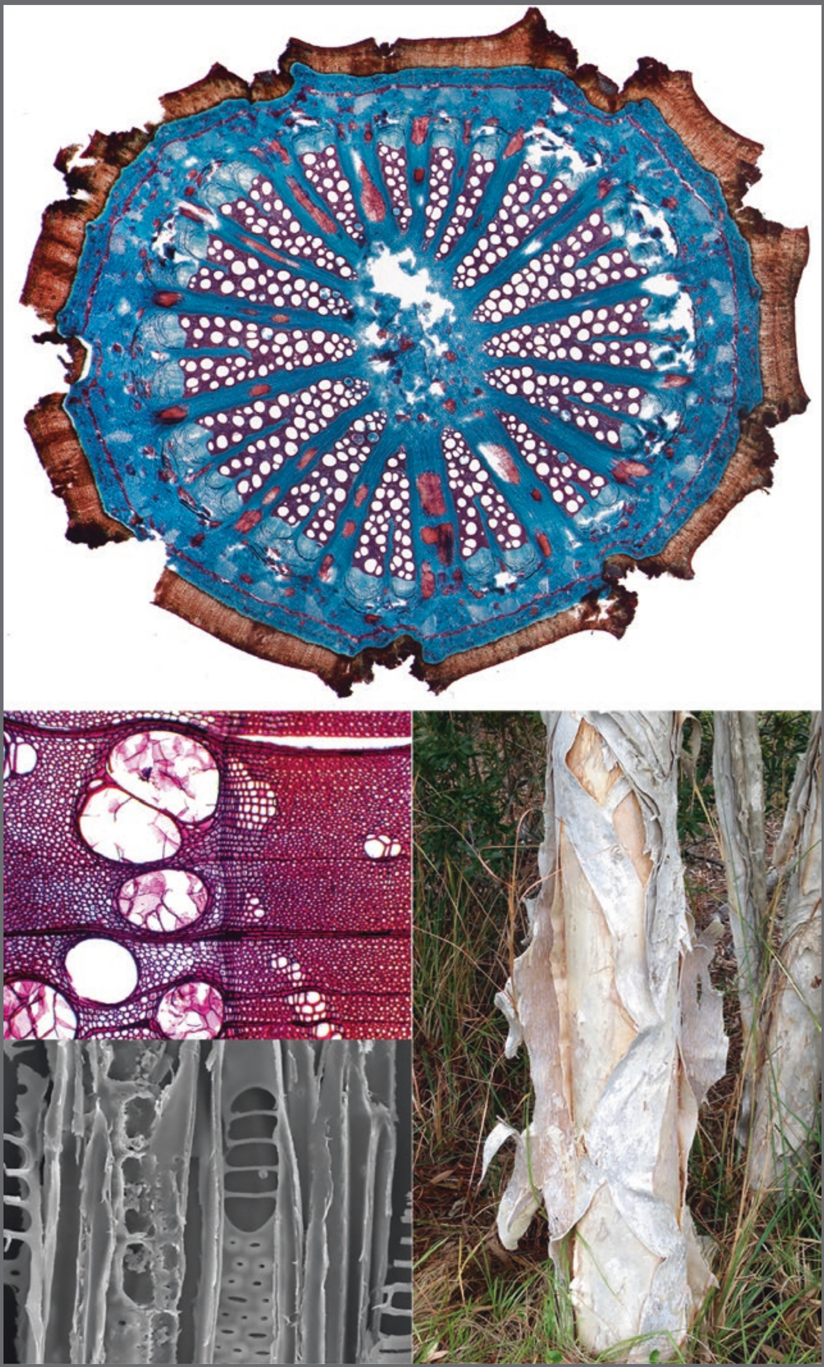
Secondary Vegetative Growth



LM of Dutchman's pipe (*Aristolochia maxima*) stem. LM of Persian silk tree (*Albizia julibrissin*) wood cross section. SEM of tulip tree (*Liriodendron tulipifera*) xylem vessel. Photograph of melaleuca (*Melaleuca quinquenervia*) periderm. (All images by RR Wise.)

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Introduction

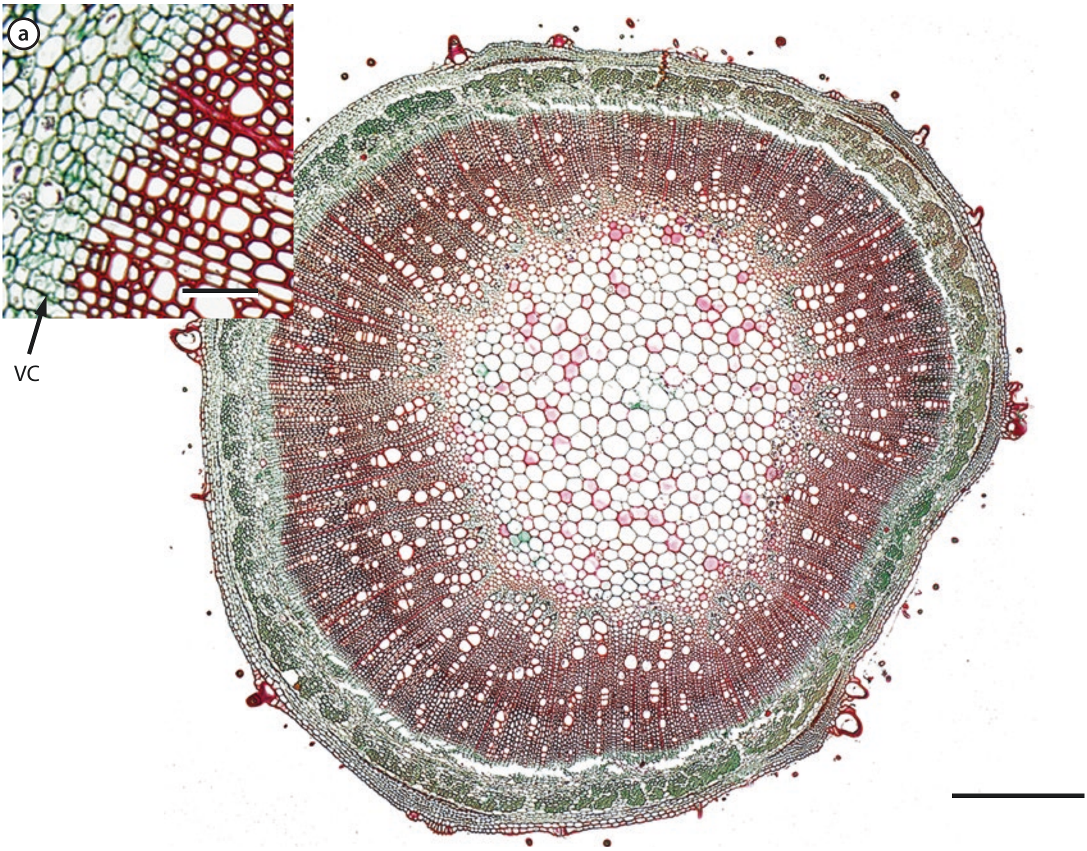
Primary growth, as discussed in ► Chap. 4, is responsible for the growth and development of the initial plant and drives increases in height and length. The primary growth of the shoot and root vascular systems is initiated by the procambium in the shoot and root apical meristems and produces primary xylem and phloem. Monocots and herbaceous eudicots do not add vascular tissues beyond that point, although monocots may have small amounts of cambium in the scattered vascular bundles. Gymnosperms and woody eudicots, because of their perennial nature, must increase the amount of vasculature to accommodate an increase in stem and root diameter and an increased need for vasculature to serve a large shoot and root system. This is called secondary growth and is provided by the vascular cambium, a cylinder of meristematic cells that lies between the xylem and phloem tissues in the shoot and root.

The girth increase fueled by secondary growth allows the plant to grow to greater heights. While this allows a plant to grow above the shade of understory plants and obtain more light for photosynthesis, it also requires an increase in the transport of water, food materials, and other compounds involved in maintenance, growth, and development. Activity of the vascular cambium provides for an increase in diameter of the stem or root that in turn increases both the support and the transport of the plant.

14.1 The Vascular Cambium Is a Single-Layer Cylinder of Meristematic Cells

The vascular cambium (like the cork cambium, ► Chap. 16) is a lateral meristem. While there may be dozens, or even thousands, of root and shoot apical meristems on a single plant, there is basically only one vascular cambium. It is a continuous cylinder of meristematic tissue that lies between the xylem and phloem (◘ Fig. 14.1a) and runs from the roots to the shoot. If damaged, for instance, by impact (◘ Fig. 14.1b, c) or herbivory, it cannot be rejuvenated. Therefore, the future of the plant relies on maintaining a healthy vascular cambium.

Mitosis is a risky process that can lead to somatic mutations in daughter cells and therefore all the progenitors of those daughters. Given its longevity and the fact that it cannot be replaced, the vascular cambium functions as a single-layer repository of meristematic cells that rarely divide, perhaps as infrequently as only once or twice a year. Mitosis of the vascular cambial cells produces daughter cells called initials—**xylem initials** (also called xylem mother cells) to the adaxial side and **phloem initials** (phloem mother cells) to the abaxial side. These initials undergo the subsequent multiple rounds of mitosis needed to provide the cells that contribute to the girth of the mature stem and root. The true vascular cambium is only one cell layer thick (**uniseriate**), but it may appear to be several layers in thickness due to the fact that the



■ **Fig. 14.1** **a** Hemp (*Cannabis sativa*) stem shown in cross-section. The vascular cambium (VC) is a single layer of cells between the pale green phloem to the outside and the red xylem tissues to the inside. Scale bars = 250 µm in main panel and 50 µm in inset (RR Wise)

adjacent initials look similar until they differentiate into mature xylem or phloem tissues. This apparent thickness has given rise to the use of the term **cambial zone** for the microscopic view of the cambium proper and its immediate derivatives. Cambial zone thickness may vary with cambial activity being thicker at the start of a growing season (■ Fig. 14.1d) and thinner at the end (■ Fig. 14.1e).

Vascular cambial initials can divide in all three axes. In the tangential horizontal plane, they grow into a layer of cells that forms a ring around the stem or root. In the tangential vertical plane, they form an increasingly thickened zone of brick-like cells, which in the cross-sectional axis is a layer that differentiates into new cells of xylem and phloem (■ Fig. 14.1f, g). Cambial initials divide mostly periclinally and are **bifacial**, meaning they produce derivatives from both the adaxial and abaxial faces—secondary phloem derivatives to the outside (abaxial) and secondary xylem derivatives to the inside (adaxial). As the process continues, the older phloem cells to the exterior become crushed, and the xylem cells to the interior differentiate into woody tissue due to their lignified cell walls.

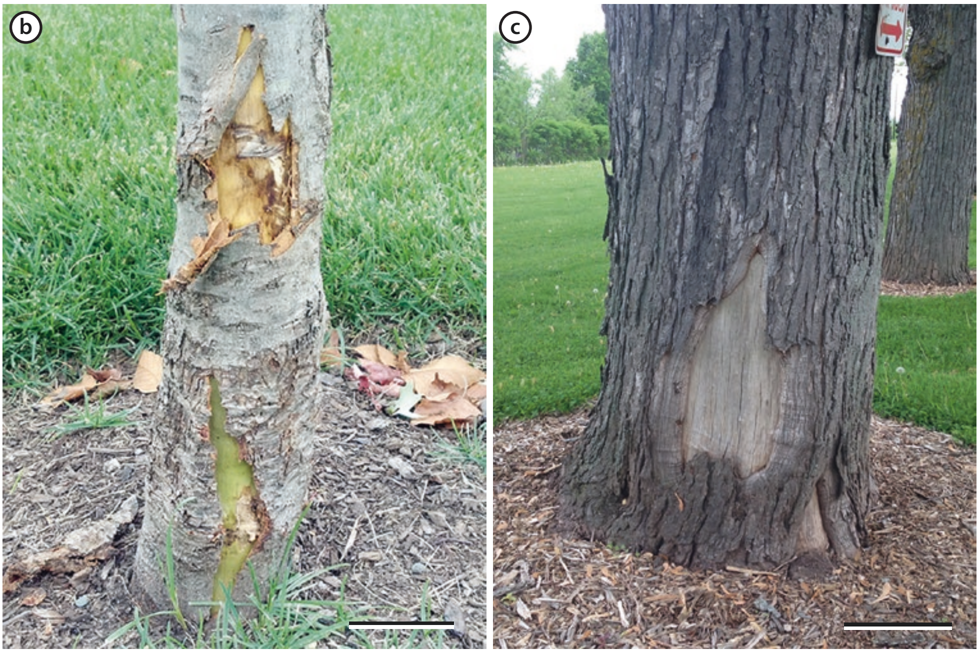


Fig. 14.1 Two tree trunks with damage to the phloem. Mechanical impacts have removed a patch of periderm, phloem, and vascular cambium on both trees. **b** A red maple (*Acer rubrum*) recently damaged by a lawn mower. **c** This sugar maple (*Acer saccharum*) was hit several years prior by a snowplow. Neither tree will be able to replace the missing vascular cambium, and the tissues it produces, although some healing is apparent at the edges of the damage seen in **c**. Scale bars = 10 cm in **b** and 50 cm in **c**. (**b** Cedarlawn Tree, A Division of Bartlett Tree Experts, Ashland, MA; **c** RR Wise)

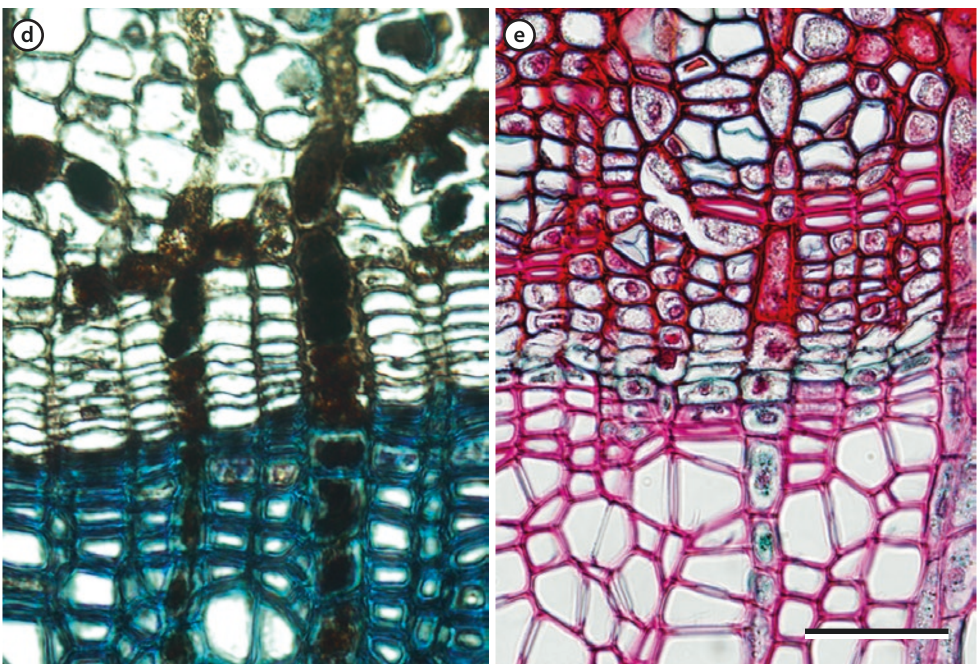


Fig. 14.1 The cambial zone includes the uniseriate vascular cambium and undifferentiated xylem and phloem mother cells to either side. **d** This oak (*Quercus alba*) stem was collected during a period of active growth and has a cambial zone that is six to seven cells wide. Only one cell in each file is a cambial initial. The others are xylem or phloem mother cells. **e** The tulip tree (*Liriodendron tulipifera*) vascular cambium is only one to two cells thick and shows few undifferentiated cells. Phloem is to the top of both images, xylem to the bottom. Scale bar in **e** = 25 μm and applies to both panels (**d**, **e** RR Wise)

14

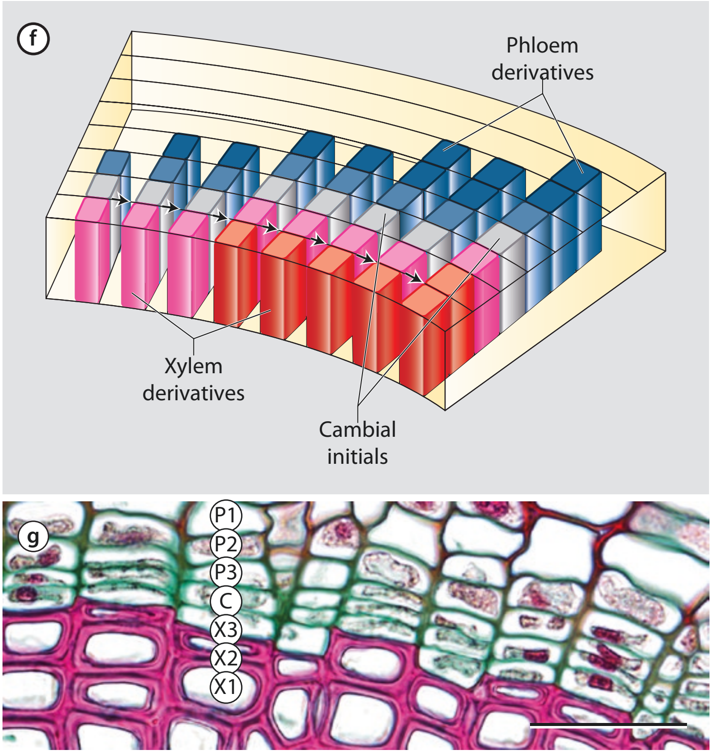


Fig. 14.1 **f** A sequence of bifacial cambial cell divisions generates xylem derivatives to the interior (X1–X3) and phloem derivatives to the exterior (P1–P3). Notice how the cambial zone gets pushed to the exterior by expansion of the xylem cells. **g** Vascular cambium of ginkgo (*Ginkgo biloba*) stem. A cambial initial (C), three xylem derivatives (X1–X3), and three phloem derivatives (P1–P3) are labeled. Xylem derivative #3 (X3) has not yet developed a secondary cell wall. Scale bar = 25 µm (**g** RR Wise)

Box 14.1 Stimulation of Genes that Influence the Vascular Tissue Influences Wood Production

Wood develops from the accumulation of xylem that originates from the vascular cambium. Until recently, the identity of the genes regulating the production of wood from the vascular cambium was unknown. By manipulating plant genes and observing the resulting phenotypes, scientists can deduce the function of specific genes. The genes PXY and CLE are involved in the production of vascular tissue in *Arabidopsis*, an annual. What role, if any, do related genes play in the secondary growth in trees?

By manipulating PXY-CLE genes in hybrid aspen trees (*Populus tremula* × *P. tremuloides*), researchers were able to discover how to stimulate woody tissue growth from the vascular cambium. Plants that have been engineered to overexpress either the PXY or CLE genes were shorter than controls, and cells of their xylem were unorganized. When both genes (PXY-CLE) were incorporated into the plant genome, about half of the plants were not impacted and appeared normal, while the others were stunted. When the genes were

coupled with a promoter that was associated with dividing cells, the resulting plants grew taller and faster and had larger diameters and biomass than control plants. Thus, it appears that the vascular cambium can be augmented by manipulating genes. These concepts could be used to combat climate change to reduce atmospheric carbon, but it could also accelerate the growth rate of trees for economic advancement in the timber industry.
Reference: Etchells et al. (2015).

14.2 The Transition from Primary to Secondary Growth Requires Lateral Expansion of the Vascular Cambium

Primary growth of the procambium leads to the generation of vascular bundles with fully functional xylem and phloem tissues. However, in monocots and eudicots restricted to primary growth, further development of the vasculature beyond primary growth is not possible. Because of this, their vascular bundles are said to be "closed" (◘ Fig. 14.2a). Plants capable of secondary growth, such as gymnosperms and woody (perennial) eudicots, can add to the vasculature via activity of the vascular cambium. In this case, the vascular bundles are "open" because they contain their own cambium—the **fascicular cambium** (◘ Fig. 14.2b).

In eudicots that develop further, parenchyma cells in the interfascicular region between the vascular bundles become meristematic, begin to divide, and form the **interfascicular cambium** (◘ Fig. 14.2c). Eventually, the fascicular and interfascicular cambia merge (◘ Fig. 14.2d) and become the continuous cylinder of the vascular cambium (◘ Fig. 14.2e, f) that is responsible for eudicot secondary growth.

14.3 The Vascular Cambium Contains Two Types of Cells: Fusiform Initials and Ray Initials

Stems and roots exhibiting secondary growth have two interconnected vascular systems, **axial** and **radial** (◘ Fig. 14.3a). The axial system, composed of fully functional xylem and phloem tissues, conducts water (xylem) and sugars (phloem) up and down the plant axis between the root and shoot. As indicated in ► Chaps. 7 and 8, angiosperm xylem tissue has three cells types (vessel elements, fibers, and parenchyma), while phloem tissue has four cell types (sieve tube elements, companion cells, fibers, and parenchyma). All of those cell types are found in the angiosperm axial vascular system; but gymnosperms lack xylem vessel elements and fibers. A tremendous amount of water (via xylem) and sap (via phloem) moves through the axial vascular system as the root and shoot systems exchange water and sugars.

The radial vascular system is much smaller in scope and complexity than the axial system, as it only serves to move water and sugars a short distance from the axial system outward to the living portion of the bark (refer to ► Chap. 16—Periderm) much like the spokes of a

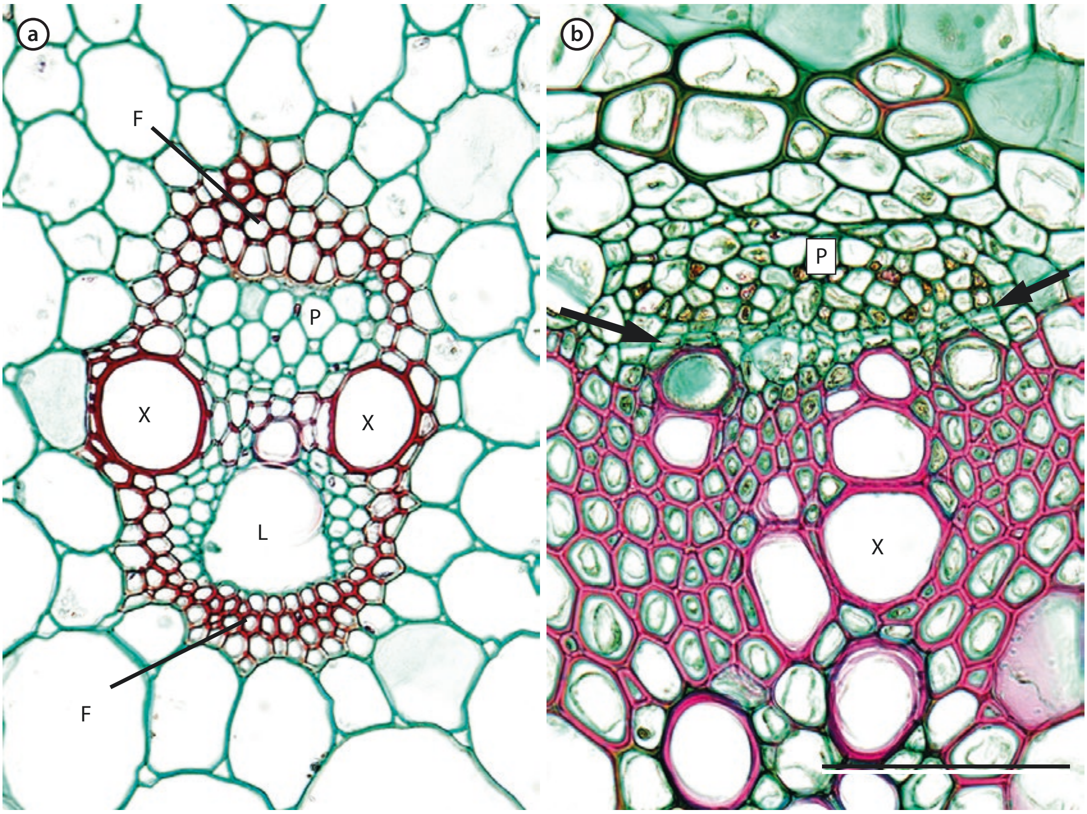


Fig. 14.2 **a** Closed vascular bundle from a maize (*Zea mays*) stem. The bundle has phloem (P), xylem (X), and fibers (F) but will not develop further. The large hole in the center is a lacuna (L) produced by the tearing of parenchyma cells during bundle expansion. **b** An open vascular bundle from beet (*Beta vulgaris*) stem. In addition to xylem and phloem, this bundle has a fascicular cambium (light-green cells between arrows) that has generated secondary vascular tissues. Scale bar in **b** = 50 µm for both panels (**a**, **b** RR Wise)

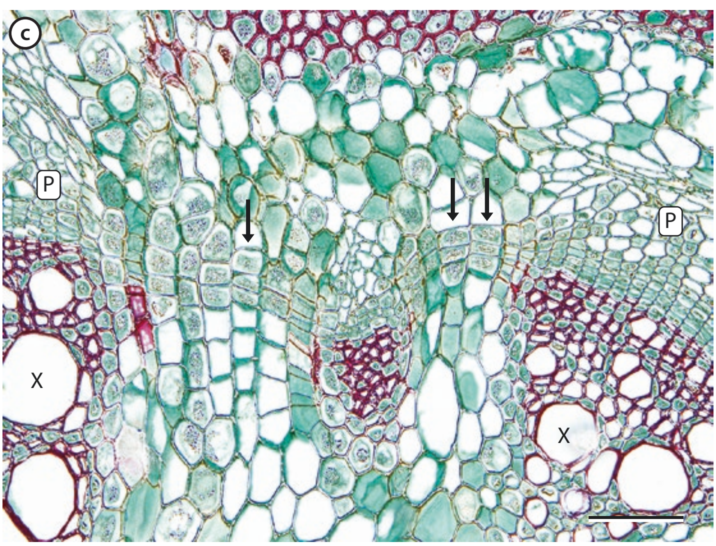


Fig. 14.2 **c** Cross-section of a Dutchman's pipe (*Aristolochia* sp.) stem showing parts of three adjacent vascular bundles (**fascicles**) with xylem (X) cells toward the inside (bottom of image) and phloem (P) to the outside. Note the division of cells (*arrow*) in-between the vascular bundles marking the beginning of interfascicular vascular cambium development. Scale bar = 50 µm (RR Wise)

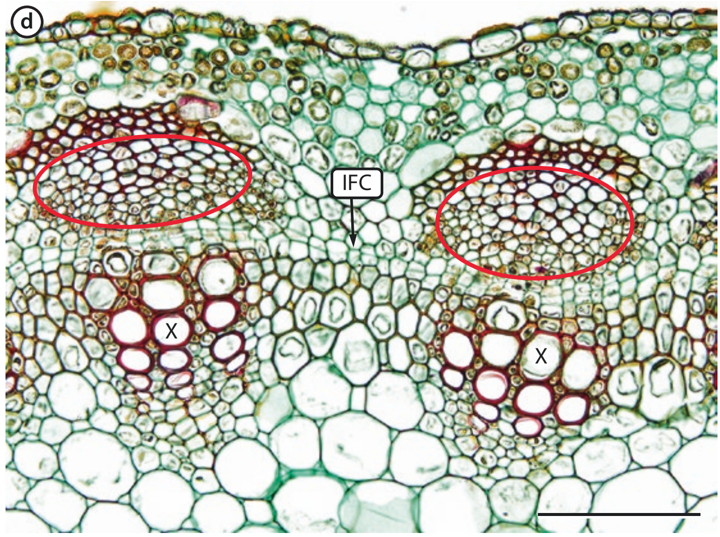


Fig. 14.2 **d** Cross-section of black medic (*Medicago lupulina*) stem showing a slightly later stage of interfascicular cambium (IFC) development than in the previous figure. Phloem (circled in red) and xylem (X) derivatives are indicated. Scale bar = 100 µm (RR Wise)

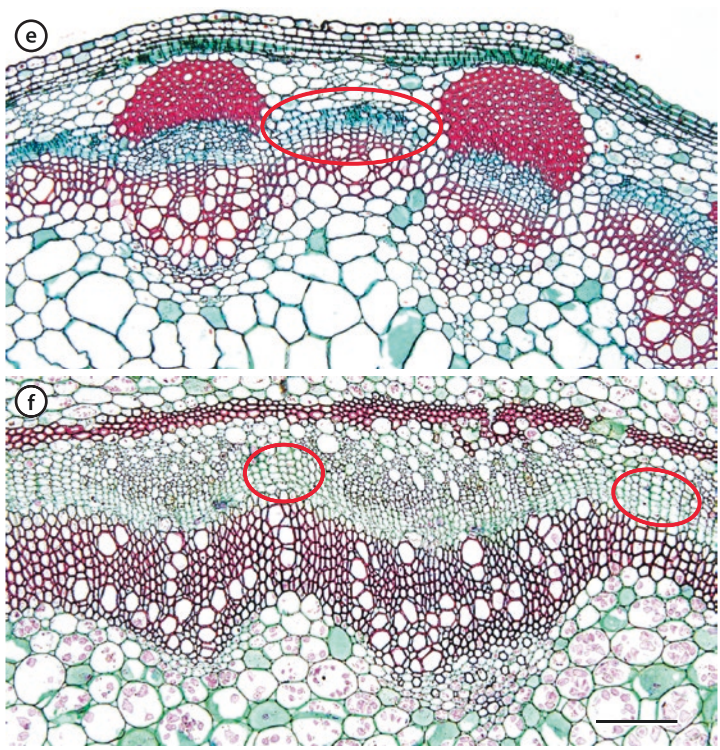


Fig. 14.2 **e**, **f** Further development of the intrafascicular cambium in **e** sunflower (*Helianthus* sp.) and **f** geranium (*Pelargonium* sp.) stems. The interfascicular cambium is circled. Bright red caps of abaxial phloem fibers (not circled) mark the vascular bundles in *Helianthus*. Scale bar in **f** = 100 µm for both panels (**e**, **f** RR Wise)

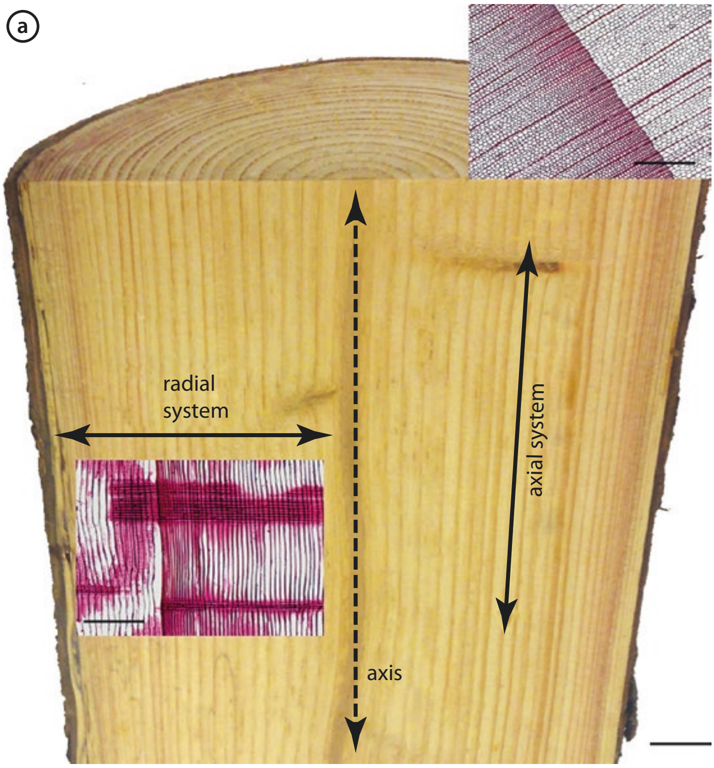
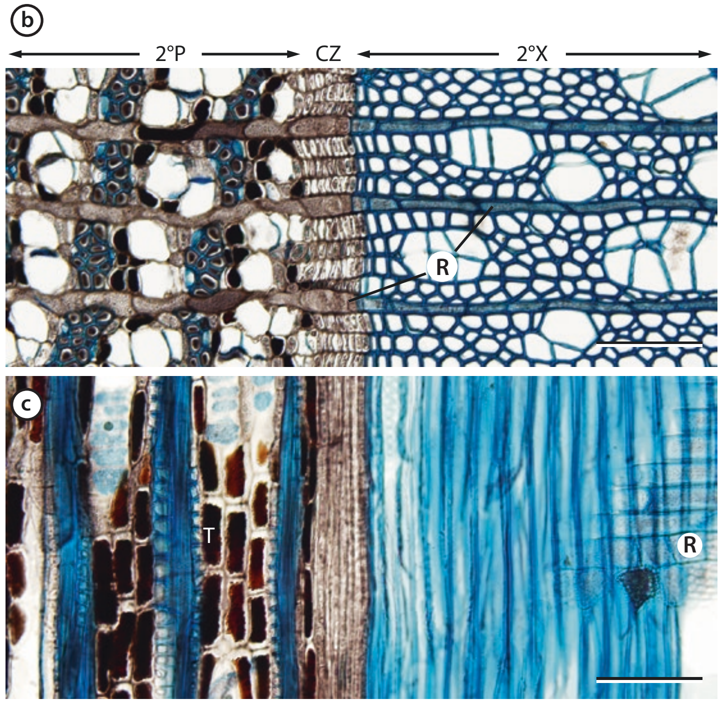


Fig. 14.3 **a** Portion of a 27-year-old white spruce (*Picea glauca*) stem labeled to show the stem axis and the orientations of the axial vascular system and the radial vascular system. Insets show a cross-section (top left) and a radial section (bottom left) from stained thin sections. Scale bars = 1 cm in main panel and 100 μm in insets (RR Wise)

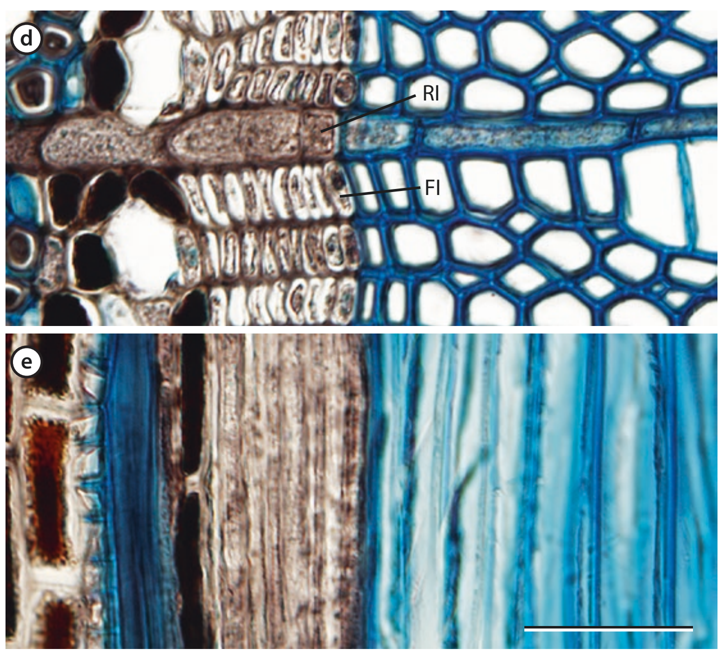
wheel extend outward from the hub to the rim. There are both **xylem rays** and phloem rays, but do not be confused; contrary to their names, xylem and phloem rays are not made of xylem and phloem tissues. Both ray types are composed almost entirely of parenchyma cells, with perhaps some sclerenchyma. Xylem and phloem rays are so named because they are found in, and extend through, the axial xylem and phloem tissues. Xylem rays are continuous with phloem rays because the same cambial initials generate them.

In order to generate both the axial and radial vascular systems, the uniseriate vascular cambium contains two cell types: **fusiform initials**, which are elongated and tapered but flattened on the tangential face, and **ray initials**, that are shorter cells, somewhat elongated along their radial axis. Fusiform initials produce the axial (or vertical) elements of secondary vascular tissues, such as the vessel elements, fibers, and parenchyma of the xylem and the sieve elements, companion cells, fibers, and parenchyma of the phloem. Ray initials generate cells of the radial vascular system (Fig. 14.3b, c).

Vascular cambium initials, both axial and radial, are parenchyma cells with primary cell walls that are never lignified (Fig. 14.3d–f). The radial walls, however, often have numerous orderly arranged primary pit fields that give the walls a "beaded" appearance (Fig. 14.3g, h). When the cells are dormant (end of



◘ **Fig. 14.3** **b**, **c** Black willow (*Salix nigra*) stem vascular cambial zone (CZ) in **b** cross-section and **c** radial section. The two planes of section have been aligned with each other. Secondary phloem (2°P) is to the exterior (abaxis, left) and secondary xylem (2°X) is to the interior (adaxis, right) of the stem. Rays (R) are indicated in both panels. Note also the tannin (T)-filled phloem parenchyma. Scale bar = 50 µm (**b**, **c** RR Wise)



◘ **Fig. 14.3** **d**, **e** Higher magnification views of ◘ Fig. 14.3b, c showing black willow (*Salix nigra*) ray initials (RI) and fusiform initials (FI). Scale bar for both panels = 25 µm (**d**, **e** RR Wise)

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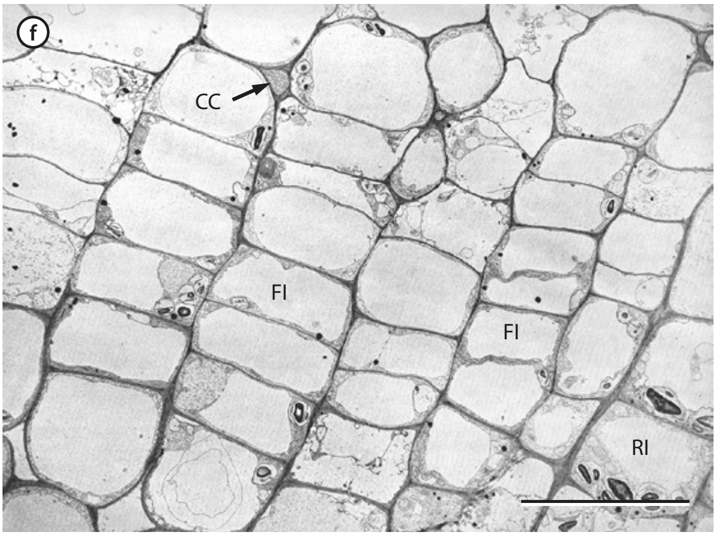
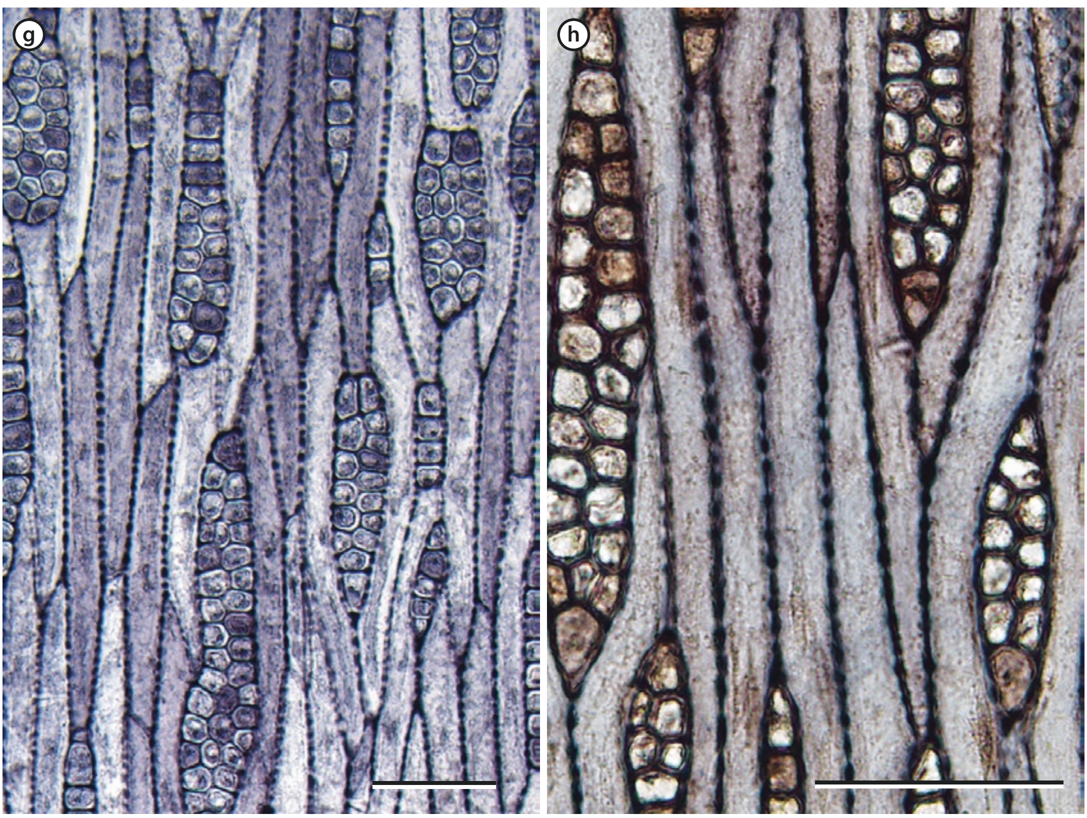


■ **Fig. 14.3** **f** Transmission electron micrograph of the cambial zone in a black locust (*Robinia pseudoacacia*) stem. Note the onset of secondary phloem as evidenced by the development of a companion cell (toward top of field of view) and the thickening of the cell walls in the secondary xylem (toward bottom). FI fusiform initial, RI ray initial, CC portion of a phloem companion cell. Scale bar = 10 µm (Image from: Ledbetter and Porter (1970), with permission)



■ **Fig. 14.3** **g**, **h** Vascular cambia seen in face view (tangential section) in **g** white ash (*Fraxinus americana*) and **h** apple (*Malus pumila*). The vascular cambium is made of vertically elongated and pointed fusiform initials and round ray initials. Note the beaded appearance in the radial walls of the fusiform initials imparted by the primary pit fields. Scale bars = 50 µm (**g**, **h** RR Wise) the growing season), they have few and small vacuoles, but in the active state (early in the growing season), they become highly vacuolated with a large central vacuole. Studies have indicated considerable variation in the proportion of fusiform initials (which produce the axial xylem and phloem) vs. ray initials in the early vascular cambium (which produce the radial xylem and phloem). Ranges of fusiform initials are from 65% to 90% of the mean tangential sectional area in the cambial zone with ray initials constituting 35% down to 10% (Esau 1953). Note the high ratio of fusiform initials to ray initials; this is in keeping with the reduced complexity and extent of the radial vascular system.

14.4 Fusiform Initials Can Be Arranged in Different Patterns

When viewed in the stem's tangential plane, fusiform initials of the vascular cambium exhibit two basic patterns that depend on the species of plant undergoing secondary growth. A **storied cambium** has fusiform initials in rows of cells that have tapered end walls all aligned in approximately the same plane (◘ Fig. 14.4a). This is a relatively uncommon arrangement and found in plants that have short fusiform initials. A **non-storied cambium** (aka **non-stratified**), in which the end walls are not aligned, is more common and associated with long fusiform initials (◘ Fig. 14.4b).

The vascular cambium also generates the cells of the xylem and phloem rays. **Multiseriate rays**, as in black locust, are two to five cells wide (◘ Fig. 14.4a), while **uniseriate rays**, as seen in sequoia (◘ Fig. 14.4b), are only one cell wide.

14.5 Anomalous Vascular Cambia Produce Atypical Growth Patterns

The "normal" vascular cambium, as described above, is a continuous ring of bifacial, uniseriate meristematic cells at the periphery of the stem that generates xylem tissue to the interior, phloem tissue to the exterior, and parenchymatous rays. Any vascular cambium not in a ring or not at the periphery is considered to be abnormal or anomalous. This is somewhat of an artificial distinction, as "normal" vs. "abnormal" is purely a human concept. In fact, anomalous cambia are found in such a number of plant species that not all botanists willingly accept the validity of the term (refer to Carlquist 2007). Nonetheless, the distinction is not without its value. Unifacial activity, no activity, and generation of parenchyma instead of vasculature are considered to be abnormal activities. Cambia possessing one or more of those characteristics of location or activity are considered to be anomalous.

Anomalous activity in eudicots is seen frequently in vines and **lianas** (climbing, woody vines, ◘ Fig. 14.5a). In most plants, xylem plays a double role of water conduction and support. Because vines and lianas use other plants or rocks for support, the structural

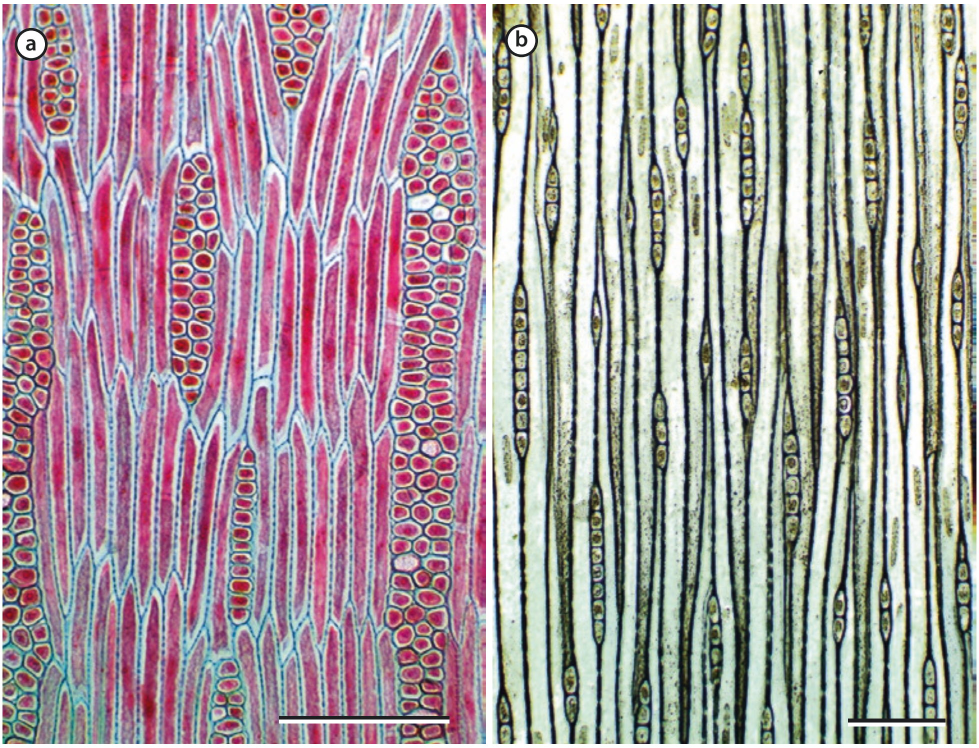


Fig. 14.4 **a**, **b** Face-on views (from tangential sections) of vascular cambia in **a** black locust (*Robinia pseudoacacia*), a eudicot and **b** sequoia (*Sequoia sempervirens*), a gymnosperm. For locust, note the storied alignment of the cells, multiseriate rays, and the short fusiform initials with beaded cell walls. Sequoia has a non-storied cambium, long fusiform initials, and uniseriate rays. Scale bar = 100 µm (**a**, **b** RR Wise)

Fig. 14.5 **a** A tangle of lianas in the tropical moist forest in the Republic of Panama. Scale bar = 20 cm (Image courtesy of Stefan Schnitzer, Marquette University)

aspect of xylem architecture is not as important, thus allowing for alternative, anomalous patterns of vascular patterning. Those patterns allow for a more flexible and bendable stem, valuable qualities for a climbing plant with secondary growth. Anomalous cambia are also commonly found in storage organs where abundant phloem, which delivers sugars for storage, is favored over xylem that primarily transports water for transpiration.

Anomalous vascular cambia can generally be considered to be of two basic types, with three "other" categories:

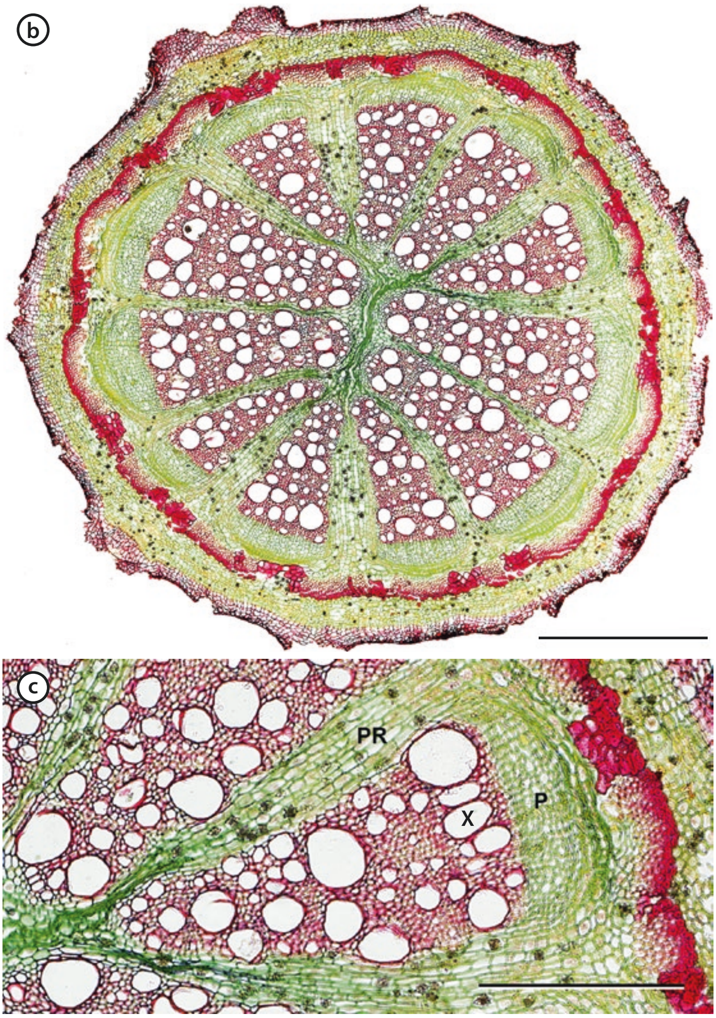
1. Normal location, abnormal activity. Cambium is in the normal location, but its activity is abnormal in that it is inactive in areas, generates only parenchyma, or is unifacial—producing only xylem or only phloem (► Sect. 14.5.1).
   - Interfascicular cambium generates parenchyma resulting in pith rays, *Aristolochia* stem (◘ Fig. 14.5b, c).
   - Xylem/pith lobes form due to differential activity, *Bauhinia* stems (◘ Fig. 14.5d, e).
2. Abnormal location, normal activity. Cambium is in an abnormal location or not ring-shaped, however with normal, bifacial activity (► Sect. 14.5.2).
   - Successive cambia within a vascular bundle, *Menispermum* (◘ Fig. 14.5f).
   - Successive cambia arise in rings at periphery of stem, *Chenopodium murale* (◘ Fig. 14.5g).
   - Double cambium, *Campsis* (◘ Fig. 14.5h).
   - Included phloem, *Bougainvillea* stem (◘ Fig. 14.5i).
   - "Winged" successive cambia in zones throughout stem, *Dillenia* (◘ Fig. 14.5j, k).
   - Multiple vascular cylinders (polystelic), *Serjania* (◘ Fig. 14.5l).

   Three "other" categories of anomalous cambia will be discussed in this section:
3. Anomalous vascular cambia in roots (*Beta vulgaris* fleshy root, ► Sect. 14.5.3.)
4. Spiral stem growth in eudicots (► Sect. 14.5.4)

14.5.1 Normal Location, Abnormal Activity

Dutchman's pipe (*Aristolochia* sp.) is a genus of eudicotyledonous twining vines with an unusual form of interfascicular cambial growth. The bifacial fascicular cambium produces xylem and phloem tissues as normal. In addition, an interfascicular cambium (IFC) forms as described above (► Sect. 14.2). However, instead of producing xylem and phloem tissues to the inside and out, the bifacial IFC generates only parenchyma cells in both directions. The result is an interrupted cambium with large pith rays separating wedges of vasculature (◘ Fig. 14.5b, c).

In passion flower (Passifloraceae), and many genera in the Bignoniaceae (◘ Fig. 14.5d, e), certain areas of the vascular cambium become inactive, while others remain active or even speed up mitotic activity. The result is a cross-shaped or lobed xylem with

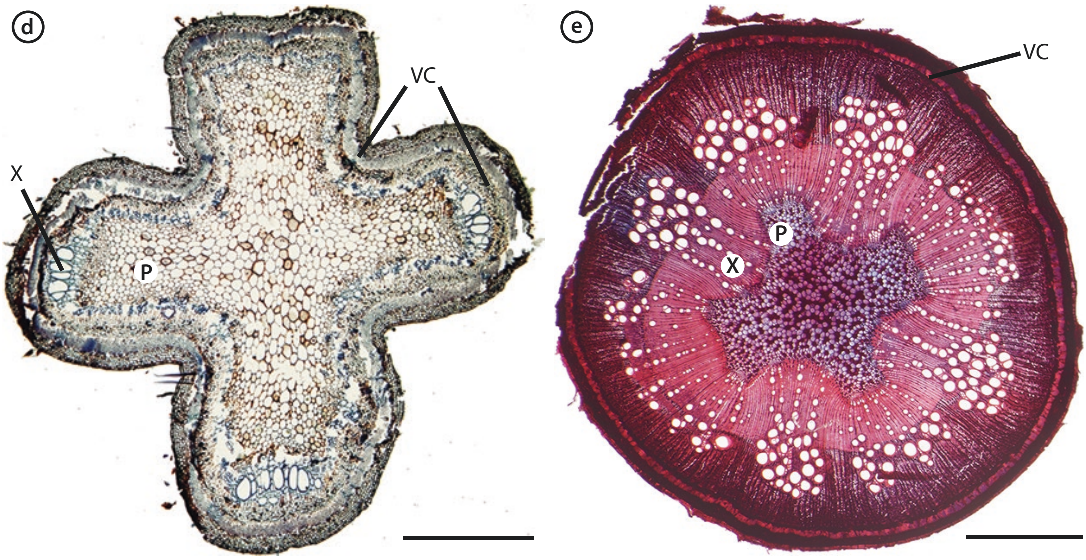


◘ **Fig. 14.5** **b**, **c** Dutchman's pipe (*Aristolochia* sp.) stem seen in cross-section at **b** low and **c** higher magnifications. The vasculature is composed of xylem (X) and phloem (P) wedges that are separated by **medullary** or **pith rays** (PR) that run from the pith at the center of the stem to the cortex. A ring of cortical sclerenchyma (stained red) composed of both brachysclereids and fibers is seen to the outside of the vascular bundles. Note the numerous druse crystals in the medullary rays and cortical parenchyma. Scale bars = 500 µm in **b**, 250 µm in **c** (**b**, **c** RR Wise)

intervening areas of phloem. In some cases, the stem takes on a lobed or star shape (◘ Fig. 14.5d). These various arrangements of structural xylem tissue create a flexible vine that can bend and wrap around a substrate as it grows.

14.5.2 Normal Activity, Abnormal Location

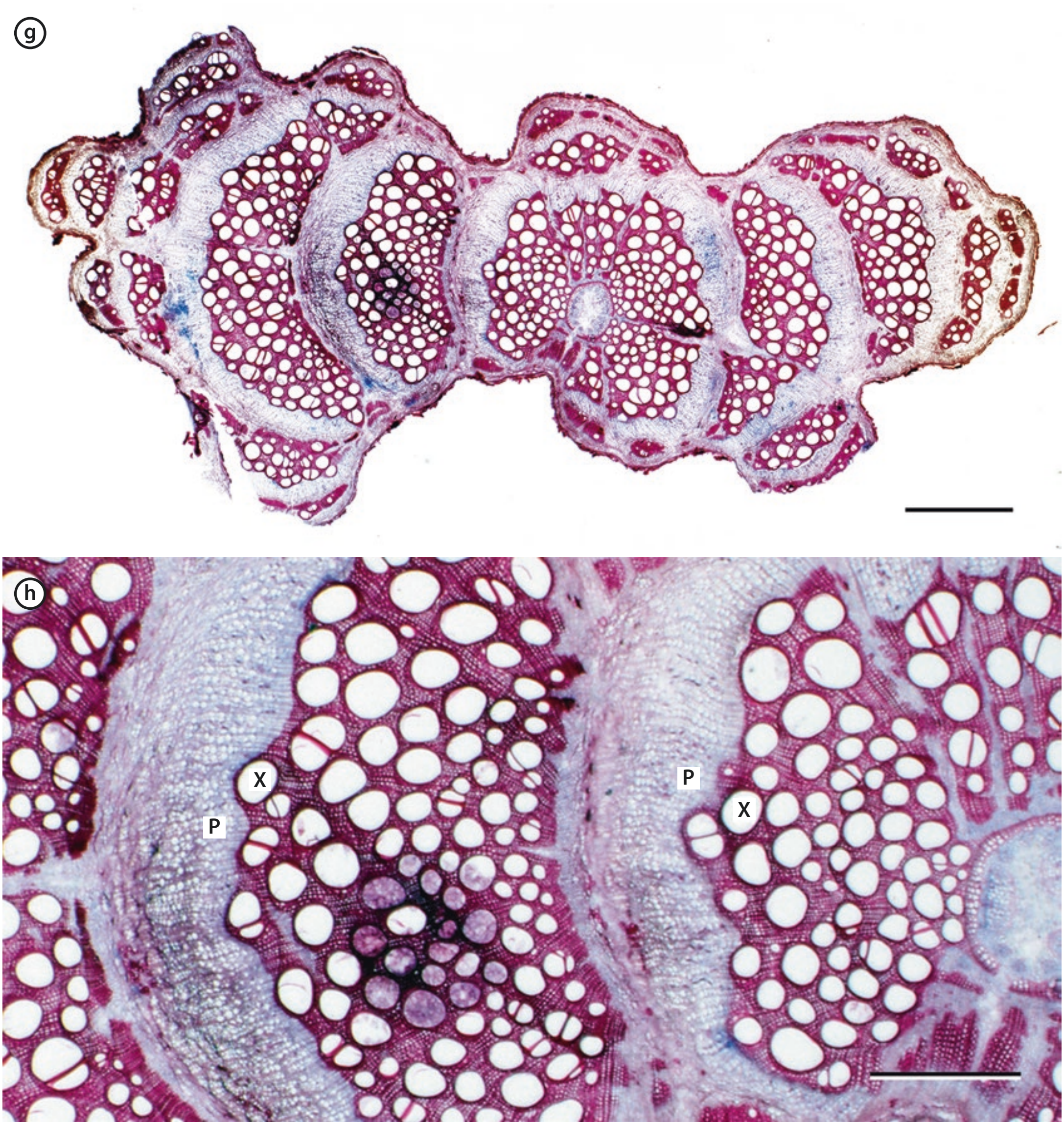
Five examples are given of normal cambia in an abnormal location: successive cambia (◘ Fig. 14.5f–h), peripheral vascular cambium (◘ Fig. 14.5i), **internal phloem** (◘ Fig. 14.5j), included phloem (◘ Fig. 14.5k), and multiple (polystelic) vascular cambia (◘ Fig. 14.5l).



■ **Fig. 14.5** **d** *Bauhinia cosmogenesis* liana has large lobes of xylem due to unequal activity of cambium. The vascular cambia (VC) between the arms went dormant as the cambia in the arms continued to produce xylem (X) and pith (P) resulting in a four-lobed stem with a four-lobed pith. **e** In *Bauhinia vahlii* growth of the vascular cambium produced a round stem, but in areas it generated substantial pith (P) to the inside instead of xylem (X) to the inside. A four-lobed pith within a round stem is the consequence. Scale bars = 500 µm in both panels. Specimens courtesy of Jack Fisher (**d**, **e** RR Wise)

■ **Fig. 14.5** **f** Cross-section of moonseed (*Menispermum* sp.) stem. This plant is a vine. With the growth of the stem, multiple successive vascular cambia will be formed progressively outward, each to produce new secondary phloem and secondary xylem. Five successive layers of xylem are indicated by rows numbered 1–5. Active phloem (P) sits to the inside of the crushed phloem (CP) that is capped with a bundle of phloem fibers (red-stained cells). Note also two darkly stained lenticels at the top and large pith rays (PR). Scale bar = 100 µm (RR Wise)

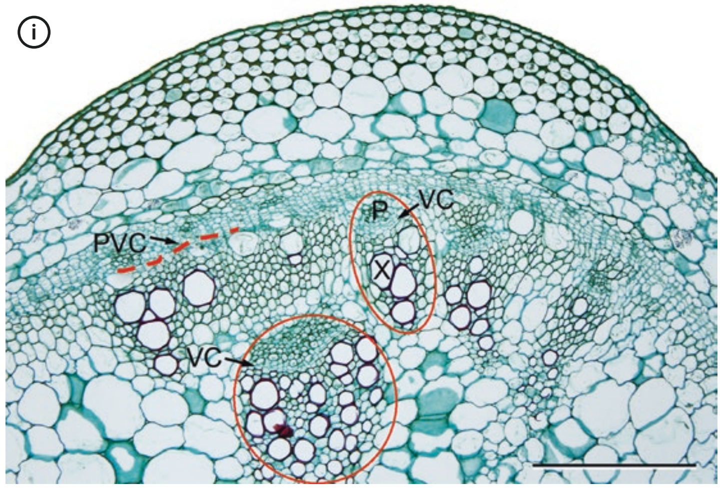
Moonseed (■ Fig. 14.5f) produces **successive cambia** within a single vascular bundle and in a single growing season. The initial vascular cambium develops normally and generates xylem to the interior and phloem to the exterior. That cambium then ceases activity, and a new (successive), bifacial cambium forms from



◘ **Fig. 14.5** **g**, **h** *Dillenia* sp. liana in cross-section exhibiting **g** a winged style of anomalous secondary growth due to **h** successive vascular cambia. X xylem, P phloem. Scale bars = 2 mm in **g** and 1 mm in **h** (**g**, **h** RR Wise)

parenchyma cells interior to the first phloem. That cambium lays down xylem (interior) and phloem (exterior) for a brief period, and then it goes dormant. The process is repeated multiple times in a single growing season. Moonseed also displays the same pith ray development seen in *Aristolochia* (◘ Fig. 14.5b).

Many lianas contain successive cambia that function for a limited time and are then replaced by a new cambium. When the cambium ceases to function, parenchyma cells in in the phloem differentiate into a new cambium and generate internal xylem and **external phloem**. Multiple rounds of successive cambium development directed to either side of the stem result in the winged growth pattern seen in *Dillenia* sp. stems (◘ Fig. 14.5g, h). Successive cam-



◘ Fig. 14.5 **i** Sowbane (*Chenopodium murale*) stem. Two primary vascular bundles are circled, and their vascular cambia (VC) lie between the xylem (X) and phloem (P). A peripheral vascular cambium (PVC, dashed red line) has just started to develop and is producing immature xylem and phloem tissues. Note also the angular collenchyma adjacent to the stem epidermis. Scale bar = 100 µm (RR Wise)

bia are also called **supernumerary cambia** (vascular cambia originating in the phloem outside the regularly formed vascular cambium). Successive cambia are widespread across taxa and organs and no doubt have an adaptive advantage by distributing phloem throughout the stem, phloem that plays a role in embolism repair under stressful conditions (Robert et al. 2011). Their ontogeny, anatomy, and diversity are considered in detail by Carlquist (2007).

In sowbane (*Chenopodium* sp.) the initial development of a vascular cambium within vascular bundles proceeds normally. Subsequently, however, a novel peripheral vascular cambium arises in the cortex (◘ Fig. 14.5i). This new, bifacial cambium generates both xylem and phloem. Upon further development, the stem of this eudicot will have a ring of vasculature with fully developed primary vascular bundles scattered in the pith, reminiscent of a monocot stem.

Trumpet creeper (*Campsis* sp.), another climbing vine, has a normal vascular cambium that generates phloem externally and xylem internally (◘ Fig. 14.5j). However, it also has a second, abnormal vascular cambium to the interior, which is reversed. It produces external xylem and internal phloem, resulting in inverted arrangement of the vascular tissues.

In *Bougainvillea,* the bifacial vascular cambium initially develops in a normal fashion, producing secondary xylem to the interior and secondary phloem to the exterior. However, that cambium eventually ceases activity altogether, and a separate (anomalous) secondary cambium forms in the phloem tissue of each vascular bundle (◘ Fig. 14.5k). Like the first cambium, it also generates xylem and phloem, but the xylem generated to the interior grows around and completely surrounds the previous phloem. The phloem thus surrounded is called **included phloem**.

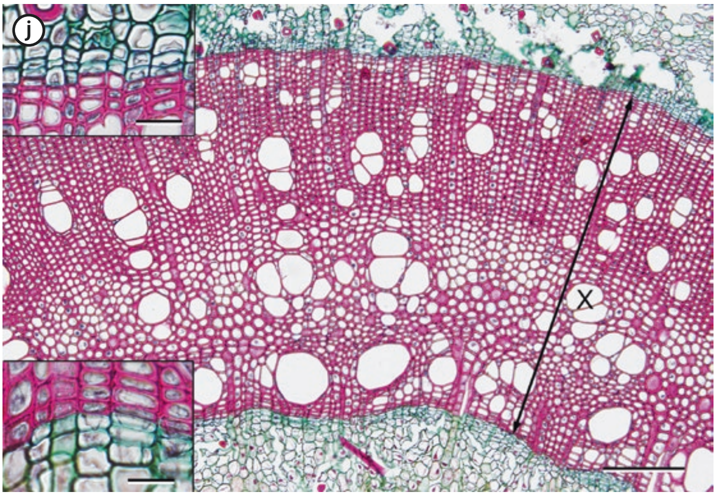


Fig. 14.5 **j** Trumpet creeper (*Campsis radicans*) double cambium. A large band of xylem (X) is indicated. The insert at the top left shows the external cambium producing phloem tissues to the exterior. The inset in the lower left shows the internal cambium producing phloem tissues to the interior. Scale bars = 100 µm in main panel and 10 µm in insets (RR Wise)

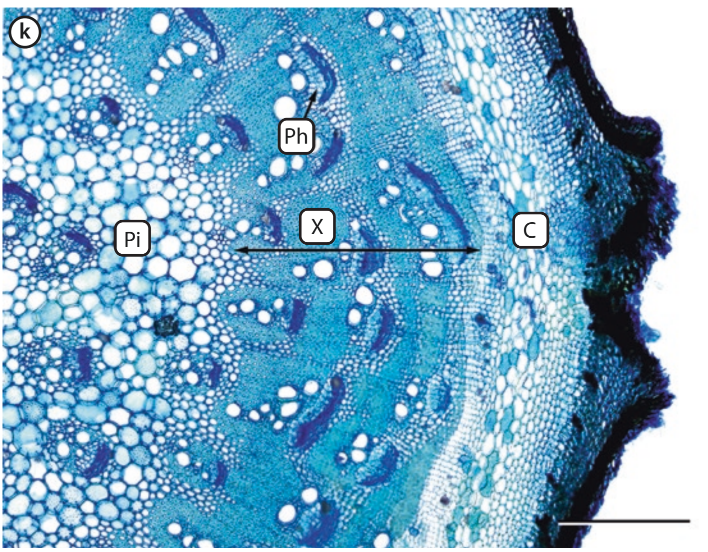
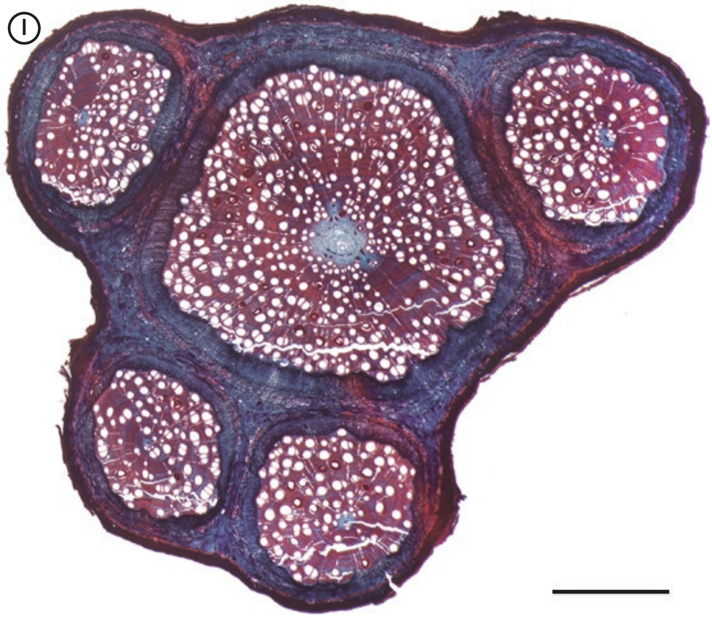


Fig. 14.5k **k** Included phloem in bougainvillea (*Bougainvillea* sp.) stem. A thick band of xylem tissue (X) lies between the parenchymatous pith (Pi) to the interior and parenchymatous cortex (C) to the exterior. A representative patch of included phloem (Ph) is indicated by the arrow, capped by a layer of phloem fibers to the exterior. Note also a lenticel to the right. Scale bar = 250 µm (RR Wise)

Some plants, again mostly vines and lianas such as *Paullina* and *Serjania*, develop multiple vascular cambia within one stem. Primary growth produces the basic eudicot stem, but then individual islands of parenchyma cells in the pith differentiate into cambial cells and form their own circular cambia that develop xylem, phloem, and pith. The result is a stem with multiple, separate vascular cylinders



◘ **Fig. 14.5** **l** Extra-stellar vascular bundles in a *Serjania polyphylla* liana. Scale bar = 2 mm. Specimen courtesy of Jack Fisher (RR Wise)

all surrounded by a singular periderm. Five separate **extra-stellar vascular bundles** are shown in the *Serjania* liana illustrated in ◘ Fig. 14.5l. This arrangement is sometimes called polystelic.

14.5.3 Anomalous Secondary Growth in Roots

The beet root is a major storage organ, with the roots of some commercial varieties attaining the size of a soccer ball. The primary beet root initially generates a ring of vascular cambium in the cortex that produces xylem and phloem. However, as the root increases in diameter, multiple successive, concentric cambia arise spaced to leave wide zones of storage parenchyma between (◘ Fig. 14.5m). Thus, there is a scarcity of xylem in the beet root. Abundant phloem is needed to transport the sugars that are stored in the thick bands of parenchyma. On the other hand, roots do not transpire; consequently the demand for xylem-supplied water is quite low.

14.5.4 Spiral Growth in Eudicots

The final form of anomalous growth has to do not with cambial location or activity, but with the shape of the fusiform initials and the derivatives generated. In this case, anticlinal divisions of the cambial initials result in stunted cells that do not grow. Thus, the adjacent cells elongate, with the result being a twisting of the growth pattern (◘ Fig. 14.5n, o). **Spiral growth** may be the result of prevailing winds or soil water availability, but the true cause has yet to be

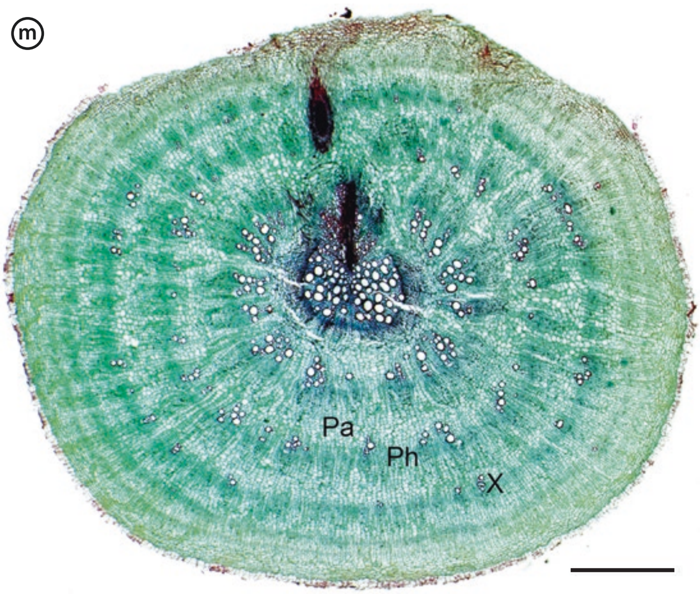


Fig. 14.5 **m** Concentric successive cambia in beet (*Beta vulgaris*) root have produced abundant phloem (Ph-darker green) interspersed with parenchymatous storage tissue (Pa-lighter green), allowing for high rates of both transport and storage. Xylem tracheary elements (to the immediate left of the X) become progressively scarcer as the root expands. Scale bar = 500 µm (RR Wise)

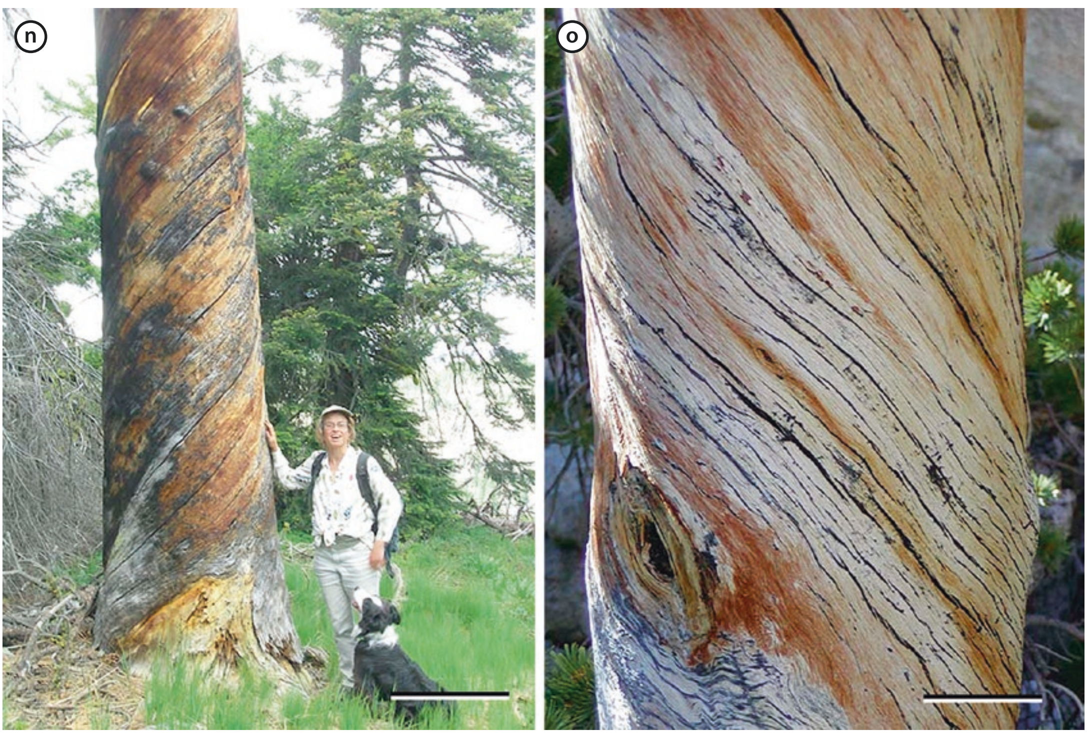


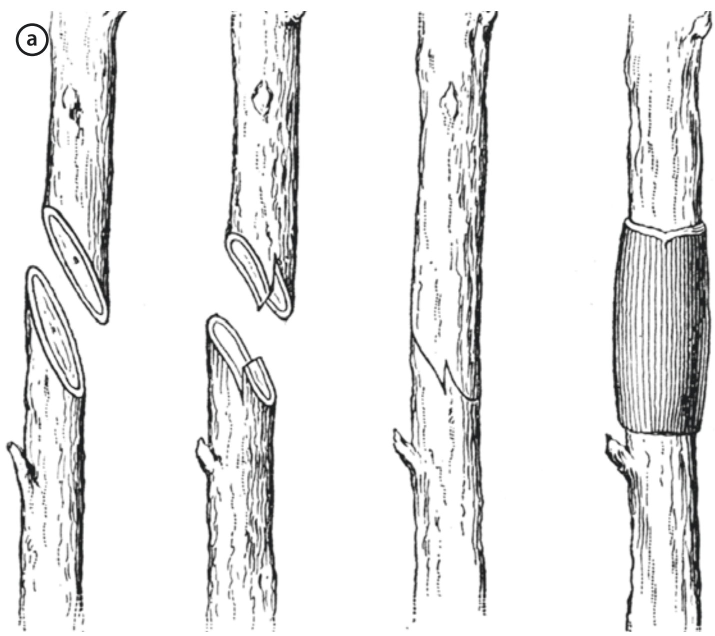
Fig. 14.5 **n** Ponderosa pine (*Pinus ponderosa*) and **o** white bark pine (*Pinus albicaulis*) displaying spiral vascular cambium activity. Note that the spiral growth may be either **n** right-handed or **o** left-handed. Scale bars = 1 m in **n** and 0.3 m in **o**. (**n**, **o** C Earle)

elucidated. Spiral growth trees may be right-handed or left-handed, although right-handed patterns seem to prevail. Such trees are worthless to the lumber industry and are actually quite dangerous to saw due to the uneven forces in the log.

14.6 Grafting Relies on the Fusion of Active Vascular Cambia

Grafting is a process by which stems of plants that have a generally close taxonomic relationship are spliced together and allowed to grow. The plant with the established root system is called the **rootstock**; the stem piece grafted to it is the **scion**. It is important that the vascular cambia of the scion and the rootstock come into as extensive contact as possible in order to allow for the development of secondary tissues between the graft where vascular transport occurs. Grafts may be between two stems of the same diameter (◘ Fig. 14.6a), or multiple small scions may be grafted onto a larger rootstock (◘ Fig. 14.6b, c).

Grafting has been used in scientific studies to study the xylem or phloem transport of plant growth regulators (specifically those involved in flowering) and viruses. In addition, non-chlorophyllous (albino) plants that normally die after their seed food is utilized can often be studied by grafting them onto the stock of a closely related wild-type plant. Grafting is also widely used in the horticultural industry (◘ Fig. 14.6b, c). In fact, the vast majority of wine grapes grown worldwide are the result of grafting a particular high-quality stem (where the fruits are borne) onto insect- and disease-resistant rootstock.



◘ **Fig. 14.6** **a** Grafting of a single scion to a stem. The two stems are cut and mated and then the joint is wrapped in tape or wax (Image from HH Cummings (1909) Nature Study by Grades, public domain)

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Fig. 14.6 Grafting of multiple scions to a single pear (*Pyrus* sp.) rootstock. Six scions were grafted on to the periphery of a single trunk and then bound with a binding wrap and covered with paint. **b** An image taken about 5 weeks after the graft. **c** Six months after grafting, the shoots have become established and leaves have developed. Bamboo support poles will be used for the first 4 or 5 years until the graft union is strong enough to hold the new limbs and the fruit they will produce. Scale bar = 10 cm (**b**, **c** Images courtesy of Michael Hamphel, Grouse Mountain Farms, Chelan, WA)

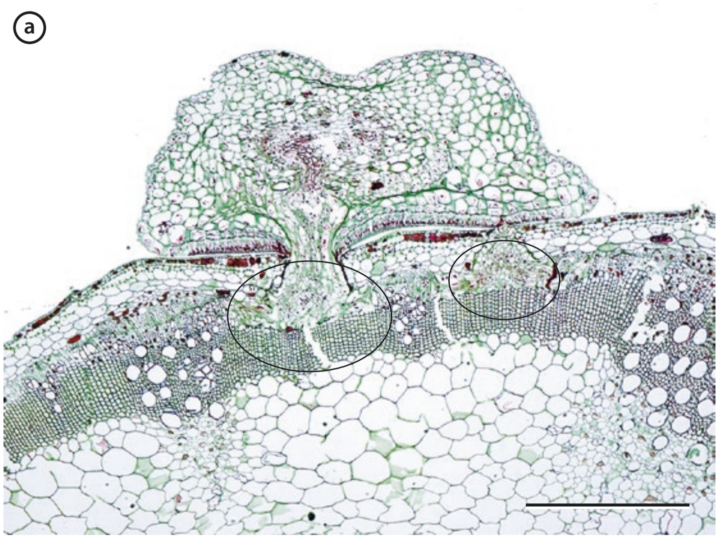
Box 14.2 Plant Grafting

The process of grafting dates well back to Biblical times as well as to ancient Greek and Chinese times. In the modern world, grafting (a shoot scion attached to a rootstock) is used to maintain fruit crops and horticultural variants and in scientific research. However, monocots do not connect to each other as they do in eudicots due to the virtual random arrangement of the vascular connections in the intermodal regions. But in eudicots, some species pairings, such as that between potato and tomato in the Solanaceae, are able to be grafted with little difficulty. If done properly, one can obtain a single plant with potatoes beneath the ground and tomato fruits on the shoots. Of course, the opposite arrangement yields neither even though the graft may be vegetatively successful. It appears that the plant growth regulator, auxin, plays a key role in promoting a successful graft. In research, long-term grafts of the same species, e.g., soybean, are useful to study the growth of a genetically based scion that is devoid of chlorophyll. Grafting is a form of wound response similar to that due to injury from herbivory or wind damage. In all cases, a callus forms, tissues

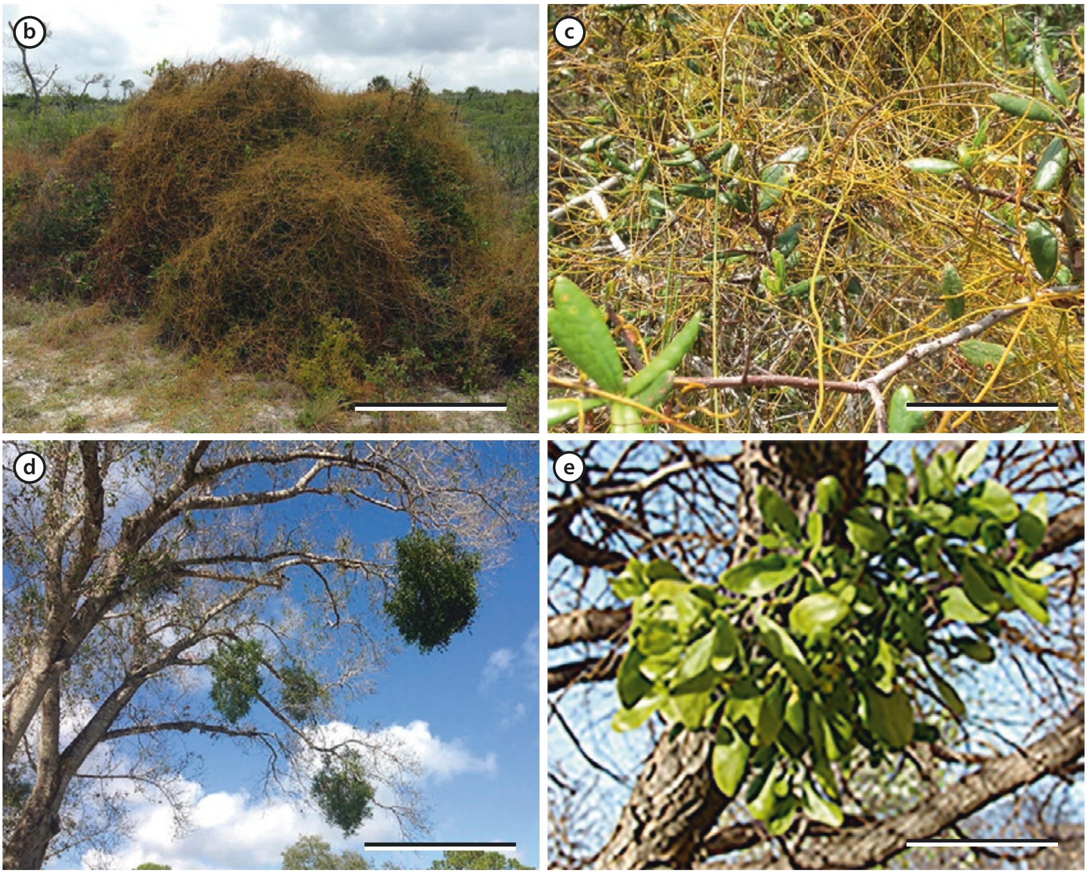
adhere, and the vascular tissue reestablishes which enables water, nutrient, and molecular transport to occur. With recent research on RNA silencing and its potential to regulate growth as well as stress resistance, plant grafting will remain an active area of research for some time to come.
Reference: Melnyk and Meyerowitz (2015).

14.7 Parasitic Plants Merge Their Vasculature with that of the Host Plant

The definition of a plant from ► Chap. 1 is any eukaryotic organism that relies on photosynthesis as a method of acquiring food. Some parasitic plants, however, violate that simple definition. The roots of parasitic plants are modified into haustoria (sing., haustorium) which penetrate a host and fuse with the host's vasculature, much like the grafting described above. There are two classes of **parasitic plants**; both are eudicots. **Holoparasites** infect a host plant and fuse both their xylem and phloem with corresponding tissues in the host plant stem or root (◘ Fig. 14.7a). They then rely on the host for both water (via the xylem) and photosynthate (via the phloem). Thus, they are heterotrophic angiosperms. Holoparasites tend to be leafless, yellow to orange stems and can completely smother and kill their host. Leaves and chlorophyll are not needed because all nutrition comes from the host. Love vine (◘ Fig. 14.7b, c) is a holoparasite, while



◘ **Fig. 14.7** **a** Penetration of dodder (*Cuscuta* sp.) haustoria (top) into unidentified host (bottom) stem and fusion of the vasculatures (circles). The larger fusion to the left is further developed than the smaller fusion to the right. Scale bar = 500 µm (RR Wise)



◘ **Fig. 14.7** **b**–**e** Two parasitic plants. **b**, **c** Love vine (*Cassytha filiformis*) is a holoparasite with yellow stems and no leaves. **d**, **e** American mistletoe (*Phoradendron leucarpum*) (shown here parasitizing a live oak—*Quercus virginiana*) is a hemiparasite with green leaves, but no root system. Scale bars = 1 m in **b** and **d** and 10 cm in **c** and **e** (**b**, **c** RR Wise; **d** OM Wise; **e** GR Rogers, Palm Beach State College)

mistletoe (◘ Fig. 14.7d, e), the second type of parasitic plant, is a **hemiparasite**. It is photosynthetically independent, but relies on the host plant xylem for water and minerals.

Plasmodesmata allow for symplastic connections between adjacent plant cells. When a host plant is infected by the haustorium of a parasitic plant, nutrients are transferred from the host to the parasite. Such nutrients are carried in the phloem sieve tube elements of the host. Anatomical studies have demonstrated numerous plasmodesmata between the cells of the parasite and cells of the host. Experiments using radiolabeled sucrose, amino acids, phytohormones, other chemical tracers, and live virus particles showed direct transfer of all these components from host to parasite. It was even possible to detect transfer between two host plants using the parasite *Cuscuta* as a bridge between the two host plants. This study provided clear evidence of the symplastic transfer of phloem solutes from parasite to host (Birschwilks et al. 2006).

14.8 Chapter Review

■ Concept Review

14.1 *The vascular cambium is a single-layer cylinder of meristematic cells.* The vascular cambium is composed of a single layer of bifacial cambial initials. They divide and produce xylem mother cells to the interior (adaxial) and phloem mother cells to the exterior (abaxial).

14.2 *The transition from primary to secondary growth requires lateral expansion of the vascular cambium.* Vascular bundles are generated by primary growth. Closed bundles can develop no further. Open bundles contain a meristematic fascicular cambium. Upon the transition to secondary growth, parenchyma cells lying between vascular bundles develop into an interfascicular cambium that grows toward and eventually connects to the fascicular cambia. Thus, the vascular cambium cylinder is produced.

14.3 *The vascular cambium contains two types of cells—fusiform initials and ray initials.* The axial vascular system transports water and sugars up and down the stem or root. The radial vascular system transports water and sugars from the center out to the living periderm. Fusiform initials generate xylem and phloem of the axial system. Ray initials generate parenchyma cells of the radial system.

14.4 *Fusiform initials can be arranged in different patterns.* Most plants have an irregular arrangement of fusiform initials, called non-storied. A storied cambium has aligned rows of cambial initials.

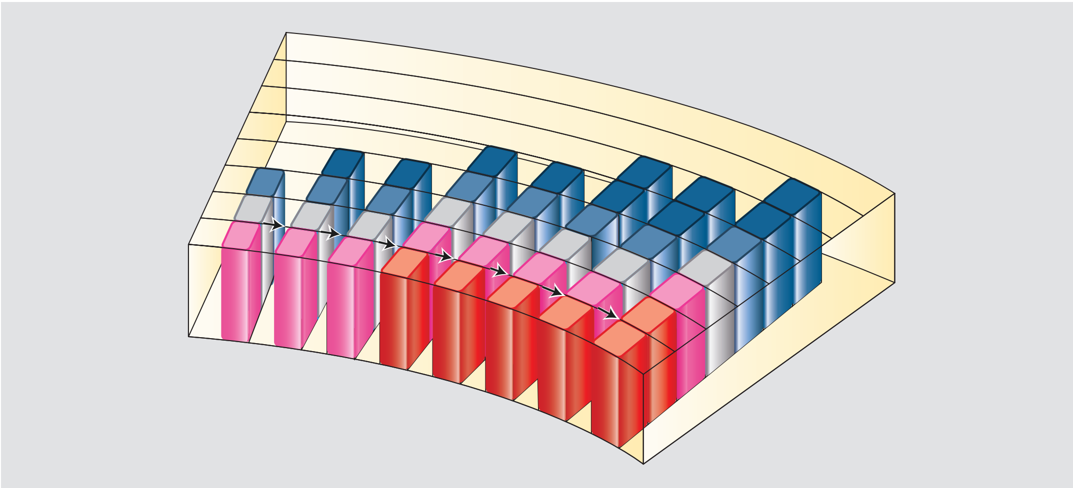
14.5 *Anomalous vascular Cambium produce atypical growth patterns.* Multiple variations of vascular cambium exist called anomalous cambia. They include (1) cambia in a normal location with abnormal growth, (2) abnormal location with normal growth, (3) anomalous cambia in roots, (4) spiral growth in eudicot stems.

14.6 *Grafting relies on the fusion of active vascular cambia.* Grafting splices a scion and a root stock together. The vascular cambia of the two tissues fuse and produce a permanent connection between the two plants. Grafting is used in both scientific studies and in the production of novel horticultural combinations of shoots and roots.

14.7 *Parasitic plants merge their vasculature with that of the host plant.* Holoparasitic and hemiparasitic plants use a modified root (haustorium) to penetrate a host plant and tap into the host's vasculature system.

Concept Connections

1. Label the cambial initials, xylem derivatives, and phloem derivatives in the figure below.



Concept Assessment

2. Which is *not* produced by fusiform initials?
   a. fibers.
   b. tracheids.
   c. rays.
   d. companion cells.
   e. axial parenchyma.

3. Hemiparasitic plants differ from holoparasitic plants in that
   a. hemiparasites are free-living; holoparasites are completely dependent on the host.
   b. hemiparasites are photosynthetic; holoparasites are heterotrophic.
   c. hemiparasites are eudicots; holoparasites are monocots.
   d. hemiparasites have a vasculature system; holoparasites lack a vasculature system.
   e. hemiparasites are colorless; holoparasites are green.

4. Interfascicular cambium is formed
   a. by the fascicular cambium.
   b. deep in the pith.
   c. only in monocots.
   d. by differentiation and division of parenchyma cells.
   e. from active dividing, primary phloem cells.

5. Cells produced by the vascular cambium toward the abaxial direction are destined to become
   a. meristematic.
   b. phloem.
   c. xylem.
   d. pith.
   e. additional cambium.

6. Uniseriate rays are characteristic of
   a. ferns.
   b. gymnosperms.
   c. eudicots.
   d. monocots.
   e. all angiosperms.

7. Theoretically, the vascular cambium is comprised of a layer of how many cells?
   a. one.
   b. three.
   c. five.
   d. seven.
   e. more than eight.

8. Most primary pit fields found in vascular cambium are found
   a. on transverse walls.
   b. after secondary wall formation.
   c. on radial walls.
   d. on tangential walls.
   e. on ray initials.

9. In order for a cambial initial to generate a derivative it must divide
   a. in a horizontal plane.
   b. in a radial plane.
   c. in a periclinal plane.
   d. in an alternate plane.
   e. in an anticlinal plane.

10. Anomalous vascular architectures are often found in lianas because climbing vines
    a. only need xylem for transpiration.
    b. are major storage organs.
    c. use the host plant for support.
    d. a and b.
    e. a and c.

11. Supernumerary cambia typically arise in the
    a. secondary phloem.
    b. pith.
    c. xylem.
    d. periderm.
    e. vascular cambium.

- **Concept Applications**

12. What is the relationship between open vascular bundles, closed vascular bundles, primary growth, and secondary growth?

13. Why are holoparasites colorless?

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Wood: Economics, Structure, and Composition

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Introduction

Wood and the trees that produce it are all around us. Humans (and other animals) have used wood for thousands of years and in thousands of applications. Wood provides shelter, tools, furniture, heat, food additives, medicines, and drugs, to name just a few of the many applications. About 20%, or 66,065, of all plant species are trees (Beech et al. 2017), the wood of which provides a wealth of possibilities. Unfortunately, many tree species are endangered due to overharvesting, habitat destruction, and global climate change. The future will see if humans can continue to exploit wood as a valuable resource and not put up too many parking lots.

15.1 Wood Has Significant Worldwide Economic Value

Wood is the multiyear accumulation of xylem growth (refer to ► Chap. 7). It functions to provide support to the plant and acts as a conduit for the transport of water from the soil to the leaves. Wood is the most widely used plant product in the world (FAO 2017) with items ranging from toothpicks to massive beams. The wide range of wood properties—strength, color, grain, and workability—make it an extremely versatile material for all manner of human uses (◘ Fig. 15.1a–u).

Wood is the product of secondary growth as revealed in annual growth rings. As is well known, wood is used in furniture making, as a fuel, in electrical generation, and even as a food supplement. In India, the export of various raw timbers, as well as finished furniture and other home products, is a major industry largely comprised of darker woods such as teak (*Tectona grandis*), meranti (*Shorea* sp.), and mahogany (*Toona* sp.). In China, the export of unfinished wood was once a growing industry, but has leveled off since 2005 in which furniture and plywood are now the primary products produced and sold on the open market. The lack of growth in the China wood industry can largely be attributed to the reduction in the amount of wood that is being harvested. The timber products from China are mostly made into furniture and plywood that are exported and shipped to other nearby Asian countries, the USA, and Europe—primarily the UK. The majority of Chinese-exported woods are from pines, fir, eucalyptus, and some birch.

The USA is also a contributor to the export of woods, but primarily as logs and lumber, mostly softwoods, which are usually assembled as already made products (e.g., casks, door frames, and prefabricated wood buildings) and fuel (e.g., wood chips). Many individuals might find it surprising that Canada is the world's leader as an exporter of softwood lumber, wood pulp, and newsprint. It is also the leading seasonal producer of Christmas trees—largely pine, spruce, and fir.

Fig. 15.1 Some examples of different types of North American hardwoods used in furniture and finished flooring applications. **a** Red maple (*Acer rubrum*), **b** sugar maple (*Acer saccharum*), **c** chestnut (*Castanea dentata*), **d** green ash (*Fraxinus pennsylvanica*), **e** butternut (*Juglans cinerea*), **f** black walnut (*Juglans nigra*), **g** sweet gum (*Liquidambar styraciflua*), **h** tulip poplar (*Liriodendron tulipifera*), **i** apple (*Malus pumila*), **j** black cherry (*Prunus serotina*), **k** white oak (*Quercus alba*), and **l** red oak (*Quercus rubra*). Scale bar in **l** = 2 cm and applies to all panels (**a**–**l** RR Wise)

15

Fig. 15.1 Nine New World and Old World tropical hardwoods, selected to emphasize the range of natural variation in color and figure: **m** Bahia rosewood (*Dalbergia nigra*), **n** eucalyptus (*Eucalyptus* sp.), **o** zebrawood (*Microberlinia brazzavillensis*), **p** wenge (*Millettia laurentii*), **q** purpleheart (*Peltogyne paniculata*), **r** padauk (*Pterocarpus* sp.), **s** Honduras mahogany (*Swietenia macrophylla*), **t** tamarind (*Tamarindus indica*), and **u** teak (*Tectona grandis*). Scale bar in **u** = 2 cm and applies to all panels (**m**–**u** RR Wise)

Brazil is another major exporter of wood products. The Brazilian wood largely comes from the forests in the Amazon region and includes pine and eucalyptus which are either processed or exported as pulp, wood chips, plywood, paper, flooring, and furniture. Like China, these products are exported to countries all over the world. However, in Brazil due to vast deforestation, certain woods are governmentally prohibited to be harvested. These woods include rosewood, nut trees, and the native brazilwood (*Caesalpinia echinata*).

15.2 A Wide Variety of Products Are Made from Wood Fibers and Wood Extracts

Various paper products may be made from wood fibers. Smooth and soft paper products like napkins, tissue paper, and absorbent towels are typically produced from debarked hardwood trees after lengthy cooking and digesting in sodium hydroxide and sodium sulfide. The pulp product is then filtered for particle size, and chalk, clay, starch, or titanium oxide may be added to meet the color and absorbency nature of the pulp. The treated pulp is then run through metal rollers, dried and cut to size. Less processed pulp (i.e., shorter digestion, larger filter size, and less chemical treatment) will result in heavier products such as boxes or pressed wood. In addition to paper products from wood, some technically non-woody materials are flax, which can be used for cigarette paper, and cotton and linens, which are used in the form of rope and textiles. Bamboo, straw, and even sugarcane, as well as linens, are used as additives to wood pulp to produce specialty paper products such as bank checks, résumé paper, and paper money.

Some wood products are exclusively composed of cellulose fibers to make artificial sponges, chewing gum from chicle sap, various types of dyes from bark, and rubber from latex derived from the phloem of the rubber tree (*Hevea brasiliensis*). Cellulose derived from wood is also used as a food thickener and is often employed in the production of ice cream. Finally, sugar, such as in maple syrup, and spices, such as cinnamon, are food products produced from woods.

A long history exists in the medical field involving the production of medical products, called **silvichemicals**, which are extracted from certain types of woods and are used in the healing or prevention of illness. Quinine, used to treat malaria, is also derived from the bark of the *Cinchona* sp. (family Rubiaceae) tree. Other medicinal extracts such as betulin from birch bark are known to have antibacterial properties, and pine compounds include sterols which may be used as additives in margarines and yogurt products and reduce cholesterol when consumed regularly. Additional drug items from trees include the ones found in cough syrup, laxatives, pain relievers, tranquilizers, and worm repellents. Many cosmetics contain a cellulose derivative called carboxymethyl cellulose (also known as cellulose gum) to help stabilized and thicken makeup creams.

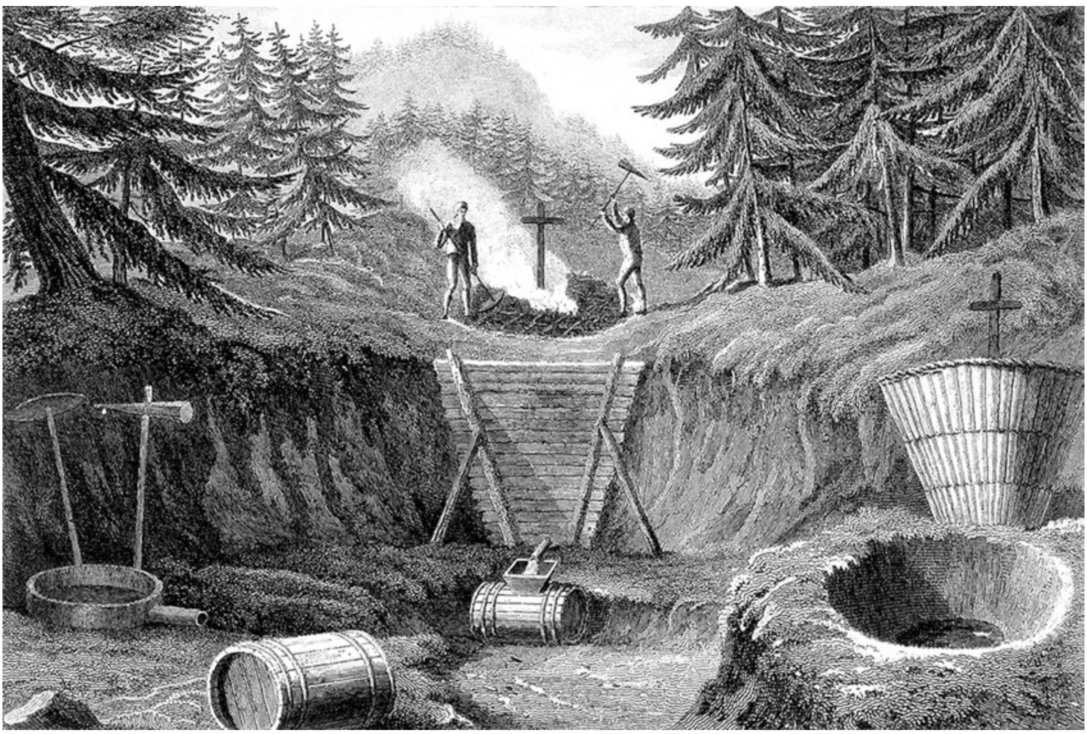
15

Box 15.1 Natural Wood Fibers Meet Modern-Day Plastics

Research at the University of Southern Mississippi's School of Polymers and High Performance Materials uses natural wood fibers to reinforce plastic products. The renewable wood fiber composites could revolutionize building construction, automobiles, and aircraft. It could also be a boon for the paper industry by providing new uses for fibers that can strengthen plastics. It further enables products to be shaped without having to melt them in the preparation. Other products, such as permanent

bonded magnets which are used in computers and cars, can develop higher energy without the use of rare earth metal alloys by designing magnetic powders with polymer matrices from wood fibers and do so at needed higher temperatures. Nanostructured hybrid organic-inorganic thermoplastic materials containing wood products can demonstrate many benefits in plastic composites without the disadvantages, giving improved energy efficiency in laser fusion systems, biomaterials, storage materials for nuclear wastes, and in load-bearing hybrid composites. Furthermore, the organic-inorganic hybrid materials make products more moisture resistant, thereby providing greater control over biodegradation processes.
Reference: Otaigbe and Naim (2014)

During the eighteenth and nineteenth centuries and the first half of the twentieth century, pine trees mostly from Finland and Sweden were extensively harvested and baked under moss or canvass in order to extract resin by heat, which was then collected in barrels as tar (◘ Fig. 15.2). The pine tar was exported throughout



◘ **Fig. 15.2** Representation of the process of making tar in the forests of Sweden. A pine tar pit is excavated in a hillside, and then piles of pine logs and branches are arranged at the lower in the pit, with the lower end covered by planks. The pile is ignited and then covered with layers of moss, earth, or a tarpaulin to eliminate air. The pine sweats tar during the burning process and drips out of the bottom of the pile, and it is collected in barrels. The wood is oxidized to charcoal. (Image from Clarke (1816), public domain) the world, especially to New York City, for use in roofing and in the construction of roads. Some was used as a sealant for wooden ship hulls, and by-products included turpentine and pine oil. Pine tar also has a long history as a topical treatment for skin conditions (Barnes and Greive 2017). The vast deforestation of this European forest resulted in a major loss of a large part of that country's native trees, such that today there are only rare sites in Finland that have native forestation.

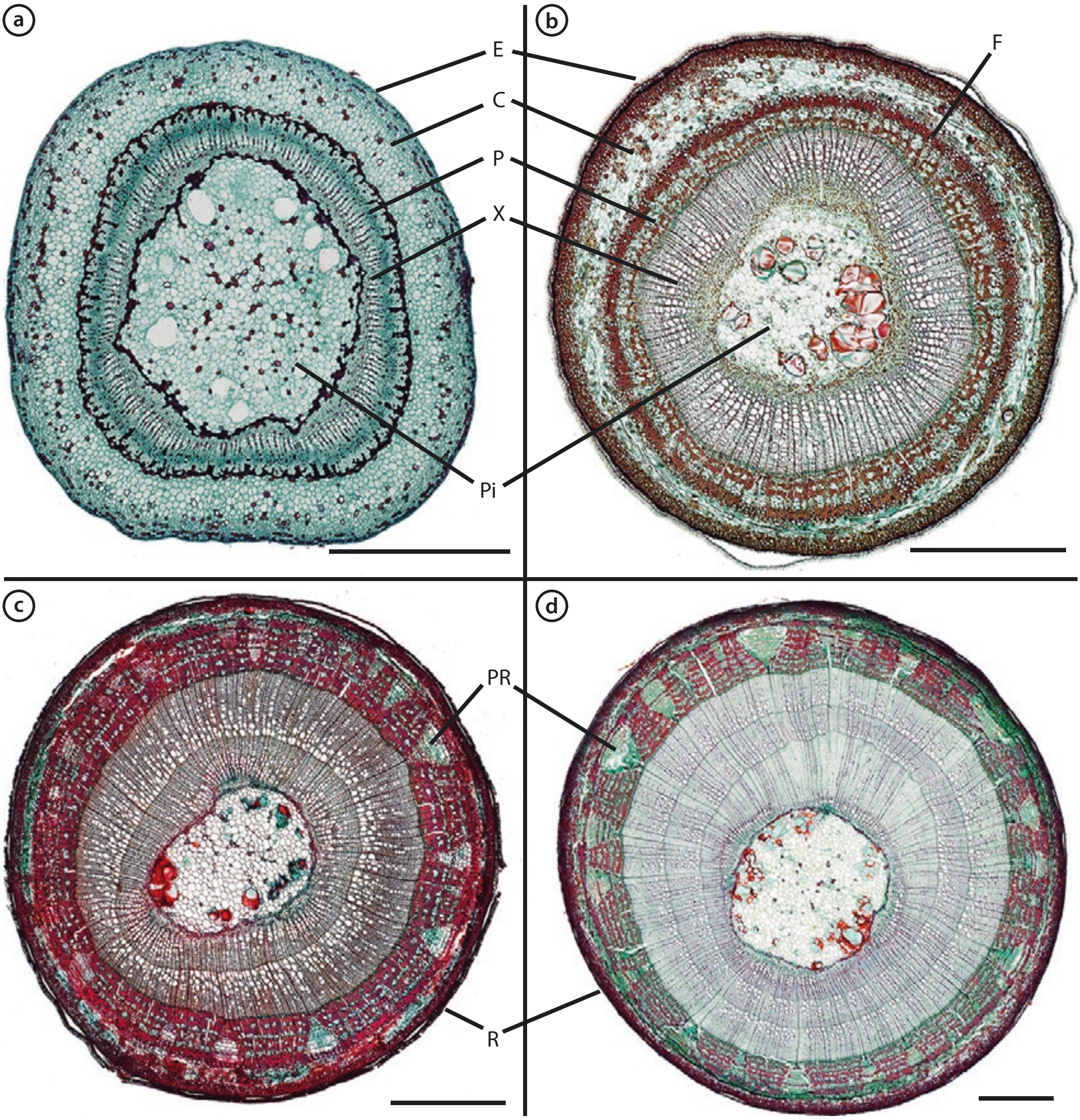
15.3 Wood Development and Composition Show Annual Cycles

Wood develops from the secondary growth of cambium in gymnosperms and woody eudicots. ◘ Figure 15.3a–d shows the progressive changes that take place during early secondary growth of a perennial eudicot stem. The cells of the vascular cambium involved in secondary growth are termed fusiform initials. They are characterized by being elongated with tapered ends and give rise to the cellular elements of the axial system in secondary woods. The manufacture of wood (secondary xylem) takes place in major steps, starting with cell division, cell expansion (elongation and radial enlargement), cell wall thickening (involving cellulose, hemicellulose, cell wall proteins, and lignin biosynthesis and deposition), and ending with programmed cell death.

Each successive year of vascular cambial activity leaves a layer of xylem to the interior and phloem to the exterior. The xylem persists and accumulates with each growing season producing one tree ring (see below), while the phloem (▶ Chap. 8) becomes crushed and incorporated into the periderm (▶ Chap. 16).

In most temperate woody species, vessel element and tracheid diameters respond to the seasonal growth conditions that reflect rapid growth in the spring, slowing of growth over the summer, and the cessation of growth in the fall (◘ Fig. 15.3e, g). This causes annual growth rings and the related wood characters called "figure" or "grain." Most conifers and temperate eudicot trees have prominent growth rings (◘ Fig. 15.3f, h). Many tropical ecosystems have little annual variation in temperature or rainfall. Therefore, tropical hardwood species such as eucalyptus and mahogany (◘ Fig. 15.1n, s) have less prominent annual growth rings and have an appearance called "smooth grained."

The science of **dendrochronology** relies on the generation of a new growth ring every year, but that is not always the case. If growth conditions are unfavorable, a tree may not lay down a continuous ring of xylem every season. A period of inactivity, followed by a resumption of activity, will result a missing ring. A false ring forms when there is a growth interruption, such as a severe spring drought, from which the tree recovers and starts a new ring later in the growing season. There will be the appearance of two rings.



■ **Fig. 15.3** **a**–**d** Cross-sections of American basswood (*Tilia americana*) stems. **a** Stem at the beginning of the first year of growth with a continuous ring of developing xylem and phloem. Pith is seen at the center of all four stems. A cortex has developed at this early stage and the epidermis is thin. **b** Stem at the end of year one. The epidermis has sclerified and a ring of phloem fibers (F) has developed. A large ring of xylem indicates the first year's woody growth. **c** Stem at the end of year two. The phloem has become progressively more sclerified, and a second growth ring surrounding the first year's woody growth is apparent. Phloem rays have expanded to accommodate the increase in stem circumference. A third layer of xylem has been produced and phloem rays have expanded. The epidermis has transformed to a rhytidome. C cortex, E epidermis, P phloem, Pi pith, PR phloem ray, R rhytidome, X xylem. Scale bar = 500 µm in all panels (**a**–**d** RR Wise)

Discontinuous rings, also called locally absent rings, form when a portion of the vascular cambium goes quiescent (but does not die) for a year or more, while other regions continue to generate xylem derivatives. The area of the spruce stem shown in ■ Fig. 15.3i, j was quiescent for 6 years before resuming growth.

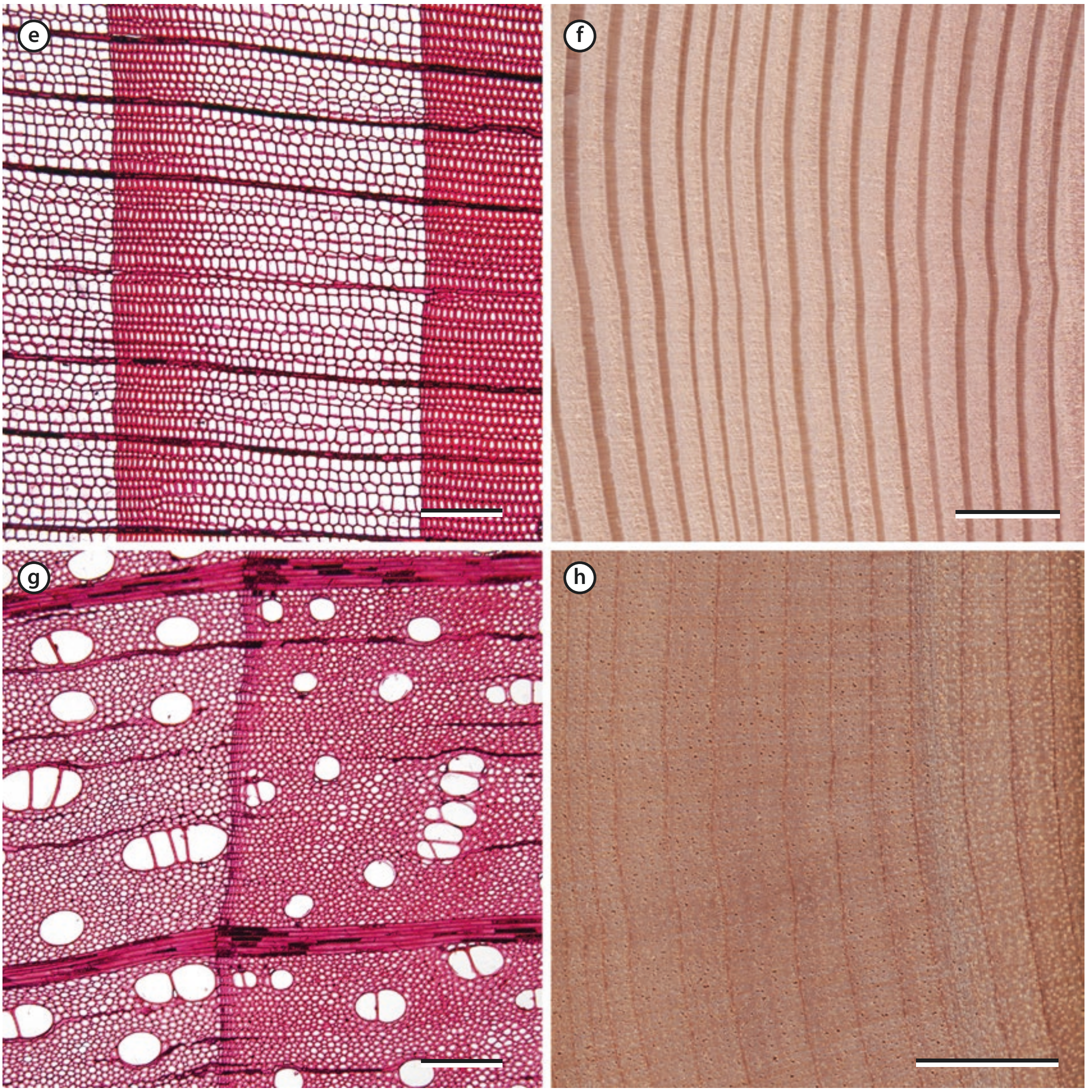


Fig. 15.3 Annual growth rings in a conifer and eudicot. **e** Annual rings of Douglas fir (*Pseudotsuga menziesii*), a coniferous softwood species, showing the springwood as the light portion and summerwood as the dark part of the rings. **f** Higher-magnification view on one growth ring. The summerwood tracheids (on the left edge of each ring) are smaller with thicker cell walls than the springwood tracheids. **g** Annual rings in sugar maple (*Acer saccharum*) accompanied with **h** an LM of the rings. Scale bars = 100 µm for **e** and **g** and 0.5 cm for **f** and **h** (**e**–**h** RR Wise)

15.4 Wood Varies in Its Architecture and Composition

15.4.1 Cross, Radial, and Tangential Planes of Section

Wood is a complex three-dimensional tissue that is best viewed in three different planes of section (Fig. 15.4a) (Meylan and Butterfield 1972). A **cross-section** is perpendicular to the long axis of the stem (or limb or trunk). It is the best section for revealing annual growth rings. A **radial section** (also called longitudinal

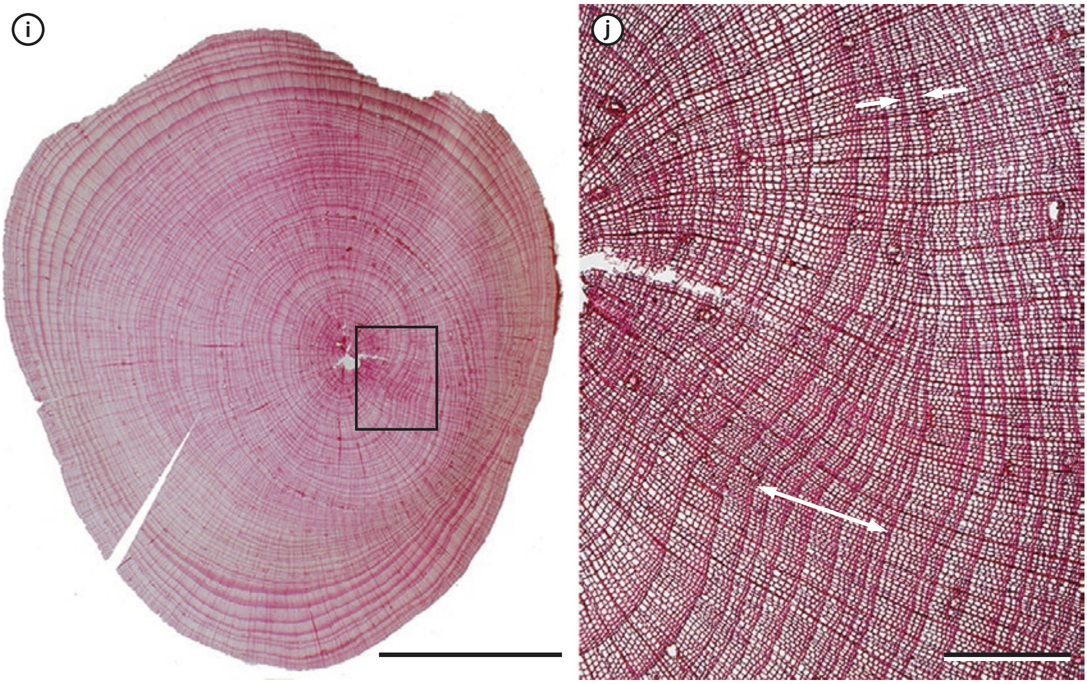


Fig. 15.3 **i** A spruce (*Picea* sp.) stem showing discontinuous tree rings. **j** A higher-magnification view of the boxed area in 15.3i. The single growth ring at the top of the image (*between arrows*) connects with seven growth rings at the bottom of the image (*arrow*). This particular stem has several areas of discontinuous growth rings; only one is highlighted. Scale bars = 0.5 cm in **i** and 250 μm in **j** (**i**, **j** RR Wise)

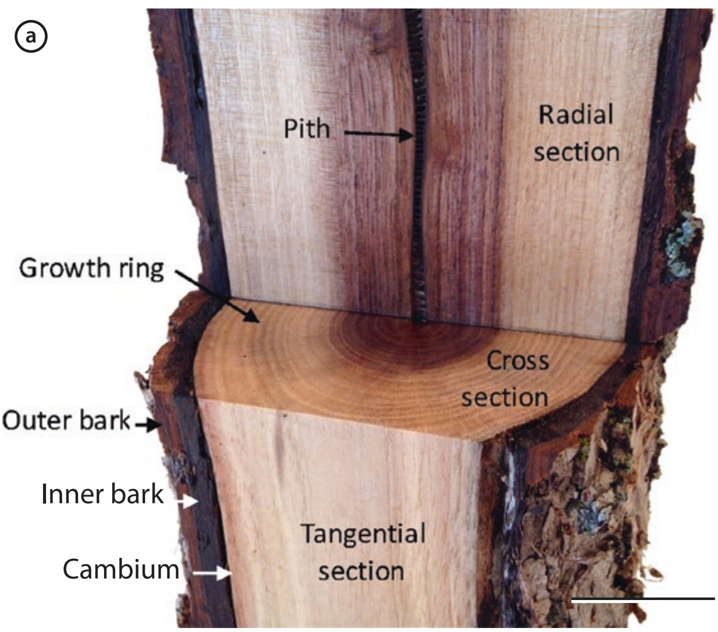


Fig. 15.4 **a** A 28-year-old black walnut (*Juglans nigra*) stem cut to expose the three planes of section—cross-section, radial section, and tangential section. Dark heartwood is at the center and lighter sapwood to the periphery. The location of growth rings, **outer bark**, **inner bark**, cambium, and pith are indicated. The age of the stem was determined by counting the annual **growth rings**. Scale bar = 2 cm (RR Wise)

section) is parallel to the longitudinal axis and runs through the center of the stem. The surface exposed by a radial section is therefore side view of the rays that extend from the center of the stem to the exterior. A **tangential section** is also parallel to the longitudinal axis, but is off-center. This plane of section allows for a visualization of ends of the rays as they run from the center to the exterior. The different planes of section reveal different information. For instance, because pits connect tracheids via the anticlinal walls, they are best viewed in a radial (c.f. ◘ Fig. 15.5g) or tangential section (c.f. ◘ Fig. 15.5l, m).

15.4.2 Softwood vs. Hardwood

It should be evident that not all woods are the same. Of course, the taxonomic nature of the species has much to do with the overall internal structure of wood, but other factors such as environmental conditions (e.g., temperature, humidity, and elevation) along with age and nutrition also play key roles. To begin with, most individuals have heard the terms "**softwood**" and "**hardwood**." While there is often a true difference in the physical hardness of woods, the term softwood is used in both the common and commercial senses to mean gymnosperm, while the hardwoods are angiosperm eudicots. Density is a common measure of wood hardness, and most hardwoods have a higher density than softwoods, but that is not always the case (◘ Fig. 15.4b). The primary difference is not necessarily the physical hardness of the wood but rather the presence of vessel elements (aka pores) and fibers in hardwoods vs. the lack of such cell types in softwoods. In addition, softwoods typically have a

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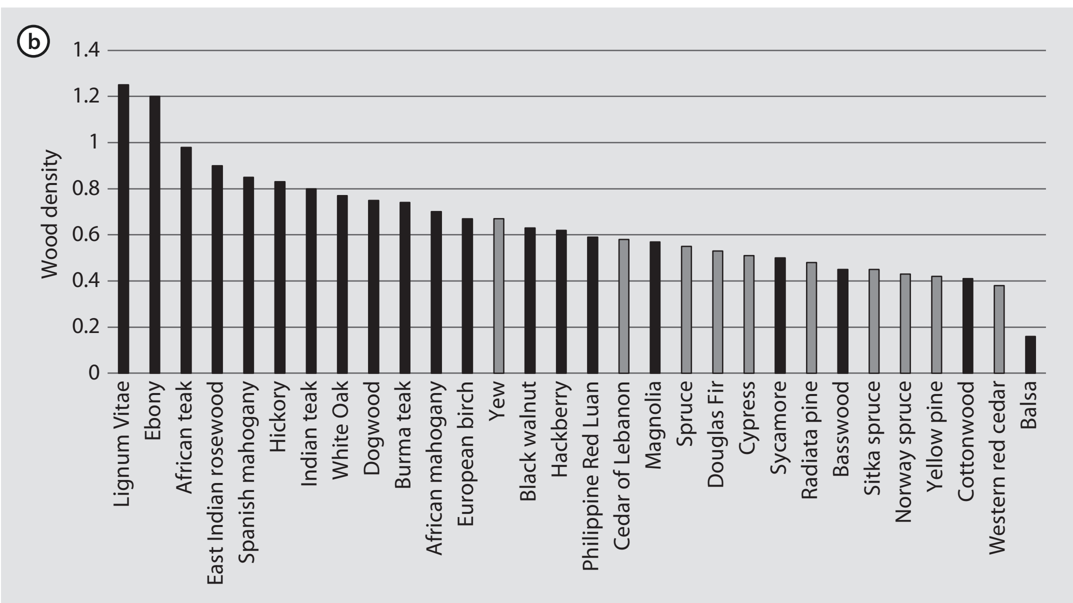
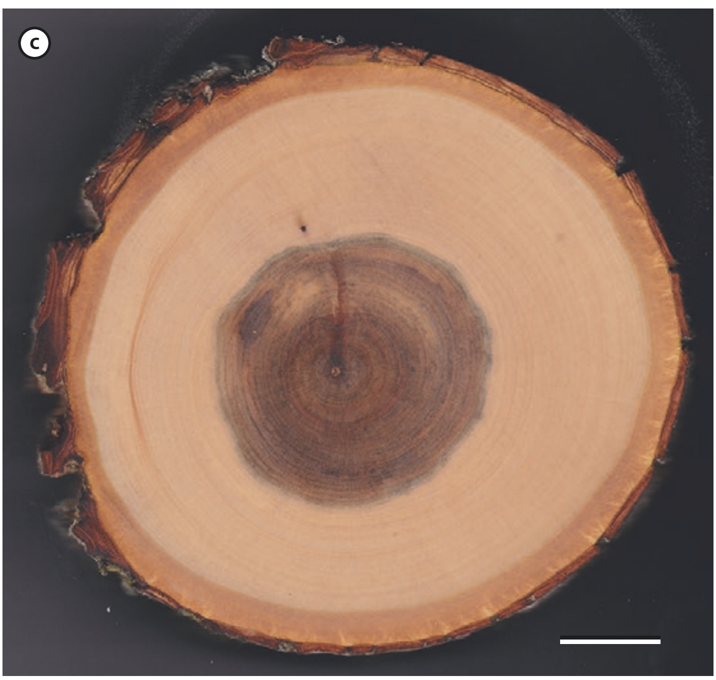


◘ **Fig. 15.4** **b** Specific gravities of selected eudicot (black bars) wood and gymnosperm (gray bars) wood. Note that not all hardwoods are high in density and not all softwoods are low in density. Units of wood density are 103 kg m^{-3}. (Figure compiled from publicly available data) (RR Wise) faster rate of growth than hardwoods, which is related to their lower density. Some common examples of softwoods are pine, spruce, Douglas fir, and juniper. Typical hardwoods are eudicots such as oak, maple, beech, ash, walnut, and hickory. There are exceptions to the eudicot = hardwood definition; balsa tree (*Ochroma pyramidale*) is a eudicot in the Malvaceae family with extremely soft- and low-density wood.

15.4.3 Sapwood vs. Heartwood

Another common distinction that is made in wood is age-related and often revealed by a difference in pigmentation (◘ Fig. 15.4c). For trees of several years of age, and then throughout the rest of their standing existence, an outer portion of wood, the **sapwood**, may appear lighter in color, has a relative high level of moisture due to the active transport of water by some living cells, and stores some energy reserves. Transpirational water moves through the open cells of the sapwood. Such wood is also often designated as living wood. Alternatively, the innermost region of wood, which is often darker in color, has less water and mineral reserves and is no longer active in translocation (i.e., dead tissue) and is designated as the **heartwood**. The darker color of heartwood is due to the buildup of resins, terpenes, and polyphenolic compounds as the wood ages.



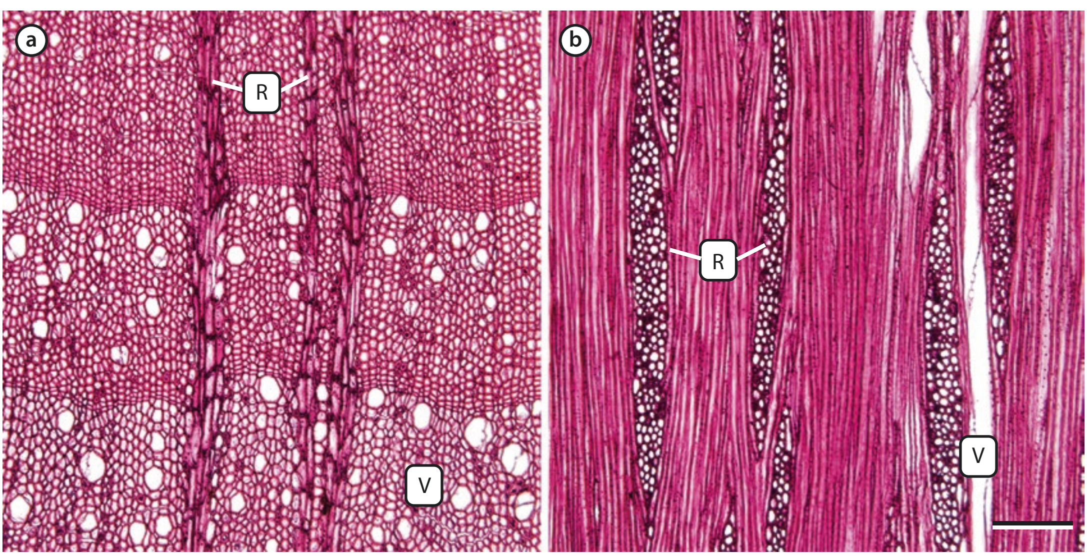
◘ **Fig. 15.4** **c** Cross-section of a Norway maple (*Acer platanoides*) stem showing a central, dark heartwood core surrounded by lighter sapwood. The sample has 58 annual growth rings, which are too small to be seen here. The first 28–30 years of growth have been converted to heartwood, while the subsequent ~30 years of growth remain as sapwood. Scale bar = 2 cm (RR Wise)

The center of the heartwood may be a small central region of soft, spongy-like material, which represents pith from the first year's primary growth that eventually becomes obscured in most species by being crushed. In a few cases, such as black walnut (*Juglans nigra*), it remains as a chambered pith (refer to ◘ Fig. 11.5j) but has no true function. Over the course of time, the heartwood becomes the dominant portion of a tree trunk. Because of its color, density, and strength, heartwood is usually the preferred type of wood for the purposes of furniture fabrication. The strength is largely due to the very low water content, since sapwood warps and shrinks somewhat when dried. Sapwood is also prone to decay and staining due to fungal infections. Those trees that have more rapid growth typically have more sapwood than heartwood, whereas the opposite is usually the case with slower growing species or in individuals where environmental conditions favor slow growth.

15.5 Conifer Wood Has Tracheids, Parenchyma, and Rays

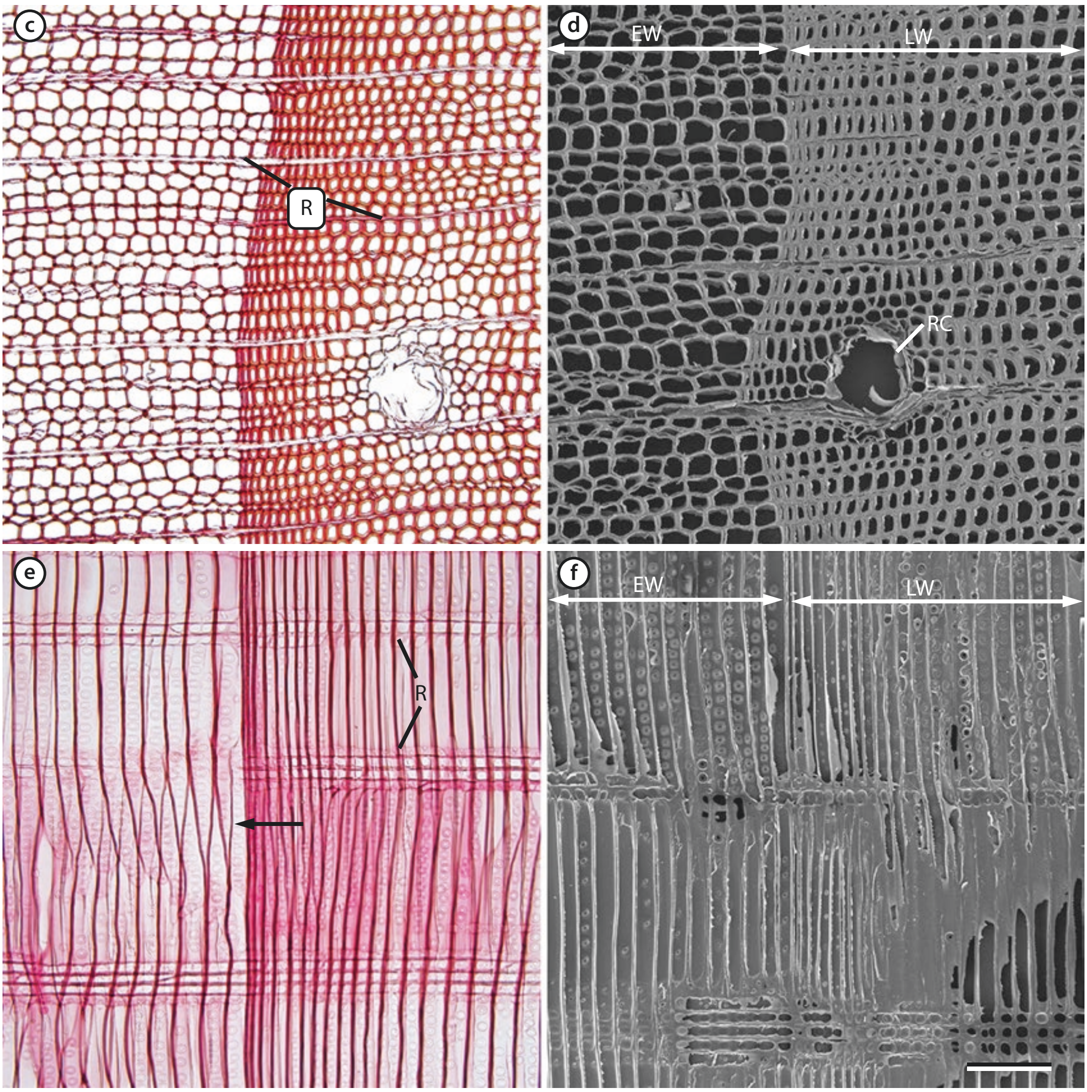
Xylem vessel elements (perforate tracheary elements; refer to ► Chap. 7) are a common feature of most angiosperm species but are only rarely found in gymnosperms. The gnetophytes (phylum Gnetophyta) which include three genera—*Ephedra*, *Gnetum*, and *Welwitschia*—are the only gymnosperm taxa that contain vessels (◘ Fig. 15.5a, b) (Carlquist 2001); all other gymnosperms only have tracheids (imperforate tracheary elements) as water-conducting cells.

Tracheids in the axial system of a gymnosperm stem act as conduits for the movement of transpirational water from the roots to the leaves. Their structure has been detailed in ► Chap. 7 (Xylem) and will be briefly reviewed here.

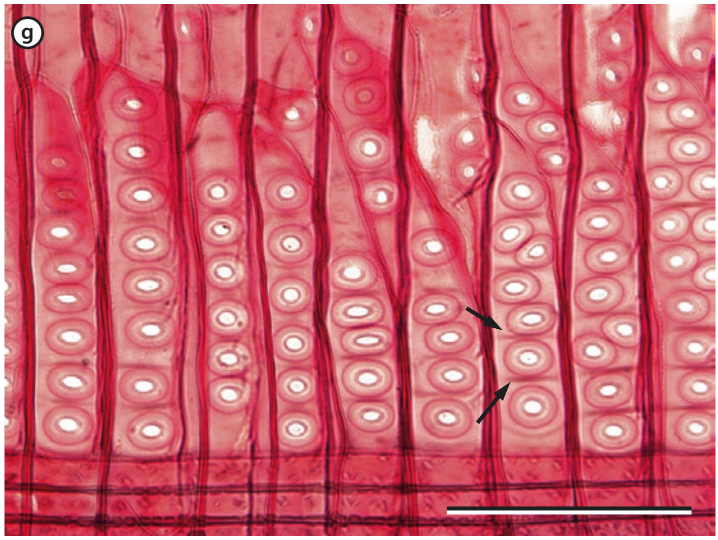


◘ **Fig. 15.5** **a**, **b** Joint fir (*Ephedra trifurca*, Gnetophyta) wood in **a** cross-section and **b** tangential section showing presence of vessel elements (V). Rays (R) are also apparent in both images. Scale bar in **b** = 100 μm and applies to both panels (**a**, **b** RR Wise)

The basic features of gymnosperm wood are shown in ◘ Fig. 15.5c–f. Tracheids have the typical long and narrow shape with tapered ends. Abundant water at the beginning of the growing season allows for larger tracheids with thinner walls, so-called earlywood. As the growing season progresses and water becomes more limiting, smaller tracheids develop with thicker walls, latewood. This growth pattern produces the **annual rings** seen in ◘ Fig. 15.3e, f. The tapered ends overlap with those of tracheids both above and below in the stem of the tree. Lateral movement of water from one tracheid to the next is via **circular bordered pits** in the anticlinal walls (◘ Fig. 15.5g). ◘ Figure 15.5g also shows **crassulae** (also called bars of Sanio for the seminal work of Sanio, 1872) which are cellulose thickenings found between individual pits.



◘ **Fig. 15.5** **c**–**f** Gymnosperm (*Pinus* sp.) wood seen in cross-section **c**, **d** and radial section **e**, **f**. **c**, **d** The cross-sectional views cover a boundary between annual growth rings with thinner-walled tracheids in the earlywood (EW) and thicker-walled tracheids in the latewood (LW). Axial resin canals (RC) are lined with secretory parenchyma. **e**, **f** *Pinus* rays are a mixture of parenchyma and tracheids. Refer to ◘ Fig. 15.5g, h for a higher-magnification view of a single ray. Note the tapered and overlapping tracheids in **e** (*arrow*). Scale bar in **f** = 100 µm and applies to all panels (**c**–**f** RR Wise)



◘ **Fig. 15.5** **g** Circular bordered pits and crassulae (*arrows*) in a radial section of Norway spruce (*Picea abies*) wood. Note the tapered ends of the tracheids and that a ray traverses the bottom of the figure. Arrows indicate crassulae. Scale bar = 50 µm (RR Wise)

Tracheids lack the perforation plate found in angiosperm vessel elements, so axial water movement between cells occurs through pits in the long overlapping areas at the tapered ends (◘ Fig. 15.5e). Xylem **resin canals** (◘ Fig. 15.5c, d) are an evolutionary advancement not found in the earliest fossil gymnosperm wood or in extant species such as the firs (*Abies* sp.) that are considered to have primitive features (Carlquist 2001). Lacking the ability to produce resin in the xylem, fir wood has poor resistance to insect damage and rot and therefore not well suited for outdoor construction.

Gymnosperm axial resin canals may be simple, with a single layer of **epithelium** or more complex with two or more layers of epithelial cells (◘ Fig. 15.5h, i). The presence of resin imparts insect and rot resistant, two characteristics that are important in determining the commercial and practical uses of the woods.

Tracheids in the ray system of a gymnosperm stem act as conduits for the movement of water in a radial direction from the stem out to the vascular cambium and periderm. Most of the rays in gymnosperm wood are uniseriate; only those rays with resin canals are multiseriate. Uniseriate rays are clearly seen in a radial section (◘ Fig. 15.5j, k). They may be composed exclusively of parenchyma cells, or may be a mixture of parenchyma and ray tracheids, depending on species. Both ray parenchyma and ray tracheids are said to be procumbent (i.e., with their long axis in a horizontal plane) and share circular bordered pits with adjacent **axial tracheids**. Rays are the source of water and minerals for the living tissues that lie to the exterior of the vascular cambium, i.e., the phelloderm and phellogen of the periderm (► Chap. 16).

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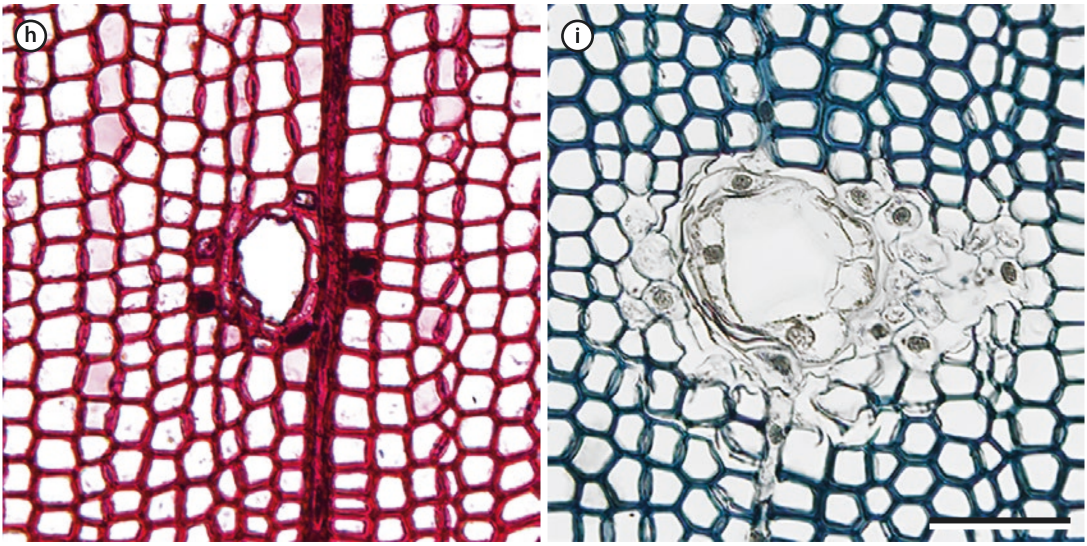
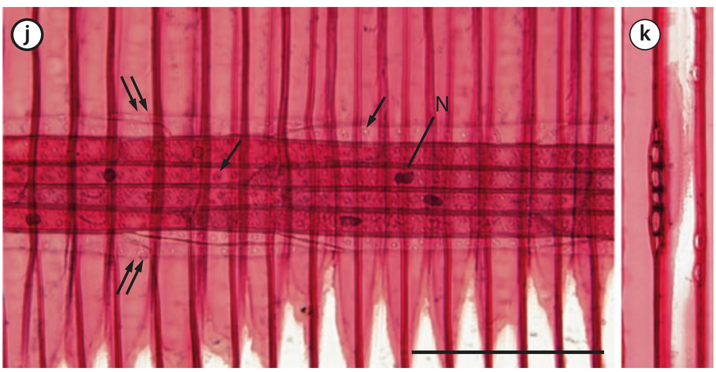


◘ **Fig. 15.5** Cross-sectional views of resin canals. **h** The canals in Douglas fir (*Pseudotsuga menziesii*) have a thin layer of epithelial parenchyma cells. **i** Resin canals in white pine (*Pinus strobus*) are much larger with a thick epithelial layer. Scale bar in **i** = 50 µm and applies to both panels (**h**, **i** RR Wise)



◘ **Fig. 15.5** **j**, **k** Radial **j** and tangential **k** views of xylem rays in the wood of Norway spruce (*Picea abies*). **j** Axial tracheids can be seen running in a vertical direction in the background, and a ray runs horizontally. The ray has three rows of ray parenchyma with conspicuous nuclei (N) bordered by a row of ray tracheids on the top and bottom (*double arrows*). Simple pits connecting the ray cells to the axial tracheids are indicated by single arrows. Note that the ray parenchyma cell ends are blunt and the ray tracheid end walls are tapered. **k** The uniseriate ray is viewed in tangential section and has the same number of rows of ray parenchyma and ray tracheids as in **j**. Scale bar in **j** = 100 µm and applies to both panels (**j**, **k** RR Wise)

Many gymnosperms, particularly the pines, have radial resin canals, in addition to the axial resin canals described above. Resin canals containing rays are multiseriate (◘ Fig. 15.5l, m) due to the biosynthetic nature of the tissue. The axial and radial resin canals are the tissues that synthesize the compounds that are extracted as pine tar, discussed in ► Sect. 15.2.

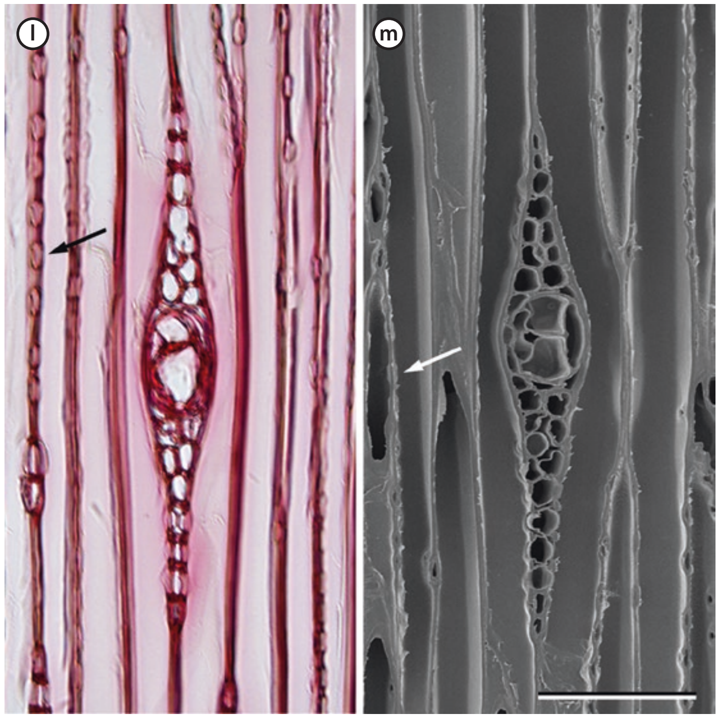


Fig. 15.5 **l**, **m** Two radial resin canals seen in tangential section in the wood of pine (*Pinus* sp.). Note the bordered pits on the tracheid anticlinal walls (*arrows*). Scale bar in **m** = 100 μm and applies to both panels (**l**, **m** RR Wise)

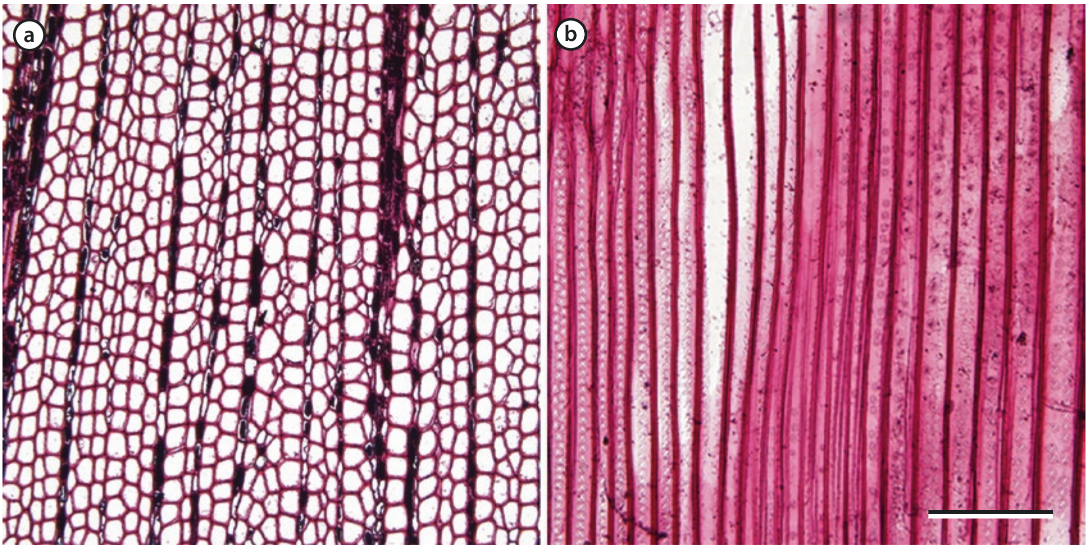
The presence, abundance, or absence of xylem axial resin canals, radial resin canals, ray parenchyma, ray tracheids, and crassulae are of value to the identification and systematics of both extant and extinct gymnosperm species.

15.6 Eudicot Wood Is Characterized by Vessel Elements, Tracheids, Parenchyma, and Rays

Eudicot wood identification is based on several characters that are visible with a simple 10x hand lens. Those characters include (1) the distribution of vessel elements (also called "pores" here and "perforate tracheary elements" in ► Chap. 7) within a single growth ring, (2) the arrangements of individual vessels as solitary or grouped regardless of where they are in the annual growth ring, (3) the pattern and distribution of xylem parenchyma, and (4) ray architecture. It should be noted that there are a number of angiosperm taxa that lack rays entirely, a characteristic called "raylessness," which has been related to the mechanical and functional needs of the stem (Carlquist 2015).

15.6.1 Patterns of Xylem Vessel Element Distribution

Just as not all gymnosperms are vessel-less, not all angiosperms possess vessel elements. Pepperbush is a shrubby, primitive, vessel-less



◘ **Fig. 15.6** **a**, **b** Purple pepperbush (*Tasmannia purpurascens*) wood seen in **a** cross-section and **b** longitudinal section. Note abundant tracheids and lack of vessel elements. Scale bar in **b** = 100 μm and applies to both panels (**a**, **b** RR Wise)

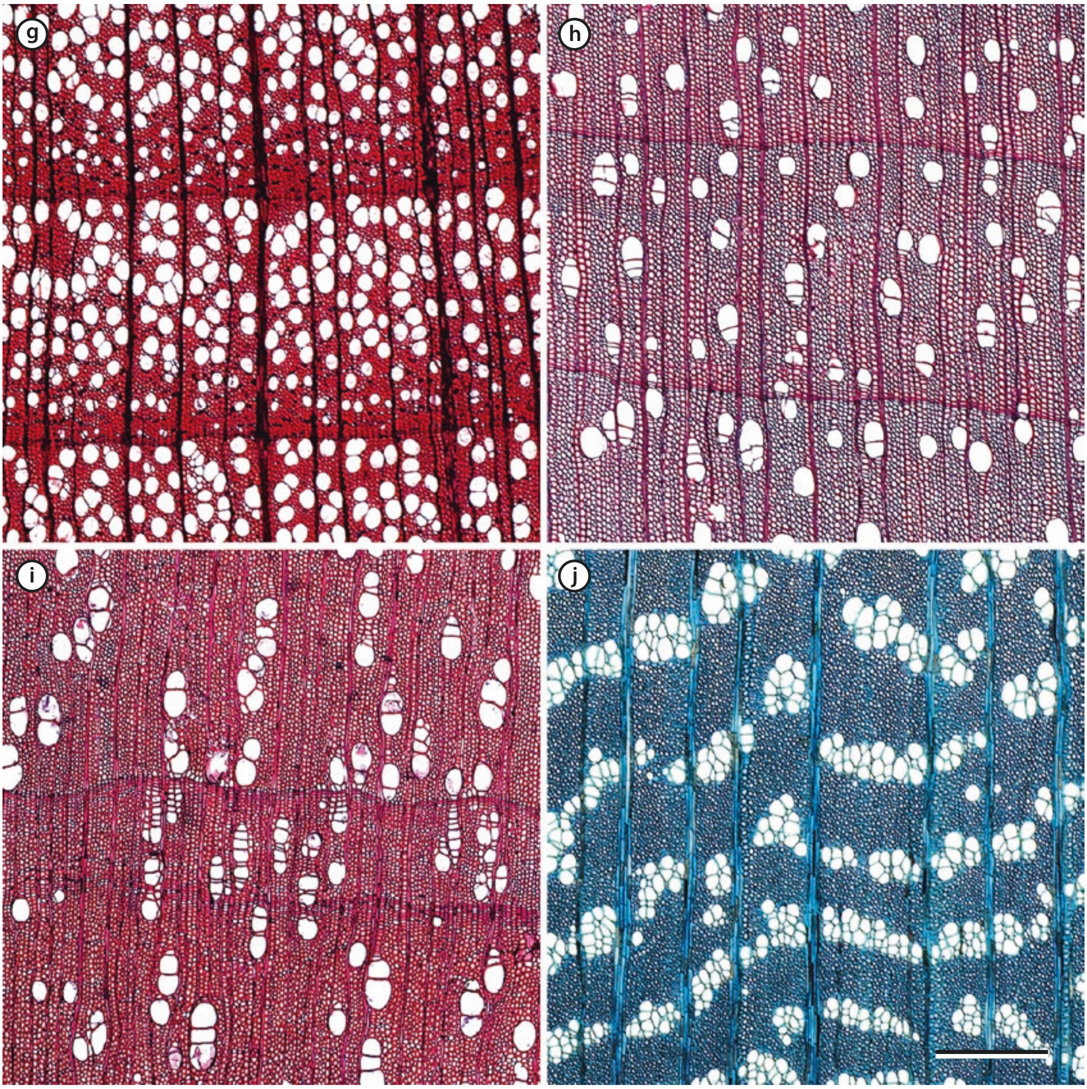
eudicot (◘ Fig. 15.6a, b) in the Winteraceae family. Both the vessel-containing gymnosperms, such as *Ephedra* (◘ Fig. 15.5a, b), and the vessel-less angiosperms have been studied extensively for clues to the evolution of xylem vessels.

◘ Figure 15.6c–f shows four basic patterns of vessel element distribution in growth rings when observed in cross-sections. Woods such as catalpa, ash, oak, and hickory have their largest pores develop in the early (spring) wood and microscopically appear to form a ring pattern at the juncture of the annual growth rings. Thus, such a pattern is termed "**ring-porous**" (◘ Fig. 15.6c). Alternatively, in other angiosperms, the pores are generated uniformly throughout the growing season, giving rise to their designation as "**diffuse-porous**" wood (◘ Fig. 15.6d). These include common species such as birch, cherry, maple, and poplar. In many hardwoods such as chestnut, black walnut, and magnolia, pores are less grouped together at the starting sites of the annular rings but rather trail off throughout the growth season, giving rise to a designation as "**semi-ring-porous**" (◘ Fig. 15.6e). A "**dendritic**" pattern (from the Greek *dendron*, meaning tree or branched) is one in which vessel elements branch out from the earlywood to the latewood. Intermediate patterns exist and species may share features of more than one pattern. White oak (◘ Fig. 15.6f), for instance, is a ring-porous wood with dendrites of vessel elements spread across the growth ring.

15.6.2 Vessel Grouping

Vessel elements may be solitary, as in beech (◘ Fig. 15.6g), found in small clusters of two to three cells which are common in the birches (◘ Fig. 15.6h), or arranged in radial files of three to ten or more cells as seen in hornbeam (◘ Fig. 15.6i). Elm is characterized as having large clusters of vessel elements (◘ Fig. 15.6j). A single species

Fig. 15.6 **c**–**f** Cross-sections of **c** ring-porous hardwood from northern catalpa (*Catalpa speciosa*), **d** diffuse-porous hardwood from paper birch (*Betula papyrifera*), **e** semi-ring-porous hardwood from horse chestnut (*Aesculus hippocastanum*), and **f** ring-porous with dendrites in white oak (*Quercus alba*). The central axis of the tree is toward the bottom in all four images. The tissues at the top of panel **f** are phloem and bark. Scale bar in **f** = 250 µm and applies to all panels (**c**–**f** RR Wise)



■ **Fig. 15.6** **g**–**j** Groupings of vessel elements. **g** Solitary in American beech (*Fagus grandifolia*), **h** small clusters in silver birch (*Betula alba*), **i** radial files in American hop hornbeam (*Ostrya virginiana*), **j** large, multi-vessel clusters in American elm (*Ulmus americana*). Scale bar in **j** = 250 µm and applies to all panels (**g**–**j** RR Wise)

may exhibit one or more of the vessel element patterns shown. For instance, while most of the vessel elements in beech are solitary, a few exist as pairs (■ Fig. 15.6g).

15.6.3 Patterns of Xylem Parenchyma

Like xylem vessel element distribution, the pattern or xylem parenchyma is a species-specific trait very useful in wood identification. Xylem parenchyma cells, which function as storage sites as well as aiding in the transport of water and dissolved substances, are scattered throughout the sapwood in several recognizable patterns. The parenchyma cells may be found individually or in aggregate

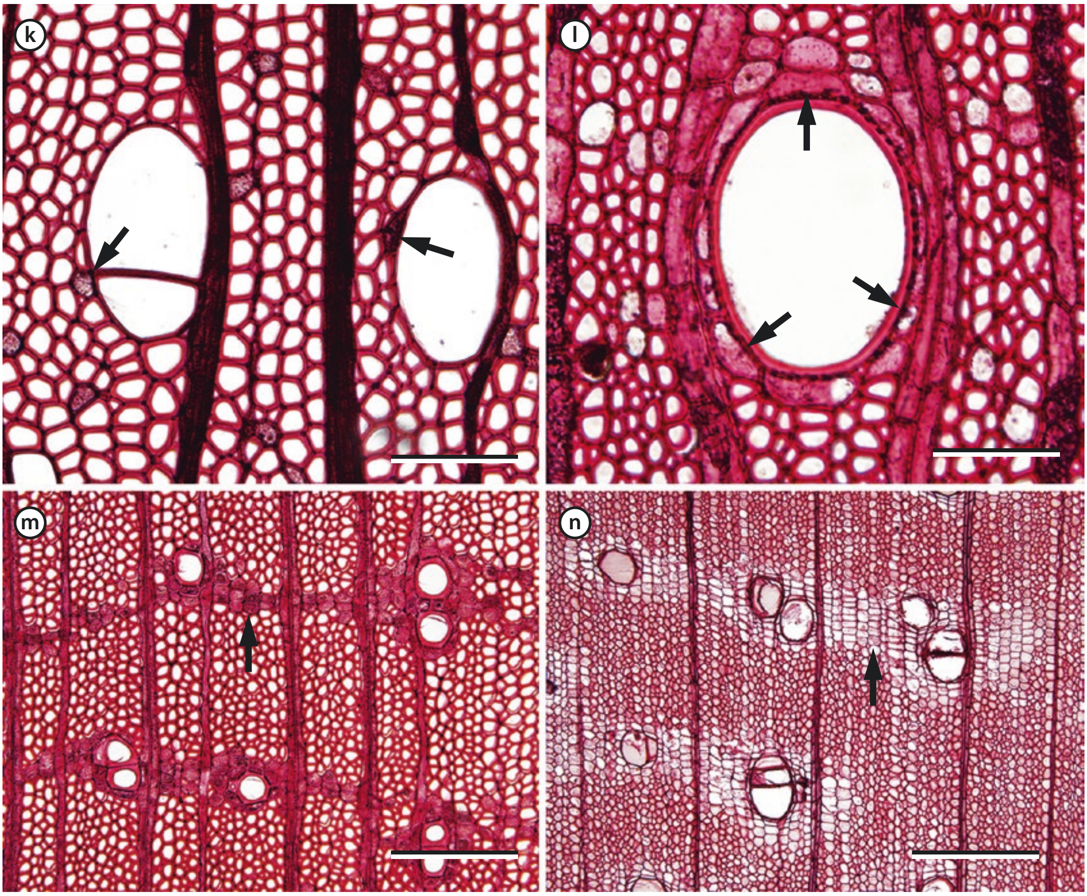


Fig. 15.6 **k**–**n** Various forms of paratracheal parenchyma, e.g., parenchyma associated with a vessel element. **k** Scanty paratracheal parenchyma in paper birch (*Betula papyrifera*); note also the apotracheal parenchyma in the field of view. **l** Pecan (*Carya illinoinensis*) wood has vasicentric paratracheal parenchyma completely surrounding a vessel element. **m** Ash (*Fraxinus* sp.) is characterized as having narrow bands of confluent paratracheal parenchyma that appear darker than the surrounding tracheids. **n** The broad bands of confluent paratracheal parenchyma in the foxglove tree (*Paulownia tomentosa*) are lighter than the surrounding tracheids. Arrows indicate the location of the parenchyma. Scale bars = 50 µm in **k** and **l**, 100 µm in **m**, and 200 µm in **n** (**k**–**n** RR Wise)

clusters throughout the wood. They may also be found oriented in the longitudinal axis along the length of the tree trunk or in rays that appear along the radial axis. Parenchyma cells that are associated with xylem vessels are called **paratracheal** parenchyma (Fig. 15.6k–n). They may be scanty (only one or two per vessel element, Fig. 15.6k), **vasicentric** (completely surrounding a vessel element, Fig. 15.6l), or **confluent** (extending from one vessel to another). Confluent xylem parenchyma may be in narrow (Fig. 15.6m) or broad bands (Fig. 15.6n), depending on the species. Paratracheal parenchyma may be further classified as **aliform** (winged) if it forms, as seen in cross-sections, tapered extensions on the sides of a vessel element (not shown) or as **scalariform** parenchyma if it forms narrow bands between rays (Fig. 15.6m). Multiple types of xylem parenchyma may be seen in one image. Indeed, Fig. 15.6m shows confluent, scalariform, and paratracheal parenchyma.

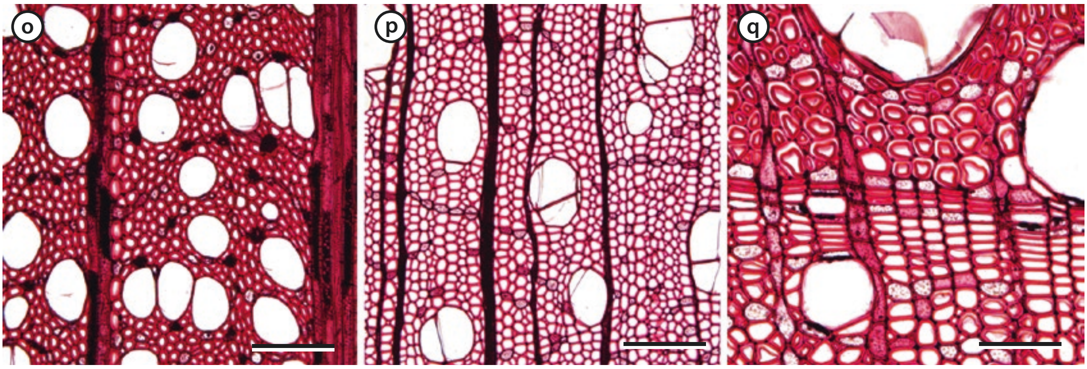


Fig. 15.6 **o** Diffuse apotracheal parenchyma in sycamore (*Platanus occidentalis*), **p** banded apotracheal parenchyma in paper birch (*Betula papyrifera*), **q** terminal apotracheal parenchyma in black walnut (*Juglans nigra*). Scale bars = 100 µm in **o** and **p** and 50 µm in **q** (**o**–**q** RR Wise)

Those parenchyma cells not associated with a vessel element are called diffuse or **apotracheal** parenchyma, meaning not associated with vessel elements (Fig. 15.6o–p). They may be **diffuse** (Fig. 15.6o), **banded** (extending between rays, Fig. 15.6p), or **terminal** (found at the boundary of an annual growth ring, Fig. 15.6q). Regardless of its specific pattern—paratracheal or apotracheal—parenchyma cells constitute approximately the same relative volume (~10%) in both softwoods and hardwoods. Wood is a tissue whose primary functions are support and long-distance water conduction. Parenchyma contributes to neither of those functions, thereby placing a limit on their abundance.

15.6.4 Ray Architecture

Rays are groups of xylem cells generated by the vascular cambium (specifically, **ray initials**) that transport xylem sap (water and minerals, but not photosynthate) through wood in a radial direction. Similar to gymnosperm rays, eudicot rays are joined to the axial xylem system via numerous interconnecting pits (Fig. 15.6r). The main direction of the sap flux is from the axial system, through pits, to the ray system and interior toward the exterior. Rays may be composed of living (parenchyma) and dead (tracheids) cells and function for a number of years. Most of the living cells in wood are those found in rays, the exception being the paratracheal or apotracheal parenchyma of the axial system.

Homocellular rays have a single-cell type, either parenchyma or tracheid. Rays in maple, sycamore, and alder are homocellular and composed of only procumbent ray parenchyma cells. **Heterocellular rays** have a mixture of parenchyma (upright or procumbent) and/or tracheids, such as found in walnut, oaks, and willow (Fig. 15.6r, s).

Rays can vary considerably in height and width due to the number of cells comprising the ray; tangential sections offer the best view of ray size (Fig. 15.6t–v). Ray height is designated as short

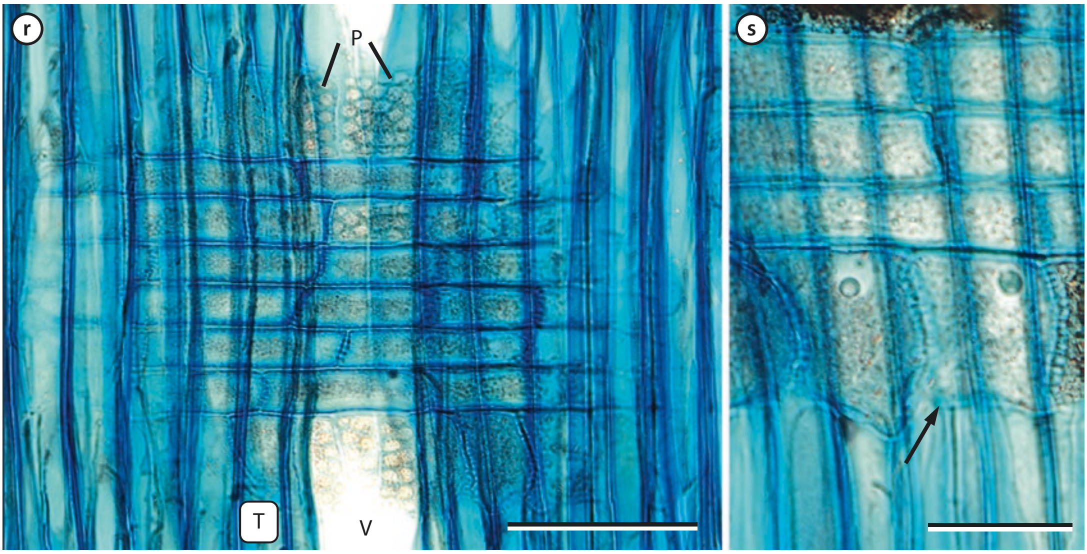


Fig. 15.6 **r** Heterogeneous willow (*Salix nigra*) ray with six rows of procumbent parenchyma cells in the middle and top and bottom rows of upright (square) marginal cells. Numerous pits (P) connect the marginal cells with a vessel element (V). Tracheids (T) are to either side of the vessel element. **s** Higher magnification of a similar specimen showing upright cells (*arrow*) in the margin of ray. Scale bars = 50 µm in **r** and 25 µm in **s** (**r**, **s** RR Wise)

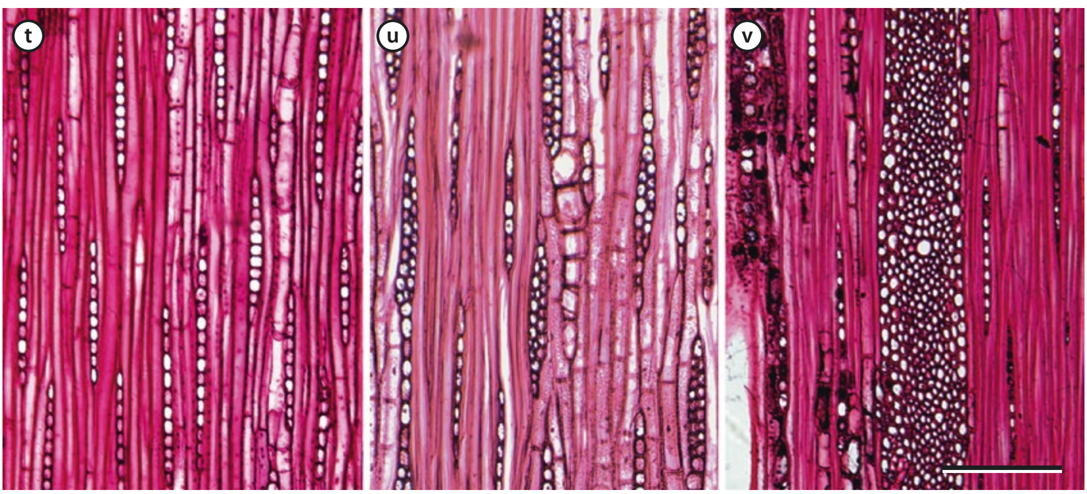
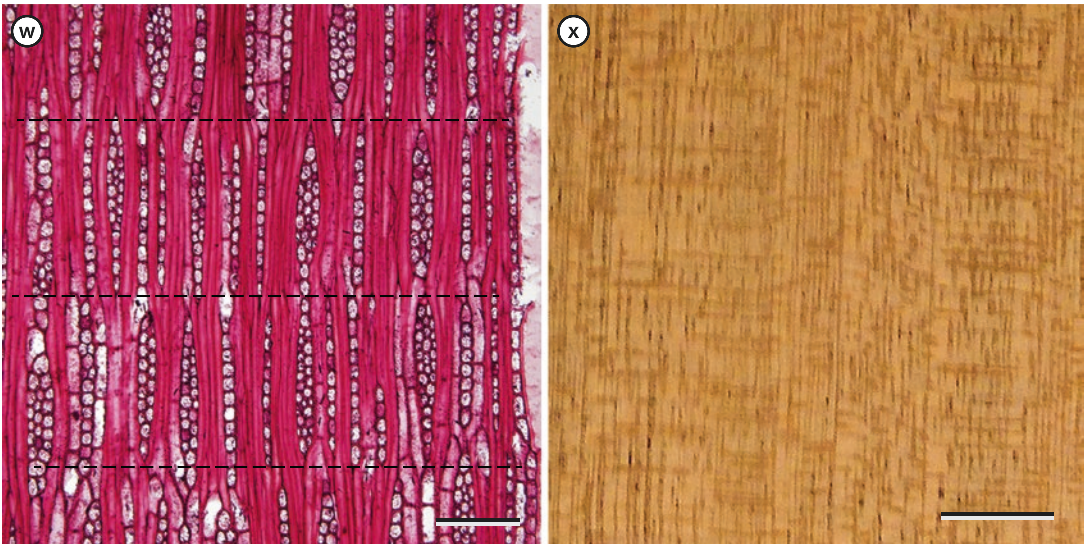


Fig. 15.6 Tangential sections showing wood rays. **t** American chestnut (*Castanea dentata*) wood has uniseriate rays. **u** Black walnut (*Juglans nigra*) has both uni- and biseriate rays. **v** Red oak (*Quercus rubra*) has numerous uniseriate rays as well as large aggregate rays. Scale bar in **v** = 100 µm and applies to all panels (**t**–**v** RR Wise)

or tall. Short rays have 2–10 cells in a vertical direction, and tall rays have ten to several hundreds. Narrow rays may have only one to three cells in width, whereas relatively wide rays can be more than ten cells in width. The width of rays as determined by the cell number is often referred to as the seriate number, as in **uniseriate**, **biseriate**, etc. In a number of species (e.g., oak, *Quercus*; hornbeam, *Carpinus*; alder, *Alnus*; etc.), rays may merge to form aggregate rays, some of which may not only be very wide, but extremely tall (Fig. 15.6v).



◘ **Fig. 15.6** **w** Tangential wood section of persimmon (*Diospyros virginiana*) revealing the storied nature of the rays, both uniseriate and multiseriate. Dashed horizontal lines highlight the stories of rays. **x** A flat-sawn (i.e., radial section) sample of sapele (*Entandrophragma cylindricum*), a hardwood tree native to tropical Africa, showing ripple marks caused by storied rays. Scale bars = 100 µm in **w** and 2 cm in **x** (**w**, **x** RR Wise)

Different planes of section, cross, radial, and tangential, can show strikingly different views of wood anatomy, even to the naked eye. Flat-sawn boards have the tangential surface exposed. In some hardwood species, such as a number of tropical trees, the rays are generally aligned in horizontal rows or tiers (◘ Fig. 15.6w). These are called storied rays, and they impart stripes of alternating light and dark bands, called ripple marks (◘ Fig. 15.6x). In other woods, ripple marks may also result from similar patterns of fibers or parenchyma cells.

15.7 Reaction Woods Develop in Response to Gravity

Wood, despite its natural strength due to lignified secondary cell walls, is still subject to forces of nature including high winds, gravity, weight-bearing loads, leaning, and other environmental factors. Such situations, however, vary between wood from gymnosperms and that of angiosperms and result in changes in the structure and composition of cell walls, which is generically termed as **reaction wood**. Gymnosperms and angiosperms (woody eudicots) contain uniquely different types of reaction wood.

Reaction wood is a development response driven by directional transport of the hormone indoleacetic acid (IAA). Statocysts in the endodermis (refer to ◘ Fig. 11.5m) settle to the bottom of the stem, which causes the transport of IAA in the same direction. In gymnosperms, the relatively higher IAA concentration at the lower side of the stem induces the vascular cambium to produce thicker cell walls and increased deposition of lignin, which gives greater strength to

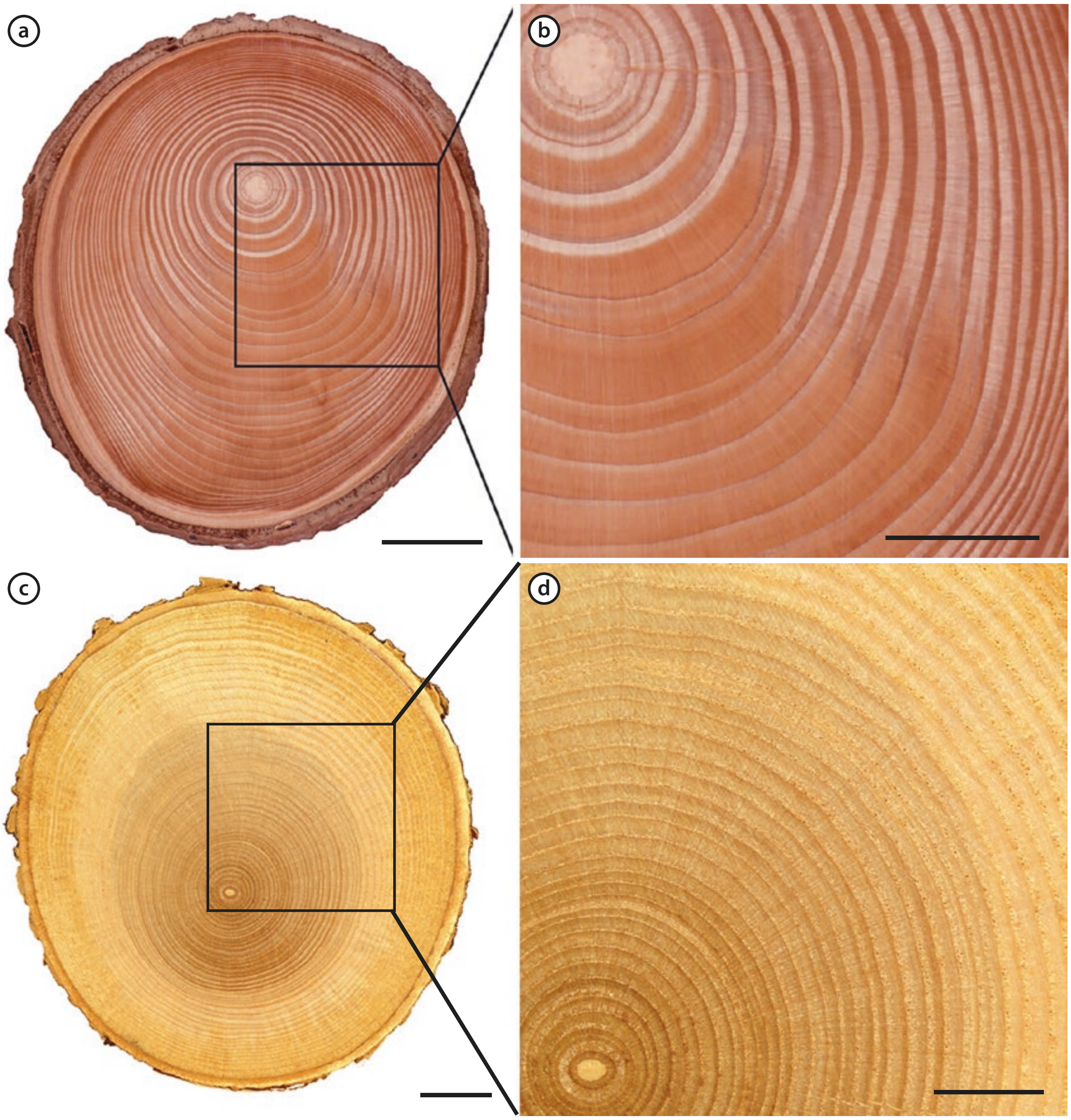


Fig. 15.7 **a**–**d** Two forms of reaction wood. **a**, **b** Compression wood develops at the bottom of gymnosperm stems and limbs. Norway spruce (*Picea abies*) is shown. **c**, **d** Tension wood develops on the upper part of the stem of a horizontal or leaning woody eudicot stem, as shown in this cross-section of a green ash (*Fraxinus pennsylvanica*) limb. Scale bars = 2 cm in **a** and **c**, 1 cm in **b** and **d**. (Images **a** and **b** by Michael Rosenthal, Technische Universität Dresden – Rosenthal and Bäucker (2012), CC BY-SA 3.0, images **c** and **d** by RR Wise)

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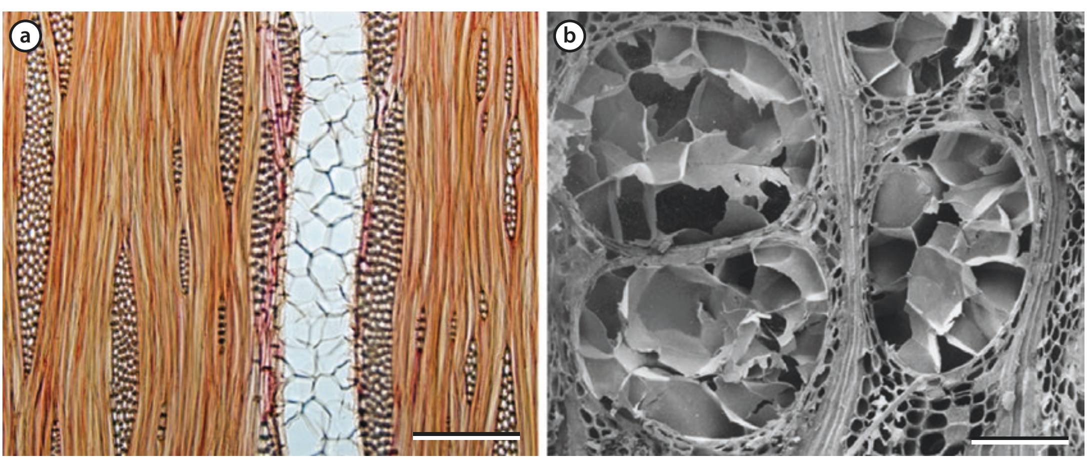
the site of stress. Specifically, the reaction wood of conifers is termed "**compression wood**." The compression wood may have the appearance of a dark stain (Fig. 15.7a, b). On the other hand, the reaction wood of eudicot angiosperms is designated as "**tension wood**" and develops on the upper side of branches (Fig. 15.7c, d) where it is found as **gelatinous fibers** (see also Fig. 6.7g) (recall that gymnosperms lack fibers) and greater amounts of cellulose, but with reduced amounts of lignin. That condition exists when the concentration of indoleacetic acid is low.

The composition of reaction wood enables a branch to become more flexible and resist breaking in high winds or other forms of stress. The tension wood of eudicots, like the compression wood of gymnosperms, is also produced by stimulated cambial activity, but on the opposite side of a branch or affected tree trunk. Because of the unique patterns of darkened wood and cellular distributions, reaction woods are highly sought after for their use in furniture and wooden panels. The compression wood of gymnosperms, on the other hand, is considered to be of lower quality than normal wood due to uneven drying and warping of lumber. It can be dangerous to saw and machine. Reaction wood has also been reported in some roots for both gymnosperms and eudicots and most recently has been found in cycads (a primitive gymnosperm) indicating that reaction wood may have been formed at an early evolutionary period in seed plants.

15.8 Tyloses and Crystals May Be Found in Some Woods

A **tylosis** (pl: tyloses) is a vascular occlusion in a vessel element or tracheid caused by the protoplasm of an adjacent xylem parenchyma cell extending through a shared pit and filling the cell lumen (◘ Fig. 15.8a, b). In the formation of wood, paratracheal parenchyma cells are adjacent to vessel elements, where they largely function in food storage. However, as vessels age, or when an infection takes place, and when drought or mechanical damage may occur to the wood, the cell walls of the parenchyma may protrude through pit pairs in a matter of hours due to the production of enzymes that dissolve the pit membrane. The protrusion in a balloon-like manner extends throughout the lumen of the vessel element (and in a few cases into tracheids), thus blocking of the passage of water and dissolved substances, but also blocking the passage of any infectious materials.

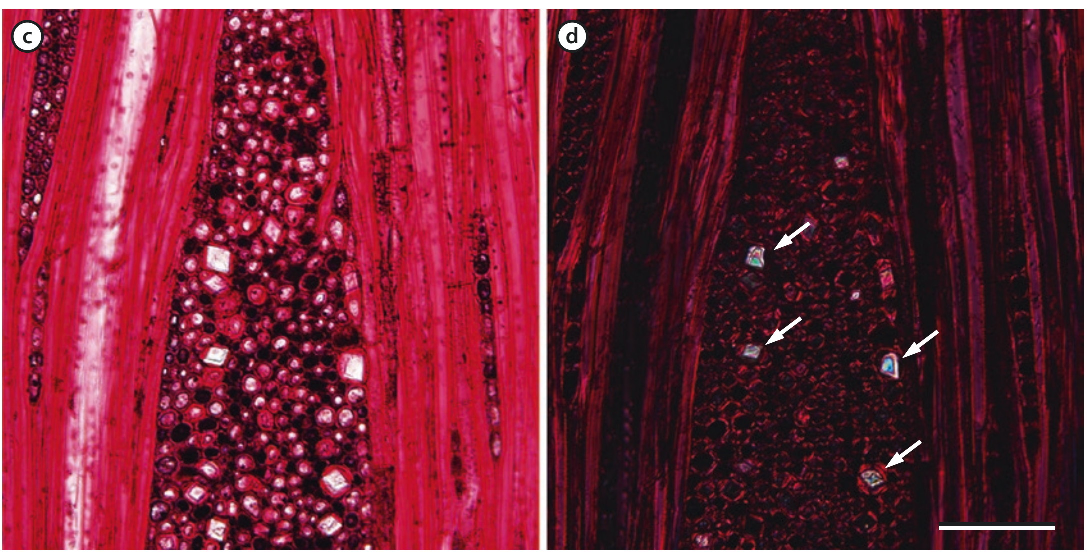


◘ **Fig. 15.8** **a**, **b** Black locust (*Robinia pseudoacacia*) wood with tyloses in **a** longitudinal section and **b** cross-section. The tyloses developed from parenchyma cells adjacent to the vessel elements. Scale bars = 100 µm in **a** and 50 µm in **b**. (**a** RR Wise; Image **b** courtesy of John Curtis)

While they often form in response to infection, some woods naturally form tyloses. For instance, white oak (*Quercus alba*) has abundant tyloses in the heartwood that are no longer participating in water conduction. Red oak (*Quercus rubra*), on the other hand, has few. Coopers (makers of wooden barrels, kegs, and casks) learned early on that a barrel made of red oak would leak, whereas a white oak barrel would not.

The bacterium *Xylella fastidiosa* is spread by biting insects and causes Pierce's disease, a deadly disease of peaches, grapes, citrus, and other plants (Baldi and La Porta 2017). The bacterium enters the xylem conducting tissue and multiplies. The plant's response is to produce tyloses in the infected tissues, which block transpiration and cause leaf and, ultimately, plant death. There is currently no treatment or cure for Pierce's disease, although some plants show significant resistance, meaning there could be a genetic basis for protection that could be transferred to susceptible varieties or species (Svyantek et al. 2016).

In addition to tyloses, mineral crystals may be found in the lumen of vessel elements such as red mulberry (*Morus rubra*) and teak (*Tectona grandis*) and have been observed in parenchyma cells of wood rays as in the American beech (◘ Fig. 15.8c, d) and numerous other species. The chemical composition of these crystals has been found to be calcium oxalate or magnesium oxalate. Other crystals may be composed of silicon dioxide (Carlquist 2001).



◘ **Fig. 15.8** **c**, **d** Tangential section of a ray in American beech (*Fagus grandifolia*) wood viewed under **c** bright-field and **d** polarized illumination. Arrows in **d** mark the birefringent crystals in the ray parenchyma cells. Scale bar = 50 µm (**c**, **d** RR Wise)

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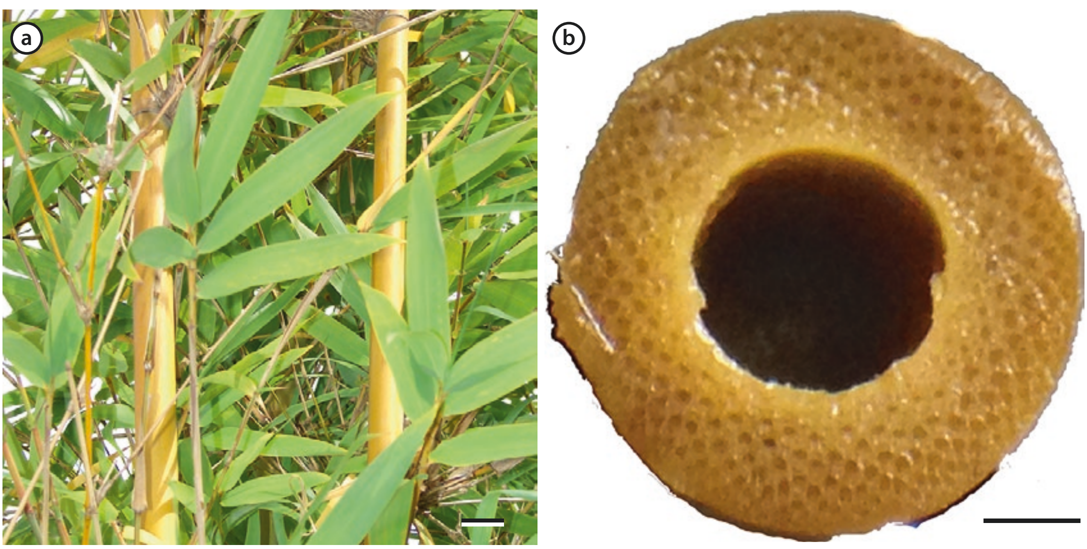
15.9 Monocot "Wood" Does Not Come from True Secondary Growth

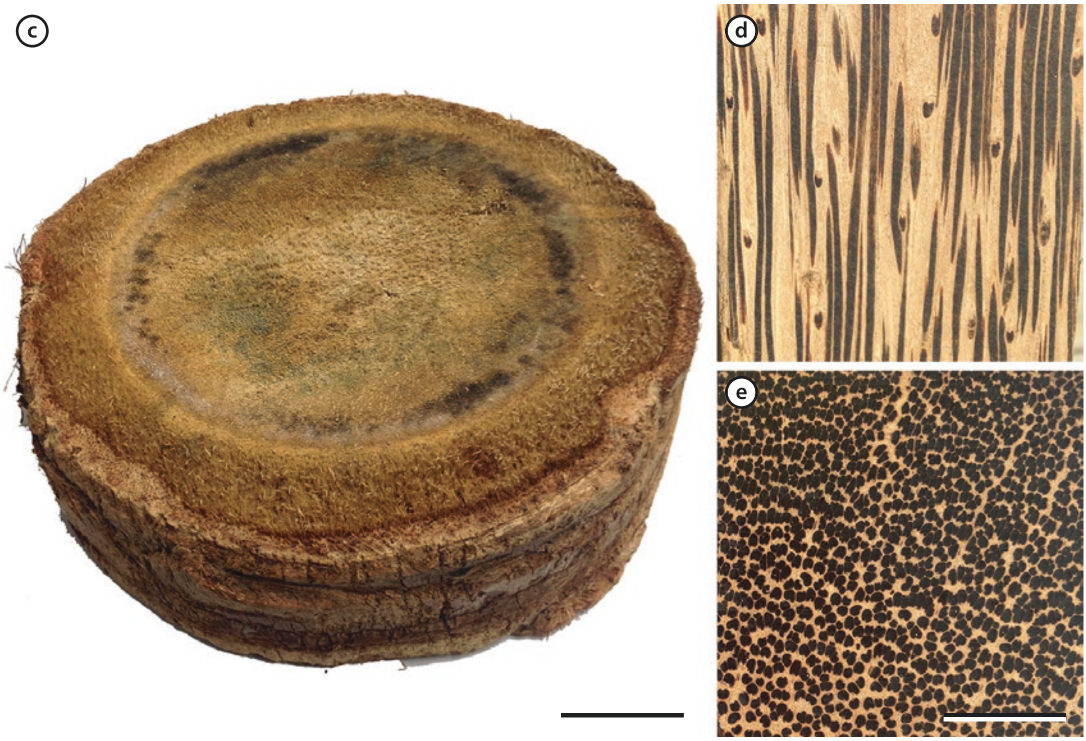
As discussed in ► Chap. 11, stems of monocotyledonous plants are characterized by their disordered distribution of vascular bundles throughout the cross-sectional organization—a pattern that does not give rise to the annual layered secondary growth seen in woody eudicots. Thus, monocots cannot form true wood. However, some perennial monocots such as bamboo (Poaceae, subfamily Bambusoideae) and the palms (Arecaceae) can produce a very strong, long-lasting stem or trunk.

Monocots lack a vascular cambium encircling the stem (► Chap. 11), which is the source of true wood in eudicots. However, they do have a cambium in each of the many vascular bundles. Therefore, monocots increase stem strength by heavy sclerification of the fiber caps on each bundle, not by sclerifying the entire stem and steadily increasing stem diameter with each growing season, as woody eudicots do. The result is a mass of supportive tissues that, taken together, constitute monocot "wood."

Bamboo (*Bambusa* sp.), a common fast-growing monocot, has a hollow stem (referred to as a 'culm' in monocots) with thick walls (◘ Fig. 15.9a, b). It has numerous vascular bundles comprising xylem, phloem, and fiber caps embedded in parenchymatous tissues (refer to ◘ Fig. 11.5e–g). It is the fiber caps that provide mechanical



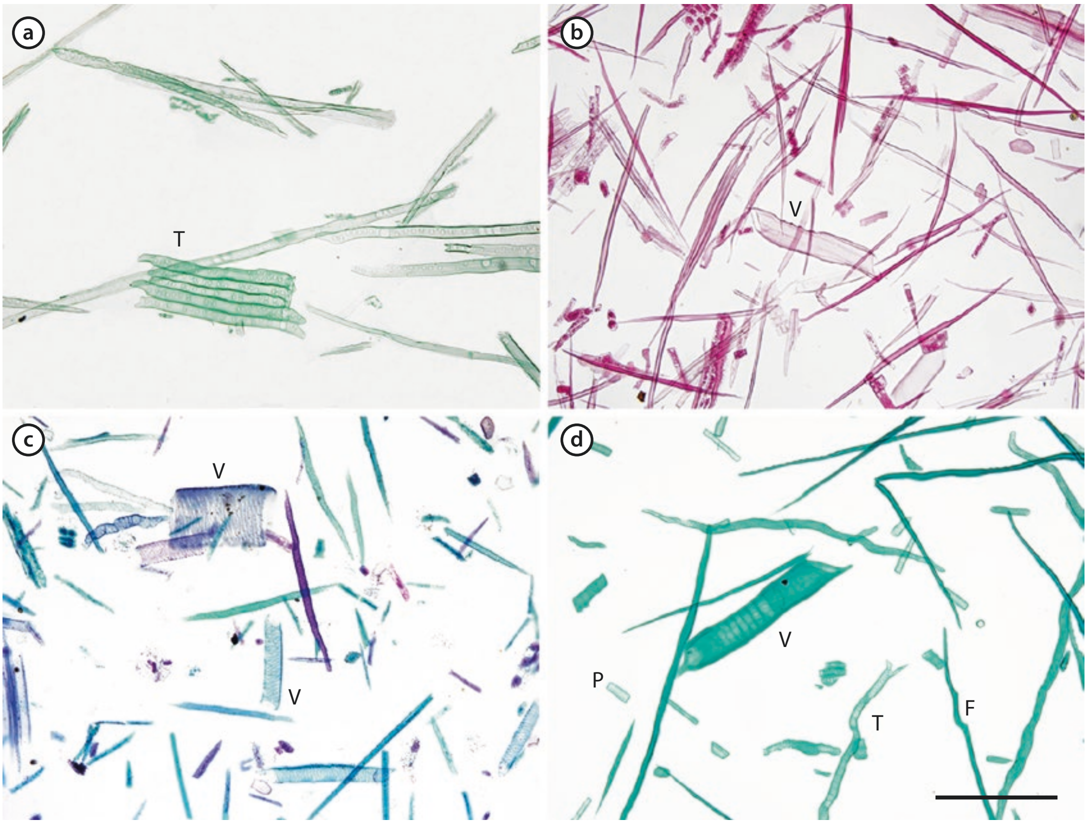
◘ **Fig. 15.9** **a**, **b** Photographs of weaver's bamboo (*Bambusa textilis*) culms. **a** Side view showing leaves arising from nodes. **b** End view showing end-wall thickness. Scale bars = 2 cm in **a** and 2 mm in **b** (**a** Forest and Kim Starr, CC BY 3.0; **b** RR Wise)



◘ **Fig. 15.9** **c** Cross-section of a cabbage-palm (*Sabal palmetto*) "tree trunk." The stem is solid with several radial zones that represent different ratios of fiber to parenchyma. **d** Cross and **e** longitudinal section of black palm (*Borassus flabellifer*) "wood." The dark brown streaks in **d** and spots in **e** are sclerified vascular bundle fiber caps. The intervening tan tissue is parenchyma. Scale bars = 5 cm in **c** and 1 cm in **d** and **e** (**c**–**e** RR Wise)

support for the stem, particularly where they are concentrated at the periphery and where bending stress is typically the greatest. As the plant ages, new cell wall material is deposited to the fibers with increasing amounts of lignin in alternating layers that contributes additional strength. The abundance of heavily sclerified vascular bundles makes for an extremely strong stem. It is worth noting that many of the vascular bundles converge in the internodal regions to form a complex, intertwined arrangement that adds strength to the stem. In Asia, bamboo scaffolding is often used in building construction, frequently in high-rise buildings more than 20 stories high, attesting to its considerable strength (Lo et al. 2008) and its availability as an inexpensive, lightweight, and easily assembled material.

Palm "trees" have a solid stem which, like bamboo, is composed of heavily sclerified vascular bundles embedded in a matrix of parenchyma cells (◘ Fig. 15.9c). Palm trees may reach considerable size (refer to ◘ Fig. 1.19). For some species, the percent fiber is so high that the lumber, when cured and dried, can be made into flooring and siding in building construction. Black palm (◘ Fig. 15.9d, e) is one example. The almost 3000 species of palms have numerous other uses. Palm leaves can be used for thatched roofs, oil, wax, and many types of straw hats. The tree trunks can also provide sap for sugars and for fermented drinks. Due to their rapid growth, palms



◘ **Fig. 15.10** **a**–**d** Macerations of **a** pine (*Pinus* sp.) wood, **b** ephedra (*Ephedra* sp.) wood, **c** Dutchman's pipe (*Aristolochia* sp.) stem, and **d** red oak (*Quercus rubra*) wood showing isolated parenchyma (P), tracheids (t), and vessel elements (V). Scale bar in **d** = 100 µm and applies to all panels (**a**–**d** RR Wise)

have been used for the production of biodiesel fuel. Palms are major food sources with coconut (liquid and hardened endosperm) and date (fleshy fruit) being the primary examples.

15.10 Wood Macerations Are Useful for Species Identification, Product Identification, and Forensics

In order to visualize the individual cells of wood from virtually all directions, a process of cellular separation is often employed that chemically and/or enzymatically dissolves the middle lamella and then allows for the individual cells to be viewed. This process is termed maceration. ◘ Figure 15.10a–d reveals such structures from a variety of woods. The maceration process typically involves treating small pieces of wood with 10% nitric and/or chromic acid or potassium chlorate, which breaks down the middle lamella but does not damage the primary and secondary walls. After up to 24 h in that solution, the cells are washed in distilled water and can be examined by light (or laser confocal) microscopy. If greater contrast is required, staining with safranin (red) or methyl green solutions can be employed.

In addition to wood, other plant tissues can be treated by maceration such as stem or leaf materials that contain a large number of sclereids of different nature. It has also proven useful to combine maceration with polarizing microscopy to show birefringence and, therefore, the orientation of cell wall layers. It is common in the paper industry to test competitors' paper products to determine the amount and ratios of wood fibers used in production. Knowing the physical nature of fibers in wood from paper has also been utilized in forensic studies to document papers that may, or may not, share a common origin.

15.11 The Study of Tree Rings Is Important in Archeology, Climatology, and Forensics

Dendrochronology is the science that studies annual tree rings in the secondary growth of gymnosperms and eudicots in order to reveal past climate and environmental changes year by year. When there are good years with plentiful water and a favorable, long growing season, the annular growth rings in the secondary xylem will be wider. However, if the conditions are not favorable, the width of the growth rings will be considerably narrower. Thus, the cross-sectional view of the secondary xylem can be used to trace the overall environmental conditions over the life of a tree, regardless of whether it is a gymnosperm or a woody eudicot. In most cases, it is not necessary to cut an entire cross-section of a trunk in order to count and examine the growth rings. Instead, an increment borer can be used to drill into the living tree to obtain the same information, but without killing the tree. Of course, the missing rings, false rings, and discontinuous rings discussed in ► Sect. 15.3 will complicate such studies.

Data from growth rings coupled with studies of entrapped carbon dioxide specimens from ice sheets and the bleaching of corals have shown that temperatures in the tropical oceans, and in the air above the northern hemisphere, began to rise in the 1830s, much earlier than first thought (Jacoby and D'Arrigo 1997).

Using dendrochronology, which was first employed in the early twentieth century by A. E. Douglass, a process termed archeological dating has developed; that is a precise means of using the information to determine archeological conditions over the course of long periods of time (e.g., approximately 10,000 years being the longest dating time recorded). The tree growth rings can also be used in conjunction with radiocarbon (^{14}C) dating due to the natural carbon content present in the rings. Since most trees only live for 100–200 years, the longer time spans of information are obtained by visually matching rings from living trees with older samples of preserved specimens by examining the parts that show overlapping growth ring patterns (◘ Fig. 15.11a). In a similar manner, those can also be matched with even older ones, and so on as far back as ancient

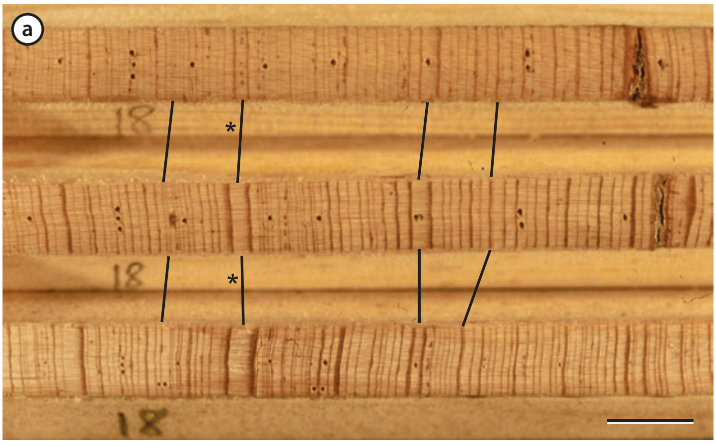


Fig. 15.11 **a** Increment cores taken from three Douglas fir (*Pseudotsuga menziesii*) trees growing at El Malpais National Monument, New Mexico, USA. The "18" indicates the location of the year 1800, marked by three dots in all three cores. The vertical lines connect corresponding narrow and wide rings, demonstrating cross dating between the trees. The thickest ring on all three cores (indicated with an asterisk) is the year 1816, the "Year Without a Summer." The Mount Tambora volcano in Indonesia erupted on April 10, 1815, causing widespread global cooling. In the USA Southwest, cooler atmospheric temperatures led to increased soil moisture and increased growth in the year after the eruption. Scale bar = 0.5 cm. (Image courtesy of Henri D. Grissino-Mayer, The University of Tennessee, Knoxville)

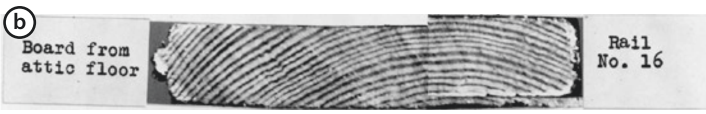


Fig. 15.11 **b** Wood cross-section from attic floor of presumed Lindbergh kidnapper on the left and the matching wood from the home-made ladder rail used by the kidnapper on the right (Forest History Society, Durham, NC)

specimens of the same species can be obtained. Dendrochronology has been used to assign dates to buildings, ships, musical instruments, and artworks, in some cases verifying or refuting the authenticity of the piece.

The pattern of growth rings as seen in cross-sectional view can also be used in forensic investigations, perhaps the most famous of which was in the kidnapping and murder trial of the Charles Lindbergh baby in 1932. The suspected kidnapper used a home-made ladder to reach the upstairs bedroom window of the young child and left it at the site. A part of the ladder was not made from the same wood as the rest, and, when analyzed via matching tree rings, it was found to be from wood of the kidnapper's attic—ponderosa pine (*Pinus ponderosa*) (◘ Fig. 15.11b). On that basis, and additional forensic analysis of the wood samples, the kidnapper was sentenced and later executed.

Box 15.2 Advances in Forensic Wood Identification

When plant material is confiscated and inspected for illegal trade, law enforcement officials use traditional anatomical, morphological, and/or fluorescent techniques to identify wood samples. However, distinguishing closely related species that may be endangered and banned from trade may be impossible to accomplish unless more sophisticated techniques are used, especially when the origin of the wood is unknown. This presents an important problem in some areas of the world, particularly in the Amazon, where 80% of the total harvest was estimated to be illegal.

Direct Analysis in Real Time Time-of-Flight Mass Spectrometry (DART-TOFMS) may provide a means to identify unknown wood samples in the field by ionizing samples using a DART ion source followed by mass spectrometry using the TOFMS. Unknown specimens can be identified to species by comparing the DART-TOFMS output with specific chemical signatures of reference samples. In the Amazon and other areas, wood products from protected trees can easily be confused with trees that are unprotected due to similarity in appearance. To test this technique, Lancaster and Espinoza (2012) identified chemical signatures of 13 tree species, tested unknowns using DART-TOFMS, and analyzed differences in species using linear discriminant analysis. The techniques were highly reproducible for correctly identifying species 91 to 100% of the time. Thus, DART-TOFMS may provide a means of rapidly identifying protected plants to solve problems in forensic botany.

Reference: Lancaster and Espinoza (2012)

15.12 Chapter Review

15

Concept Review

15.1 *Wood has significant worldwide economic value.* Wood is extremely versatile and the most heavily used plant product in the world. It is used in energy production, building construction, furniture, plywood, flooring, paper, and many other applications.

15.2 *A variety of products can be made from wood fibers and wood extracts.* Wood can be digested to produce wood fibers. The resulting fibers are used in many different types of paper and in food products as thickeners and extenders or to affect the food texture, clumping, and consistency. The extraction of chemicals from wood yields tars, resins, pharmaceuticals, dyes, syrup, and spices.

15.3 *Wood development and composition show annual cycles.* The growth of wood reflects the annual cycle of growing seasons, especially in temperate climatic zones. Each season of growth leaves behind a layer of xylem to the interior and generates a new layer of phloem to the exterior. Wood "grain" is a result of seasonal variation in the size of vessels and tracheids. Dendrochronology is the science of using tree rings to reconstruction climate history.

15.4 *Wood varies in its architecture and composition.* Wood is best studied by examination of cross, radial, and tangential sections. Woody eudicots produce "hardwood," while conifers produce "softwood." Waste products and tannins are deposited in the older, inner layers, resulting in "heartwood." Transpiration takes place in the younger, outer layers called "sapwood."

15.5 *Conifer wood has tracheids, parenchyma, and rays.* Tracheids serve for water conduction and support in gymnosperms. They are long and narrow and tapered at the ends, tapered to the extent that they lack end walls. Tracheids have numerous pits in the side walls through which water moves from one tracheid to the next. Resin canals secrete and store rot- and insect-deterring resins; they may be axial or radial. Gymnosperm xylem rays are composed of a mixture of tracheids and parenchyma.

15.6 *Eudicot wood is characterized by vessel elements, tracheids, parenchyma, and rays.* Woody eudicots contain vessel elements, which may also be called "pores." The size and arrangement of pores is both genetically and environmentally control and very useful in taxonomy and in determining the structural, mechanical, and functional properties of the wood. Pore arrangement may be ring-porous, diffuse-porous, semi-porous, or dendritic. Vessels may be grouped in recognizable patterns or scattered randomly throughout the wood, depending on the species. Likewise, xylem parenchyma distribution shows species-specific distribution patterns. Xylem rays are composed of tracheids and parenchyma and serve to transport water and nutrients to the periderm.

15.7 *Reaction woods develop in response to gravity.* Reaction wood develops in response to sustained gravitational pull. Gymnosperms develop compression wood on the lower side of a horizontal trunk branch, while angiosperms develop tension wood on the upper side. The S2 layer of the secondary cell wall is the main area to see thickening in reaction woods.

15.8 *Tyloses and crystals may be found in some woods.* Tyloses occur when the protoplasm of a paratracheal parenchyma cell extends through a pit into the lumen of an adjacent vessel element. They form naturally in some species and in response to infection in other species. Calcium oxalate, Mg oxalate, or SiO_2 crystals may be found in the vessels or parenchyma of some species.

15.9 *Monocot "wood" does not come from true secondary growth.* Wood is generated by the vascular cambium during secondary growth. Even though monocots lack true secondary growth, some such as palm trees and bamboo develop thick layers of fibers around each of the dozens or hundreds of individual vascular bundles scattered throughout the stem. The end result is a structurally strong and tough stem that can be used in many of the same ways that true eudicot wood is used.

15.10 *Wood macerations are useful for species identification, product identification, and forensics.* Maceration is the process of dissolving out the lignin that holds together the tracheids, fibers, and vessel elements of wood. This is a simple and easy way to study the individual cells of the wood and is valuable in species identification and in determining the composition of paper products.

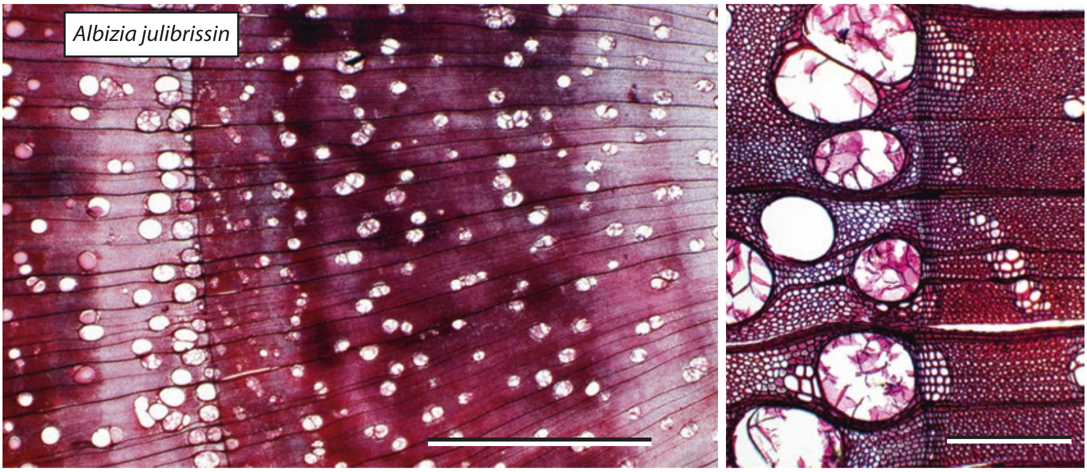
15.11 *The study of tree rings is important in archeology, climatology, and forensics.* Because growing conditions have a large effect on tree ring thickness, morphology, and composition, and tree rings accumulate on an annual basis, every tree contains a historical environmental record. The science of dendrochronology has been able to reconstruct thousands of years of continuous climatological record. It can also be used to date in buildings, ships, musical instruments, and artworks.

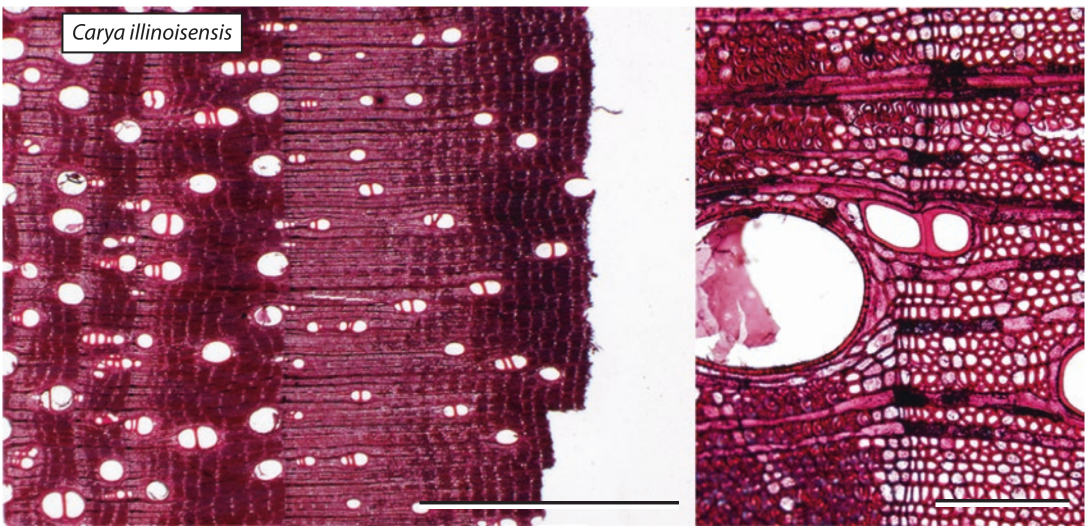
▪ Concept Connections

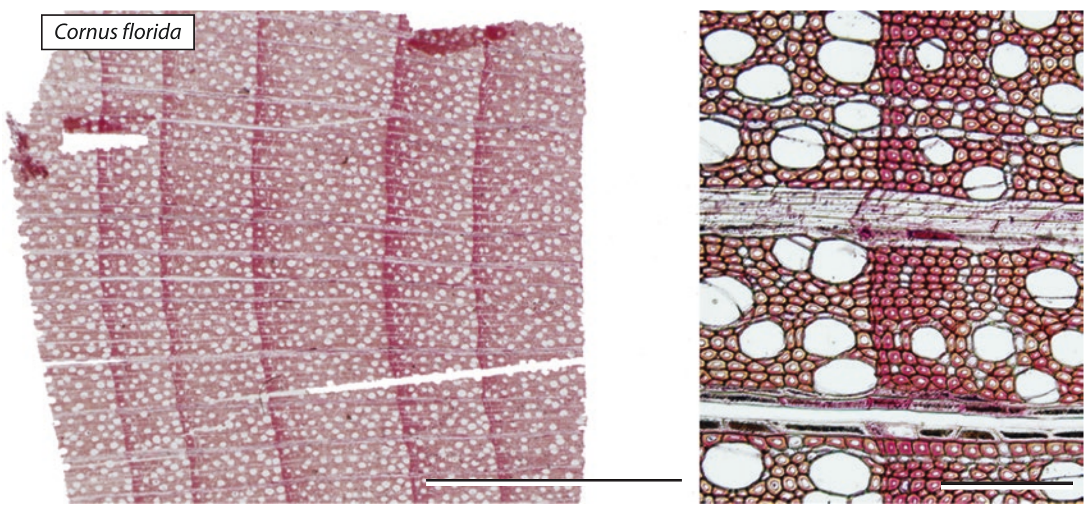
? 1. Match the description of the wood anatomy given in the table to the proper image that follows beneath (Descriptions from The Wood Database – ► www.wood-database.com)

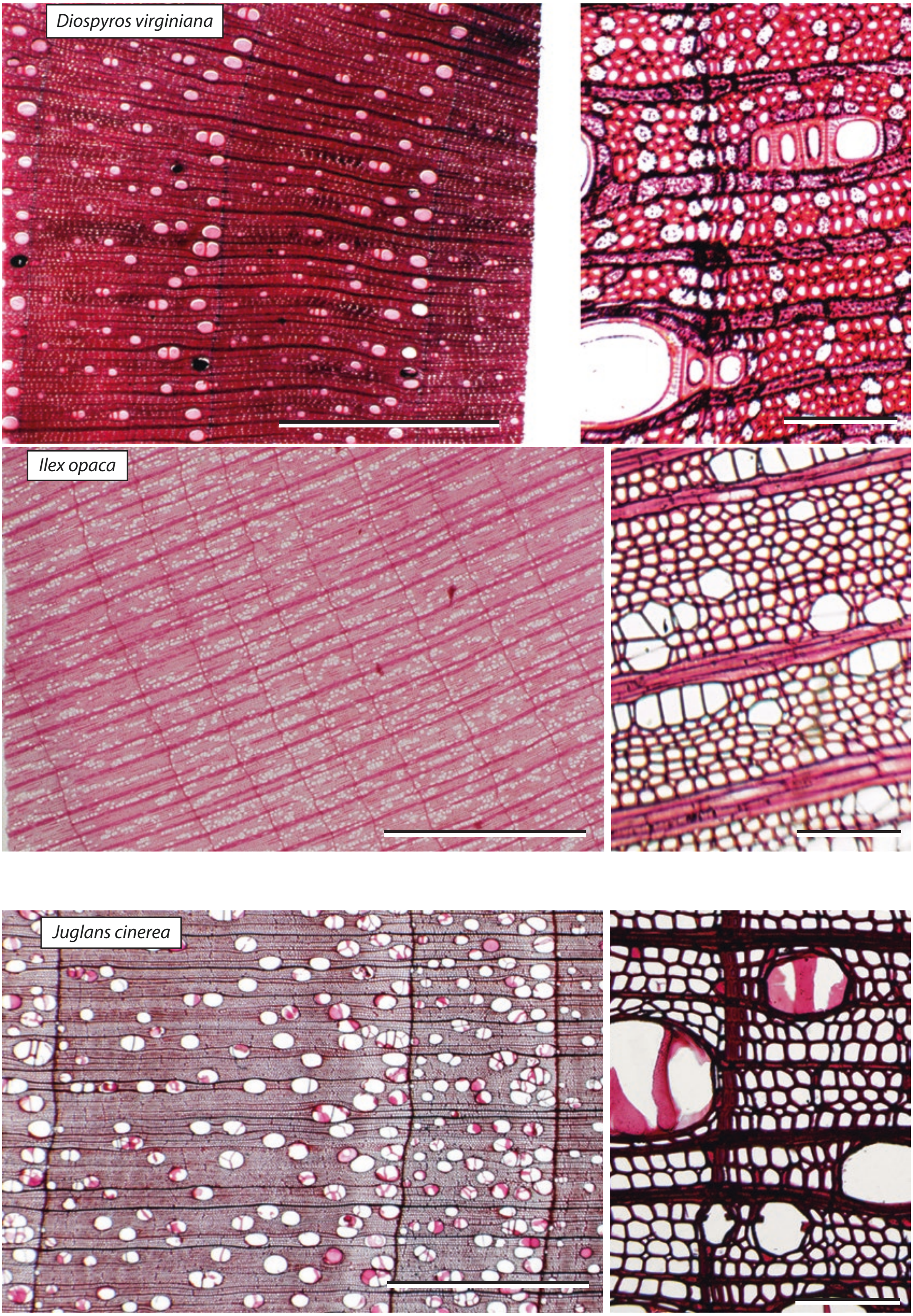
	Description
a	Ring-porous; large earlywood pores three to six rows wide, small latewood pores solitary and radial multiples of two to four; tyloses common; growth rings distinct; rays visible without lens; parenchyma around latewood pores vasicentric, aliform (winged), and confluent
b	Ring-porous; two to four rows of large, exclusively solitary earlywood pores, numerous small latewood pores in radial arrangement; tyloses absent; growth rings distinct; rays large and visible without lens; apotracheal parenchyma diffuse in aggregates (short lines between rays)
c	Ring-porous to semi-ring-porous; large to very large earlywood pores in a single intermittent row, medium to small latewood pores solitary and radial multiples of two to three, few; tyloses common; parenchyma reticulate (bands absent from earlywood row in true hickory group, but present in pecan hickory group); narrow rays, close spacing

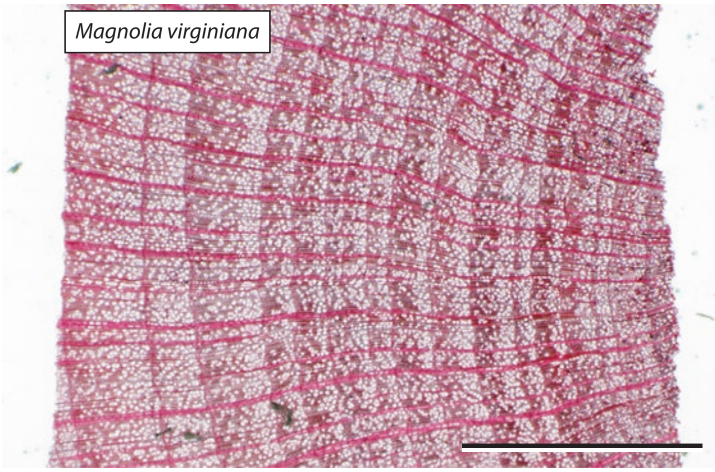
	Description
d	Semi-ring-porous; medium to large earlywood pores sometimes form broken rows, latewood pores medium to small; solitary and radial multiples of two to three; growth rings usually distinct; rays not visible without lens; parenchyma diffuse in aggregates, vasicentric, and banded (reticulate and marginal).
e	Semi-ring-porous; medium to large earlywood pores gradually decreasing to small latewood pores; solitary and radial multiples of two to three; tyloses occasionally to abundantly present; growth rings distinct; rays barely visible without lens; parenchyma banded (marginal); apotracheal parenchyma diffuse in aggregates (sometimes very faint and barely visible even with lens)
f	Diffuse-porous or semi-ring-porous; small to medium pores predominantly in radial multiples of two to four, commonly arranged in radial rows, moderately numerous to numerous; growth rings may be distinct due to an intermittent row of earlywood pores; rays in variable sizes from narrow to very wide, normal to fairly close spacing; parenchyma not typically visible with lens
g	Diffuse-porous; small to very small pores tending to occur in increased frequency in earlywood zone; exclusively solitary; growth rings distinct; rays usually not visible without lens; parenchyma not typically visible with lens
h	Diffuse-porous; solitary and radial multiples; large to very large pores in no specific arrangement, very few; tyloses abundant; parenchyma vasicentric, lozenge, confluent, and marginal; narrow to medium rays, spacing normal
i	Diffuse-porous (growth rings generally distinct due to gradually decreasing pore density in latewood); small to medium pores in no specific arrangement, moderately numerous to numerous; exclusively solitary; tyloses occasionally present; parenchyma not visible; medium to wide rays, spacing normal
j	Diffuse-porous; small to medium pores in no specific arrangement, numerous; solitary and radial multiples of two to three; growth rings distinct; narrow rays visible without lens, normal spacing; parenchyma marginal
All scale bars = 1 mm for left panels and 100 μm for right panels	

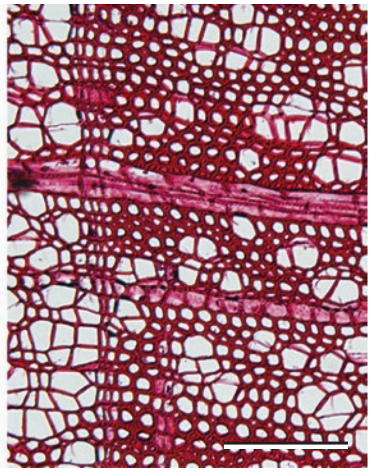

Albizia julibrissin

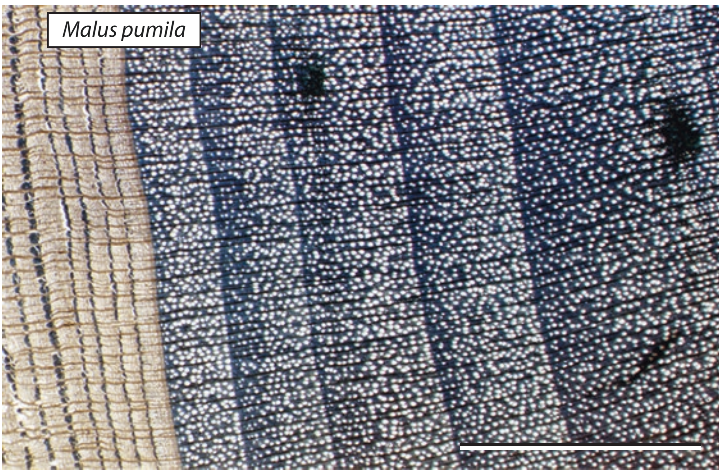

Carya illinoisensis

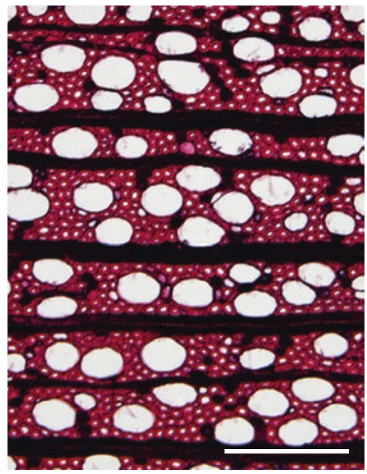

Cornus florida


Diospyros virginiana
Ilex opaca
Juglans cinerea

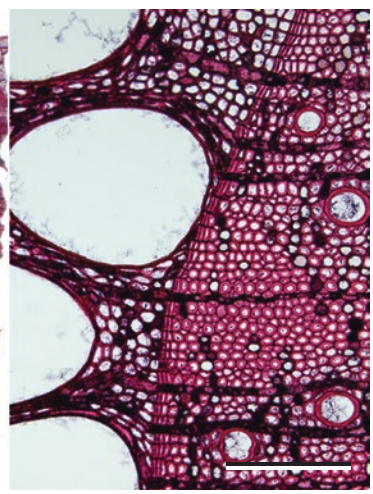

Magnolia virginiana

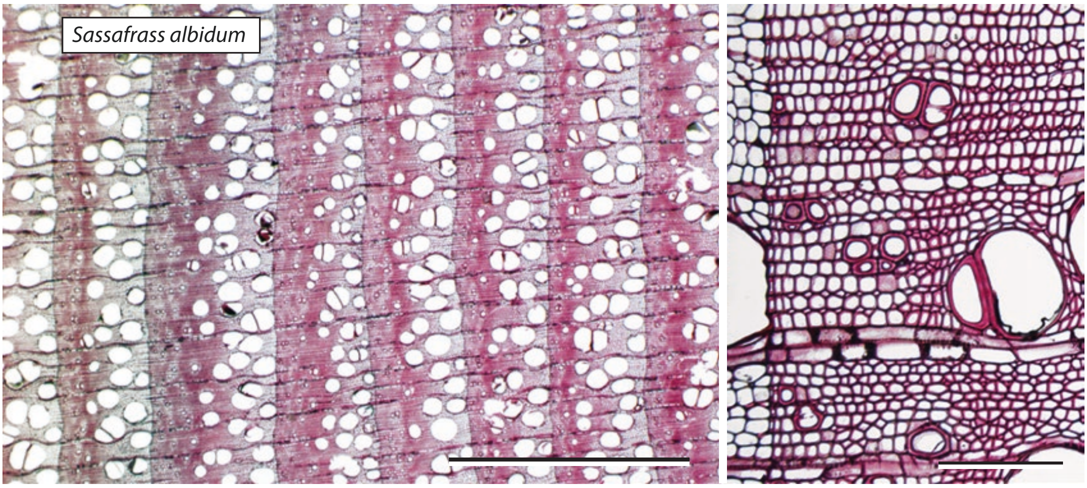



Malus pumila




Quercus rubra





■ **Concept Assessment**

2. Summerwood is
   a. the same as heartwood.
   b. found to the outside of each annular ring of xylem.
   c. found to the inside of each annular ring of xylem.
   d. formed throughout the growing season.
   e. only found in monocots.

3. Monocot "wood" is the result of
   a. secondary growth.
   b. heartwood.
   c. dedifferentiation of phloem fibers.
   d. massive fiber development of fiber caps.
   e. conversion of fibers to fiber tracheids.

4. All gymnosperms lack vessel elements
   a. true.
   b. false.

5. Paratracheal parenchyma may be found
   a. at the interface of spring and summerwood.
   b. around wood rays.
   c. in phloem.
   d. in conifers.
   e. around vessels.

6. Heterocellular rays contain
   a. vessels and tracheids.
   b. fibers and vessels.
   c. fibers and tracheids.
   d. vessels and parenchyma.
   e. tracheids and parenchyma.

7. An example of a diffuse-porous wood would be
   a. oak.
   b. sugar maple.
   c. elm.
   d. osage orange.
   e. ash.

8. Wood pulp may contain
   a. vessel members.
   b. libriform fibers.
   c. tracheids.
   d. fiber tracheids.
   e. all of the above.

9. Gymnosperm resin is produced by
   a. the vascular cambium.
   b. epithelial cells.
   c. tracheids.
   d. vessel elements.
   e. fibers.

10. Trees from tropical climates show less "figure" than trees from temperate climates because
    a. most tropical trees are monocots.
    b. temperate trees grow slower than tropical trees.
    c. the tropics have less seasonal variation in growth conditions.
    d. tropical trees grow faster than temperate trees.
    e. figure is a result of variations in phloem development.

11. Most transpiration is via the
    a. heartwood.
    b. summerwood.
    c. sapwood.
    d. reaction wood.
    e. hardwood.

Concept Applications

12. Imagine you have the ability to genetically engineer poplar trees (*Populus tremuloides*) to express any anatomical character you wish. Which anatomical traits would you select if you were to engineer poplar for the boat building industry, the furniture industry, or the paper industry?

13. Wood has been called the ultimate recycling material, but cutting down trees kills them and many trees are threatened or endangered. Use the Internet to research "sustainable lumber," and write a minute paper on those efforts (a minute paper is a brief summary of a specific topic).

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Periderm

16.1 Periderm Comprises a Large Component of Bark and Adds a Protective Layer to Plants – 554

16.2 Phellogens Originate De Novo by Dedifferentiation of Existing Cells in the Epidermis, Cortex, Phloem, or Pericycle – 557

16.3 Phellem Cells Are Suberized, Dead, and Generated to the Exterior of the Phellogen – 560

16.4 Phelloderm Cells Are Living and Generated to the Interior of the Phellogen – 562

16.5 The Polyderm Is an Internal Protective Tissue Composed of Alternating Rows of Suberized and Lignified Cells – 563

16.6 Lenticels Are Formed in Areas Where the Periderm Has Ruptured due to the Buildup of Filling Tissue, Facilitating Gas Exchange – 563

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Introduction

On herbaceous plants, the epidermis is the outer protective covering of all portions of the plant—roots, shoots, and flowers (▶ Chap. 9). Thus, the epidermis is of primary origin. In contrast, the periderm and bark are of secondary origin and are found on the stems and roots of woody eudicot plants, gymnosperms, and, in a different form, in some monocots. In this chapter we will identify the origin, components, development, and characteristics of periderm, consider the structure and function of lenticels, and describe the nature and composition of the rhytidome in its various forms.

16.1 Periderm Comprises a Large Component of Bark and Adds a Protective Layer to Plants

Of all plant anatomical structures, the **periderm** seems to have the most, and the most difficult to master, terminology. With this in mind, ◘ Table 16.1 and ◘ Fig. 16.1a, b may help better define the

◘ **Table 16.1** Layers of the epidermis, periderm, and rhytidome, starting from the outside of a stem or root and moving inwards

Technical terminology	
Phellem (cork)	2° growth produced by the phellogen to the exterior; usually multiple cell layers
Phelloid cell	Phellem cells that do not contain suberin; scattered throughout the phellem; may be sclereids in some species
Phellogen	aka cork cambium; the 2° meristem that gives rise to phellem and phelloid cells to the exterior and phelloderm to the interior
Phelloderm	2° growth produced by the phellogen to the interior; usually one to a few cell layer
Periderm	Sum of the phellem, phelloid cells, phellogen, and phelloderm
Polyderm	A specialized, multilayered tissue found in some roots and rhizomes; dead outer layers, but with non-suberized inner layers of storage cells; found in a select group of plant families
Rhytidome	A (sometimes) thick accumulation of dead tissue found on mature stems and roots, mostly outer layers containing periderm (produced by the phellogen) and secondary phloem (produced by the vascular cambium); everything to the outside of the most recent phellogen; roughly equivalent to bark
Nontechnical terminology	
Bark	All of the tissues to the exterior of the secondary xylem or wood
Inner bark	Living tissues of the vascular cambium and phloem and periderm
Outer bark	All dead tissues to the exterior of the inner bark

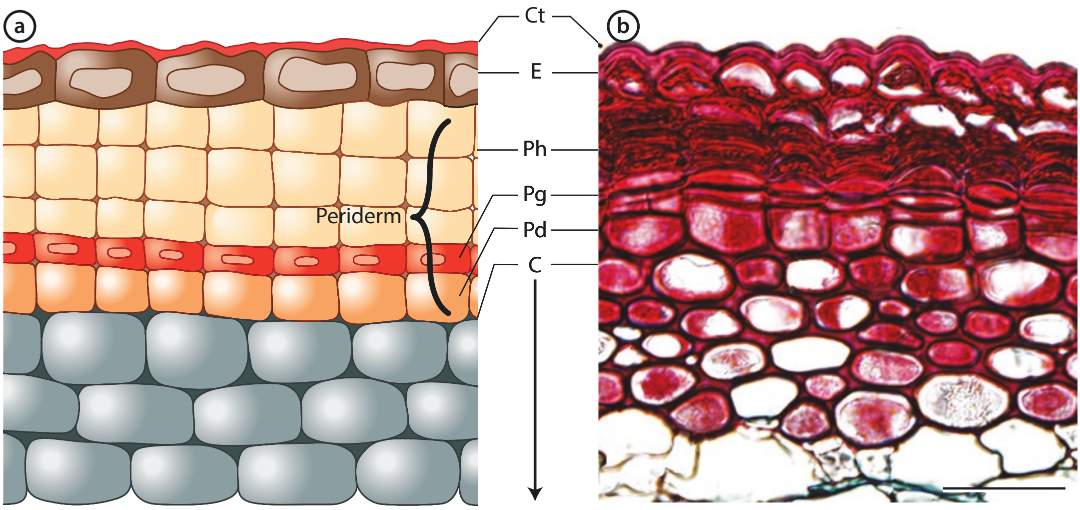


Fig. 16.1 **a** Drawing of epidermis, periderm, and cortical layers in a young stem. **b** A cross-section of a 1-year-old American basswood (*Tilia americana*) stem at the outer surface. The cuticle (Ct) and epidermis (E) have not been shed yet but will when the periderm has fully developed. The phellem (Ph) is composed of heavily suberized and partially collapsed cork cells. The phellogen (Pg) is meristematic and shows periclinal divisions, producing phellem to the exterior and phelloderm to the interior. The phelloderm (Pd) is a single layer of large cells that align in a radial direction with the phellogen. The cells in the outer layer of the cortex (C) do not align with the phelloderm/phellogen but are becoming suberized. The large, innermost cortical cells are parenchymatous. Phelloid cells, located in the phellem when found, are not shown in either **a** or **b**. Scale bar in **b** = 25 µm (**a**, **b** RR Wise)

tissues and layers that make up the periderm and associated tissues. The structure and function of the individual layers will be discussed in detail in the following sections of this chapter.

All woody plants begin with primary growth and have an exterior covering at the initial stage of the **epidermis** (► Chap. 9) and, perhaps, a **hypodermis** (refer to ► Sect. 11.5). Upon the initiation of secondary growth, cells in the epidermis, cortex or secondary phloem of the stem (depending on the species and organ), or the pericycle of the root become meristematic and differentiate into a cambial zone called the **phellogen** (or **cork cambium**). The phellogen gives rise to **phellem** tissue (also called "cork") to the outside and **phelloderm** tissue to the inside (Fig. 16.1b). The periderm proper is thus the sum of the phellem, phellogen, and (if present) phellogen (which is dead at maturity). **Bark** is a nontechnical term used for all tissues to the exterior of the xylem, regardless of their origin. This includes the periderm, cortex (if present), active phloem conducting elements of the current growing season, as well as previous season's crushed conducting elements and phloem fibers. Therefore, even though the phloem tissues are not generated by the phellogen, it is common to call all of the living tissues between the xylem and the phellogen the "inner bark" and the dead tissues to the exterior of the phellogen the "outer bark" (Fig. 16.1b).

The periderm does not always form a continuous ring around a root or stem. Certain zones of the phellogen in the burning bush (aka winged wahoo) become extremely active and generate large extensions of cork off of the stem (Fig. 16.1c, d). While the function of such extensions is unknown, from their appearance alone, it has been postulated that it may function as browse deterrents.

■ **Fig. 16.1** **c**, **d** These photographs demonstrate corky "wings" of the burning bush (*Euonymus alatus*), a native of China that is widely used as a landscape plant. The wings result from localized activity of the phellogen along the longitudinal axis of the stem. Scale bars = 2 cm in **a** and 0.5 cm in **b** (**c**, **d** RR Wise)

Box 16.1 High-Tech Potato Periderm Assessment

Potato (*Solanum tuberosum*) is one of those most important and widely grown crops in the world, with over 420 million tons of the starchy, tuberous rhizome produced each year. The potato tuber has a thin, corky periderm which has multiple variations—smooth, rough (russeted), brown, red, purple, or yellow—and has been the subject of intensive study for over a century. Growth, harvesting, and subsequent handling can damage the tuber periderm and degrade the quality, storage, and marketability of the crop. Therefore, potatoes are subject to postharvest grading and sorting, processes that benefit from sophisticated automated inspection based on image capture and computer-assisted evaluation. Riza et al. (2017) have moved beyond simple video-based inspection methods and conducted research on validating the use of measuring diffuse light reflectance across the range of ultraviolet (UV) to visible light (vis) to near infrared (NIR). Their goal was to develop a technology capable of simultaneously detecting multiple periderm flaws such as the presence of soil clods on the tuber surface, mechanical damage, greening, and three forms of common scab lesion (CSL), clear CSL, superficial CSL, and deep

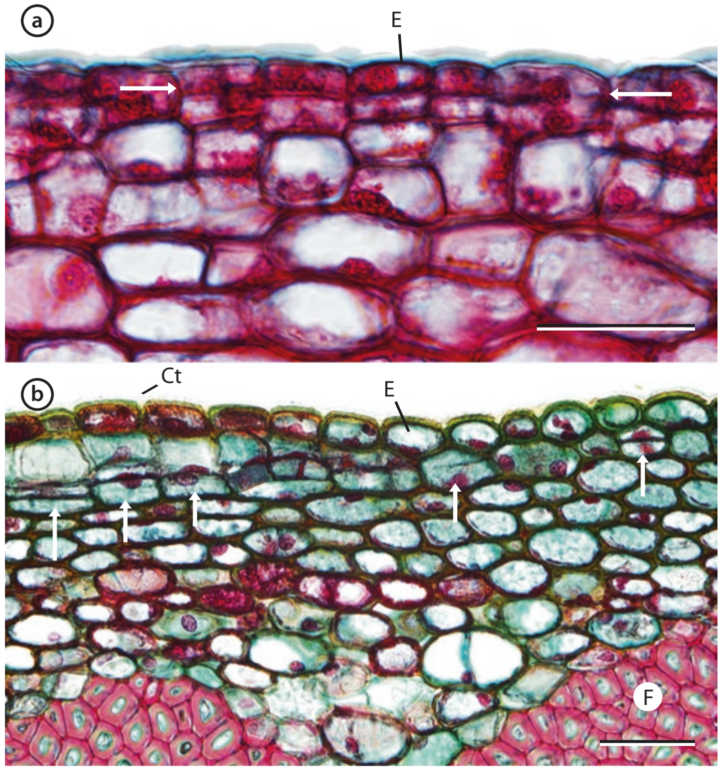
CSL. They found the most accurate results were obtained using detection at six different wavelengths and processing those images using a machine learning process (specifically, subspace discriminant classifier) to separate the periderm defects into different classes. The use of diffusive reflectance measurements at specific wavelengths, and the processing of those signals through a statistically based classification system, can identify each of the periderm defect types and may contribute to the development of automated systems for multiple defect discrimination.
Reference: Riza et al. (2017).

16.2 Phellogens Originate De Novo by Dedifferentiation of Existing Cells in the Epidermis, Cortex, Phloem, or Pericycle

Similar to the secondary vascular cambium (▶ Chap. 14), the phellogen is a lateral, cylindrical, meristematic tissue. However, it is different in that it is a temporary meristem and a new phellogen must differentiate each growing season. In contrast, the vascular cambium persists for the life of the plant. The phellogen is typically just one cell layer thick and usually bifacial in stems (producing new tissues to both the inside and outside—phellem and phelloderm) and unifacial in roots (producing new tissues only to the outside—phelloderm).

The stem phellogen originates when mature parenchyma cells in the epidermis, cortex, or phloem parenchyma dedifferentiate, i.e., revert to a meristematic state. Periclinal divisions are necessary to produce phellem to the exterior and phelloderm to the interior. When the phellogen is situated at or near the surface, it is called a **superficial phellogen**. Superficial phellogens may arise in the epidermis, as seen in pear fruit (◘ Fig. 16.2a), or in cortical cells just interior to the epidermis (◘ Fig. 16.2b). **Deep-seated** phellogens originate to the interior of the stem when phloem parenchyma cells dedifferentiate and become meristematic (◘ Fig. 16.2c, d). As the periderm develops, it will cut off the supply of water and nutrients to the cortex, fiber caps, and the external periderm, which will be shed (◘ Fig. 16.2e). Multiple phellogens may arise in a single growing season from epidermal, cortical, or phloem cells, and few survive until the next growing season. Woody perennials start with a superficial phellogen in their first year or two of growth (as in the sycamore seen in ◘ Fig. 16.2b) and then transition to developing deep-seated phellogens as layers of periderm encircle the stem and the original epidermis and cortex are shed.

In roots, the deep-seated periderm always arises in the pericycle through the process of dedifferentiation and redifferentiation of parenchymatous meristematic cells. As the phellogen produces phellem (◘ Fig. 16.2f), the endodermis, cortex, and rhizodermis that were the



■ **Fig. 16.2** **a**, **b** Superficial origin of the phellogen. **a** The phellogen of pear (*Pyrus communis*) fruit originates as periclinal divisions of the epidermal cells (E). Five pairs of epidermal/phellogen cells are shown between the two white arrows. **b** This 1-year-old sycamore (*Platanus occidentalis*) stem shows the phellogen originating as periclinal division of cells in the subepidermal cortex (white arrows). The cuticle (Ct) and epidermis (E) are still intact. The parenchymatous cortex lies between the phellogen and the large fibers (F) that cap the phloem (not shown). Scale bars = 20 µm in **a** and 25 µm in **b** (**a**, **b** RR Wise)

result of primary growth are shed (■ Figs. 10.9c and 16.2g). The development is primarily unifacial in cell production, and the derived cells typically lack intercellular spaces. Typically, the pericycle will develop a new phellogen every growing season, and the periderm will accumulate to seal off the root from the soil.

Box 16.2 Defense Components Found in the Periderm
Periderm replaces the epidermis early in tuber development, as in potato, and becomes the skin. In order to identify proteome factors (sets of proteins expressed by an organism) that may play a role in skin development and its defensive characteristics, proteins with high potentials were isolated and tested against biotic and abiotic stresses. High levels of patatin proteins (glycoproteins for storage and able to cleave fatty acids) were found in the young skins which exhibited antifungal resistance. It is believed that the skin may contain different isoforms of the proteins. The phelloderm (inner cell layers of the

periderm) contains high levels of glycoalkaloids which are toxic secondary metabolites active against a number of insect pests as well as pathogens. Periderm development is common among stems and roots of many seed plants and serves as a battery of defensive elements as the tissue increases in thickness by secondary growth as well as in lenticels and following wounding. Thus, the potato tuber skin may have functional implications for other periderm systems. Reference: Barel and Ginzberg (2008).

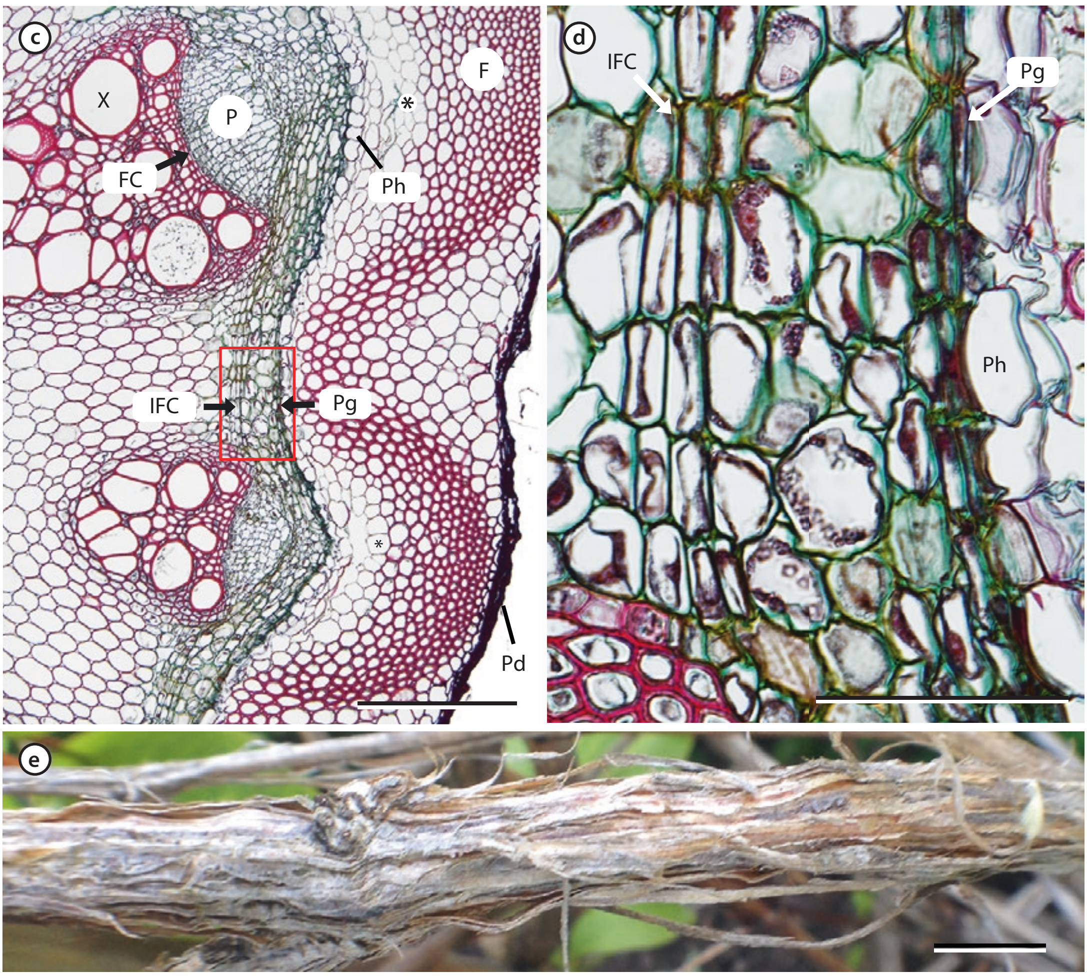


Fig. 16.2 **c**–**e** Deep-seated origin of the phellogen in a clematis (*Clematis* sp.) stem. **c** This low magnification view shows two vascular bundles containing xylem (X) and phloem (P) separated by a fascicular cambium (FC). Each bundle is capped by a group of fibers (F). An interfascicular cambium (IFC) has developed between the two bundles, and a phellogen (Pg) encircles the entire stem. Large phellem cells (Ph) are visible between the phloem and fibers toward the top of the image. Note how the parenchyma cells just interior to the fiber caps (labeled with *) show tearing. The original periderm (Pd) will be lost as the tissues to the exterior of the deep-seated phellogen mature. The red box indicates the area of **d**. **d** At a higher magnification, the early stage of development of the interfascicular cambium (IFC) and phellogen (Pg) can be seen. The IFC derivatives are still parenchymatous, not yet having matured into xylem (to the inside) or phloem (to the outside). The phellogen has produced a single layer of developing phellem (Ph) cells to the exterior. **e** Strips of periderm can be seen shedding off this 4-year-old *Clematis* stem. Scale bars = 100 µm in **c**, 50 µm in **d**, and 1 cm in **e** (**c**–**e** RR Wise)

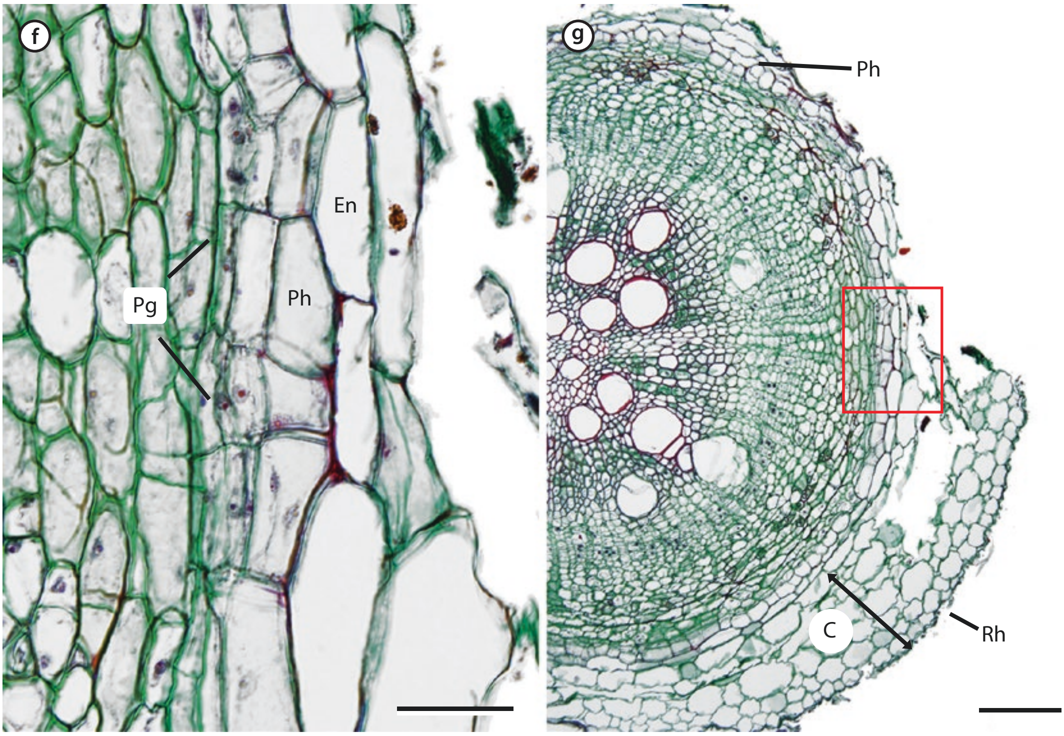


Fig. 16.2 **f**, **g** Root phellogen initiation. **f** High magnification view of a castor bean (*Ricinus communis*) root pericycle at the start of periderm formation. The phellogen (Pg) has generated a few phellem cells (Ph) to the exterior, adjacent to the endodermis (En). **g** At a lower magnification, it can be seen that while portions of the original rhizodermis (Rh) and cortex (C) remain on this specimen, some has been shed. Short radial files of phellem cells (Ph) are evident in areas. Red rectangle indicates the area of Fig. 16.2f. Scale bars = 25 µm in **f** and 100 µm in **g** (**f**, **g** RR Wise)

16.3 Phellem Cells Are Suberized, Dead, and Generated to the Exterior of the Phellogen

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Characteristically, phellem (cork) cells produced to the exterior of the phellogen have the same shape as their initials and are aligned in radial brick-like columns with no intercellular spaces (Fig. 16.3a, b). The cell wall of cork cells contains suberin, a waxy protective substance that causes the cell to be impervious to water and gases. Upon functional maturity, cell death occurs accompanied by blockage of the plasmodesmata and emptying of the contents of cell lumens which are then filled with air, tannins, or resins. The elderberry phellem cells shown in Fig. 16.3a are mostly filled with tannins, while those of geranium (Fig. 16.3b) are collapsed and air-filled.

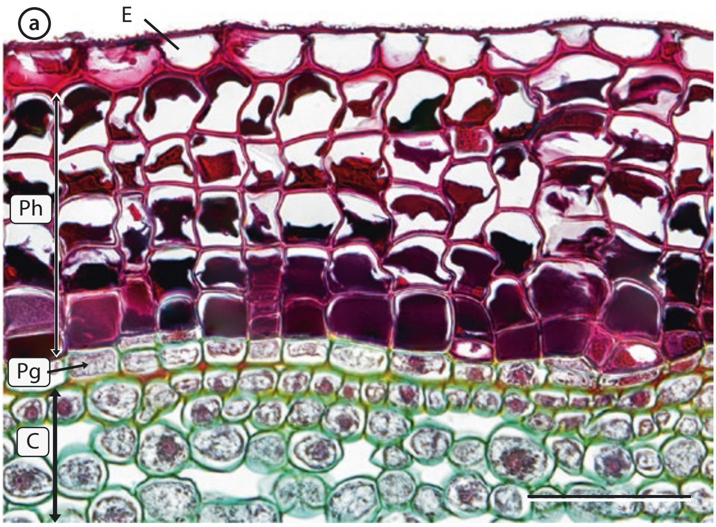


Fig. 16.3 **a** The periderm on this elderberry (*Sambucus* sp.) stem has one layer of epidermis (E), five to six layers of phellem (Ph) produced by the phellogen (Pg), and no phelloderm. Note the extensive suberization of the cell walls in both the epidermis and the periderm and lack of intercellular air space. Most of the phellem cells have extensive tannin deposits. Scale bar = 50 µm (RR Wise)

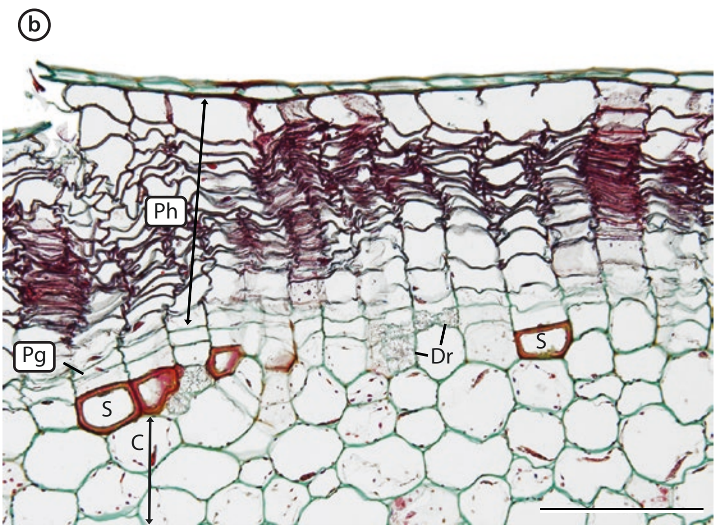
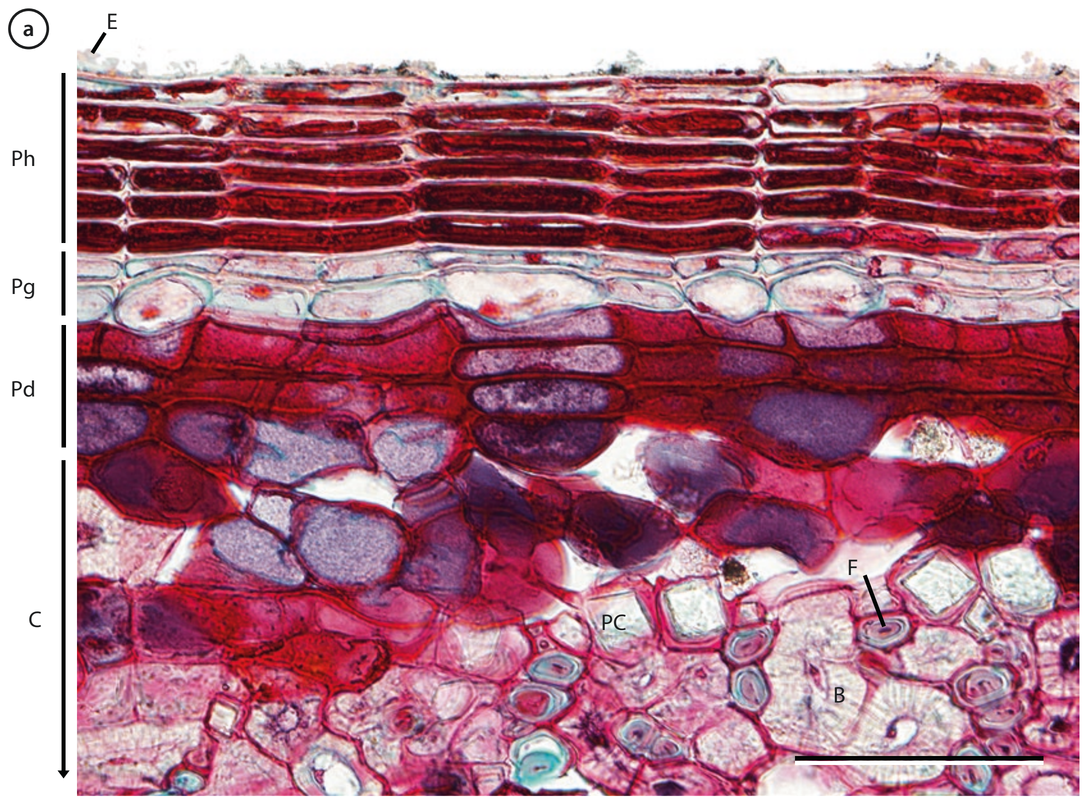


Fig. 16.3 **b** Phellem development in a geranium (*Pelargonium* sp.) stem. The phellogen (Pg) is loosely organized and not easily distinguished from the other layers. The phellem (Ph) cells are dead with the outer cells being crushed by the growth of the stem. Note that some of the phelloderm cells have developed in to sclereids (S), while others are filled with druse crystals (Dr). C cortex. Scale bar = 100 µm (RR Wise)

16.4 Phelloderm Cells Are Living and Generated to the Interior of the Phellogen

The phelloderm is a layer of parenchyma cells in the periderm generated by the phellogen toward the interior, opposite the phellem cell, and to the exterior of the cortex (◘ Fig. 16.4a). Not all species generate a phelloderm. The phelloderm is sometimes called a "secondary cortex" which reflects the overlap in function.

Phelloderm cells are shaped and arranged like phellogen cells but are larger and tend to be aligned in radial files that reflect their origin from the phellogen. They are parenchymatous, living cells at maturity and often are the sites of starch storage. Usually, the phellogen generates more phellem cells than phelloderm cells resulting in only one (refer back to ◘ Fig. 16.1b) to two or three layers of phelloderm (◘ Fig. 16.4a). However at sites where the phellogen is particularly active, such as where it underlies a lenticel, multiple layers of phelloderm may be produced (◘ Fig. 16.4b). Because they are living, phelloderm cells can undergo further development. Some mature into sclereids, while others may store starch or produce druse crystals (refer to ◘ Fig. 16.3b).



◘ **Fig. 16.4** **a** The phellogen (Pg) activity is directed primarily toward phellem (Ph) production to the exterior with smaller amounts of phelloderm (Pd) to the interior, as illustrated here for a 2-year-old tamarack (*Larix laricina*) stem. There are six layers of phellem and two to three layers of phelloderm. Remnants of the epidermis (E) can be seen at the stem surface. Note also the prismatic crystals (PC), fibers (F), and brachysclereids (B) in the cortex. Scale bar = 50 µm (RR Wise)

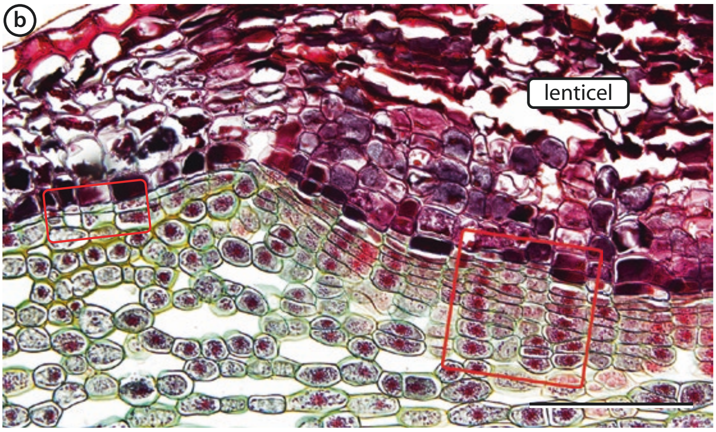


Fig. 16.4 **b** In this elderberry (*Sambucus canadensis*) stem, the phelloderm is only one layer thick where there is no lenticel (*red box to left*) but up to six layers thick where it underlies a lenticel (*red box to left*). Scale bar = 100 µm (RR Wise)

16.5 The Polyderm Is an Internal Protective Tissue Composed of Alternating Rows of Suberized and Lignified Cells

A **polyderm** is, as its name implies, a multilayered cylinder of cells that serves as a bounding layer in or around stems and roots, being more common in the latter. It is composed of alternating layers of suberized and non-suberized cells (often, but not always, lignified). The polyderm is generated by the pericycle in roots, which explains its position to the interior of the endodermis in young roots of the wax apple (*Syzygium samarangense*, Myrtaceae) tree (Fig. 16.5). A polyderm may have up to 20 layers, and, upon maturation of the root or stem, and loss of the cortex, it assumes the role of a periderm (Esau 1953). A polyderm may also develop in immature buds and serve as a barrier to fungal infection (Williamson 1984).

16.6 Lenticels Are Formed in Areas Where the Periderm Has Ruptured due to the Buildup of Filling Tissue, Facilitating Gas Exchange

Lenticels are interruptions within the periderm that extend through the phellem and allow for gas exchange between stems, roots, and fruits and the atmosphere (Fig. 16.6a, b). Given that the periderm phellem cells are nearly impermeable to gasses and water, lenticels provide a means for gas exchange by providing openings in the periderm for carbon dioxide produced via cellular respiration to exit and for oxygen needed for mitochondrial respiration to enter.

Lenticels form in areas where the epidermis has ruptured (Fig. 16.6c, d). The cork cambium beneath lenticels is more active, producing loosely arranged cells called **filling tissue** (Fig. 16.6e–h). The area on stems containing the filling tissue often gives way to the

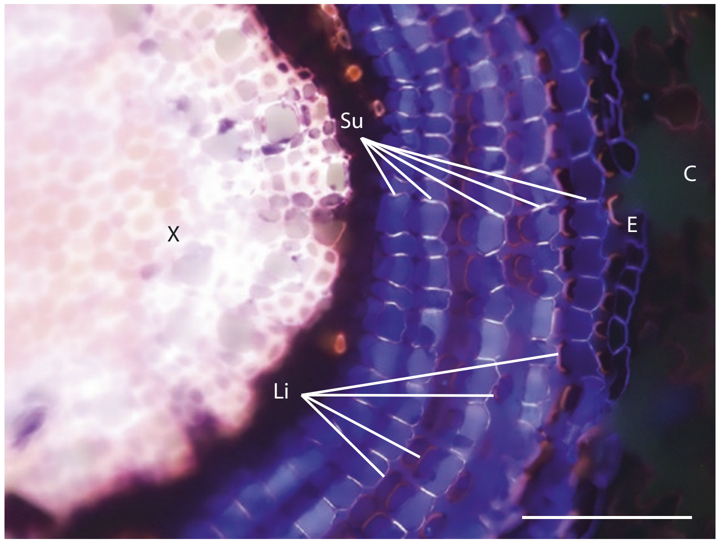


Fig. 16.5 A multilayered polyderm (P) developed in this young wax apple (*Syzygium samarangense*) root between the xylem (X) to the interior and the endodermis (E) to the exterior. The five suberized (Su) layers alternate with four lignified (Li) layers. The section was treated with a stain that fluoresces white in the presence of suberin and red in the presence of lignin. Scale bar = 100 µm. (A Tuladhar, Meijo University, Nagoya, Japan)

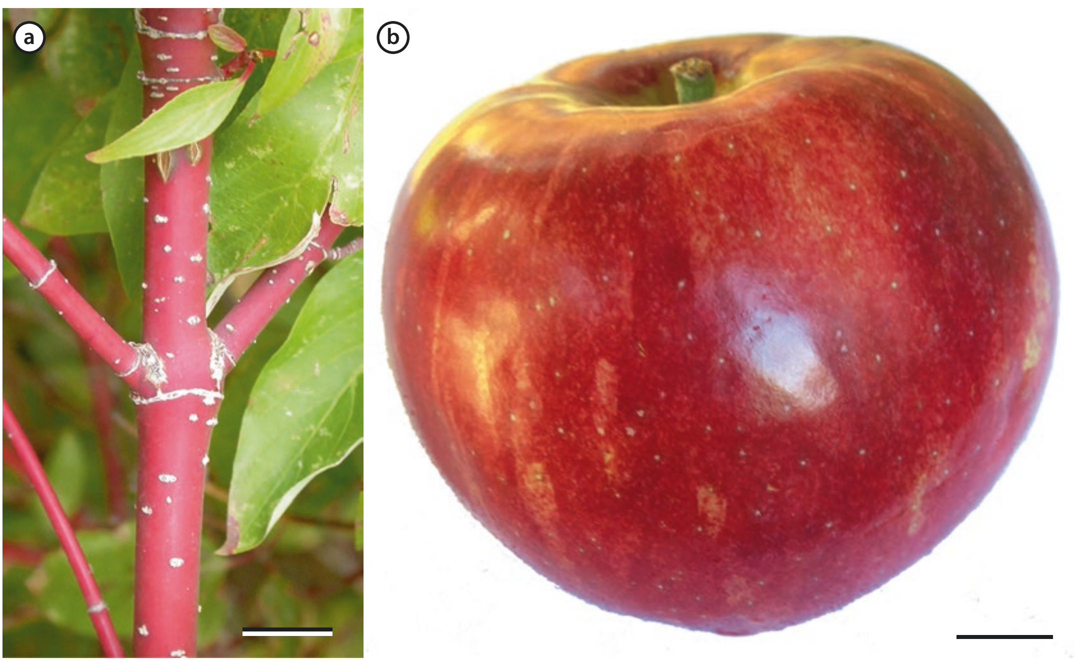


Fig. 16.6 **a** The outer morphology of lenticels is shown here in red osier dogwood (*Cornus sericea*). The lenticels are small and light colored. Their filling tissue is composed of very loosely arranged colorless cells with non-suberized cell walls. **b** Apples (fruit of *Malus domestica*) have extensive numbers of small, dot-like lenticels on the periderm surface. Scale bars = 1 cm (**a** Matt Lavin from Bozeman, Montana, USA, CC BY-SA 2.0; **b** S Lyons-Sobaski)

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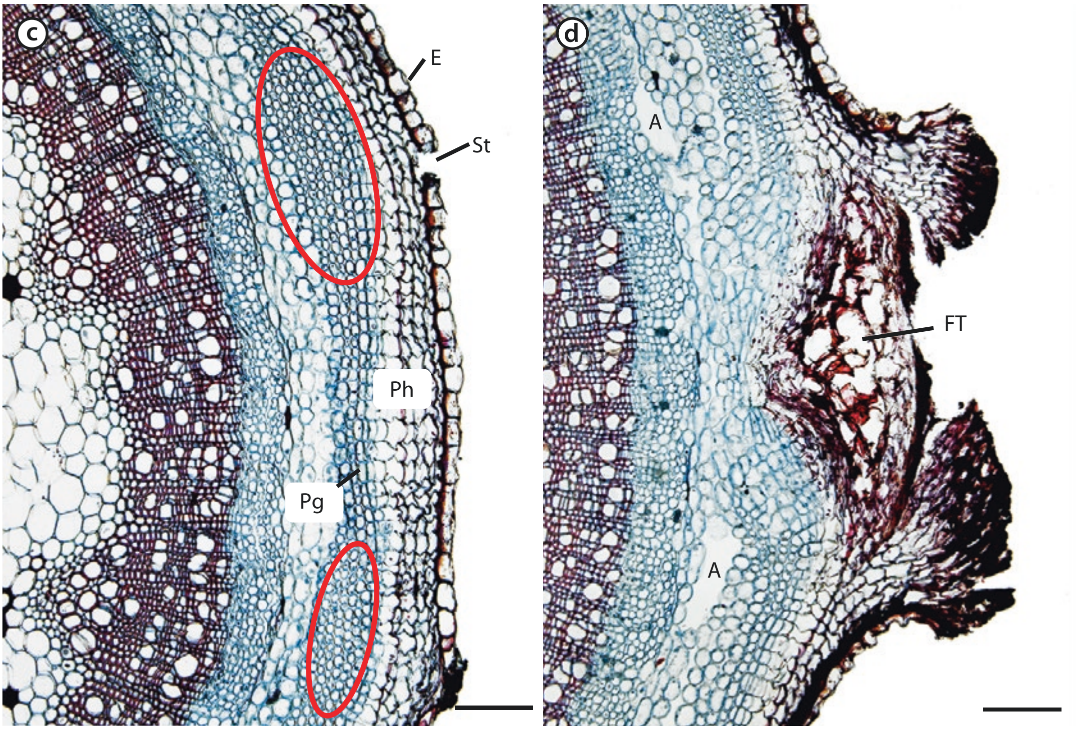


■ **Fig. 16.6** Lenticel structure and development in elderberry (*Sambucus canadensis*) stem periderm. **c** Two lenticels are shown at an early stage of development. The lenticel toward the top of the image is apparent by the degradation of the stoma (St) and the proliferation of small parenchyma cells in the cortex (red ellipse). The lenticel to the bottom of the image is lightly more advanced. The phellem has started to push against the epidermis (E) and create a bump on the stem surface. Cortical parenchyma has proliferated (red ellipse). **d**. A mature lenticel has ruptured the stem surface and is composed of dead cells of the filling tissue. Air spaces (A) have developed in the cortex. Scale bars = 100 µm (**c**, **d** RR Wise)

pressure, and thus, the outer tissue ruptures forming the lenticel. It is common to see that lenticels have formed underneath stomata.

Lenticels get their name from the Latin term, "lens," due to the lens-like shape of these structures (Esau 1953). They are often used in species identification which may be especially helpful during winter months (■ Fig. 16.6i, j). Lenticels are found in the periderm as long as it continues to grow; new lenticels will replace old ones. As the rhytidome is formed (see ► Sect. 16.7), lenticels become less active and usually blend into the corky tissue.

16.7 The Rhytidome Is a Multiyear, Multilayered Accumulation of Dead Tissues

The rhytidome is commonly called bark, although the two terms are not exactly synonymous. Bark is a nontechnical term for the thick, corky tissues on the outside of a plant, extending from the surface of the xylem (wood) to the surface of the stem or root. From an anatomical standpoint, there are multiple and different layers in bark. If you recall from earlier in the chapter, bark is made of both inner and outer bark. Inner bark extends from the cells immediately

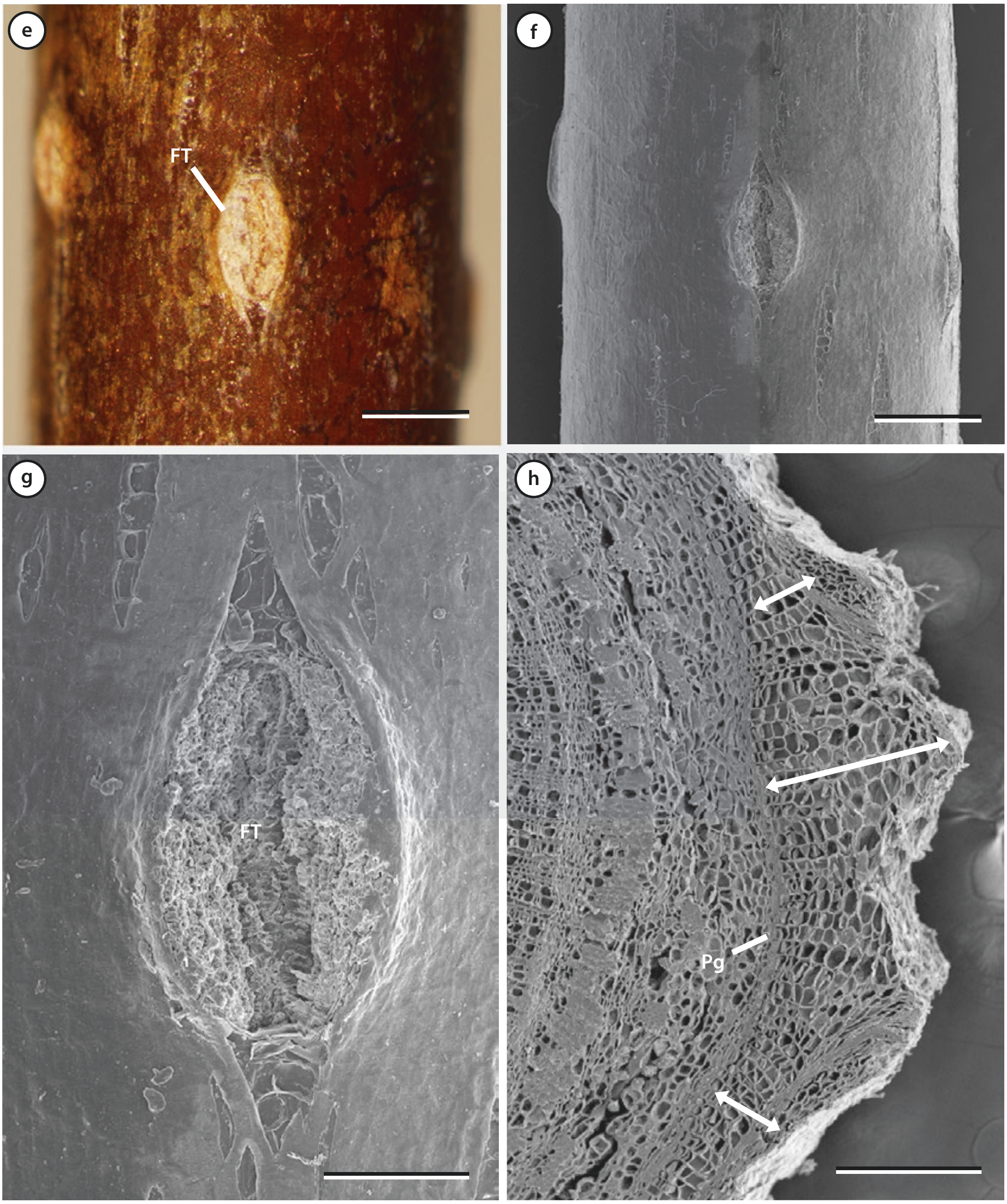


Fig. 16.6 **e**–**h** Four different views of lenticels on a young stem of a katsura tree (*Cercidiphyllum japonicum*). **e** Light macrograph showing the light color of the filling tissue (FT), as compared to the reddish bark. **f.** SEM of three lenticels, one in face view and two in side view. **g** SEM of filling tissue and the rupture in the epidermis and periderm caused by growth of the lenticel. Several smaller splits can be seen in the epidermis. **h** Cross-section SEM of a lenticel. The phellem of the filling tissue (*double-headed arrows*) extends from the phellogen (Pg) to the stem surface. Scale bars = 500 µm in **e** and **d** and 250 µm in **g** and **h** (**e**–**h** RR Wise)

◘ **Fig. 16.6** **i**, **j** Lenticels found in the surface of **i** white poplar (*Populus alba*) and **j** sweet cherry (*Prunus avium*). Scale bars = 2 cm (**i, j** RR Wise)

outside of the vascular cambium to the innermost cork cambium; thus, the inner bark extends from one secondary cambium to another secondary cambium (◘ Fig. 16.7a). The rhytidome (rhytis = Greek for "wrinkle") is the outer bark; it is not wood because it is not made of secondary xylem tissue. It is composed of dead cells immediately external from the cork cambium to the outside of the stem or root. It includes the present year's phellem and any secondary phloem, crushed primary phloem, crushed cortex, prior periderms, and crushed epidermis from previous years. Given enough time, the rhytidome can become quite thick.

◘ Figure 16.1a, b and most of the text in this chapter have described the development of a periderm during a single growing season in which a phellogen becomes active, produces phellem and (sometimes) phelloderm, and then dies. Superficial phellogens produce a periderm at the surface of the stem. Conversely, deep-seated phellogens in the stem and phellogens in the root produce a periderm inside the organ and to the exterior of the phloem (refer to ◘ Fig. 16.2c–g). Therefore, the periderm layers generated by those phellogens will cut off the supply of water and nutrients to any tissues to the exterior and they will die. Each growing season a new deep-seated phellogen arises and pushes the previous year's growth further outward. The accumulation of multiple years of periderms and the tissues they cut off (crushed phloem conducting elements and fibers) constitutes the rhytidome. Examples of the exterior and internal structure of the rhytidomes of several common tree species are given in ◘ Fig. 16.7b–i.

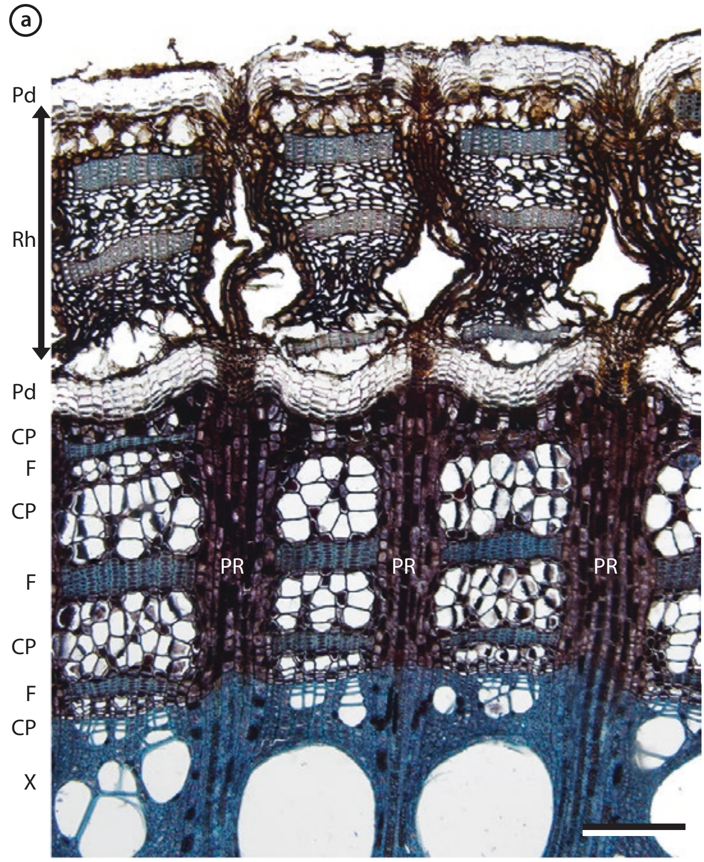


Fig. 16.7 **a** A cross-section of grape (*Vitis* sp.) rhytidome. Xylem (X) lies to the interior of the stem. Moving outward there are four layers of conducting phloem (CP) interspersed with three layers of phloem fibers (F). Those seven layers represent the phloem generated in the most recent year's growth. The vascular cambium (not shown) lies between the xylem and the first layer of conducting phloem. The periderm (Pd) appears in the form of colorless arches interrupted by narrow dark zones in which cork cells have pigmented contents. In the white zones, the phellogen was initiated in the secondary phloem axial parenchyma, while in the darker areas it originated in phloem rays (PR). The periderms are composed mostly of phellem cells. The zone of dead cells lying outside the innermost periderm is the rhytidome (Rh). This grape specimen only has one layer in its rhytidome. Scale bar = 100 µm (RR Wise)

16.8 Cork Is a Commercially Important Rhytidome

Cork is a portion of the bark from the cork oak tree (*Quercus suber*) indigenous to southern Spain, Portugal, and parts of northern Africa. The outer bark from the cork oak is sustainably harvested about every 9 years, leaving the inner bark intact, and thus, the trees may live to about 250 years old (Fig. 16.8a). From the cork, a number of commercial products are derived including bottle cork and stoppers, bulletin boards, dart board backers, flooring, fishing floats, insulation wall tiles, insulating hot pads and coasters, shoe wedges, and cork flooring among other products.

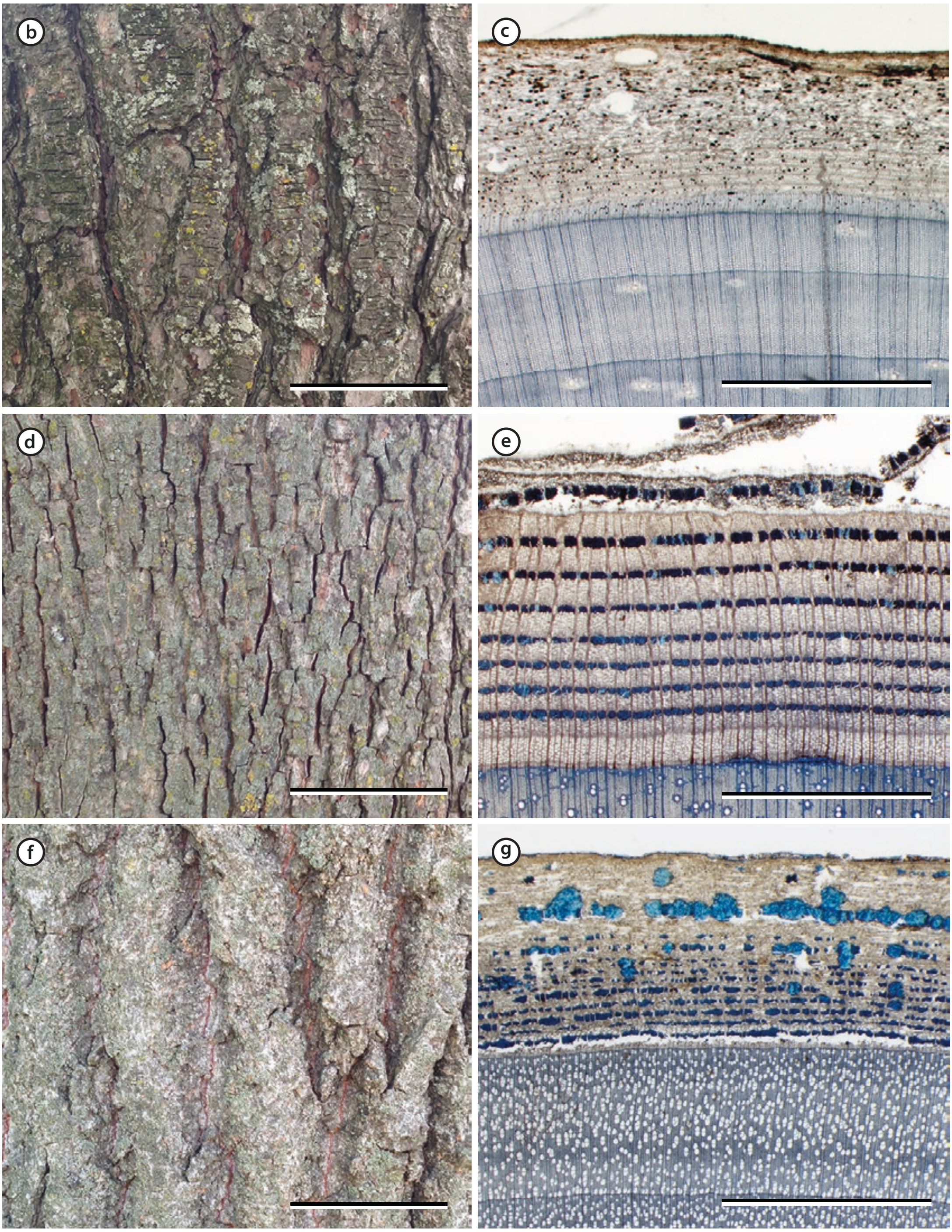


Fig. 16.7 **b**, **c** White pine (*Pinus strobus*), **d**, **e** green ash (*Fraxinus pennsylvanica*), **f**, **g** big-tooth aspen (*Populus grandidentata*), **h**, **i** white oak (*Quercus alba*). Scale bars = 5 cm in all left panels and 100 µm in all right panels (**b**–**i** RR Wise)

Cork cells are derived from phellogen initials and are developed in the radial direction. The tangential growth of the phellogen mother cell is reflected in the daughter cells. A highly suberized

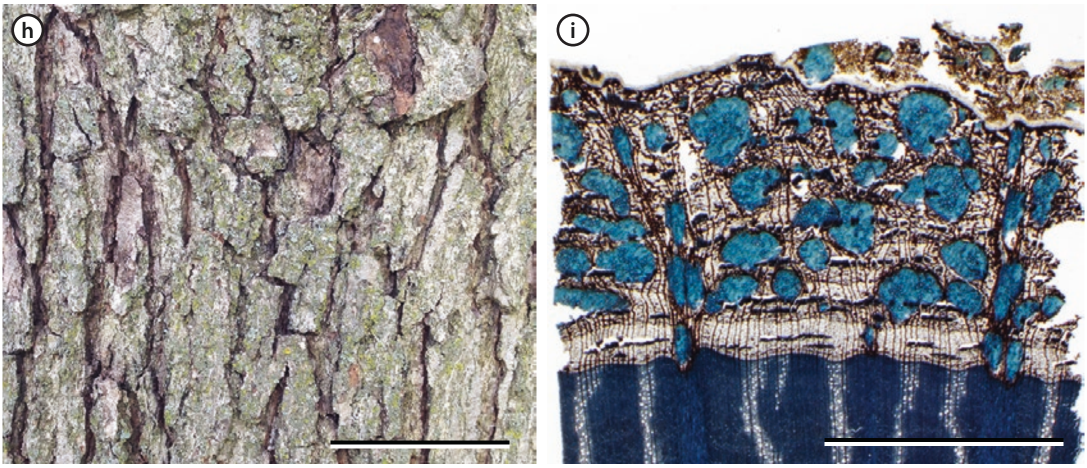


Fig. 16.7 (continued)

Fig. 16.8 **a** It requires manual skill, strength, and care to harvest the cork layer from the *Quercus suber* tree. With care, the cells grow back into new layers for harvesting about every 9 years. **b**. Individual layer of cork tissue showing the vertical extent of lenticel development as dark lines penetrating the homogeneous cork cells. (**a** Juan Carlos Cazalla Monijano, CC BY-SA 3.0; **b** Sallyofmayflower, CC BY-SA 3.0)

secondary wall is formed, and the cell contents are virtually devoid of cytoplasm and water, leaving only an air-filled lumen. The phellogen is functional during the growth months of the year and, in temperate zones, is not active during winter seasons. Thousands of cork cells can be found in a thin section of cork when viewed under the light microscope, and it was Robert Hook's famed observations of the compartmentalization of cork that gave rise to the name of "cells" as a unit of biological structure (refer to ► Chap. 2).

Cork has annual rings, although they may be difficult to always identify. While cork tissue is typically homogeneous in terms of cell types, lenticels interrupt the cork with cracks and irregular spaces brought about by the exchange passageways for air and other gasses (◘ Fig. 16.8b). The cells formed during the most active growth seasons are elongated in the radial axis with thin cell walls, while those formed in the end of the growth period are flattened radially with thicker walls. Cork development is promoted by periods of increased rainfall and higher temperatures.

16.9 Chapter Review

■ Concept Review

16.1 *Periderm comprises a large component of bark and adds a protective layer to plants.* The periderm is composed of a meristematic tissue called the phellogen that generates phellem cells to the exterior and phelloderm cells to the interior. The periderm is of secondary origin, and a new layer is generated each growing season.

16.2 *Phellogens originate de novo by dedifferentiation of existing cells in the epidermis, cortex, phloem, or pericycle.* The phellogen is a unique meristem—it does not persist from year to year and must arise anew via cellular dedifferentiation each growing season. Stem phellogens may arise in the epidermis or cortex (in younger stems; called superficial phellogens) or in the phloem (in older stems; called deep-seated phellogens). Root phellogens always arise in the pericycle.

16.3 *Phellem cells are suberized and dead at maturity.* Phellem cells are dead and their walls are heavily suberized. Therefore, they are impervious to water and gases. The cells themselves also contain air, tannins, or resins.

16.4 *Phelloderm cells are living cells generated to the interior of the phellogen.* Phelloderm cells are cork parenchyma. In contrast to the phellem, these cells are living and function in starch storage, contain calcium oxalate crystals, or develop into sclereids.

16.5 *The polyderm is an internal protective tissue composed of alternating rows of suberized and lignified cells.* This tissue type is not commonly found in many plants, but it plays a protective role in preventing fungal infections. It is usually restricted to the roots where it originates in the pericycle, interior to the endodermis.

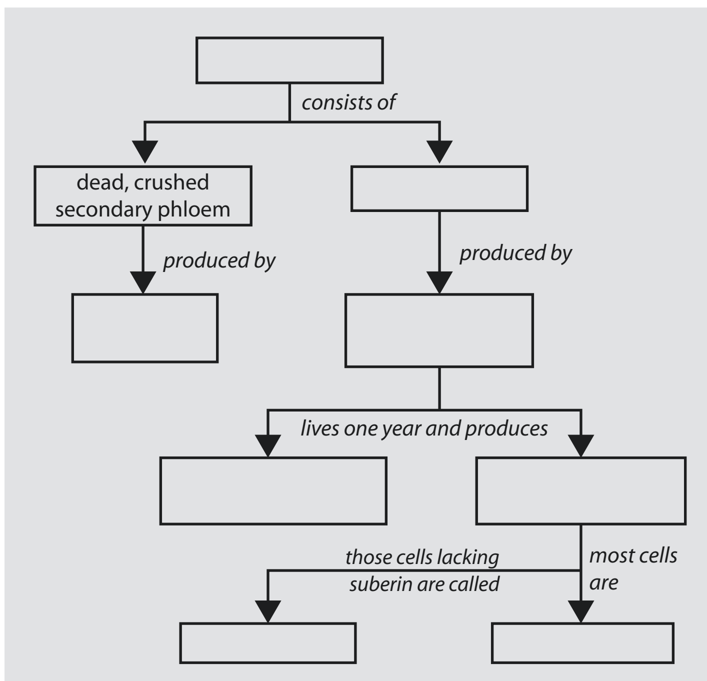
16.6 *Lenticels are formed in areas where the periderm has ruptured due to the buildup of filling tissue, facilitating gas exchange.* The periderm is impervious to gases and water. However, the living cells of the inner bark need oxygen to support respiration. Therefore, in certain localized areas, the phellogen will produce a large mass of phellem and phelloderm that pushes out and ruptures the surface of the stem or root, producing a structure called a lenticel. The lenticel is filled with loosely pack phellem cells that allow for the diffusion of O_2 into the stem or root and diffusion of CO_2 outward.

16.7 *The rhytidome is the outer bark and consists of dead cells.* Woody perennials generate a series of deep-seated phellogens over the course of their growth. The phellem and phelloderm produced by each successive phellogen cut off the living and dead tissues to the exterior. Over time, a multiyear, multilayered accumulation of dead periderms and phloem fibers accumulates at the stem or root surface. This is the rhytidome.

16.8 *Cork is a commercially important rhytidome.* Cork as an economic commodity is sustainably harvested from the cork oak tree (*Quercus suber*). Cork has a variety of applied uses as bottle stoppers, flooring, bulletin boards, and fishing floats to name a few.

Concept Connections

1. Use the following terms to complete the concept map below: cork cambium (phellogen), periderm, phelloderm to the inside (adaxial), phellem to the outside (abaxial), phelloid cells, rhytidome, suberized, vascular cambium.



Concept Assessment

2. From the perspective of a plant anatomist, the terms bark and periderm are synonyms.
   a. true; they refer to identical structures.

b. false; bark is made up of both living and nonliving components in contrast to periderm that is made up of only nonliving cells.
c. false; periderm is composed of the phellogen, secondary phloem, and vascular cambium only.
d. false; periderm contains the living cells of the cork cambium and nonliving cells of the cork; bark is more inclusive and also contains secondary phloem from the vascular cambium.
e. false; the periderm includes the vascular cambium and all the structures external from it whereas the bark does not include the vascular cambium.

3. Generally speaking, cork cells are impermeable to gasses and water because of
   a. the presence of suberin.
   b. air-filled cells in the lumen of the periderm.
   c. the cork cambium.
   d. the presence of sclereids in the cork tissue.
   e. the presence of lenticels.

4. In stems, the development of periderm often starts
   a. with the pericycle.
   b. as a branching of the vascular cambium.
   c. with the parenchyma cells differentiating into the cork cambium.
   d. as epidermal cells that morph directly into cells of the outer bark.
   e. both a and c.

5. Which of the following analogies is most appropriate?
   a. periderm : phellogen :: phellem : phelloid cell.
   b. phelloid cells : phellogen :: vascular cambium : cork cambium.
   c. rhytidome : phloem :: phellem : phellogen.
   d. phelloid cells : xylem :: polyderm: phellogen.
   e. phellogen : phellem :: vascular cambium : phloem.

6. Where does the periderm begin development in root systems?
   a. vascular cambium.
   b. phellogen.
   c. pericycle.
   d. xylem.
   e. phloem.

7. In the potato tuber, the periderm of the underground stem originates from the
   a. pericycle.
   b. epidermis.

c. starch-filled parenchyma cells.
d. vascular cambium.
e. secondary phloem.

8. The primary function of lenticels is to
a. produce cork cells within the phellem.
b. regulate the production of oxygen in the periderm.
c. produce suberin and prevent oxygen from exiting the plant.
d. allow for the exchange of gasses through an otherwise impermeable cell layers.
e. form the rhytidome.

9. The cork that is harvested for cork products such as bottle stoppers, bulletin boards, and flooring is harvested from which plant species:
a. *robinia pseudoacacia.*
b. *betula pendula.*
c. *quercus alba.*
d. *tilia americana.*
e. *quercus suber.*

10. Why can cork be used as fishing bobbers/floats?
a. because cork contains air-filled cells that allow the tissue to be buoyant in water.
b. because the suberin present within the cells is less dense than water.
c. because the suberin contained within the cells doesn't allow for water to enter cells.
d. both a and c.
e. all of the above.

11. Why are spaces and cracks found within cork?
a. the spaces were caused by insects boring into the periderm.
b. the spaces are lenticels and allow for gas exchange within the periderm.
c. the spaces are caused by drought conditions causing disruptions in the periderm during the growing season.
d. nutrient deficiency as the bark develops leads holes within the periderm.
e. the spaces are the result of viral infections that occur commonly among many plant species.

Concept Applications

12. Explain why harvesting cork from cork oak trees is sustainable and doesn't lead to premature death of the tree. What if cork from a cork oak tree was overharvested? What would happen if the inner bark was removed? What if the secondary phloem was removed? Finally, explain what would happen if the vascular cambium was removed? What would be the fate of this tree following the three different scenarios and why? Explain.

13. Compare the role, and longevity, of the vascular cambium to the cork cambium (phellogen) in terms of their contributions to the rhytidome.

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Flowering and Reproduction

SEM of a flower from the lyre-leaved sand cress (*Arabidopsis lyrata*). LM of a young apple (*Malus pumila*) fruit in cross section. SEM of a pollen grain from a northern catalpa tree (*Catalpa speciosa*). Photograph of a fruit from a breadfruit (*Artocarpus altilis*) tree. Photograph of a string of bleeding heart (*Lamprocapnos spectabilis*) flowers.
(All images by RR Wise.)

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R. Crang et al., *Plant Anatomy*, https://doi.org/10.1007/978-3-319-77315-5_17

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Introduction

A flower may be treated as a highly shortened shoot that is modified for sexual reproduction within angiosperms (*syn.* flowering plants). It is a characteristic system of reproductive organs in which two basic processes of sexual reproduction, meiosis and the fusion of male and female gametes, occur resulting in the production of a new generation, the **embryo**. Floral sterile parts, e.g., **sepals** and **petals**, as well as stamens (male structures) and sometimes pistil (female structures) are homologous to leaves. In this chapter, the first focus will be on the basic floral anatomy of the flower. Emphasis on the male anatomy of angiosperms will then be covered with female reproductive structures following in ► Chap. 18.

17.1 Flowers Possess Parts Arranged in Whorls That Vary Within and Among Species and Are Supported by a Receptacle

Flower anatomy is as diverse as the members of the angiosperm clade. A conceptualized flower will be discussed in this section, with the proviso that there are literally hundreds of variations on the basic theme shown.

Floral parts are typically borne in whorls (circular patterns) on the axis of the flower stalk known as the **receptacle**—a modified stem. From the outside, moving to the center, the three main whorls of floral organs are the perianth ("surrounding flower," sum of sepals and petals), the androecium ("male household," sum of all the stamens), and the gynoecium ("female household," sum of all the **carpels**) (◘ Fig. 17.1a).

Flowers may or may not have all three whorls. Perfect flowers have both an androecium and a gynoecium. Imperfect flowers have one or the other and are termed **pistillate** if they contain female reproductive structures or **staminate** if only male reproductive structures. Monecious (meaning "one household") plants have both male and female reproductive structures on the same plant. The flowers may be perfect or imperfect. Examples of monecious angiosperms with imperfect flowers include squash (Cucurbitaceae) and the grasses (Poaceae). Dioecious ("two households") plants have some individuals with only staminate flowers and some with only pistillate flowers, such as the honey locust (*Gleditsia triacanthos*). Obviously, all of the flowers on a dioecious plant are imperfect.

In contrast, most conifers (gymnosperms) are monoecious with unisexual reproductive structures appearing on the same plant. For example, most plants within the pine family (Pinaceae) are examples of monoecious gymnosperms, since their individuals contain both male and female cones (◘ Fig. 17.1b–e) and lack flowers. For comparison, ginkgo (*Ginkgo biloba*) is an example of a dioecious gymnosperm, since individuals have either male or female reproductive structures, but not both types. Having reproductive structures that contain only male or female reproductive structures is one way plants can avoid the negative impacts of inbreeding.

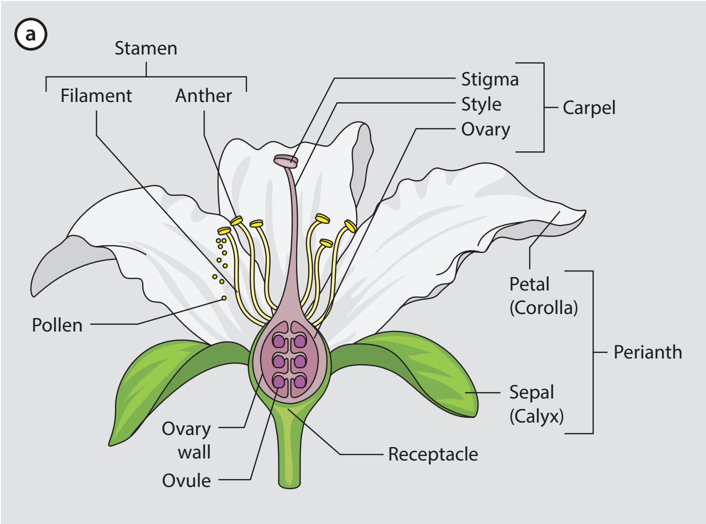
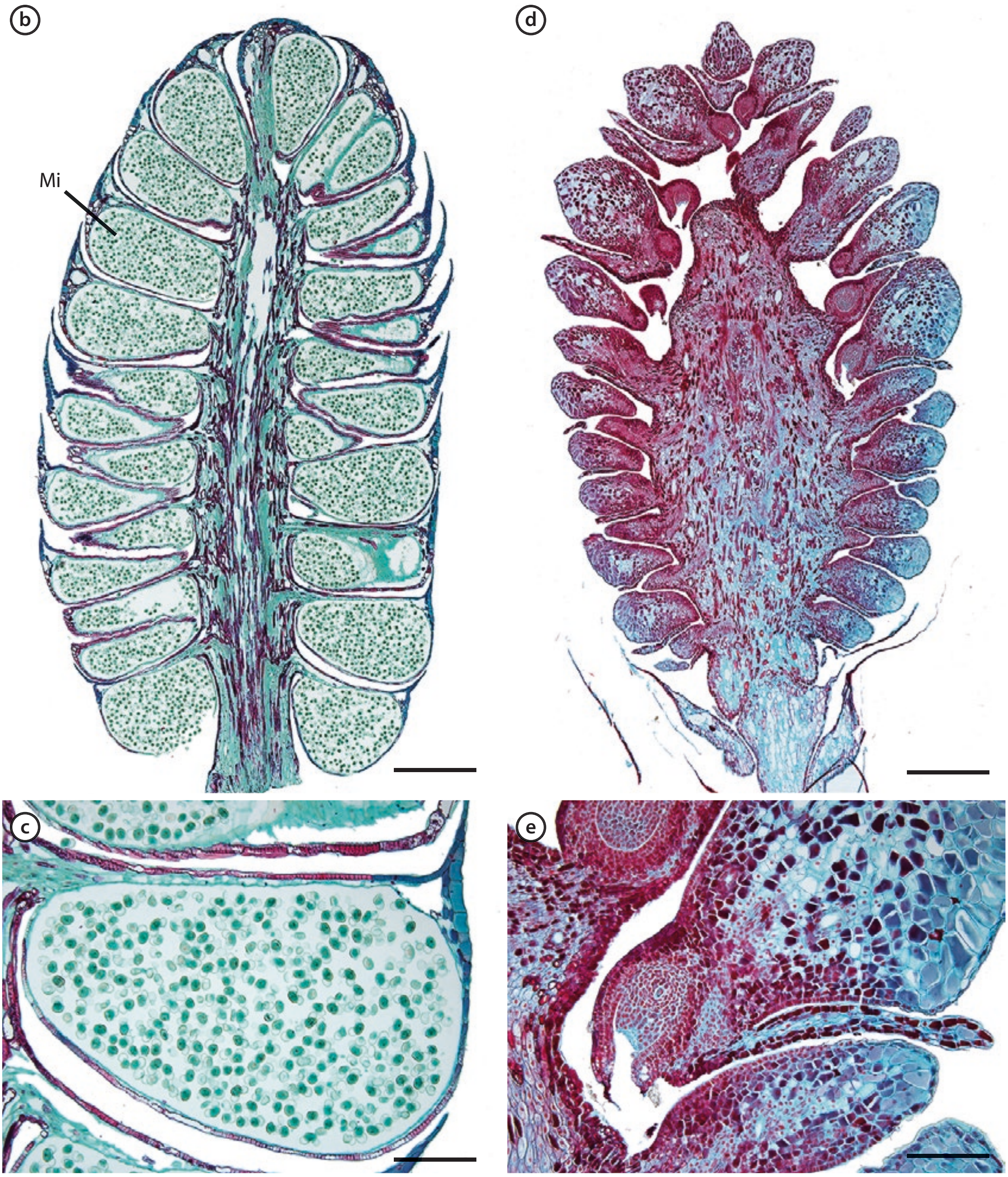


Fig. 17.1 **a** Conceptualized eudicot flower. The flower sits on a receptacle. The perianth includes the sepals and petals. The androecium is the sum of all the stamens, each of which is composed of a filament topped by an anther. Pollen cell production takes place inside the anther. The gynoecium is the sum of all the pistils, which are made of a stigma, style, and ovary. Finally, the ovary is surrounded by an ovary wall and individual egg-containing ovules that project into an inner space called the locule. (Redrawn from Crang and Vassilyev 2003)

Sepals collectively form the **calyx**, which represents the outermost whorl of the flower. Sepals serve to protect the developing flower from desiccation and herbivory. Although they are often green, they contribute little to the overall carbon economy in most plants. The next internal whorl is the **corolla** and is composed of petals. The role of petals in most plants is pollinator attraction, hence the bright colors. Together, the calyx and corolla make up the **perianth**. The sepals and petals are more or less similar to foliage leaves in their basic anatomy with a homogenous mesophyll and have veins enclosed between the adaxial and abaxial epidermises. In some species, such as tulips (*Tulipa* sp.), the sepals and petals are indistinguishable in their appearance and are thereby collectively designated as **tepals** (Fig. 17.1f). The perianth may also have stomata, trichomes, and/or various types of inner secretory cells much like typical vegetative leaves.

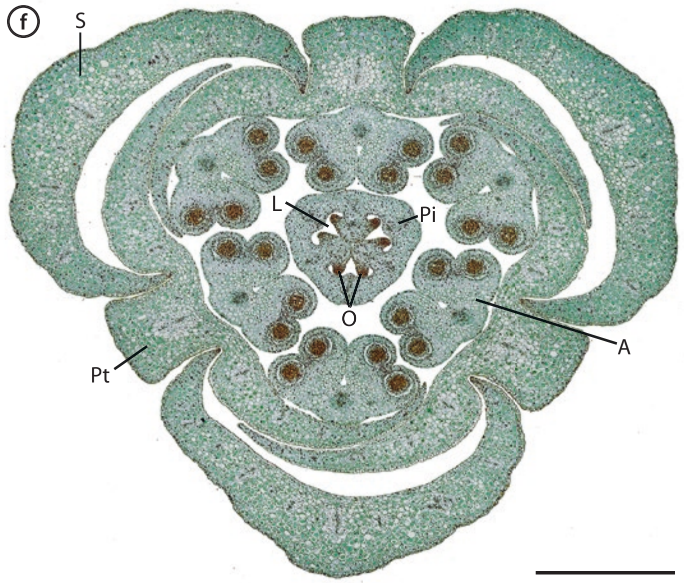
17

Petal color varies from taxon to taxon and often is important in attracting pollinators. Pigments are characteristically contained within chromoplasts (carotenoids) or vacuoles (anthocyanins). With carotenoids that normally may show red, yellow, or orange colors (Fig. 17.1g), their genetic suppression often gives rise to white petals which then result from the predominance of intercellular spaces in the petal mesophyll and are often associated with attracting pollinators that become active at dusk or during nighttime, such as moths. In many cases, the epidermal cells of petals (or tepals) differ from vegetative leaves by having softer cell walls with cellular papilla that protrude (Fig. 17.1h).

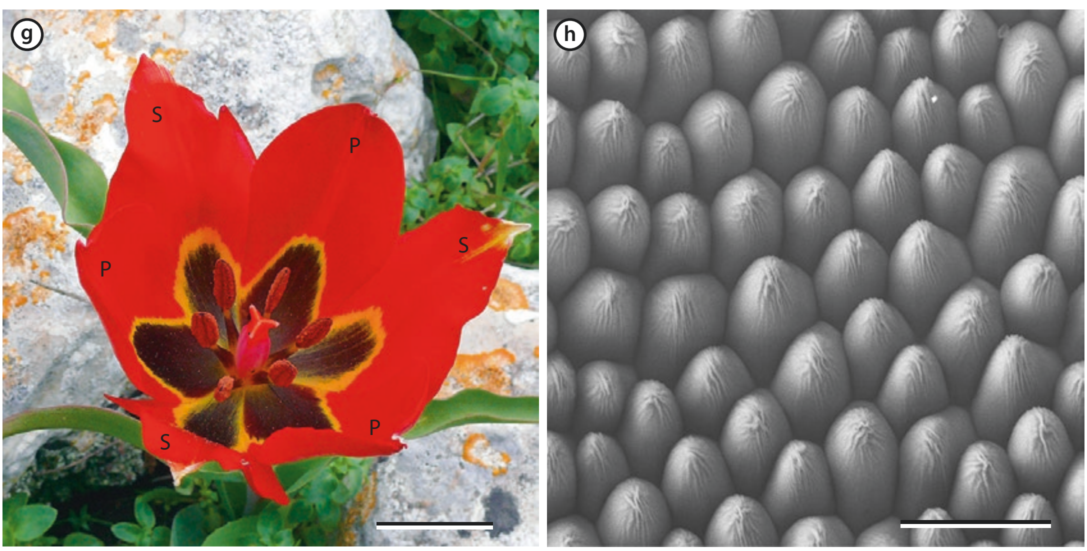


◘ **Fig. 17.1** **b**–**e** Longitudinal sections of pine (*Pinus* sp.) male and female reproductive structures. **b** A male (staminate) cone with a large microsporangium (Mi) subtending each microsporophyll. The developing pollen grains can be seen in **c**. **d** A female (pistillate) cone showing bare ovules on scalelike bracts termed megasporophylls (i.e., ovuliferous scale). Scale bars = 500 µm in **b** and **d** and 200 µm in **c** and **e**. (**b**–**e** RR Wise)

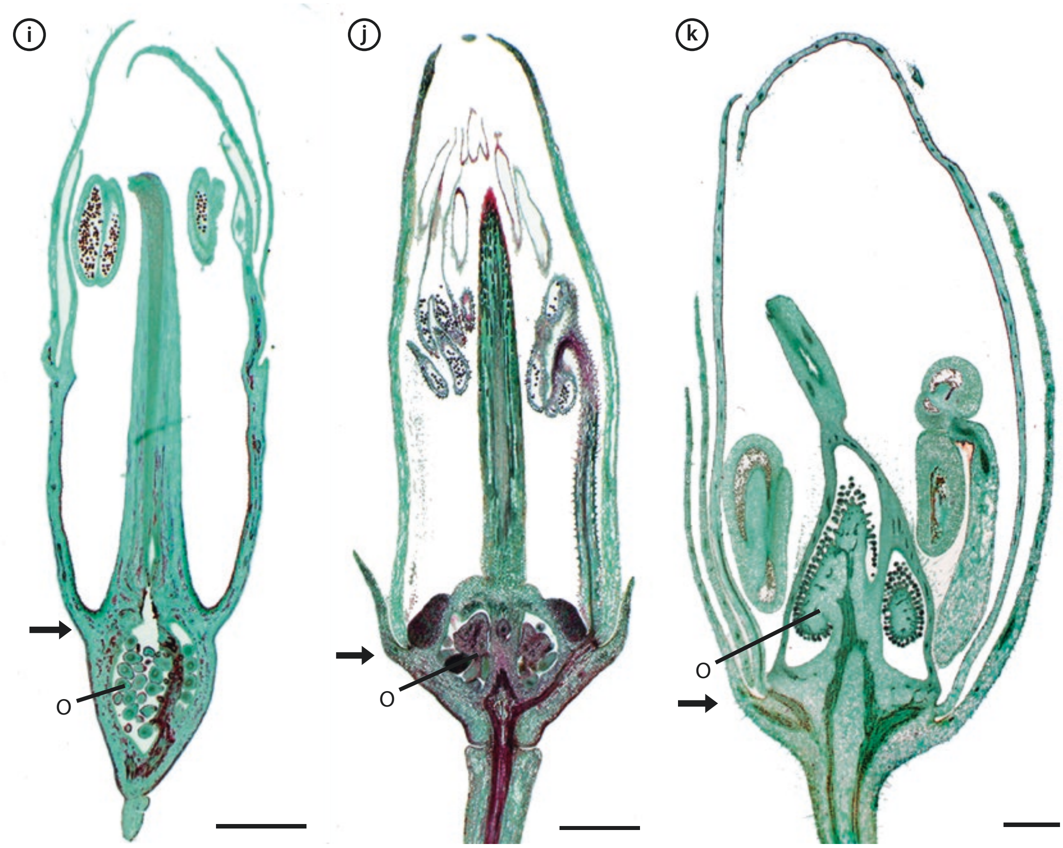
The position of the ovary relative to the surrounding floral parts is of relevance to the taxonomic status of the species such that if the ovary is above the whorls, it is termed **superior** or hypogynous (◘ Fig. 17.1i). If the whorls are attached midway, the position is **half inferior** or perigynous (◘ Fig. 17.1j). If the whorls are attached at the top of the ovary, leaving it beneath, the ovary is termed **inferior** or epigynous (◘ Fig. 17.1k).



■ **Fig. 17.1** **f** Cross-section of a perfect flower from lily (*Lilium* sp.). The flower was sectioned at a level that shows six tepals (three sepals (S) plus three petals (Pt)), six anthers (A), and one pistil (Pi) with three locules. Each locule (L) in the pistil has two ovules (O). Scale bar = 0.5 mm. (RR Wise)



■ **Fig. 17.1** **g** In this tulip (*Tulipa* sp.) flower, the sepals (S) lie to the outside of the petals (P). Because they are almost identical in structure and function, they are collectively called tepals. This arrangement is common in many monocotyledons (Zachi Evenor and MathKnight, CC BY 3.0). **h** Scanning electron microscopy of an adaxial petal surface of a rose (*Rosa* sp.) petal. Each epidermal cell forms a protuberance, the **papilla**, which gives the petals a soft texture and a “velvety” appearance. Scale bars = 2 cm in **g** and 50 µm in **h**. (**g** Zachi Evenor and MathKnight, CC BY 3.0; **h** RR Wise)



◘ **Fig. 17.1** **i** Inferior flower from black currant (*Ribes americanum*). **j** Half inferior flower from cranberry (*Vaccinium macrocarpon*). **k** Superior flower from purple foxglove (*Digitalis purpurea*). The insertion of the perianth (*arrow*) in relation to the ovary (O) is shown. Scale bars = 0.5 mm in all panels. (**i**–**k** RR Wise)

Box 17.1 What Did the Oldest Flower Look Like?
Angiosperms are the family of flowering plants that utilize flowers for sexual reproduction resulting in the production of fruits to promote seed dispersal. Fossil evidence of the earliest angiosperms goes back into the Cretaceous, about 130 million years ago; however, the common ancestor of angiosperms is thought to date back from about 250–140 mya, and no fossil evidence is known from this time period (Magallon et al. 2015). To better understand what the first flower may look like, scientists used molecular genetic analysis coupled with anatomical features from fossil data to model what the first flower may have looked like. So, what did the first flower look like? The model hypothesizes that the first flower was radially symmetrical and bisexual. The proposed floral structure was complex and composed of multiple whorls each of tepals, stamens, and carpels. This study by Sauquet and colleagues (2017) does provide a basis for further research in the morphology of the earliest flowers which is an important area in the field of evolutionary plant biology. (Figure redrawn from Sauquet et al. (2017)) (◘ Fig. 17.1l).

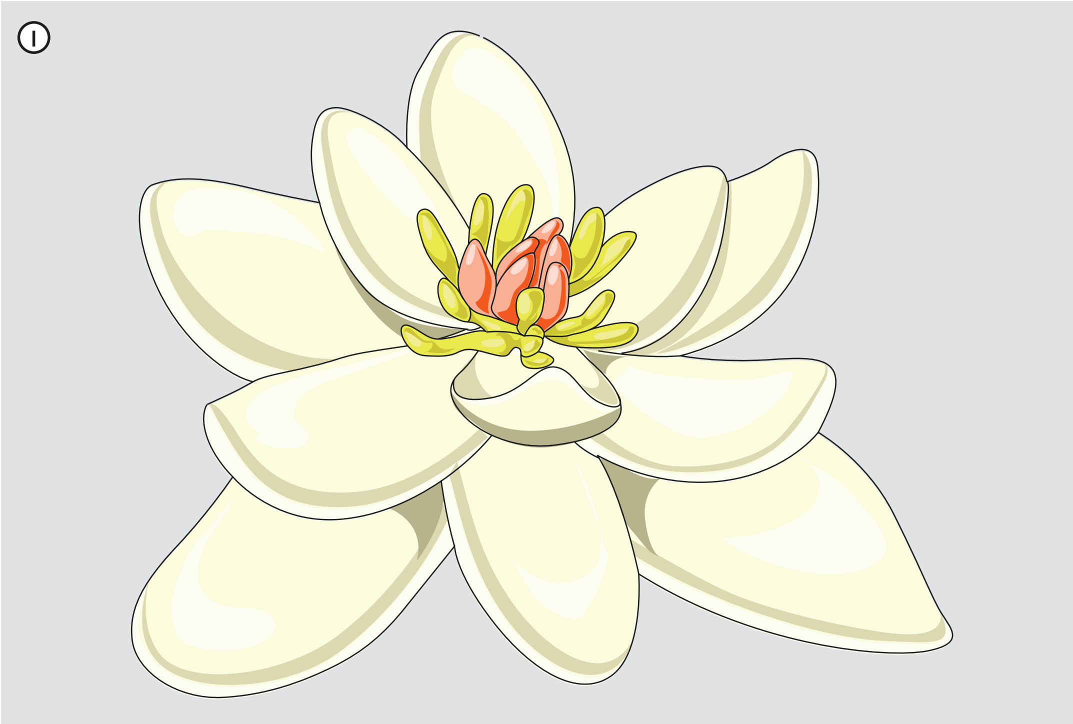


Fig. 17.1 **l** Model of earliest flower based upon molecular and fossil evidence. (References: Magallon et al. 2015; Sauquet et al. 2017)

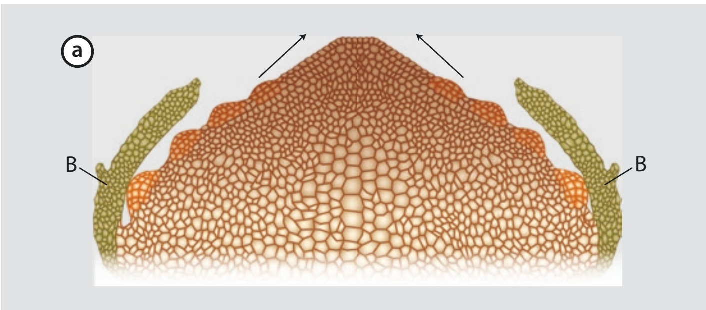
17.2 Floral Development Starts with Increasing Cell Divisions in Apical Meristems and Initiating Organs in an Acropetal Sequence

Reproductive development of a plant begins with the transition of its shoot apical meristem from producing leaves to producing inflorescence branches, floral bracts, and flowers. The organs of the flower are initiated as protrusions on the floral apex in the following sequence: bracts, calyx, corolla, androecium, and gynoecium. One of the most obvious signs of transition from vegetative to floral apex is the rise in mitotic activity of cells.

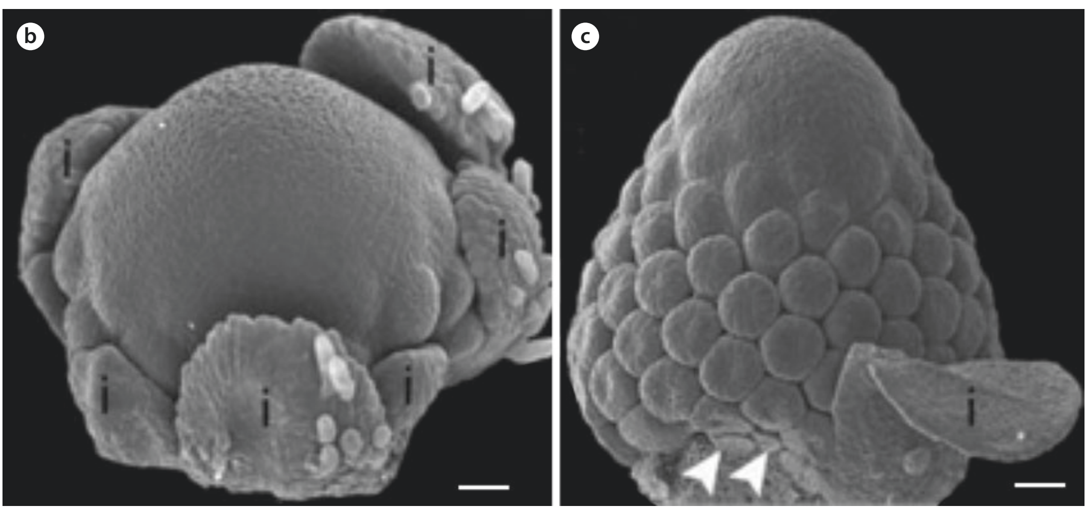
Unlike the cells of the shoot apical meristems, a characteristic feature of the floral apical meristem is its **determinate growth** when all of its cells are eventually differentiated into the floral organs. Floral ontogeny has become a new source of characters for identifying phylogenetic affinities among plants.

The organs of a flower develop in an **acropetal** sequence from the base to the apex of the floral meristem. Thus, the organs of the flower are initiated as cylindrical protrusions at the periphery of the floral apical meristem. Acropetal development is apparent when comparing the development of the petal and stamen primordia relative to each other, as well as to the carpel primordia.

The acropetal sequence of development is also noted in the floral apex of inflorescences in many angiosperms. Thus, flowers developing at the base of the inflorescence mature before those in the center. Examples that follow include head stages from *Calendula officinalis* (◘ Fig. 17.2a) and *Anacyclus homogamos* (◘ Fig. 17.2b, c). In the examples that follow, notice the changes in the structures in the developing inflorescence as well as development occurring in acropetal sequence.



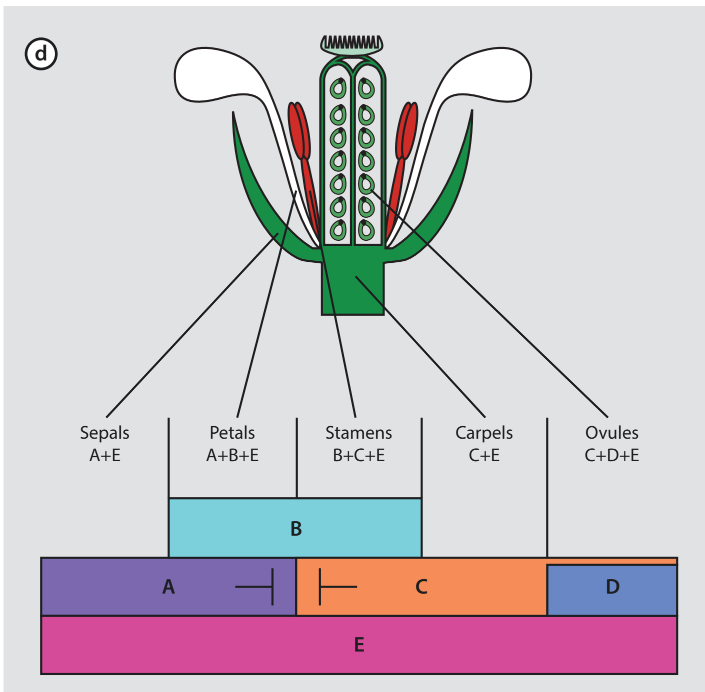
◘ **Fig. 17.2** **a** A diagram showing the initiation and early developmental stages of the inflorescence, the head, as would be found in English marigold (*Calendula officinalis*). The entire developing inflorescence would be wrapped in green bracts **B** to protect the floral primordia, indicated as orange bumps on the surface of the developing head. The two arrows indicate the direction of initiation of floral primordia with the youngest flowers in the center of the head; maturation is in the opposite direction. (Redrawn from Crang and Vassilyev 2003)



◘ **Fig. 17.2** **b**, **c** SEM micrographs of the pattern of flower initiation and early development of the inflorescence, the head, of *Anacyclus* (*Anacyclus homogamos*). **b** is a side view of a head with involucral bracts initiating helically. **c** shows a later successive developmental stage of head. Scale bar = 40 µm. (Illustration from: Bello et al. 2013)

Box 17.2 The ABCs of Floral Development: Genes Regulate Flower Development

Floral development progresses in a structured pattern that is controlled by a handful of genes (◘ Fig. 17.2d). In this basic model of *Arabidopsis* floral development, a suite of genes, "A" genes, interact to ultimately form the calyx, the outermost whorl. "A" and "B" genes interact to form the petals and stamens. "B" and "C" genes interact to form the petals and stamen. "C" genes are important for carpel and ovule development. Other genes also play a role in floral development. A group of "G" genes are involved with ovule development, and "E" genes are important for all aspects of floral development. The array of interacting genes is responsible for converting leaves into the floral parts. Changes in the genes responsible for floral development lead to differences in expression of the proteins and thus floral parts. For example, the "A" genes apply to *Arabidopsis* and close relatives and less so to other angiosperms. Not all angiosperms have perfect flowers and thus will have differences in the expression of interacting genes. Thus, the expression of genes that give rise to flowers of plants related to apples with showy flower petals will be very different than genes that lead to the formation of flowers in grasses.

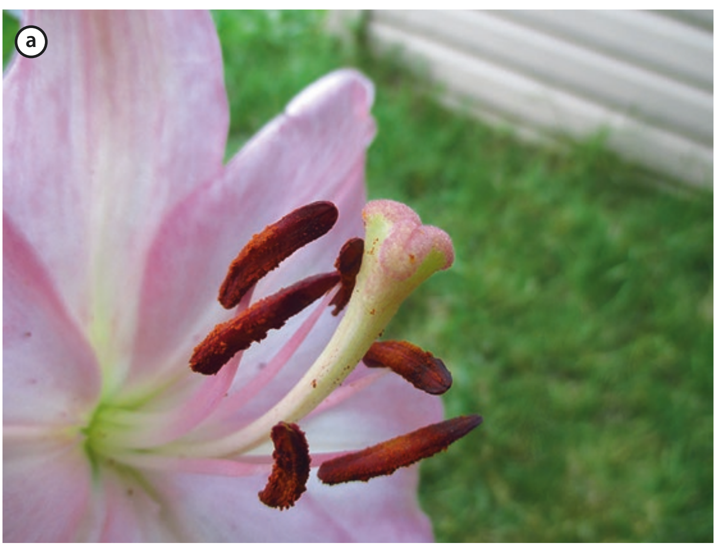


◘ **Fig. 17.2** **d** Model of the ABCs of floral development. Each uppercase letter and corresponding color code designate a suite of genes that are important for development of flowers in *Arabidopsis*. Individual genes are identified within colored circles. In the rings, "A" genes determine sepals, "A" and "B" genes determine petals, "B" and "C" genes produce stamens, "C" genes alone determine carpels, and C and D genes produce carpels. "E" genes are required throughout for normal development. (Modified from Litt and Kramer 2010)

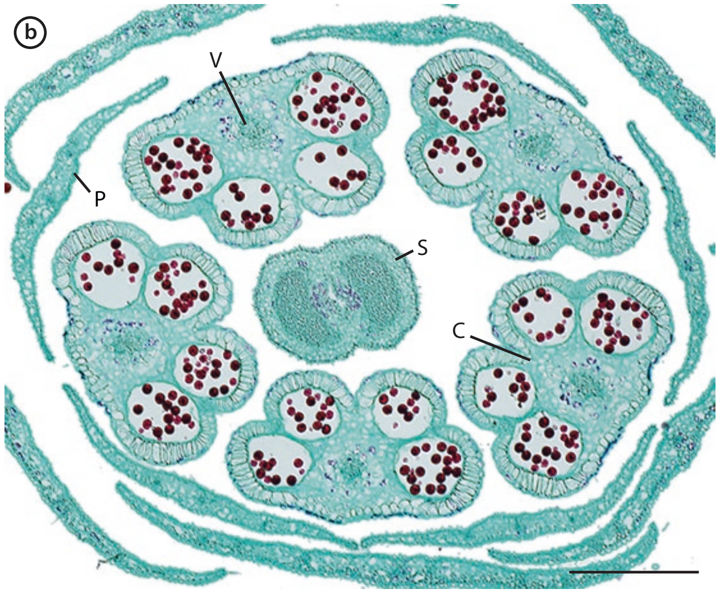
17.3 Male Reproductive Structures Give Rise to Pollen Within the Anther

Stamens are the male reproductive structures of angiosperms, and are made of pollen-containing **anthers** that are located on the tips of stalks called **filaments**. They comprise the third whorl within a flower, between the second (petals) and fourth whorls (carpels). The male reproductive structures are involved in the production of pollen grains, which give rise to male gametes, i.e., sperm cells or simply sperms. Pollen grains (the male gametophyte) develop and mature inside the anthers located at the terminal portion of the filament (◘ Fig. 17.3a, b). Pollen dispersal is facilitated by wind, animals, or, in some cases, water. After a **pollen grain** reaches a stigma, it germinates and, if it is compatible with the stigma, it forms a pollen tube capable of growing to the egg cells in the ovule(s). The surface of the stigma creates an optimal physiological condition for compatible pollen grains to germinate inasmuch as sugary secretions along with a variety of attractants and enzymes are released along the surface. Both the stigma and the pollen grain coatings are involved in the process of recognition that allows pollen grains to germinate and produce successful pollen tubes in compatible combinations (see ► Chap. 18).

In its earliest stage, the anther consists of a uniform mass of meristematic cells. Soon, in this homogeneous meristem, four separate groups of cells, the sporogenous tissue, by the process of meiosis, become discernible. The sporogenous tissue is composed of numerous **microspore mother cells**. Thus, unlike the nucellus (megasporangium) where a single megaspore mother cell and then single megagametophyte (embryo sac) are formed (refer to



◘ **Fig. 17.3** **a** A view of a lily (*Lilium* sp.) flower with a prominent style and shorter stamens bearing the anthers. The anthers have dehisced to release pollen grains (orange-red pigmented), giving the anthers a fluffy appearance. (S Lyons-Sobaski)

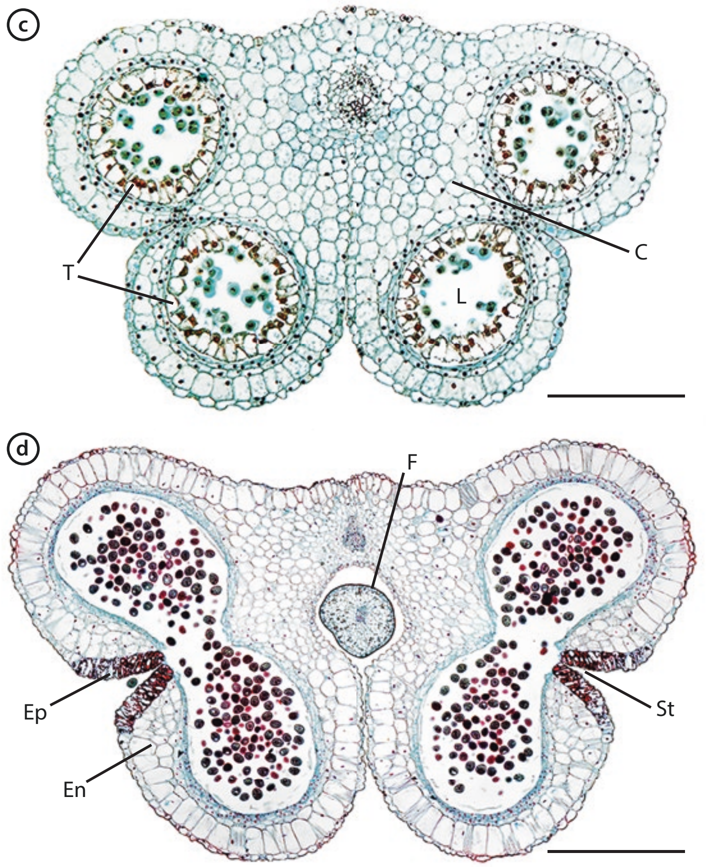


◘ **Fig. 17.3** **b** Cross-section through the upper part of the flower bud of gooseberry (*Ribes americanum*) showing petals (P) to the exterior, the central style (S), and five anthers, each with four pollen sacs (microsporangia) bearing pollen grains. Each anther has a connective (C) and a vascular bundle (V). Scale bar = 250 µm. (RR Wise)

► Chap. 18), sporogenous tissue is composed of many microspore mother cells surrounded by tapetum microspores, and then numerous **microgametophytes** (pollen grains) develop within a pollen sac (the **microsporangium**). The tapetum is a layer of cells that line the locules of the anthers, providing nutrition to the developing pollen.

The anther usually has two longitudinal lobes that are united by a band of parenchyma cells called the **connective** tissue (◘ Fig. 17.3c), which is a continuation of the filament. Each anther lobe contains two longitudinal **pollen sacs** (or locules) within which the pollen grains are produced. A single vascular band extends from the filament into the center of the connective and continues into the anther.

At the final stage of pollen grain maturation, and immediately before **anthesis** (the time of maturation of the male and female organs of the flower), the filament undergoes rapid elongation resulting in the disruption of the tracheary elements in the vascular bundle and, therefore, the cessation of the water supply to the anther, and thus, the process of anther and pollen desiccation commences. Just before anther maturation, conspicuous secondary wall thickenings are deposited on the anticlinal and inner cell walls of the subepidermal cell layer of the anthers, often termed as the **endothecium** cells (◘ Fig. 17.3d). These cells line the cavity of an anther and secrete materials for maturation of pollen grains.



Figs. 17.3 **c** Cross-section of an immature lily (*Lilium* sp.) anther showing region of the connective (C) as well as four locules (L). The thick callosic walls of the microspore mother cells stain light green. Note the thick tapetal (T) layer. **d** A cross-section of a mature lily anther showing the filament (F). Mature pollen grains are stained red, and the septum between neighboring locules has broken down. Epidermal (Ep) and endothecium cells (En) near the stomium (St) have multiplied and thickened in preparation for anther anthesis and pollen dehiscence. The tapetum and other anther wall layers are greatly reduced in size and thickness and appear as a thin internal lining of the endothecium. Scale bar = 500 µm in both panels. (**c**, **d** RR Wise)

They are densely cytoplasmic with little or no vacuoles. To facilitate pollen dispersal, each of the two anther lobes splits by a longitudinal slit called a **stomium**. The thickenings of the endothecium cells cause tangential shrinkage during anther desiccation, leading to the rupture and outward bending of the anther wall at the stomium; in other words, the drying of the anther causes it to dehisce and release pollen (Fig. 17.3d). The endothecium cells do not develop secondary thickenings in the region of the future stomium, thereby providing for the specific location and orientation of the slit for dehiscence and release of mature pollen grains.

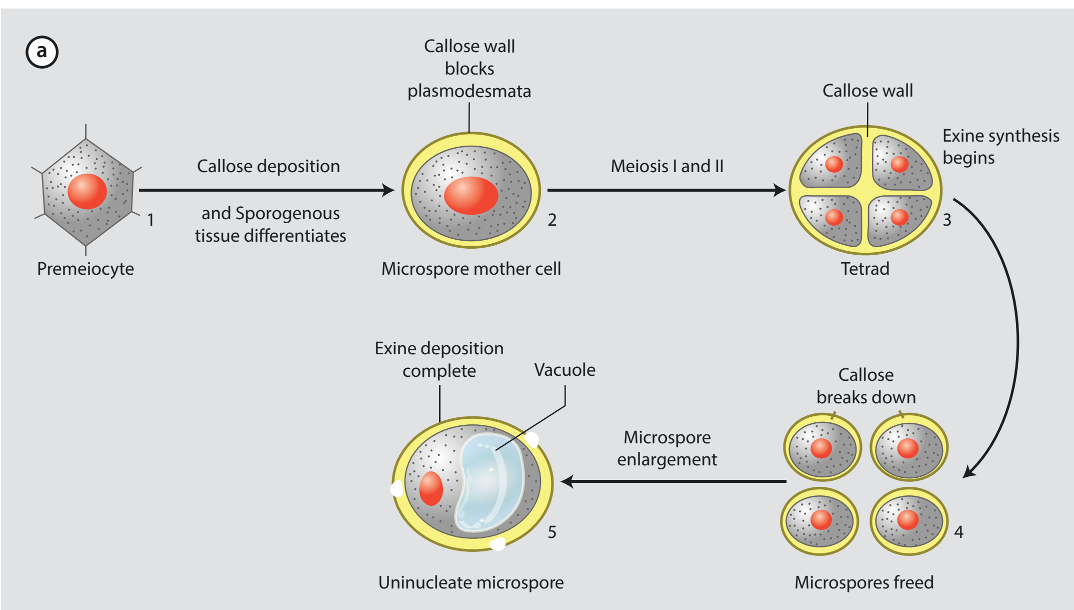
17.4 Pollen Grain Formation Begins with Microsporogenesis Followed by Microgametogenesis

The process of pollen grain formation includes **microsporogenesis** and microgametogenesis. During microsporogenesis, **microspore mother cells** (or microsporocytes) are formed in the sporogenous tissue of the anther. These cells undergo meiosis to produce tetrads of haploid, uninucleate microspores.

Microgametogenesis comprises the subsequent mitoses and development of microspores into microgametophytes. The microgametophytes in turn produce male gametes (or **sperm cells**). During microgametogenesis, microspores divide mitotically once (or less frequently twice) and become the male gametophytes or **microgametophyte** (pollen grains). In this section, microsporogenesis and microgametogenesis will be covered in detail.

17.4.1 Microsporogenesis Is the Formation of Microspore Mother Cells

The process of microsporogenesis may be subdivided into five phases (◘ Fig. 17.4a) leading to the formation of uninucleate haploid **microspores**. The first phase begins with the differentiation of compact sporogenous tissue with thin cellulosic walls and numerous plasmodesmatal connections between microspore mother cells. In the second phase, each microspore mother cell is isolated by a callosic wall in which the plasmodesmata become



◘ **Fig. 17.4** **a** The development of microspores occurs in five phases. Numbers within illustration correspond to each phase. (Redrawn from Crang and Vassilyev 2003) blocked. The conversion from tissue structure to individual cells that undergo meiosis I and II also occurs within this second phase (◘ Fig. 17.4b–g). The third phase is noted by the formation of tetrads, four young haploid microspores that become encapsulated in the **callosic wall**. **Exine** (a highly sculptured and decay-resistant outer wall layer of pollen) synthesis in the pollen wall begins providing rigidity to the pollen grains. The fourth phase is recognized by the dissolution of callose and the release of microspores from tetrads. The fifth phase is marked by the vacuolation and enlargement of microspores with the completion of exine deposition and pollen wall development.

17.4.2 Microgametogenesis Results in the Development of the Microgametophyte: The Pollen Grain

During the formation of microgametes (or male gametes or sperm cells) in angiosperms, microspores undergo two successive mitoses that lead to the formation of the microgametophyte (male gametophyte), the pollen grain (◘ Fig. 17.4h). The first division occurs within the anther. The second division follows pollination, forms two sperm cells, and occurs within the pollen tube. This second division may occur following pollination, but in many species, it occurs prior to being shed from the anther, giving rise to a three-nucleate condition of a pollen grain. On rare occasions, both mitoses will occur inside the microspore. Following pollination, the two sperm cells may be directly involved in the process of double fertilization (refer to ► Sect. 17.7 and ► Chap. 18), with the formation of a diploid zygote and triploid endosperm (◘ Fig. 17.4i–l).

Microgametogenesis can be subdivided into four general phases. The haploid vacuolated microspore represents phase 1 which undergoes unequal mitosis giving rise to a two-celled immature pollen grain. This immature microgametophyte consists of a **vegetative cell** and a small lens-shaped **generative cell** appressed to the microspore wall, giving rise to phase 2. The vegetative cell occupies the major portion of the former microspore. In fact, it has been shown that the generative cell occupies only about 1/20 of the volume of the newly formed pollen grain. The vegetative cell undergoes de-vacuolation in phase 2 and will accumulate large amounts of starch, oil, and reserve protein by phase 4. At phase 3, the generative cell separates from the **intine** and moves to a position where it assumes a spindle-shaped form and becomes completely enveloped by the vegetative cell, thus becoming a cell within a cell prior to forming sperm cells (Yu and Russell 1992). Phase 4 is represented by the mature pollen grain (also designated as the microgametophyte) which is ready for pollination.

In phase 4, the polysaccharide cell wall of the generative cell in most species has dissolved, and the two cells (generative and vegetative) make contact with each other by their plasmalemmas

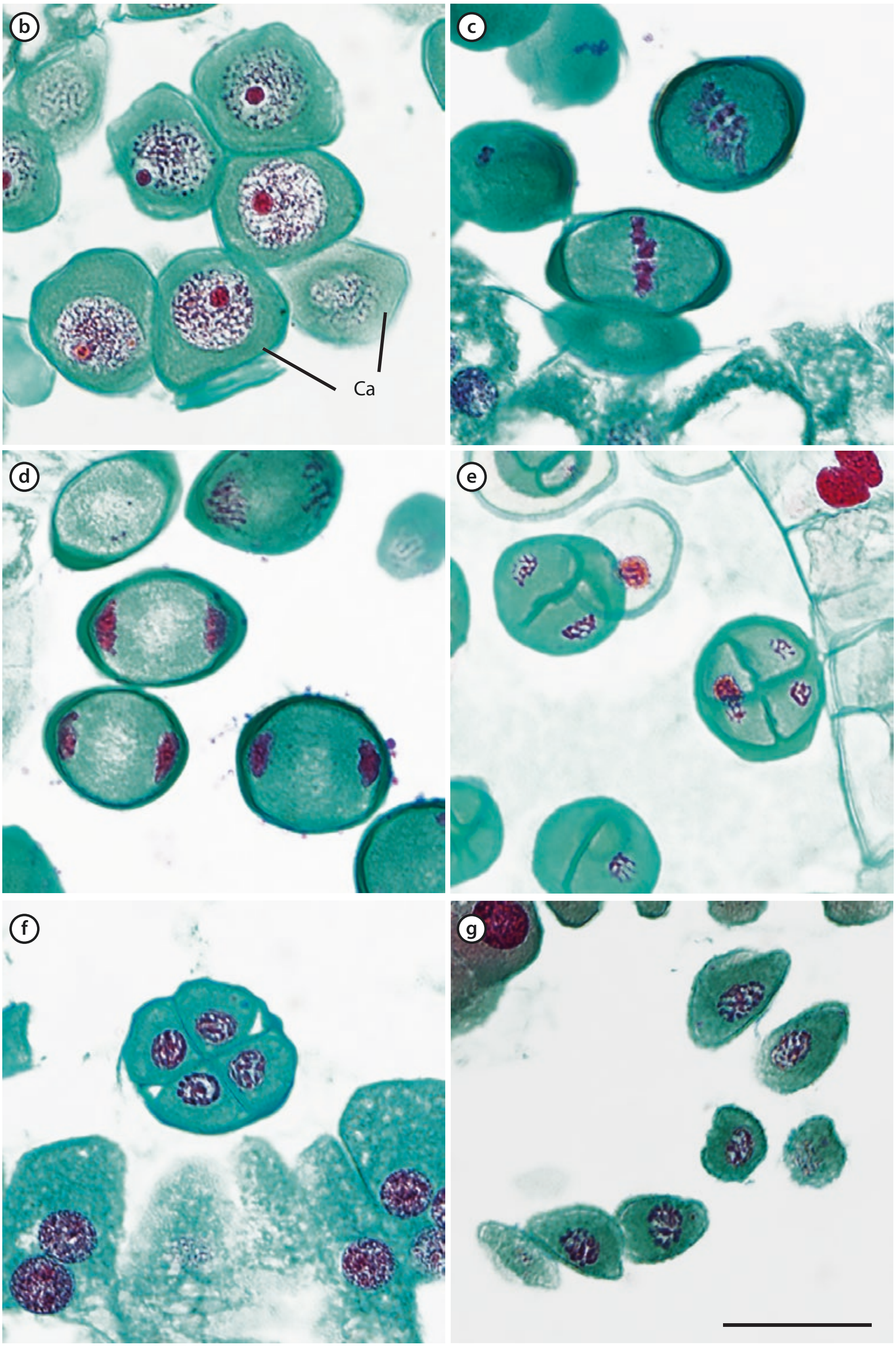


Fig. 17.4 **b**–**g** Phases of meiosis I and II during microsporogenesis in *Lilium* anthers from the premeiocyte (stage 1) to the uninucleate microspore (stage 5). **b** Early prophase I: the microspore mother cells have a thick wall of callose (Ca). **c** Metaphase I: chromosomes align at the equator. **d** Telophase I: chromosomes migrate to the cell poles; meiosis II will follow. **e** Telophase II. **f** Pollen tetrad: the four resulting haploid microspores are held together by the callosic wall, which will soon break down. **g** Uninucleate microspores: each tetrad releases four uninucleate microspores which will next proceed through microgametogenesis as described in the following section. Scale bar in **g** = 25 µm and applies to all panels. (**b**–**g** RR Wise)

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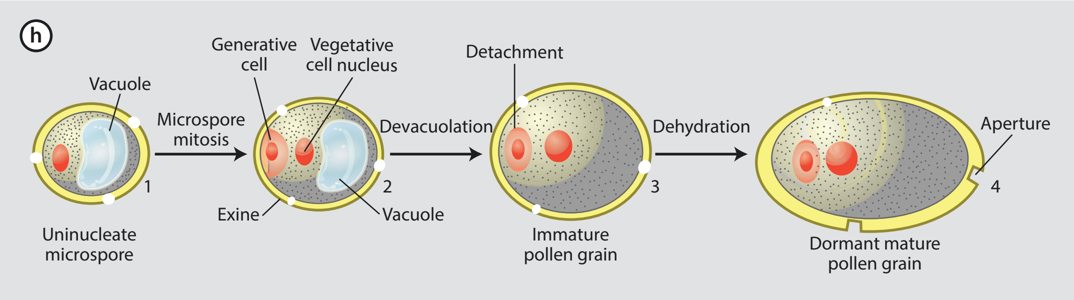


Fig. 17.4 **h** Diagram of the four phases of angiosperm microgametogenesis to form the microgametophyte. Numbers within the illustration correspond to each of four phases. (Redrawn from Crang and Vassilyev 2003)

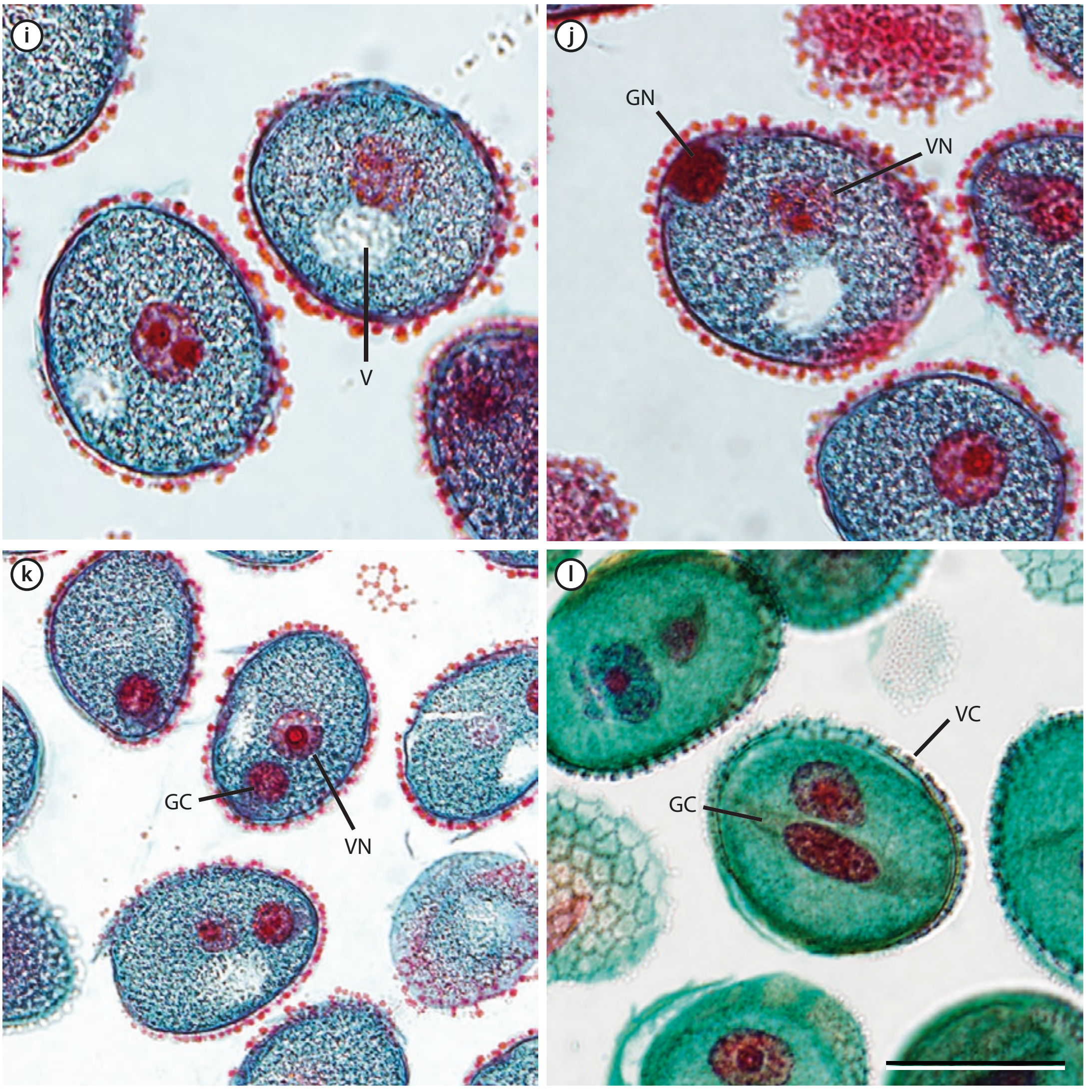


Fig. 17.4 **i** Uninucleate microspore: the cell has a single haploid nucleus (red) and a vacuole (V). **j** Developing generative cell: the nucleus has undergone one mitotic division, producing a vegetative cell nucleus (VN) and a generative cell nucleus (GN), which is attached to the intine layer. **k** Immature pollen grain: the generative cell nucleus detaches from the intine and cytokinesis is initiated. **l** Mature pollen grain: the generative cell (GC) has matured. It is housed entirely within the vegetative cell (VC) and does not form its own cell wall. Scale bar in **l** = 25 µm and applies to all panels. (**i**–**l** RR Wise)

only. The lack of a wall around the generative cell will facilitate its movement in the pollen tube following pollination. During phase 4, desiccation and transition to a dormant state occurs. At this time, the generative cell has no plastids, few mitochondria, and little cytoplasm. The pollen grain is ready to be transferred to the stigma.

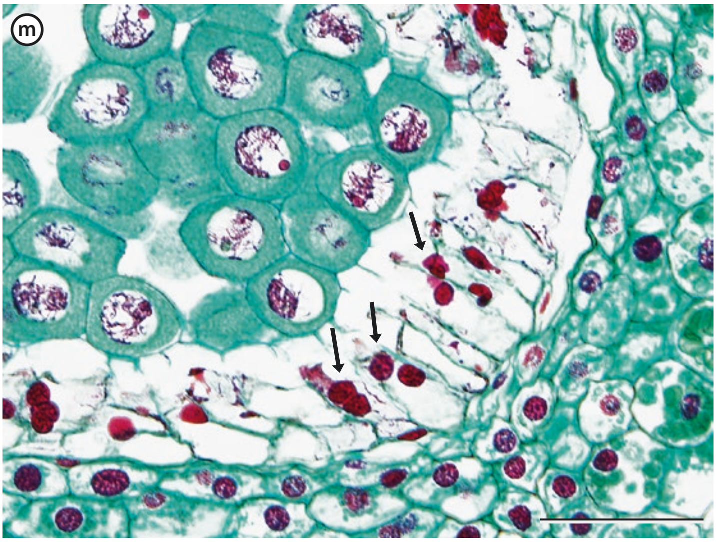
Following phase 4 but prior to pollination, some species' pollen grains are binucleate, in contrast to those that are trinucleate. If a single mitotic division occurred during microgametogenesis, the mature pollen grain consists of a large vegetative cell (developing a future pollen tube) and a small generative cell (sperm mother cell). In plants with bicellular pollen grains, the generative cell divides to form two sperm cells in the pollen tube *after* germination of the grain on the stigma. In plants with tricellular pollen grains, the generative cell divides and produces two sperms during maturation of a grain, but before pollen tube emergence. The two sperm cells allow for double fertilization of the angiosperm **embryo sac**.

As the pollen grain continues to form, a cellulosic cell wall is deposited between the generative and vegetative cells during phase 2 of microgametogenesis. If pollination occurs, this cell wall will dissolve when the generative cell moves out of the pollen grain wall as the pollen tube becomes established.

17.4.3 The Tapetum Provides Nutrition and Substances to Form the Exine

The sporogenous tissue is delineated from the anther wall by a single layer of cells designated as the **tapetum**. The cells of the tapetum enlarge and develop a complex ultrastructure, which indicates that they become very active metabolically. At the time of meiotic division of microsporocytes (◘ Fig. 17.4a stages 2 to 3), the nuclei of the tapetum cells also divide, but mitotically. However, mitosis is not followed by cytokinesis, and tapetal cells subsequently become binucleate (◘ Fig. 17.4m).

Two types of tapetum may be distinguished according to subsequent development of the cells—a **secretory tapetum** and the **periplasmodial tapetum**. The cells of the secretory tapetum remain intact and persist in situ through microgametogenesis, whereas in the periplasmodial tapetum, the cell walls break down and the protoplasts intrude into the pollen sac eventually forming a coenocytic (multinucleate) plasmodium around the developing microspores and early pollen grains. The tapetum is involved in the nourishment of the microsporocytes and pollen grains and in the synthesis and deposition of **sporopollenin** and other wall materials onto the surface of the developing exine. The tapetal cells also synthesize and secrete **callase**, an enzyme responsible for the dissolution of callose around the microspore tetrads. Before an anther matures, the tapetum degenerates, and its remains are deposited on the pollen grain surface.



■ **Fig. 17.4** **m** Lily anther. The enlarged cells of the tapetum, some with two nuclei (*arrows*), lie between the microspore mother cells to the top left and the connective tissue to the bottom right. Scale bar = 50 µm. (RR Wise)

17.5 The Structure of Pollen Grain Cell Walls Changes During Development from Microspore to Macrogametophyte, and Callose Is Deposited and Then Sporopollenin and Adhesives

Successive changes in the structure and composition of their cell walls during development are characteristic of pollen grains. First, the amorphous polysaccharide callose is deposited in meiocytes to the inside of very thin cellulosic cell walls and is also laid down after meiosis around each microspore of the tetrad during microsporogenesis. During callosic wall formation, all of the plasmodesmatal connections are lost, and the cells become isolated from the maternal sporophyte.

Prior to exine establishment, a thin layer of non-sporopollenin material, the primordial exine (or primexine), forms on the outer surface of the spore plasmalemma. The primexine serves a template for exine patterning. While still within the tetrad and encapsulated by callose, the **exine** begins to be deposited (■ Fig. 17.5a).

The exine is largely composed of sporopollenin, a complex organic hydrophobic biopolymer that is highly resistant to degradation (Dominguez et al. 1999). The tapetum contributes to the deposition of sporopollenin onto the outer surface of the exine. Upon the establishment of a first layer of sporopollenin that starts to form the young exine, dissolution of the callosic wall begins during microsporogenesis.

The rate of deposition of sporopollenin increases after the liberation of microspores from the tetrad. Exine deposition is largely absent over the pore sites through which pollen tubes emerge during germination; ■ Fig. 17.5b. Pollen grain **apertures** form early,

◘ Fig. 17.5 **a** A transmission electron micrograph of a tetrad of African violet (*Saintpaulia ionantha*) during the deposition of exine. Each microspore is encapsulated in callose (C). However, the microspore wall, i.e., the sporopollenin exine (E), is being deposited to the inside of the callosic wall. Sporopollenin can be seen on the outer surface of the exine (*arrowheads*). Note the remnants of the cellulosic cell wall (CW) of the former pollen mother cell around the tetrad and outside of the callose layer. L leucoplast, N nucleus, T tapetum, arrows = primexine. Scale bar = 10 µm. (MC Ledbetter and KR Porter 1970)

during callosic wall deposition and before exine initiation, and leave depressions in the wall (◘ Fig. 17.5c). The apertures may be circular or furrow-like, and the number of them varies from one in monocotyledons to three or more in dicotyledons. These apertures are important as they provide an opening for the pollen tube to emerge. They are covered with a plate termed the **operculum**. The microspores grow in circumference and, finally, an inner cellulosic cell wall, the intine, is deposited (◘ Fig. 17.5d). The intine is similar in composition to the primary wall of typical plant cells. Mature pollen grains are enveloped with both exine and intine (◘ Fig. 17.5e).

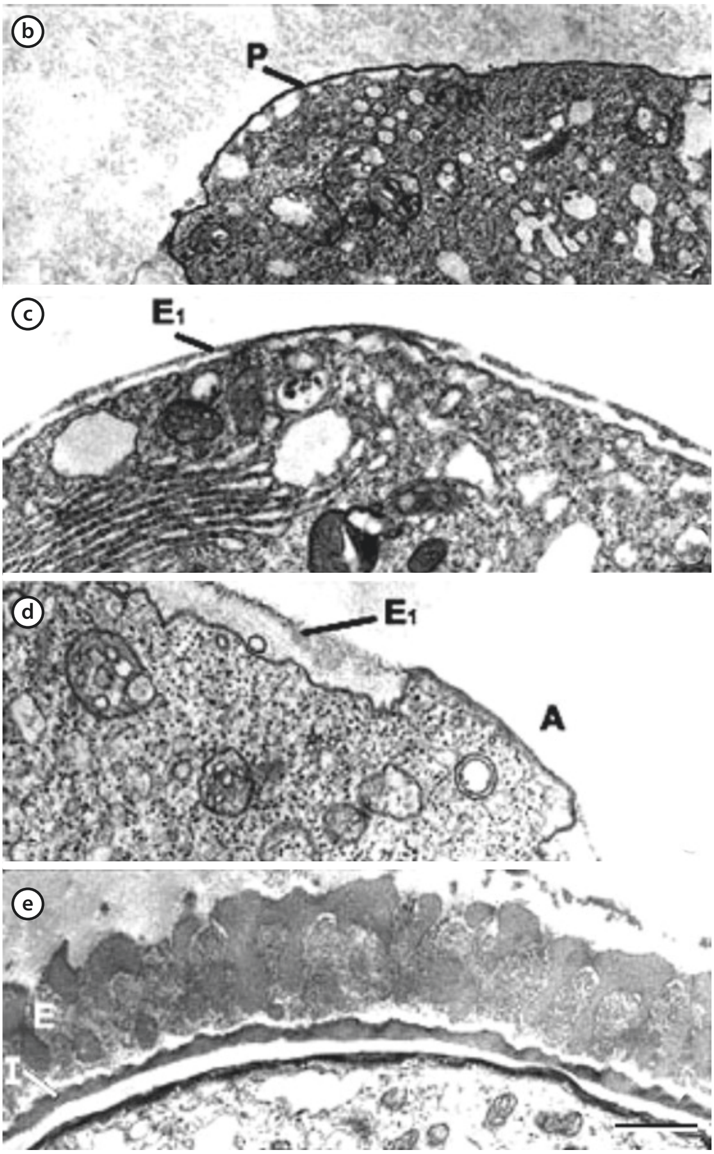


Fig. 17.5 **b**–**e** This series of electron micrographs captures exine initiation in white campion (*Lychnis alba)*. Panels **b**, **c**, and **d** represent early tetrad phases. In panel **b**, the primexine (P) is shown with differentiation on the microspore plasmalemma. In panel **c** the early exine (E_1) is seen. Also evident is an electron-transparent space between the plasmalemma and the exine (E_1) that is filled with sporopollenin precursors. Panel **d** portrays the future pollen grain aperture (A), which makes a depression in the callosic wall. This implies that the aperture was initiated during callosic wall deposition, i.e., before exine initiation. Panel **e** represents a nearly mature pollen wall consisting of exine (E) and intine (I). Scale bar = 5 μm. (**b**–**e** RC Crang)

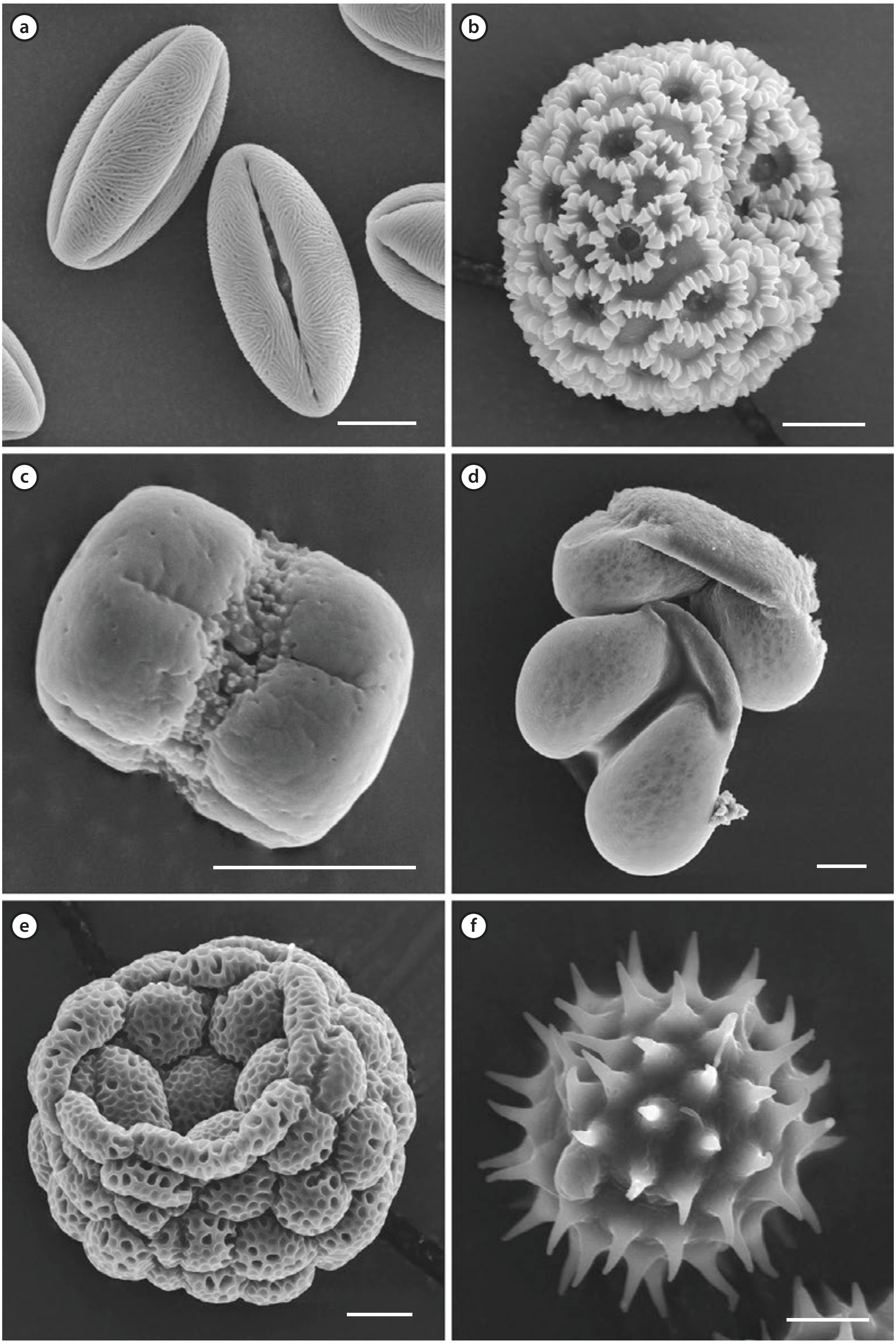
While sporopollenin produces a tough physical- and chemical-resistant wall material in the exine, another material termed **pollenkitt**, a hydrophobic lipid, provides a sticky adhesive surface enabling pollination and adherence to the stigma of pistils prior to pollen tube growth (Pacini and Hesse 2005). Two types of sticky pollen coat material exist in angiosperms, both produced by the anther tapetum. Pollenkitt is the most common adhesive material present around pollen grains of almost all angiosperms pollinated by animals. But in the case of the Brassicaceae, it is substituted by **tryphine**, a mixture of both hydrophobic and hydrophilic substances, and produced by the plasmodial tapetum upon its degeneration. Both pollenkitt and tryphine are produced by the tapetum. If tryphine is formed, the tapetal cell protoplasts lose their individuality at the microspore stage. If pollenkitt is formed, their contents degenerate at later stages. Cell content of pollen is totally reabsorbed, when ripe pollen is not surrounded by any gluing material. Pollenkitt becomes functional when the anther dehisces and becomes nonfunctional when the pollen rehydrates on the surfaces of the stigma following pollination.

17.6 The Surface Characteristics of Pollen Grains Are Taxon Specific

The cells within the pollen grain differ in structure, function, and ploidy from most cells in the plant body. The vegetative cell in the mature pollen grain is irregular in shape with many protrusions and invaginations. The small generative cell is immersed inside the vegetative cell and is separated from the vegetative cytoplasm only by two plasmalemmas with a very narrow space between. The generative cell within a pollen grain typically does not contain plastids, which explains why chloroplasts are often maternally inherited in most angiosperms as no "male" plastids are involved in fertilization and contained in the new embryo.

The shape and size of pollen grains varies greatly among species. The pollen grain may be spherical, ellipsoidal, threadlike, etc. The size of pollen grains also varies, from a few micrometers to as much as a quarter of a millimeter. Differences in properties associated with pollen grains are often related to the mechanism of pollination. Angiosperms that are underwater have been noted to lack apertures and have relatively thin exines in contrast to species that are found on land.

The surface of the exine is ornamented with a complex pattern of spines, netlike ridges, and/or other projections. These ornamentations vary greatly, but, at the same time, the pattern is constant in plant taxa of various ranks (taxon specific) and may be used for taxonomic purposes. From the analysis of pollen, it is possible to determine which plants have grown in a certain geographical region and during a certain geological time. Thus, scanning electron microscopy is very helpful in **palynology** (the study of plant pollen and spores from both living and fossil forms) because it shows the surface characteristics of pollen grains useful in comparative descriptions for various plant taxa, especially from past geological times. Compare the pollen grain surfaces within ◘ Fig. 17.6a–f.



■ **Fig. 17.6** **a–f** Scanning electron microscopy of pollen from six species. From top left to bottom right, pollen from **a** buckeye (*Aesculus glabra*), **b** Japanese spurge (*Pachysandra terminalis*), **c** Jack Frost (*Brunnera macrophylla*), **d** white pine (*Pinus strobus*), **e** catalpa (*Catalpa speciosa*), and **f** pale purple coneflower (*Echinacea pallida*). All species shown are pollinated by insects, with the exception of the **d** white pine (gymnosperm). Scale bars = 5 µm in (c) and 10 µm in all other panels. (RR Wise)

17.7 Pollen Dispersal, Germination, and Pollen Tube Growth Precede Double Fertilization

Various substances may accumulate on the exine surface and influence pollen dispersal. In **entomophilous** (insect-pollinated) plants, pollen grains are covered with oily, sticky, and colored materials, pollenkitt or tryphine, that facilitate the attraction of insects and the adhesion and subsequent transfer of pollen. In **anemophilous** (wind-pollinated) plants, the thickness, surface sculpturing, and stickiness of the exine are all generally reduced to enhance the buoyancy of the pollen in the air (see winglike structures of white pine pollen in ◘ Fig. 17.6d).

When a pollen grain is released from the anther, it exists as an extremely reduced haploid male plant (male gametophyte) until it is carried to the stigma either by wind or insects or directly by contact of the anther with the stigma. The interaction between pollen and the pistil starts with the adhesion of pollen grains to the stigmatic surface. This is facilitated by the sticky nature of the pollen surface and an exudate on the stigmatic surface. Adhesion of pollen grains to a receptive stigma is soon followed by the uptake of water through the apertures in the exine. This imbibition of water brings about the breaking of dormancy, mobilization of food reserves, and activation of metabolism in the vegetative cell including the release of proteins from the pollen wall. These proteins participate in recognition reactions between the pollen and the stigma. In incompatible combinations, pollen germination is suppressed, or newly emerged pollen tubes fail to penetrate the stigma.

Germination occurs by the emergence of a pollen tube from one of the apertures (◘ Fig. 17.7a). In culture, two or three pollen tubes may be formed (◘ Fig. 17.6d), but only the one with the generative sperm is active for growth and fertilization. The wall of the growing pollen tube (i.e., the wall of the vegetative cell) is cellulosic and both similar to and continuous with the intine of the pollen grain. Thus, the emerging pollen tube first appears as a bulge of the intine protruding through the germination aperture since the polysaccharide tube wall is essentially a continuation of the intine (◘ Fig. 17.7a, b). The nucleus of the vegetative cell and then the sperms, in plants with three-cellular pollen grains (◘ Fig. 17.7d, h), are soon moved into the growing pollen tube by the cytoskeleton. In plants with bicellular grains (◘ Fig. 17.7a), the second division of the microgametophyte resulting in the formation of two sperm cells occurs in the pollen tube (◘ Fig. 17.7c).

After recognition and acceptance of the pollen on the stigma, the pollen tubes (carriers of the sperm cells) grow through the stigma to the stylar transmitting tissue and then down to the ovary. Such growth may be through a hollow style, along surface transmitting tissue (aka **stigmatoid tissue**; refer to ► Chap. 18, ► Fig. 18.5a) or within the papillae cell wall initially (◘ Fig. 17.7i). When the tubes reach the ovary, they grow along the surface of the placenta toward the ovules. Occasionally, more than one pollen tube may be formed by a pollen grain, but only a tube containing sperm cells continues its growth; the other is soon blocked.

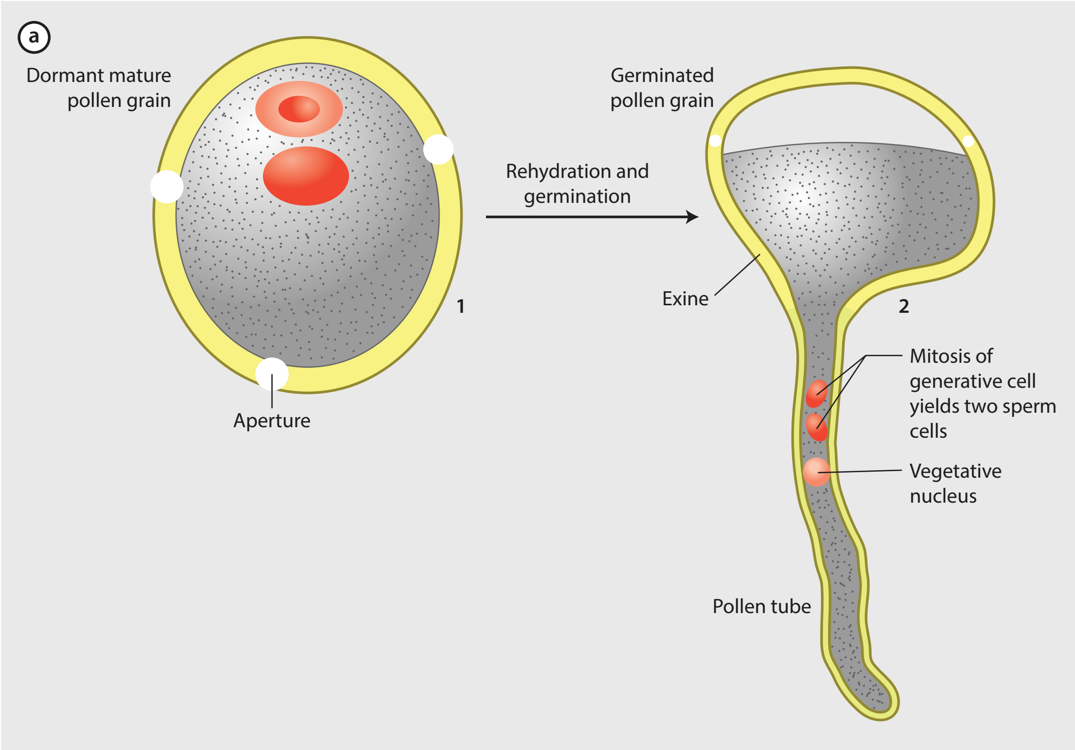


Fig. 17.7 **a** Diagrammatic representation of germination of pollen grain followed by mitosis of generative cell. After the arrival on the stigmatic surface of the pistil, the dormant pollen grain (1) adheres to a papilla, absorbs water (rehydration), and swells. The germination of the pollen grain takes place by the emergence of the pollen tube through one of the apertures (2). (Redrawn from Crang and Vassilyev 2003)

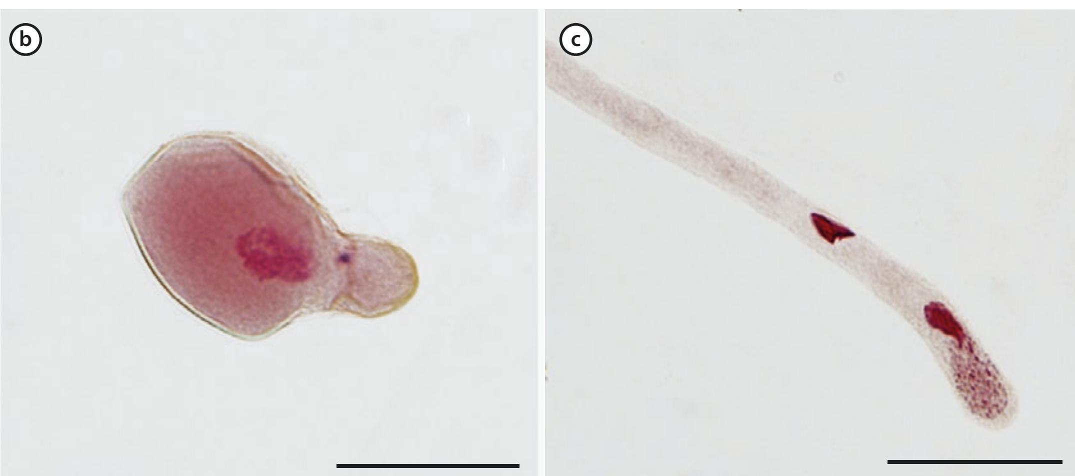


Fig. 17.7 **b**, **c** Micrographs of germinating Solomon's seal (*Polygonatum* sp.) pollen grains in vitro. Nuclei are stained in dark pink. **b** A pollen grain that has just started germinating with the vegetative nucleus at the early end of the new pollen tube. The wall of the tube is essentially an extension of the pollen grain intine. **c** Illustration shows a pollen tube with two sperms (dark red) and tube nucleus (pale pink) at tip of the tube. Scale bar = 25 µm. (**b**, **c** RR Wise)

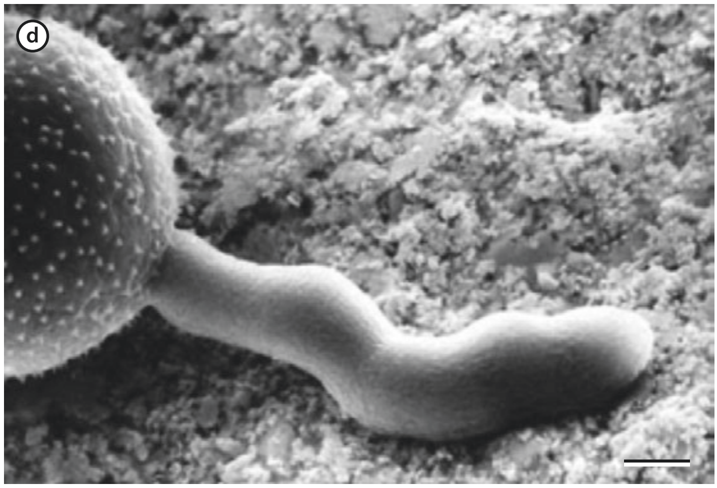


Fig. 17.7 **d** In this scanning electron microscope view, the pollen tube has grown a short distance from the pollen grain of white campion (*Lychnis alba*). The lump shown near the end of the pollen tube is most likely the site of the vegetative nucleus with the sperm cells following. Scale bar = 10 µm. (RC Crang)

The pollen tube emerges from the pollen grain by growth through the pollen aperture, which is covered by a thin layer of sporopollenin called the **operculum** (Fig. 17.7e). The pollen tube pushes against the operculum causing it to bulge (Fig. 17.7f) and eventually rupture. After pollen tube emergence, the operculum remains attached to the base of the pollen tube as an artifact of pollen germination (Fig. 17.7g).

17.8 Pollen Tube Growth Is Restricted to the Tip Region

As in other freely growing cells such as root hairs or fungal hyphae, the growth of the pollen tubes is restricted to the extreme tip (Fig. 17.8a, b). This **apical tip growth** occurs very rapidly and may reach a rate of 1 cm per hour in some plants, such as corn pollen tubes in laboratory culture. However, the actual growth zone is only a few micrometers long. This zone is filled with secretory Golgi vesicles (dictyosomes) that export the cell polysaccharides and membranes, which supply the growing wall and plasmalemma with new materials. The rate of the vesicle production has been estimated to be as high as 5000 per minute. The subapical zone is also rich in dictyosomes, the producers of secretory vesicles, as well as mitochondria and endoplasmic reticulum. Posterior to the growing tip, callose plugs form that keep the cellular contents and the generative cells growing toward the ovule (Qin et al. 2012).

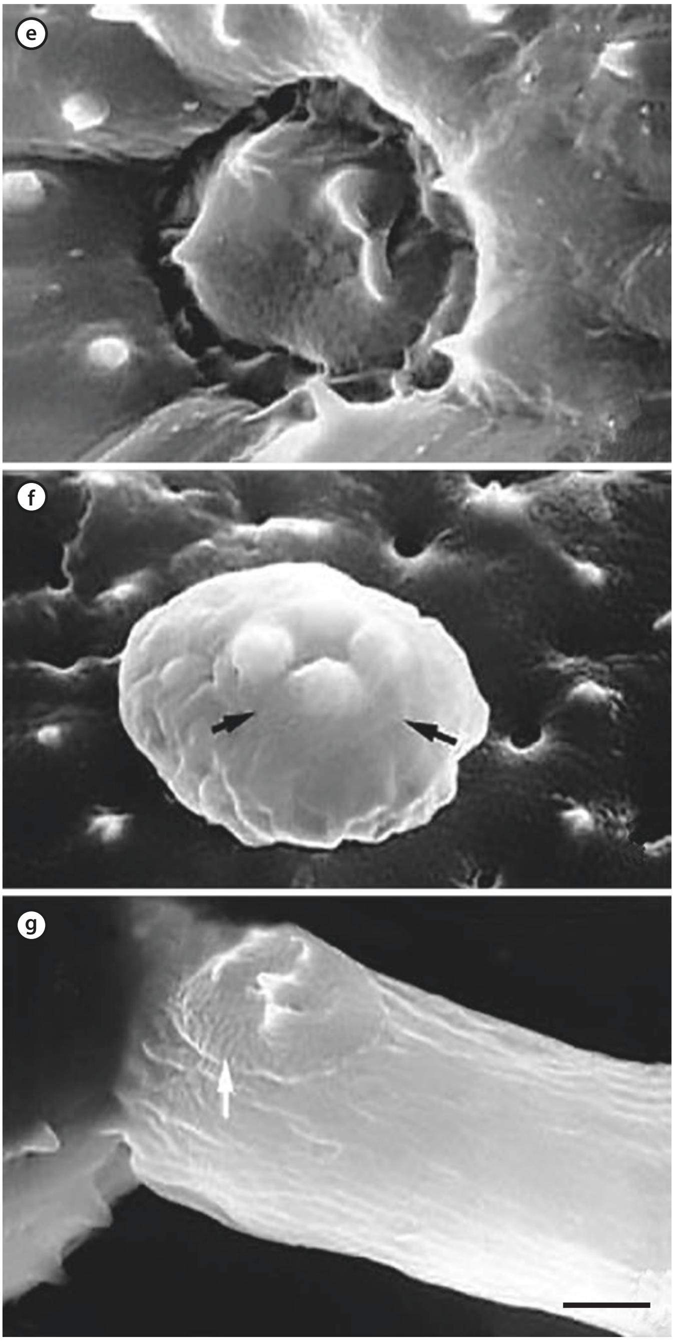


Fig. 17.7 **e**–**g** Scanning electron micrographs showing views of apertures of pollen grains in white campion (*Lychnis alba*). **e** A portion of a dry dormant pollen grain with the aperture appearing in face view as a depression in the exine. **f** A fully hydrated and activated grain immediately before pollen tube emergence. The operculum is clearly distinguishable (arrows). **g** A pollen grain with its growing pollen tube; the operculum is displaced to the side of the pollen tube. Scale bar = 1 μm and applies to all panels. (**e**–**g** RC Crang)

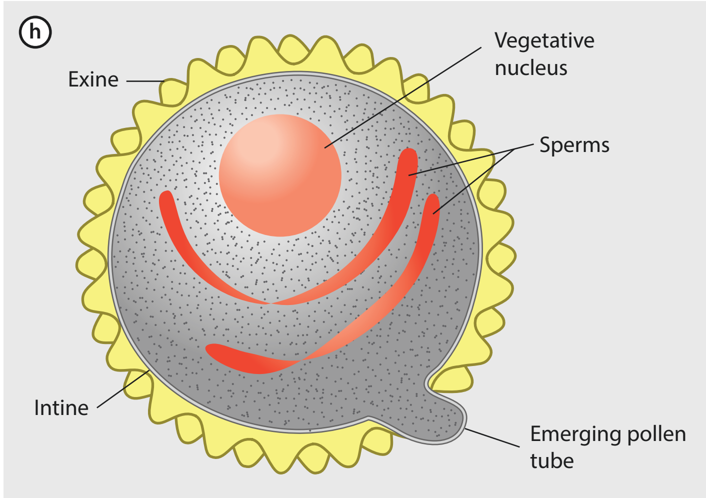


Fig. 17.7 **h** This illustration shows an early germinating tricellular pollen grain of rosinweed (*Silphium* sp.). The wall of the emerging pollen tube is in continuity with the intine. The exine is covered with sharp-pointed (i.e., echinate) spines. (Redrawn from Crang and Vassilyev 2003)

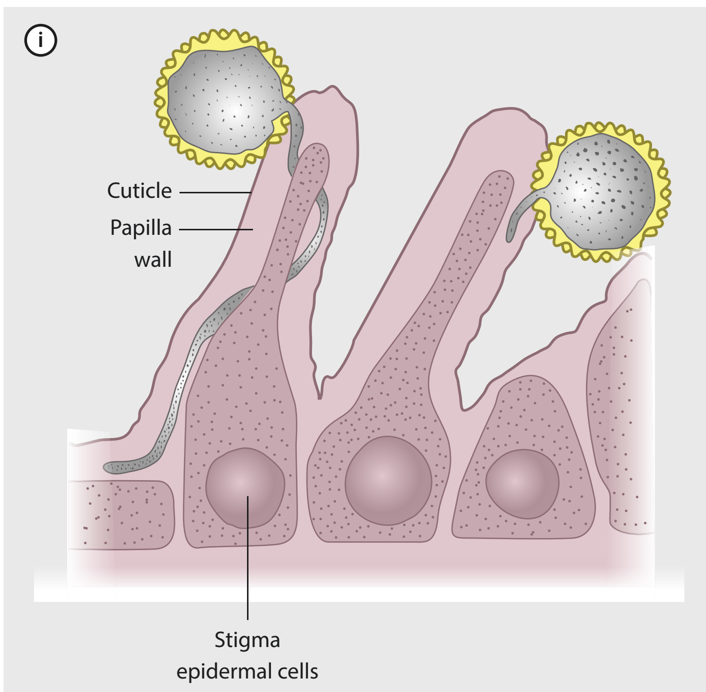


Fig. 17.7 **i** This diagram shows two pollen grains "glued" to the cell wall of a stigmatic papilla. Their pollen tubes have penetrated the cuticle (C) and grow within the papilla wall (PW) toward the stylar transmitting tissue. (Redrawn from Crang and Vassilyev 2003)

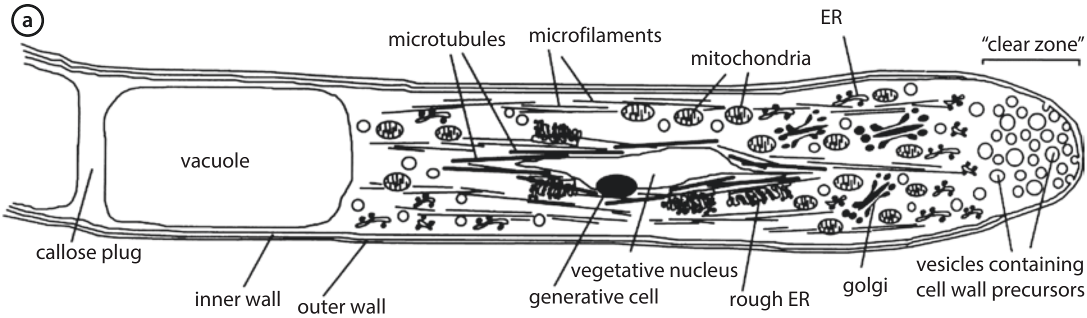


Fig. 17.8 **a** Diagram of subapical and apical tip regions of a pollen tube showing zonation. In what ways do these regions differ?. (Franklin-Tong 1999)

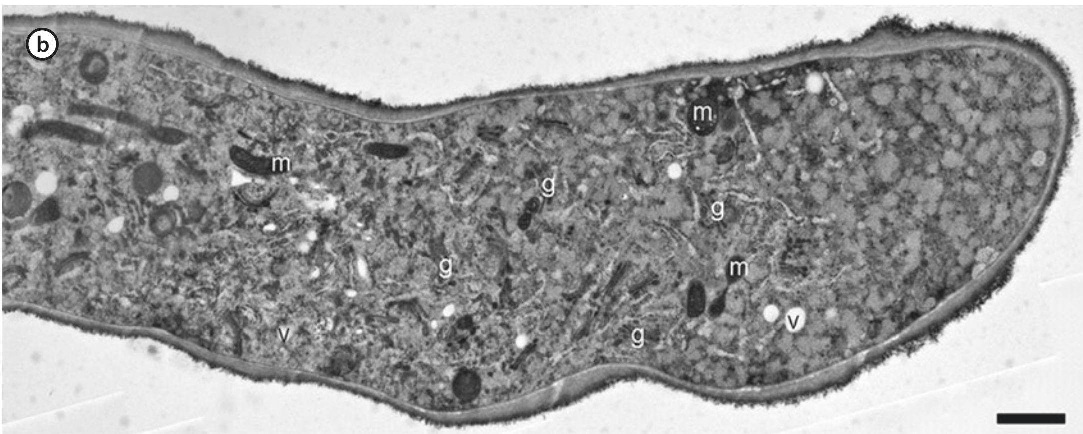


Fig. 17.8 **b** Longitudinal section of Arabidopsis (*Arabidopsis thaliana*) pollen tube apical region showing different regions of the cytoplasm. An apical cytoplasmic-clear region within 4–5 µm of the apex is full of small vesicles; large organelles are only present distally. (m mitochondria, g Golgi apparatus. Scale bar 1 µm). (Ndinyanka et al. (2017))

Similar to apically growing root hairs, pollen tubes show a distinct zonal organization (Fig. 17.8a). Usually four zones can be distinguished: (1) an apical growing zone (or clear zone); (2) a subapical zone where dictyosomes, endoplasmic reticulum, and mitochondria are concentrated; (3) a nuclear zone that includes the site of the vegetative nucleus and sperm cells; and (4) a vacuolated region.

The growing zone is filled with secretory vesicles that transport polysaccharides and membranes for the elongating cell wall and plasmalemma accordingly (Fig. 17.8a, b). These vesicles are produced by dictyosomes that are accumulated in the nongrowing subapical region. Numerous mitochondria provide energy for the active synthetic and transport processes. Endoplasmic reticulum is the site of enzyme and membrane synthesis involved in polysaccharide production and plasmalemma growth.

It has been shown that bursts of calcium (as Ca^{2+} ions) are concentrated in the central apical stream, which are essential for the release of vesicles containing the new wall materials. Longitudinally oriented microfilament bundles of the cytoskeleton are responsible for the vigorous cytoplasmic movement characteristic of pollen tubes.

After reaching the ovule, the pollen tube enters the embryo sac through the **micropyle**. The obturator, or papillate placental cells that are formed in some plants, provide a well-defined pathway that guides the pollen tube to the tip of the ovule. It is generally assumed that the directed growth of the pollen tube occurs due to chemotropically active substances produced and secreted by the **synergid** cells. After its arrival to the embryo sac, the pollen tube enters one of the synergids through its intracellular filiform apparatus. When the pollen tube is within the synergid cytoplasm, it bursts and the vegetative nucleus and both sperm cells are discharged into the synergid. Thereafter, double fertilization occurs forming the diploid zygote and triploid endosperm (refer to Female Reproductive Structures and Embryogenesis, ► Chap. 18 for more details).

17.9 Pollen Is a Major Contributor to Seasonal Allergies

Pollen is a source of allergenic proteins that elicit the formation of a specific class of antibodies, immunoglobulin E, in sensitized humans causing "hay fever." These proteins are synthesized in the vegetative cell. Many angiosperms that have inconspicuous flowers shed pollen via the air and are a cause of allergies for many. The reaction leads to a variety of symptoms, such as sneezing, stuffy nose, and watery eyes. North American plants that are associated with seasonal allergies include many species of maple, elm, and oak that shed pollen in the spring along with many prairie plants. Massive amounts of conifer pollen produced by male cones are also especially abundant typically in the spring of the year, although generally less of an allergen than most angiosperm pollen. During late summer and early fall, at least three species of ragweed (*Ambrosia* sp.) are typically to blame. Allergy shots help the body to build resistance to pollens. Wearing a face mask, regular showering, wearing clean clothes after outdoor exposure, using recirculating air-conditioning, and not planting trees, such as catalpa, dogwood, fir, or redwoods that aggravate allergies, may help in reducing the complications (◘ Fig. 17.9).

Fig. 17.9 Ragweed (*Ambrosia* sp.) pollen is a particular bane of allergy sufferers. (With permission from Prevention CDN.NDG)

17.10 Chapter Review

Concept Review

17.1 *Flowers possess parts arranged in whorls that vary within and among species and are supported by a receptacle*. The floral parts include sepals, petals, stamens, and carpels with each species having particular floral components varying in numbers of each type from zero to many.

17.2 *Floral development starts with increasing cell divisions in apical meristems and initiating organs in an acropetal sequence*. Development from the outside inward is noted not only in the individual flower but carries on to the inflorescence.

17.3 *Male reproductive structures give rise to pollen within the anther*. A stamen includes a filament with an anther attached that contains pollen grains.

17.4 *Pollen grain formation begins with microsporogenesis followed by microgametogenesis*. Meiocytes undergo meiosis leading to the formation of four haploid microspores during microsporogenesis. Microgametogenesis follows, resulting in a multicellular pollen grain which is the microgametophyte also known as the male gametophyte.

17.5 *The structure of pollen grain cell walls changes during development from microspore to macrogametophyte, and callose is deposited and then sporopollenin and adhesives*. A thin layer of primexine is formed around the outer surface of the spore plasmalemma, followed by deposition of sporopollenin forming an exine along with adhesives.

17.6 *The physical properties of pollen grains are taxon specific*. Because of the reproductive nature of the cells within the pollen grain, the structure and function of these cells differs markedly in structure and function from those of the rest of the plant body. Exine surfaces are often distinct among taxa, and thus, pollen grains can be helpful in identifying past, even ancient, plant communities based upon the pollen sampled from ice, soil, and/or lake beds.

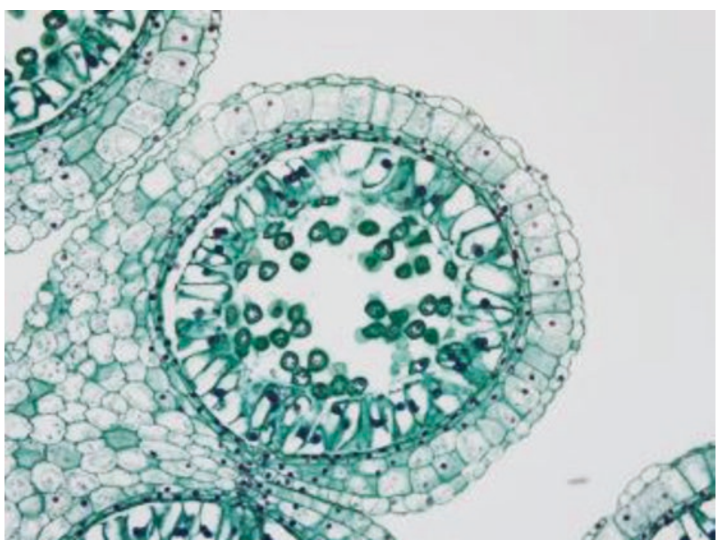
17.7 *Pollen dispersal, germination, and pollen tube growth precede double fertilization***.** The characteristics of the pollen grain surface are optimized to ensure pollen dispersal. A complicated process of pollen/stigma interaction and recognition is used to ensure that the proper pollen will germinate on the correct stigma at the right time. Germination of the pollen grain is followed by pollen tube growth through the style (which is directed by the vegetative nucleus) to the ovary to deliver the two sperm cells.

17.8 *Pollen tube growth is restricted to the tip region*. The endoplasmic reticulum, dictyosomes, and mitochondria within the pollen tube facilitate pollen tube growth via vesicles at the apical meristem of the tube cell. The synergid cells exude a chemical signal that directs the growth of the pollen tube to and through the micropyle. The pollen tube releases the two sperm cells and double fertilization follows.

17.9 *Pollen is a major contributor to seasonal allergies*. "Hay fever" is the cause of seasonal allergies as the anemophilous pollen reacts in sensitized humans.

■ Concept Connections

1. Below is a cross-section of a lily (*Lilium sp.*) flower bud showing an anther where the cells are undergoing late prophase of meiosis I during microsporogenesis at 100x magnification. Identify the epidermis, connective, tapetum, and developing microspores.



Concept Assessment

2. When flowers develop in an acropetal sequences,
   a. the stamens develop first, followed by the carpels, corolla, and calyx.
   b. the flowers develop from the inside of the flower, outward.
   c. the floral structures initially develop from the outside whorl moving sequentially inward toward the carpel.
   d. all whorls of the flower develop simultaneously.
   e. the petals are the first to develop.

3. The _______________ is the structure where pollen grains are formed.
   a. anther.
   b. filament.
   c. connective.
   d. stigma.
   e. ovary.

4. Which structure is the male gametophyte?
   a. the microspore.
   b. the megagametophyte.
   c. the microgametophyte.
   d. the pollen grain.
   e. both c and d.

5. The tapetum functions mainly to:
   a. act like adhesive tape and provide a sticky substance to facilitate dispersal of pollen grains by animal vectors.
   b. shield the sun from the damaging rays of uv light.
   c. provide nutrition to the developing pollen grain, but also produce callase to degrade the callosic walls within the tetrad.
   d. enhance the effect of the dictyosomes by contributing to the formation of the cell plate.
   e. provide the anther with support.

6. Following the various divisions of the nucleus in the formation of the male gametophyte, what is the ploidy of cells within the pollen grain?
   a. haploid.
   b. diploid.
   c. triploid.
   d. tetraploid.
   e. none of the above.

7. By phase 4 of microgametogenesis, the microgametophyte may consist of:
   a. a large generative cell and a small vegetative cell.
   b. two small generative cells and a relatively large vegetative cell.
   c. two cells that are of equal size.
   d. a small generative cell and a larger vegetative cell.
   e. both b and d.

8. Apertures on the pollen grain provide:
   a. a way for the pollen grain to get oxygen.
   b. a means for transporting polysaccharides to the sperm cell(s).
   c. an opening for the pollen tube cell to grow through.
   d. drainage for excess intine to leave the structure.
   e. a path for transportation of cellular contents between cells in the pollen sac.

9. Pollen tubes grow at the apical tip of the cell in conjunction with:
   a. dictyosome secretions migrating to the tip and depositing polysaccharides for energy for the cell.
   b. callose plugs formed behind the growing apical tip funneling the cellular contents and sperm cells forward.
   c. the endoplasmic reticulum contributing to plasmalemma growth.
   d. mitochondria in the growing region providing energy.
   e. all of the above.

10. Double fertilization leads to:
    a. the formation of a haploid zygote and diploid endosperm.
    b. the formation of a haploid zygote and triploid endosperm.
    c. the formation of a diploid zygote and haploid endosperm.
    d. the formation of a diploid zygote and diploid endosperm.
    e. the formation of a diploid zygote and polyploid endosperm.

11. The role of the synergid is to:
    a. assist in the role of the endosperm in providing nutrients to growing embryo.
    b. facilitate the distribution of the contents of the elongated pollen tube to the egg cell and central cell followings its rupture.
    c. work in synergy with the other synergids in the cell to promote the growth of the potential embryo.
    d. act as a placeholder, keeping the egg cell intact.
    e. provide nutrition to the embryo.

Concept Applications

12. Many causes of "hay fever" stem from allergies to pollen. In North America, ragweed (*Ambrosia psilostachya*) blooms at the same time as many species of goldenrod (*Solidago* sp.). Many people feel that the cause of their allergies is the goldenrod pollen because they see the plants blooming at the same time that their allergies are problematic. How can you explain that goldenrod is not the likely cause of their immediate allergic response?

13. Consider why pollen surfaces differ among taxa.

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18

Female Reproductive Structures and Embryogenesis

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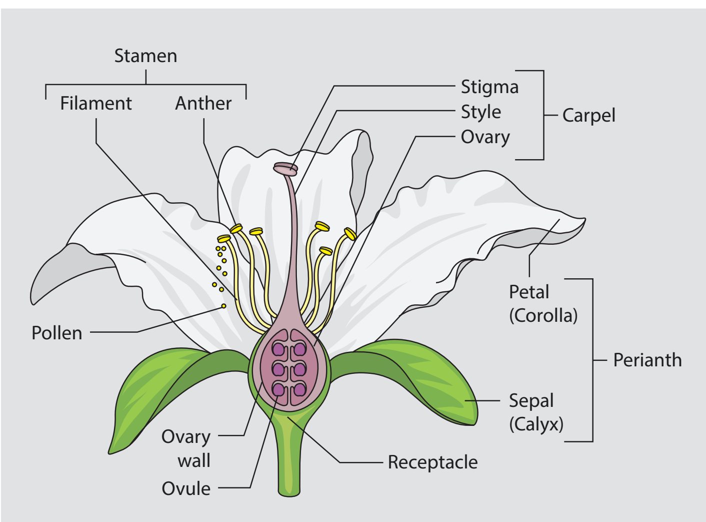
Introduction
The formation of a new seed via sexual reproduction occurs within the ovary of a flower in a series of successive steps ranging from the growth and development of an ovule to the formation of the fully mature embryo within a seed. Within this chapter, you will learn about the female reproductive structures of a flower, the formation of the embryo sac and endosperm, as well as important events including double fertilization and embryogenesis that are critical to the existence of individual angiosperms. The female structures of the flower are typically designed to enable the process of fertilization, protect the developing embryo(s), and to provide for dissemination of the species to new suitable geographical environments. All floral parts are considered to be evolutionarily modified leaves.

18.1 The Innermost Whorl of the Flower Is Typically Composed of Female Floral Parts

Female reproductive structures typically comprise the innermost whorl of floral organs in angiosperms. Primary to the design, the pistil (or carpel) has a terminal stigma, an elongated style, and a basal ovary, which in turn houses an egg cell, **central cells**, and related cells within an enclosed ovule (◘ Fig. 18.1). If only one carpel exists within an ovary, it is said to be **monocarpous**. There may be more than one ovule within an ovary and, if so, are said to be **apocarpous** if they are independent of one another or **syncarpous** if they are fused. The compilation of all carpels within the flower is collectively called the gynoecium. A pistil is a collective term for the gynoecium and, thus, may contain one or more carpels. The pistil is a modified leaf known as a megasporophyll which evolved and contains one or more ovules.



◘ **Fig. 18.1** Floral structure indicating a carpel (pistil) containing apocarpous ovules. (Redrawn from Crang and Vassilyev 2003)

Box 18.1 Sexual Selection, Reproductive Isolation, and Speciation

The genetic bases of traits such as flowering time and flower color that contribute to pre-pollination barriers have been studied in several species and, in some cases, have been shown to be involved in preventing low-fitness hybrids. Nevertheless, the role of sexual selection as a force in plant speciation is still controversial. In sexual selection, a species produces far more pollen than ovules, making for a biased sex ratio toward males as well as a species-dependent variation in ovule number per flower. As in animals, a high level of sexual selection should speed up the evolution of traits that are responsible for pre- and post-mating hybridization between species. Thus, sexual selection is believed to be tightly linked to interspecific barriers in plant speciation. It is expected that species subject to different levels of sexual selection should differ in the selectiveness of their ovules toward male gametes. Recent studies have shown that ovules from self-incompatible *Solanum* species were more selective compared to ovules from self-compatible species. Of particular importance is that new technological advances are allowing identification of the genetic targets of selection, natural or sexual, that drive the establishment of reproductive barriers between species. As a consequence, it is believed that sexual selection can produce the establishment of interspecific reproductive barriers, leading to a unidirectional gene flow between different but closely related species. Even though the origin of reproductive barriers may be elusive, ongoing sequencing studies will foster the synthesis of complementary studies involving early new speciation with the genomics of "good species."

Reference: Lafon-Placette et al. (2016)

18.2 Ovaries Are Described Based upon Position Within a Flower and May Contain Nectaries

Three types of ovaries are recognized according to their positions with respect to the lateral organs of the flower (Fig. 18.2a–c). A superior (or **hypogynous**) ovary (e.g., tulip, *Tulipa gesneriana*) is situated on the receptacle above the perianth and androecium. In flowers with an inferior (or **epigynous**) ovary (e.g., daffodil, *Narcissus pseudonarcissus*), it is positioned below the apparent points of attachments of the perianth and androecium. However, not all epigynous flowers have a hypanthium where the ovary is enclosed in the receptacle. In flowers with inferior ovaries, the lower portions of calyx, corolla, and androecium fuse into a floral tube or hypanthium, which becomes completely adnate (attached) with the whole length

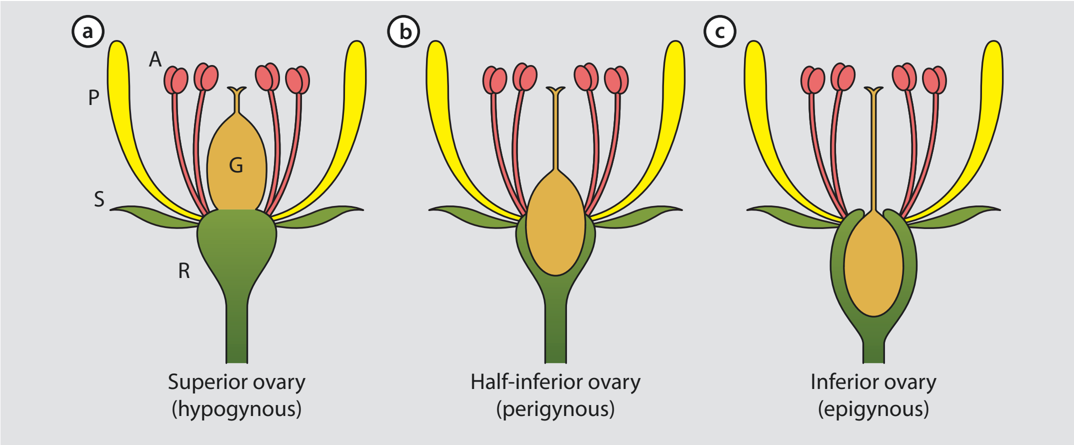


Fig. 18.2 **a**–**c** Female flowers can have one of three types of ovaries denoted by where the ovary is located relative to the sepals (calyx). *a* androecium (stamens), *p* petals, *s* sepal, *r* receptacle, and *g* gynoecium. (Redrawn from Ulf Mehlig, CC BY-SA 2.5)

Fig. 18.2 **d**–**f** A longitudinal section of a day lily (*Lilium* sp.) flower with a superior ovary. (d. natural size; e,f. magnified). The ovules and axile placentation are apparent within the hypanthium. Lily has three sepals and three petals; however, the two structures have an identical appearance, so it appears as though the flower has six petals, which is not the case. Scale bars = 1 cm in **d** and 2 mm in **e** and **f**. (**d**–**f** RR Wise)

of the ovary. In the flowers with a half-inferior (or **perigynous**) ovary (e.g., elder, *Sambucus nigra*), the hypanthium adnates (or fuses) with only the lower half of the ovary (Fig. 18.2d–f).

The ovaries of many monocots contain septal nectaries that help the flower attract animal pollinators (Fig. 18.2g, h). Septal nectar-

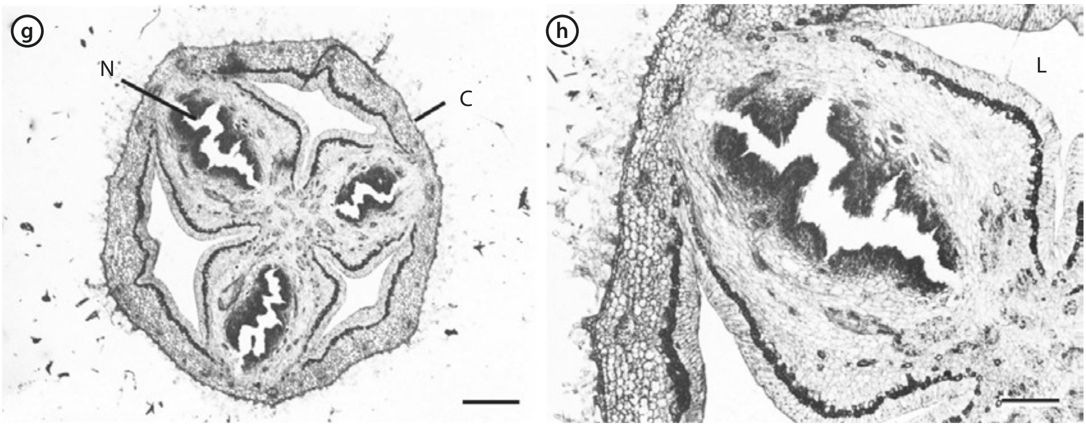


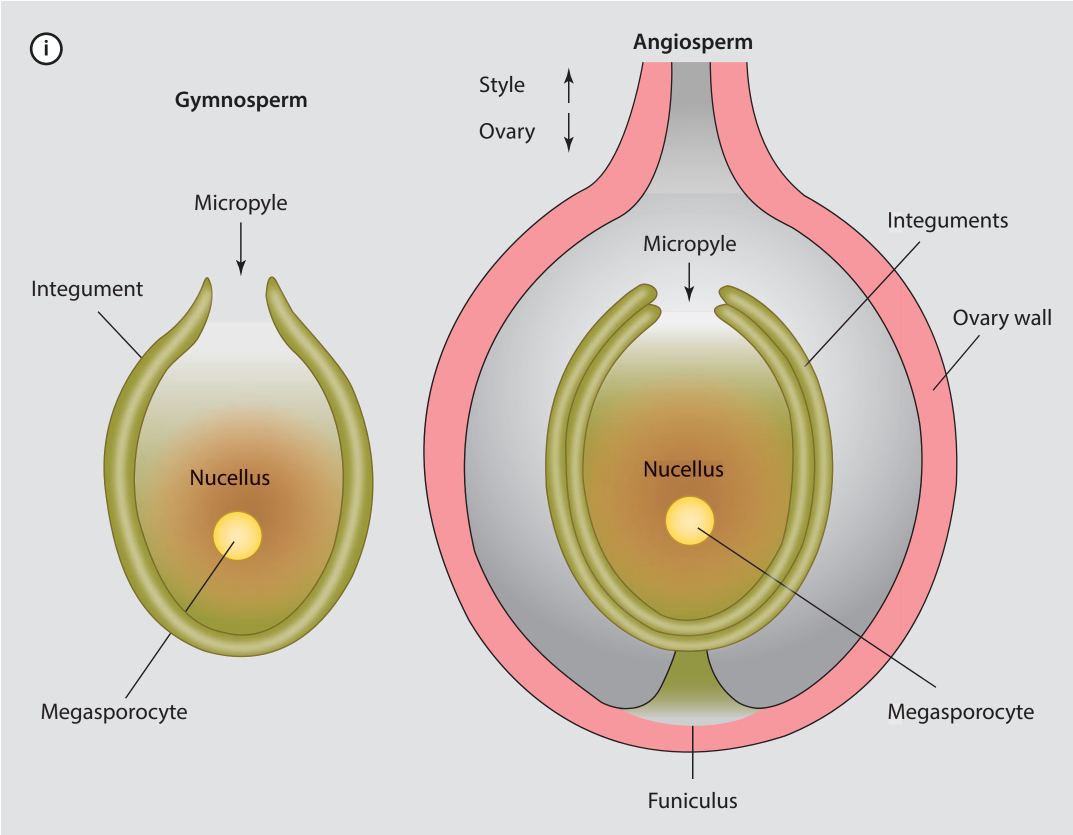
Fig. 18.2 **g**, **h** Cross-section of the ovary of black kangaroo paw (*Anigozanthos fuliginous*) showing three septal nectaries (in accordance with the number of carpels of the gynoecium). It is evident that the nectaries are formed at the interfaces of inner portions of carpels. *C* carpel wall, *N* nectary, *L* ovary locules. Scale bars = 500 µm in **g** and 200 µm in **h**. (**g**, **h** M Simpson (1993))

ies formed in the ovary wall may accompany the incomplete fusion of carpels. These nectaries represent the glandular epidermis. However, the evolution of these nectaries may parallel the formation of other forms of pollination such as "buzz-pollination" in which septal nectaries are not found. Buzz-pollination occurs in which bees and certain other insects create vibrations that obtain pollen from narrow slits of anthers and may release the pollen into non-nectary sites of the pistil. This type of pollination represents a complex adaptation of plant and insect through coevolution.

Gymnosperms, as opposed to angiosperms, are generally regarded as bearing "naked" seeds (Figs. 18.2i and 18.2j). The "naked" ovules do not mean that they are without protection. In fact, the ovules are generally borne on stalks or flattened structures (megasporophylls) that cluster together to form cones. The cones do offer some protection, but not the exclusion of pollen grains from direct contact with the ovules.

18.3 Ovules Can Be Arranged Within an Ovary in a Variety of Ways

Histologically, the ovary wall at anthesis consists of homogeneous ground parenchyma and vascular bundles and is covered from the outside and inside by the epidermis and a cuticle. The sites of the ovary where the ovules are produced are known as placentae (singular, placenta). Each ovule is attached to the ovary wall by a stalk called a **funiculus**. In angiosperms, the term locule refers to the chamber within an ovary of the flower. The number of locules present in a gynoecium may be equal to or less than the number of carpels. The locules house the ovules and later the seeds. When there are fewer locules than carpels, it is because the carpels fuse during development.



◘ **Fig. 18.2** **i** Illustration of gymnosperm and angiosperm ovules. Here you can also see how the gymnosperm ovule is "naked" and not enclosed by protective tissue, whereas the ovule of the angiosperm is enclosed within an ovary. Note the presence of the integuments, micropyle, nucellus, and funiculus. (public domain)

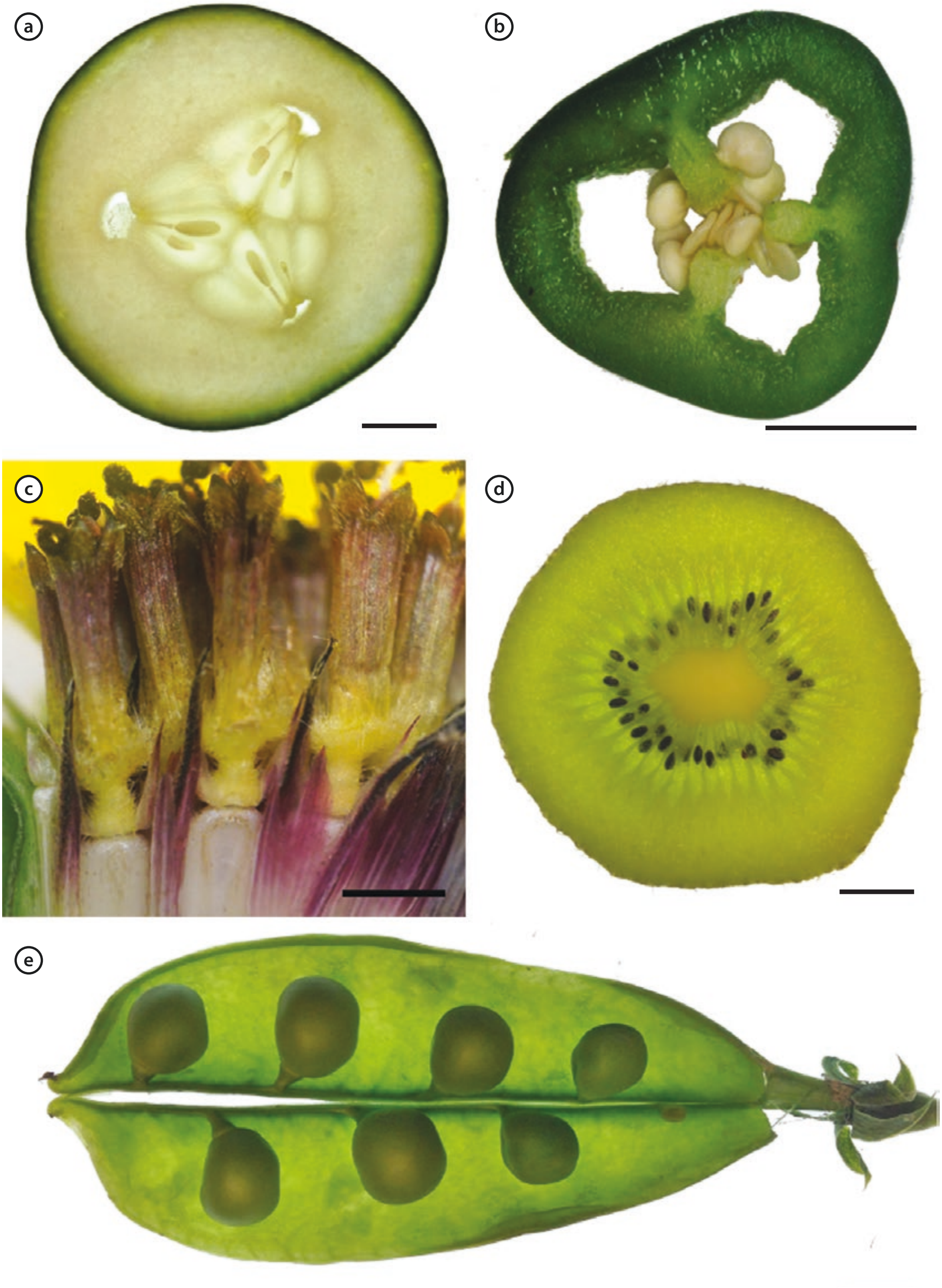
◘ **Fig. 18.2** **j** A pinyon pine (*Pinus edulis*) gymnosperm cone and exposed seeds. The seeds are borne in cones on megasporophylls and are not visible until maturity. (Curtis Clark, CC BY-SA 2.5)

Five types of placentation can be distinguished with respect to the position of placentae within the ovary and the structure of the gynoecium. In **parietal placentation**, which is often found in single-locular ovaries, the placentae and ovules are formed along the peripheral parts of the ovary at the sites of fusion of the carpel(s) margins (◘ Fig. 18.3a). Parietal placentation is found in the majority of angiosperms. **Axile placentation** (or central-angular) is found in plants with multilocular ovaries (◘ Fig. 18.3b). The partitions dividing the ovaries into locules are formed by the lateral fusion of carpels along their margins, and the placentae are formed in the angles of locules. In **basal placentation**, the ovules are attached at their base and point upright (◘ Fig. 18.3c). This is common in plants such as sunflower and carnation that have multiple flowers packed in to a flat flower head. **Free-central placentation** is characteristic of one-locular gynoecia in which the inner partitions of the ovary were lysed, leaving only a central column with placentae (◘ Fig. 18.3d). Peas and beans show **marginal placentation**, in which the ovules are arranged in a linear fashion along the seam (or suture) that forms the carpel (◘ Fig. 18.3e).

Ovules, the precursors of seeds, are derived from the placenta of the ovary wall and consist of a central **nucellus** (which represents the megasporangium), where megaspores, and later an embryo sac, are produced; one or two **integuments**, which enclose the nucellus; and a supportive stalk, the funiculus, which attaches the ovule to the placenta. Usually a single vascular strand runs through the funiculus from placenta to the lower part of the ovule (◘ Fig. 18.3f). At the free end of the ovule, a small opening, the **micropyle**, is left by the integuments. The pollen tube will pass through the micropyle before entering the embryo sac. The region where the nucellus and the integuments merge is called the chalaza. In most flowering plants, a **hypostase** is differentiated in the chalazal region (basal) of the ovule, which consists of a cluster of densely cytoplasmic cells with highly refractive cell walls. The hypostase serves as a boundary to prevent further growth of the embryo sac.

In ovules such as smartweed (*Polygonum coriarium*), the ovule consists of three main parts immediately before fertilization: (1) an outer integument, (2) an inner integument, and (3) a large multicellular nucellus (◘ Fig. 18.3g). The nucellus contains an embryo sac comprised of seven cells which include the egg and two synergids (representing the egg apparatus in the micropylar region of the sac), the central cell, and, in the chalazal region, three antipodals. Beneath the embryo sac, the hypostase can be identified as a group of cells with thickened walls and dense cytoplasm. The vascular tissue which supplies the ovule (and later developing seed) ends at the basal region of the ovule. Both integuments are thin, and each consists of only two epidermises with no mesophyll.

A minority of species hold their ovules in an **orthotropous** (upright) position (◘ Fig. 18.3h). In other species, the ovules curve during development to become perpendicular to the axis of the funiculus (**hemitropous**, ◘ Fig. 18.3i) or, as is found in the majority of plants, to the ovules become completely inverted during growth



■ **Fig. 18.3** **a**–**e** Examples of five placentation types: **a** parietal (cucumber, *Cucumis sativus*), **b** axile (jalapeno pepper, *Capsicum annum*), **c** basal (sunflower, *Helianthus* sp.), **d** free central (kiwifruit, *Actinidia deliciosa*). **e** marginal (pea, *Pisum sativum*). The funiculus can be readily observed in figures **a** and **e**. Figures **a** and **b** show fruits with three locules in contrast to fruits indicated in figures **c**–**e** with only one locule. In figure **c**, the locule is not apparent in this particular photograph. However, members of the Asteraceae form achene fruits where two carpels fuse, forming one locule that contains one seed. Scale bars = 1 cm in all images. (**a**–**e** RR Wise)

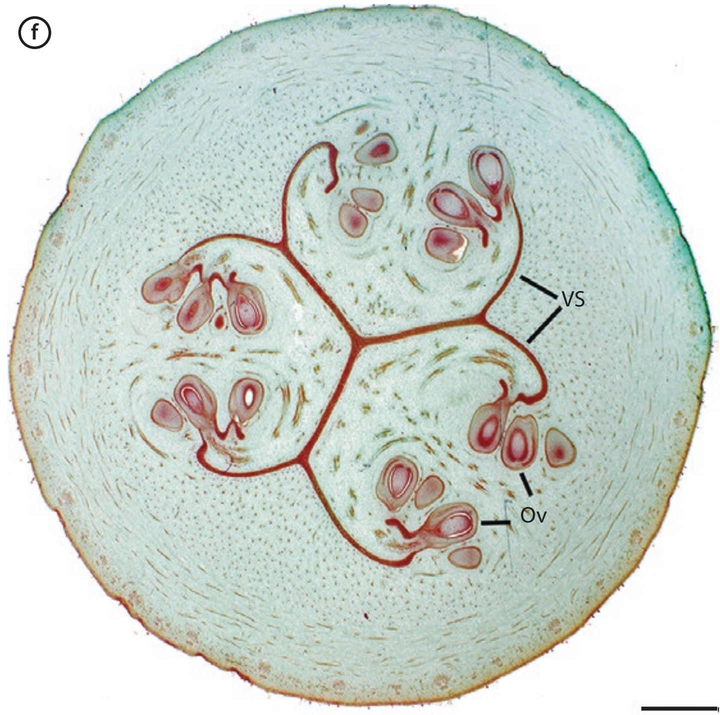


Fig. 18.3 **f** The vascular strands (VS) running to each ovule (Ov) can be clearly seen in this squash (*Cucurbita* sp.) fruit. Scale bar = 1 mm. (RR Wise)

(**anatropous**, Fig. 18.3j). The number of ovules in a single ovary varies from one to a great multitude, which ultimately provides the upper limit to the number of seeds which can be formed.

18.4 Development of the Megagamete Begins with the Differentiation of the Megaspore Mother Cell and Ends with the Formation of the Megagametophyte (Embryo Sac)

The formation of the female gamete (megagamete or egg cell apparatus), which is enclosed in the megagametophyte, can be subdivided into two stages, **megasporogenesis** and **megagametogenesis**. In megasporogenesis, a diploid **megaspore mother cell** (or **megasporocyte**) undergoes meiosis to produce four haploid **megaspores**. Megagametogenesis follows in which the four haploid megaspores undergo a complex series of mitoses and nuclear fusions to produce a variety of n, $3n$, $5n$, and even $6n$ cells that make up the mature **megagametophyte**, or **egg sac**. The number and ploidy level of the cells in the mature egg sac varies among taxa. The process in lily (*Lilium* sp.) will be detailed in this section as an example. Keep in mind, however, that numerous variations exist across the plant kingdom.

An overview of megasporogenesis in given in Fig. 18.4a–c, with details provided in Fig. Fig. 18.4d-i. Megasporogenesis starts

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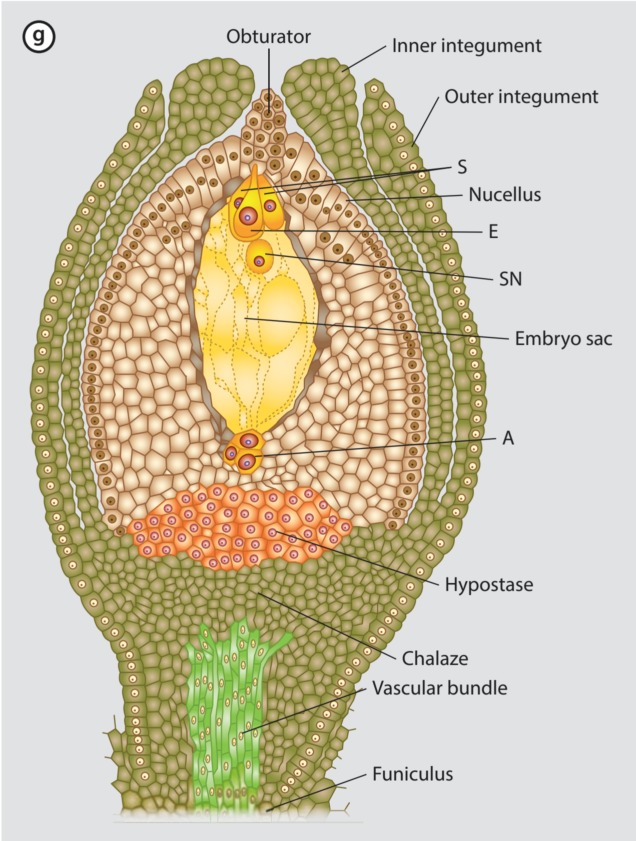


Fig. 18.3 **g** Diagram of a longitudinal section of smartweed (*Polygonum coriarium*) illustrating the orthotropous (upright) ovule immediately prior to double fertilization. *S* synergids, *E* egg cell, *SN* secondary nucleus of central cell, *A* antipodals. (Redrawn from Crang and Vassilyev 2003)

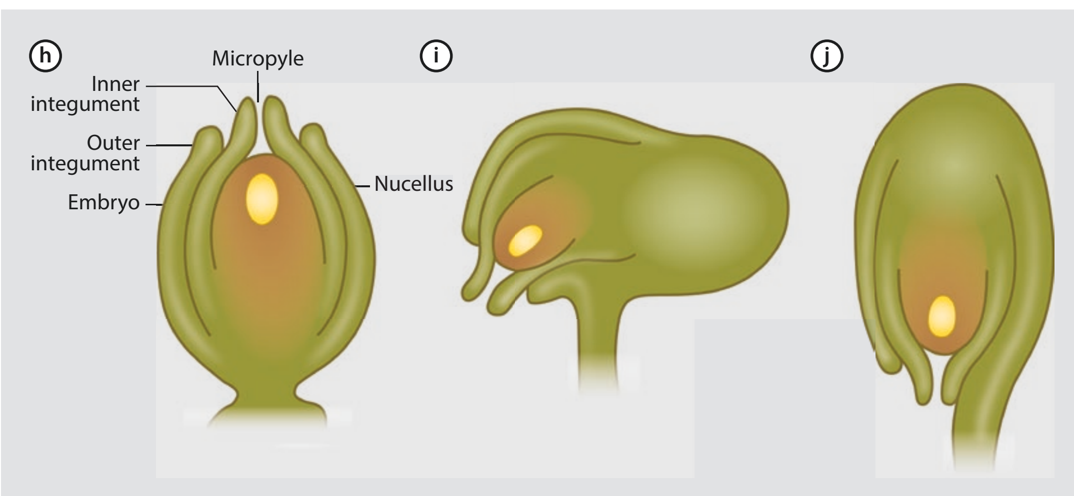
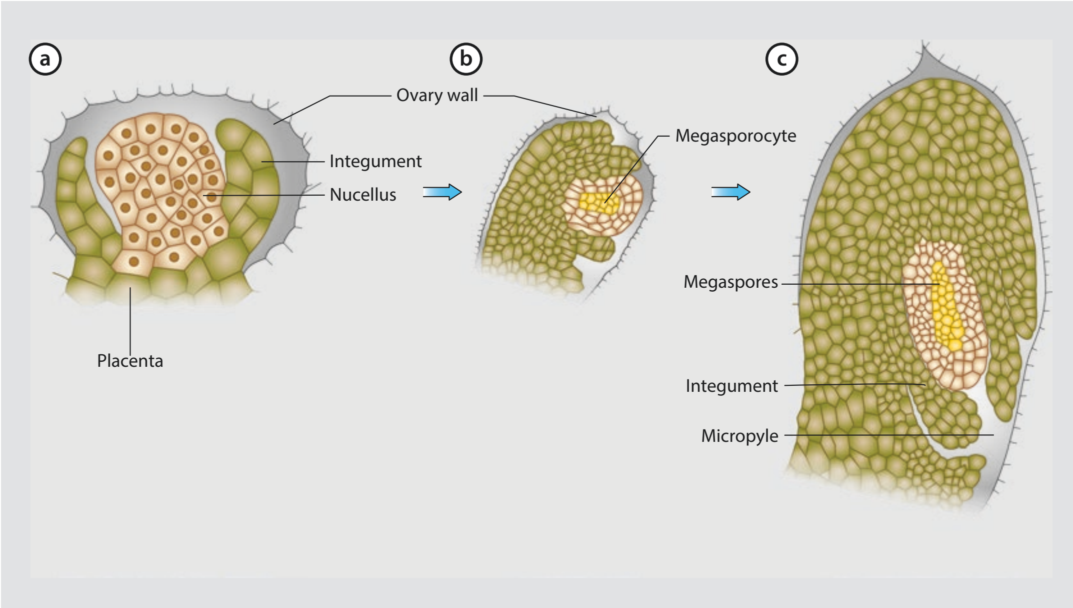


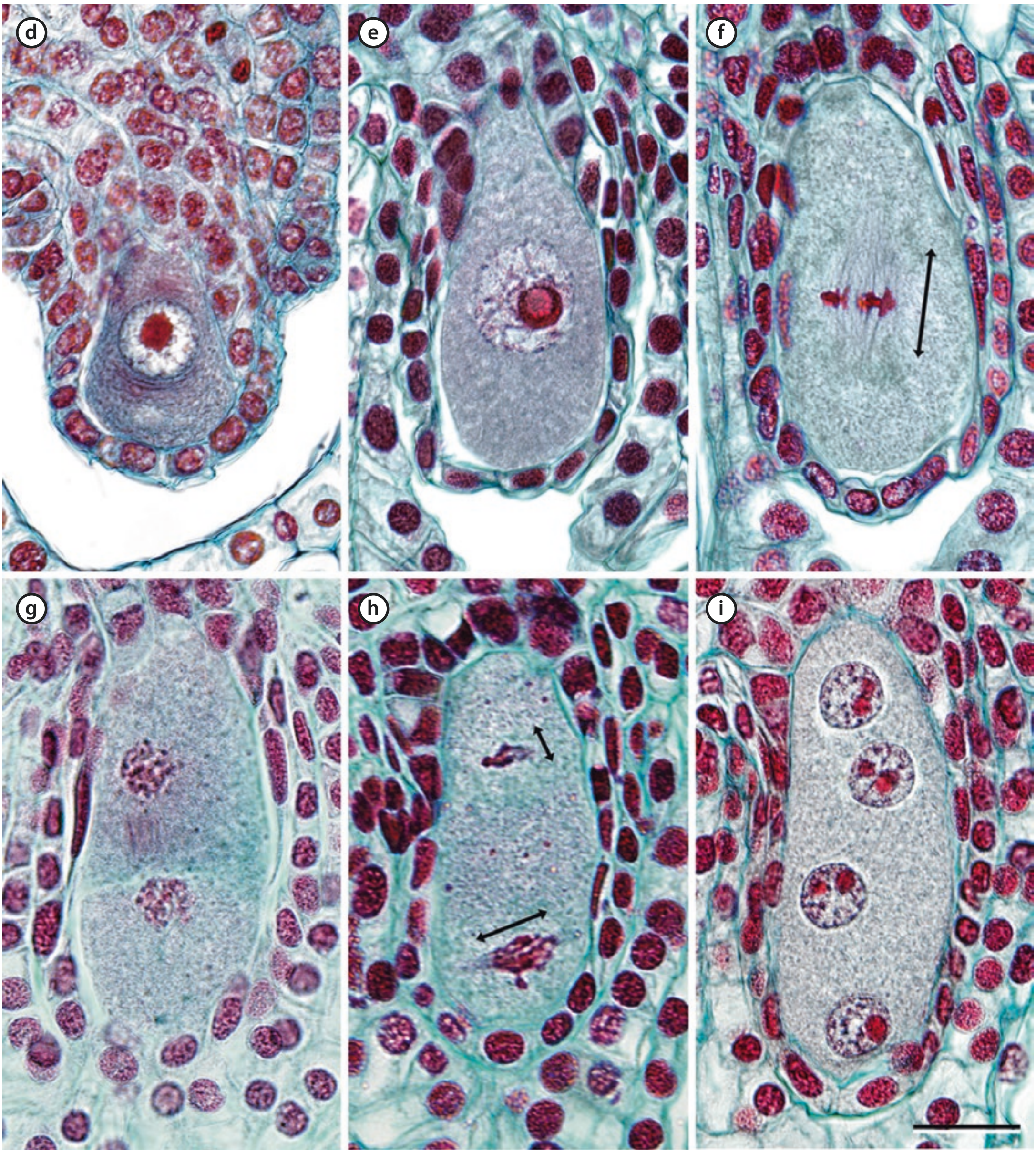
Fig. 18.3 **h**–**j** Three orientations of mature ovules, **h** orthotropous (upright), **i** hemitropous, and **j** anatropous. (**h**–**j** JM Coulter, CR Barnes and HC Cowles (1910), public domain)



◘ **Fig. 18.4** **a**–**c** In megasporogenesis a diploid megaspore mother cell (megasporocyte) undergoes meiosis to produce four haploid megaspores. This illustration portrays structural changes of an anatropous ovule of a sedge (*Carex* sp.) at three early developmental stages. Only a single ovule develops in the ovary. **a** A very young stage of development. **b** Represents the differentiation of the megasporocyte—note the change of the ovule orientation relatively to the placenta. **c** Demonstrates a postmeiotic ovule with four megaspores. The ovule is turned to such an extent that it lies near the placenta—a characteristic feature of anatropous ovules where the placenta is at the base of the ovary. (Redrawn from Crang and Vassilyev 2003)

with the differentiation of the megasporocyte in the nucellus of the young ovule. The nucellus is the central mass of diploid cells in the ovule containing the embryo sac and the developing megasporocyte. The megasporocyte is conspicuous because of its large size, dense cytoplasmic content, and prominent nucleus (◘ Fig. 18.4d). It undergoes meiosis 1 and meiosis 2, without accompanying cytokinesis, resulting in a linear array of four haploid megaspores (nuclei only), called a tetrasporic embryo sac or tetrad (◘ Figs. 18.4e–i).

Megagametogenesis then follows megasporogenesis. Megagametogenesis is a mitotic process as seen in ◘ Figs. 18.4j–o. Three of the haploid megaspores migrate to the chalazal end (◘ Figs. 18.4k) where they fuse and to form a single triploid (3*n*) mass of chromosomes (nucleus) that shares a common mitotic spindle (◘ Figs. 18.4l). The fourth haploid megaspore migrates to the micropylar end. The resulting two nuclei – one triploid and one haploid – then undergo two rounds of mitosis each (◘ Figs. 18.4m,n), resulting in four triploid nuclei at the chalazal end and four haploid nuclei at the micropylar end (◘ Figs. 18.4o). Thus, a coenocytic (lacking cell walls) eight-nucleate embryo sac is formed. Subsequent cytokinesis and cell differentiation result in a seven-cell embryo sac composed of a three-celled egg apparatus at the micropylar pole, three antipodals at the chalazal pole, and a binucleate central cell (◘ Figs. 18.4p).



◘ **Fig. 18.4** **d**–**i** Stages of megasporogenesis in lily (*Lilium* sp.). Megasporogenesis is a meiotic process composed of two rounds of nuclear division without cytokinesis resulting in a tetrad of haploid nuclei. **d** The megasporocyte is a large, conspicuous cell with a single diploid nucleus. The first division (meiosis 1) proceeds from e prophase 1 to **f** metaphase 1 to **g** telophase 1 resulting in a dyad with two nuclei. The second division (meiosis 2) begins with **h** anaphase 1 and ends with **i** telophase 2. Meiosis has generated four haploid megaspore nuclei, arranged in a linear tetrad. The chalazal end is to the top of each image, and the micropylar end is to the bottom. The double-headed arrows in **f** and **h** indicate the orientation of the meiotic spindle. Scale bar in **i** = 25 µm and applies to all panels. (**d**–**i** RR Wise)

The **egg apparatus** consists of two **synergids** (sister cells) and one egg cell (◘ Fig. 18.4p). In the synergids a **filiform apparatus** develops that consists of highly branched irregular wall protuberances protruding deeply inside the cells as seen with high-magnification light microscopy or electron microscopy. The filiform apparatus with its greatly extended plasmalemma surface is thought to be involved in the synthesis and secretion of

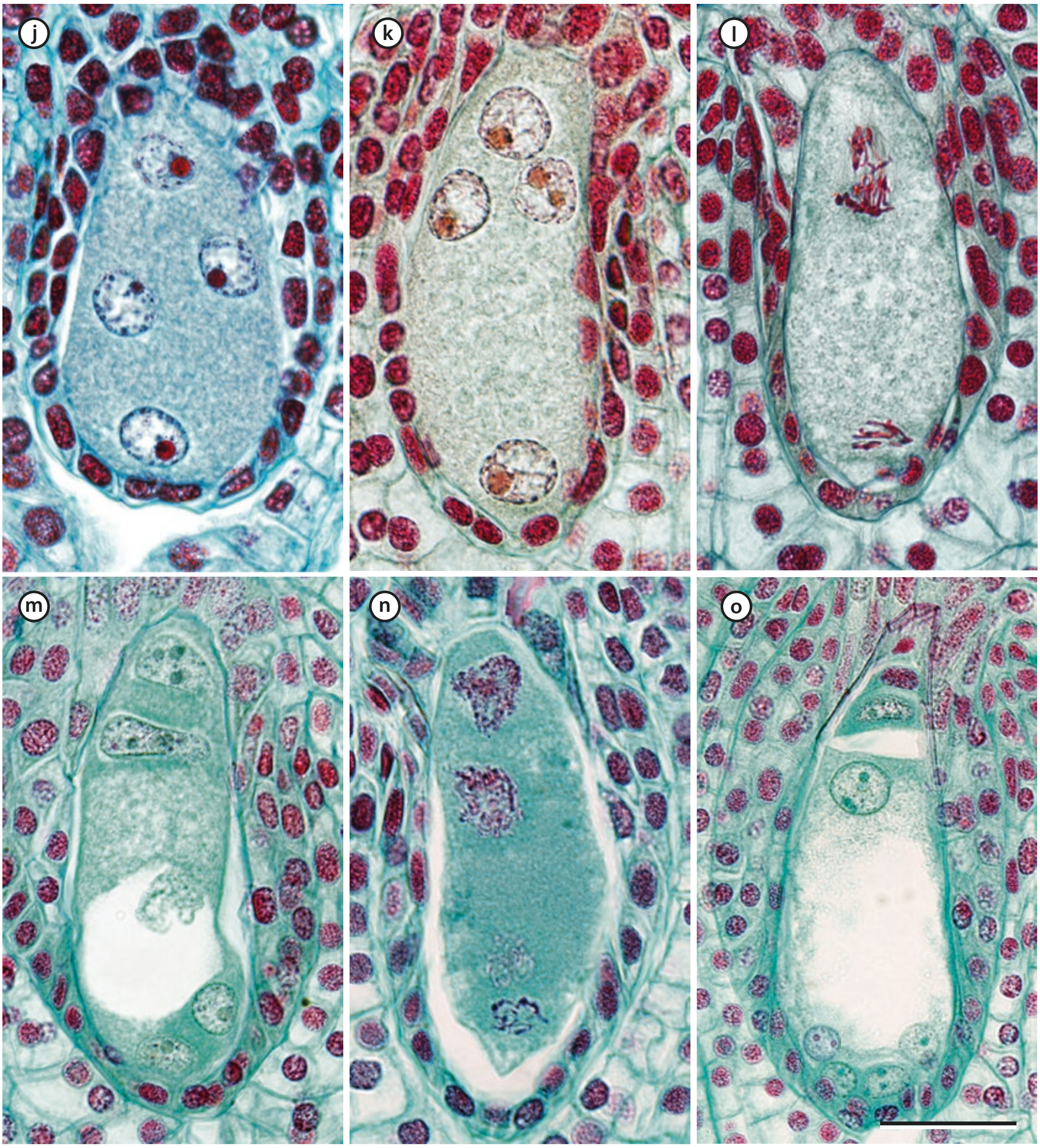


Fig. 18.4 **j**–**o** Stages of megagametogenesis in lily (*Lilium* sp.). In **j** and **k**, three of the four haploid megaspores migrate to the chalazal end and one migrates to the micropylar end. **l** The three chalazal nuclei fuse to form a single triploid nucleus. **m** Mitosis 1 generates two triploid chalazal nuclei and two haploid micropylar nuclei. **n**, **o** Mitosis 2 then generates eight nuclei (four 3*n* and four 1*n*). Scale bar in **o** = 25 µm and applies to all panels. (**j**–**o** RR Wise)

substances capable of directing pollen tube growth toward the embryo sac. In a sense, synergids may be treated as transfer cells and are further characterized by the polar distribution of cell components. Their protoplasm is concentrated in the micropylar half of the cell, while the chalazal half is highly vacuolated. The egg cell, like the synergids, also shows a specific polarity. However, in contrast to synergids, most of the protoplasm is located in the chalazal third of the cell, while the micropylar two-thirds contain a large vacuole.

The **central cell** occupies the largest portion of the embryo sac and is highly vacuolated. In the beginning, it is binucleate, and its two nuclei, along with most of the cytoplasm, are located near the egg apparatus (◘ Fig. 18.4p, q). These nuclei are called **polar nuclei**, because they are derived from groups of nuclei at the opposite poles of the eight-nucleate embryo sac. The close arrangement of polar nuclei to the egg apparatus apparently facilitates double fertilization. The polar nuclei eventually fuse with each other, but the time of fusion varies from taxon to taxon. In some plants, the fusion is completed, and the nucleus becomes diploid before fertilization. In such case, the fully mature embryo sac is seven-nucleate. But in other cases, the polar nuclei fuse only after the arrival of the sperm in the sac. The antipodals persist throughout megagametophyte development and will serve in the growth of the endosperm.

Together with the developing embryo sac, the nucellus also changes. The majority of angiosperms possess ovules in which most of the nucellus degenerates before the embryo sac reaches maturity, subsequently leaving the mature embryo sac in direct contact with the inner integument. In other cases, the inner epidermis of the integument that borders the embryo sac frequently differentiates into a specific tissue, the **endothelium** (◘ Fig. 18.4q). It consists of radially elongated cells rich in cytoplasmic content. In ovules where the nucellus is abundant, it expands by cell division during embryo sac development, and the mature embryo sac is surrounded by a massive nucellus. A general summary of the process from megasporogenesis to megagametogenesis is illustrated in ◘ Fig. 18.4r.

18.5 Pollination Is Followed by Germination of the Pollen Grain and Pollen Tube Growth

After a pollen grain reaches a stigma (whether via wind, insect, bird, etc.), it germinates, and, if it is compatible with the stigma, it forms a pollen tube capable of transporting the male gametes to their sites of fertilization. The surface of the stigma creates an

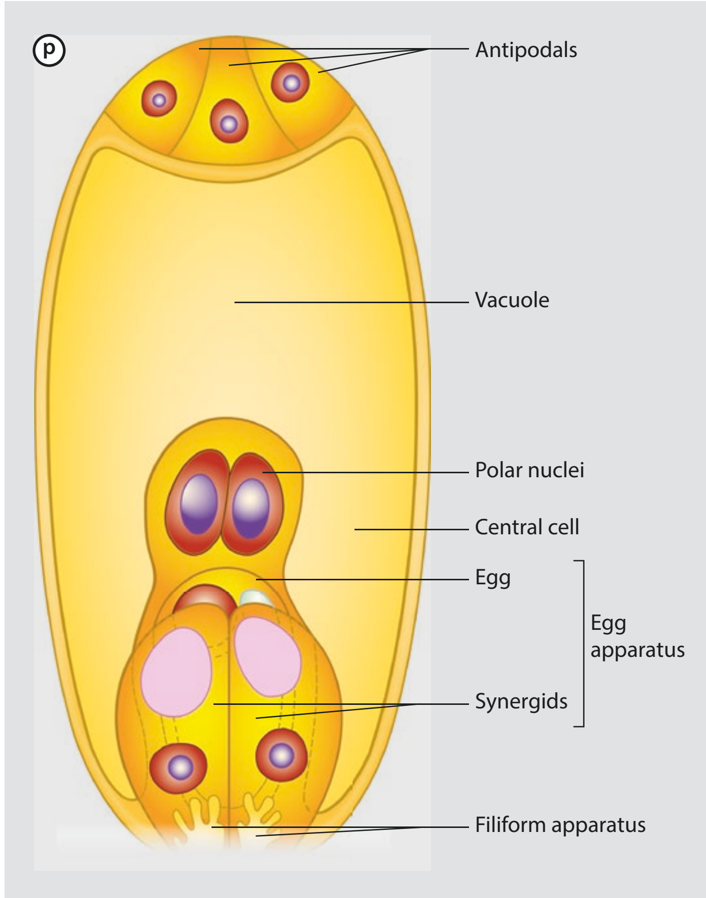


Fig. 18.4 **p** Embryo sac illustrating the highly ordered cellular arrangement that is characteristic of the majority of plants. The micropyle is at the bottom. Note the filiform apparatus in the synergids and the arrangement of the vacuoles and nuclei in synergids and egg cell. In synergids the nuclei are oriented toward the micropyle, and vacuoles are toward the chalazal end of the cells, whereas in the egg, the nucleus and most of the cytoplasm is at the chalazal end. (Redrawn from Crang and Vassilyev 2003)

optimal physiological condition for compatible pollen grains to germinate. Both the stigma and the pollen grain coatings are involved in the process of recognition that allows pollen grains to germinate and produce successful pollen tubes only in compatible combinations. In *Brassica* (as in many other plants.), two- to three-celled hairs are formed on the stigmatic surface of the carpel (Fig. 18.5a–c). The hairs secrete viscid substances that are involved in the recognition of compatible pollen. If they fit together with the substances emanating from the pollen grain wall, pollen grains germinate and produce normal filament-like pollen tubes that will grow through the style.

Fig. 18.4 **q** In rosinweed (*Silphium* sp., Asteraceae), the fully mature and ready to be doubly fertilized embryo sac is seven-celled and eight-nucleate. The densely cytoplasmic columnar cells surrounding the embryo sac comprise the endothelium (En). The three antipodals (A) at the chalazal end are prominent with darkly staining nuclei. Only the lower polar nucleus is visible in this section. The egg cell (EC) holds the sixth nucleus, and the two synergids (Sy) account for the final two, to make eight. The filiform apparatus (FA) is at the micropylar end. Scale bar = 50 µm. (RR Wise)

The style contains a stylar transmitting tissue (a.k.a. stigmatoid tissue), specialized for conducting the growing pollen tubes from the stigma toward the ovules (Fig. 18.5d, e). In styles having an open canal, the transmitting tissue lines the canal and consists of one layer of glandular cells. In solid styles, characteristic of the majority of flowering plants, the transmitting tissue forms one or more strands of elongated densely cytoplasmic cells embedded in the central ground parenchyma. The pollen tubes grow downward to the ovary through

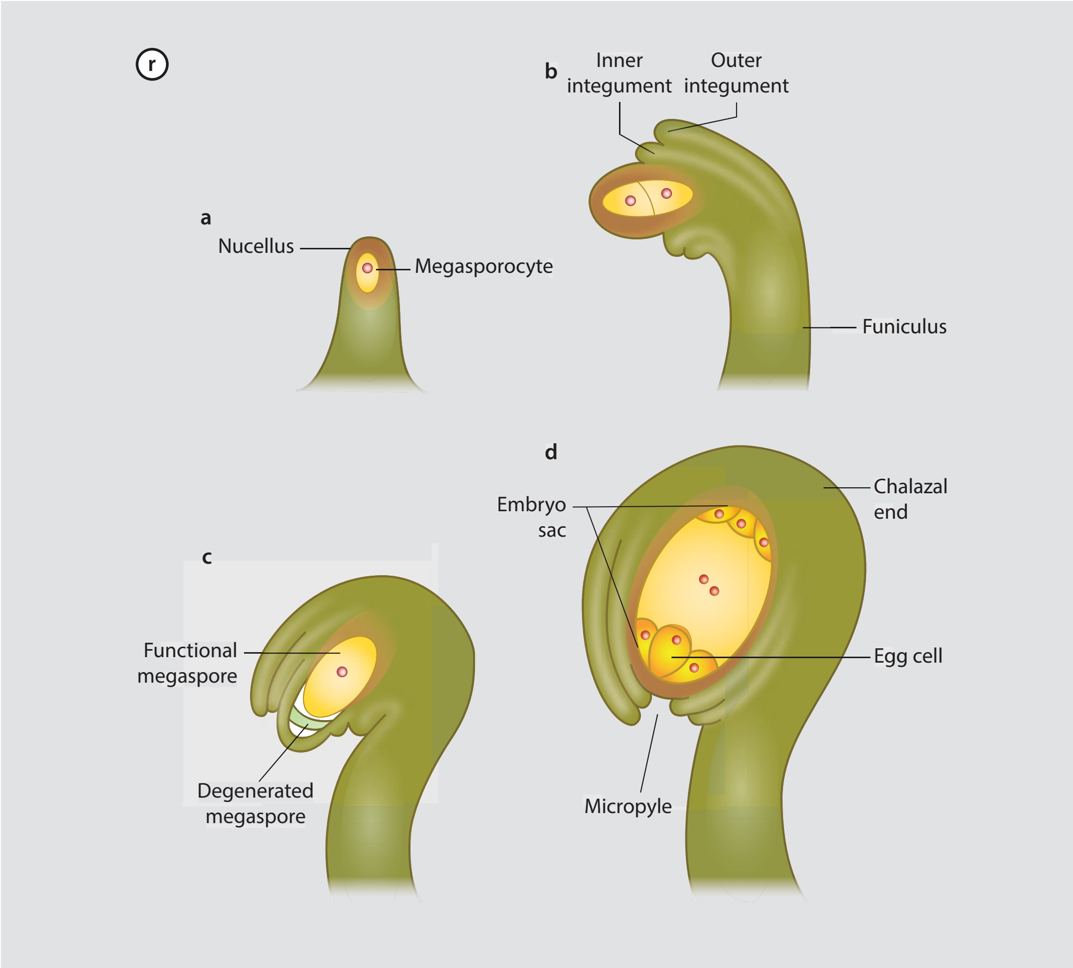
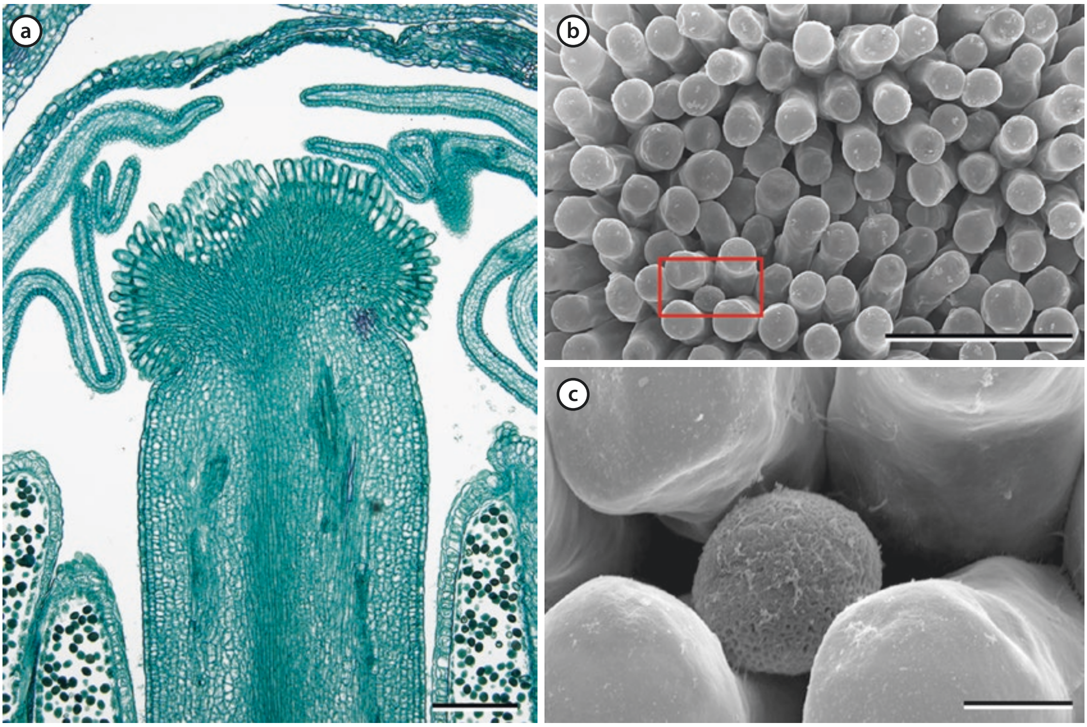


Fig. 18.4 **r** Schematic summary diagram representing the development of an anatropous ovule from the megasporocyte to the megagametophyte (embryo sac), which is characteristic of the majority of plants. Note how the orientation of the ovule changes with respect to the placenta during development. **a** Representation of an ovule shortly after initiation, showing a single megasporocyte. Note the lack of the inner and outer integuments. **b** An ovule after both integuments have started to develop. The megasporocyte has passed the first meiotic division. The axis of the nucellus is transiently at 90° to the axis of the funiculus. **c** A post-meiotic ovule. The functional megaspore at the chalazal end has expanded, and the nonfunctional megaspores have degenerated. The axis of the nucellus is now parallel to the funiculus due to unequal growth of the integuments. **d** The ovule after megagametogenesis within the megagametophyte. The mature embryo sac contains seven cells and eight nuclei. (Redrawn from Reiser and Fischer, 1993)

the thickened walls of transmitting cells which secrete wall-degrading enzymes. In hollow styles, the pollen tubes grow toward the ovary in contact with the glandular cells lining the stylar canal. This pollen transmitting tissue consists of one layer of glandular cells, which secrete various hydrophilous and lipid substances involved in nourishment and guidance of the pollen tubes as well as numerous enzymes released upon the growth of pollen tubes (Fig. 18.5d, e).



◘ **Fig. 18.5** **a**–**c** Sectional view of the stigma of *Brassica oleracea* showing a dense mat of hairs, which is the receptive surface for the pollen grains. **b** Surface view of a stigma from a flower of the lyre-leaved sand cress (*Arabidopsis lyrata*). The red box indicates a pollen grain trapped between the stigmatic hairs. **c** A close-up view of the pollen grain indicated in ◘ Fig. 18.5b. Scale bars = 500 µm in **a**, 100 µm in **b** and 10 µm in **c**. (**a**–**c** RR Wise)

18.6 Double Fertilization Results in a Triploid Endosperm and a Diploid Zygote

Double fertilization follows pollination and begins when the pollen tube, which has grown to and through the micropyle, discharges the two sperm cells into one of the synergids. Each will fertilize a cell, hence the term "double fertilization." One of the two male gametes (the haploid sperm cells) from the pollen tube fertilizes the haploid egg cell, and the other haploid nucleus fertilizes the diploid (or triploid, in the case of lily) central cell nucleus. The now diploid fertilized egg is called a **zygote** . It will give rise to the embryo and the suspensor (◘ Fig. 18.6a–c). A common feature of angiosperm embryos is that their apical basal axes are aligned according to the chalazal-micropyle axis, suggesting an orienting influence of the surrounding maternal tissues. The suspensor conveys nutrients to the growing embryo and pushes it into the lumen of the endosperm.

The typically triploid or tetraploid central cell resulting from double fertilization will become the endosperm, a nutritive tissue for the embryo. Two main types of endosperm development occur,

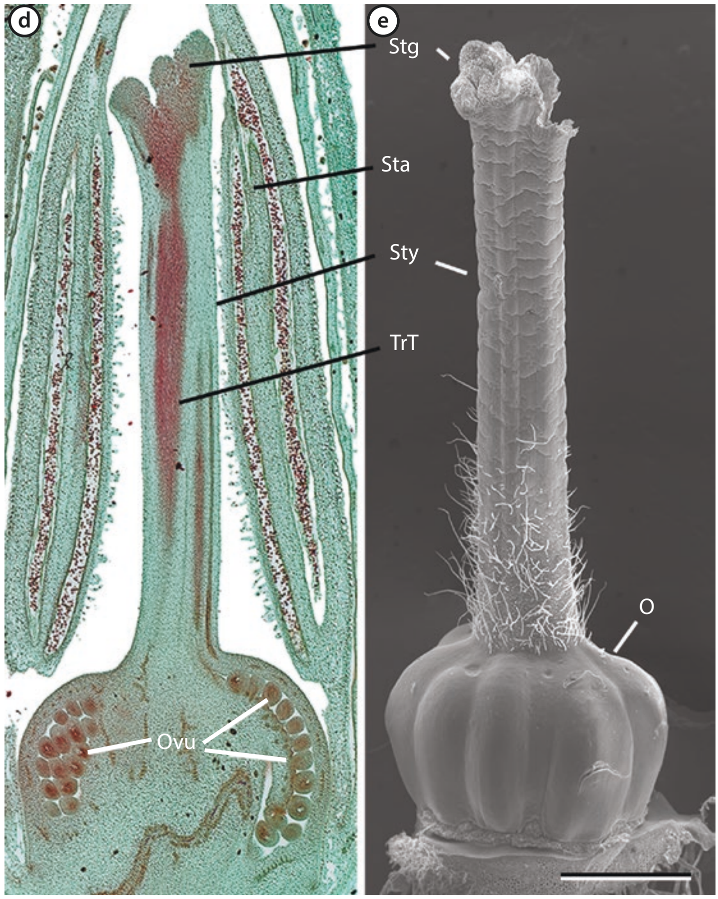


Fig. 18.5 **d** Bright-field light micrograph and **e** SEM of pistils from tomato (*Solanum lycopersicum*). *O* ovary, *Ovu* ovules, *Sta* stamen, *Stg* stigma, *Sty* style, *TrT* transmitting tissue. Scale bar in **e** = 500 µm and applies to both panels. (**d**, **e** RR Wise)

cellular and nuclear. In a **cellular endosperm**, the cell wall formation begins with the first mitosis and continues as long as endosperm is growing. In a **nuclear endosperm**, the nuclei undergo "free-nuclear division" meaning that mitoses are not accompanied by cytokinesis. In this case, cell wall formation begins only at an advanced stage of endosperm growth. Fertilization to form the endosperm is a significant evolutionary adaptation in angiosperms as plants efficiently provision for offspring only when the embryo is present.

Embryogenesis generally occurs in a series of steps from zygote to the mature embryo. These steps can be divided into three basic phases: (1) postfertilization-proembryo phase, (2) globular-cordate transition, and (3) organ expansion and maturation. Within the following section, we will focus on the embryogenesis of shepherd's purse (*Capsella bursa-pastoris*), one of the most intensely studied dicot plants for embryonic development.

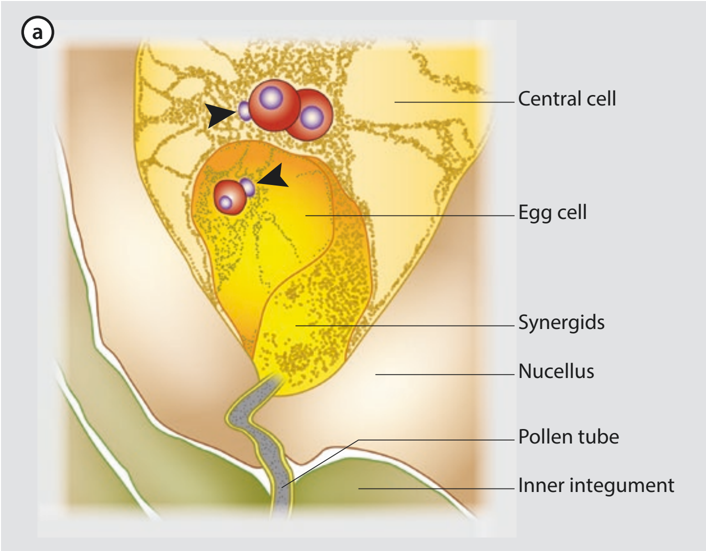


Fig. 18.6 **a** A typical illustration of the double fertilization process. The pollen tube enters through the micropyle and one of the synergids discharges its contents. Then the sperm nuclei (*arrows*) traverse the synergid and one fertilizes the egg cell to form the diploid zygote. The other sperm nucleus enters the central cell where it fuses with the two polar nuclei to form the triploid endosperm. (Redrawn from Reiser and Fischer, 1993)

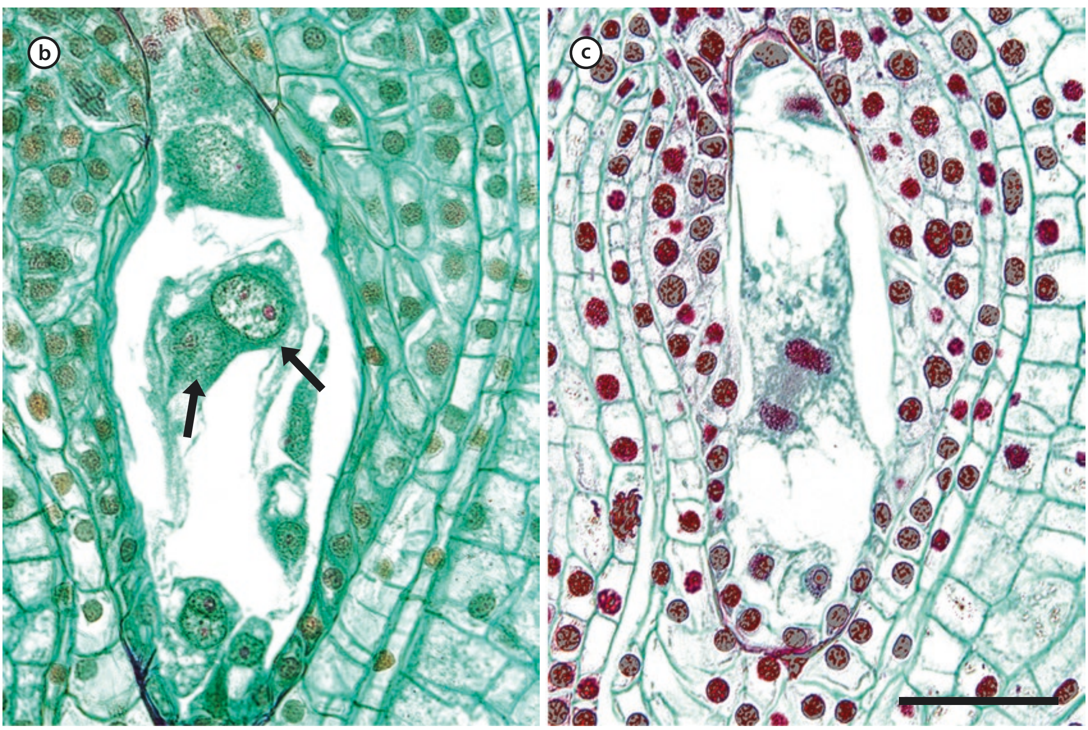
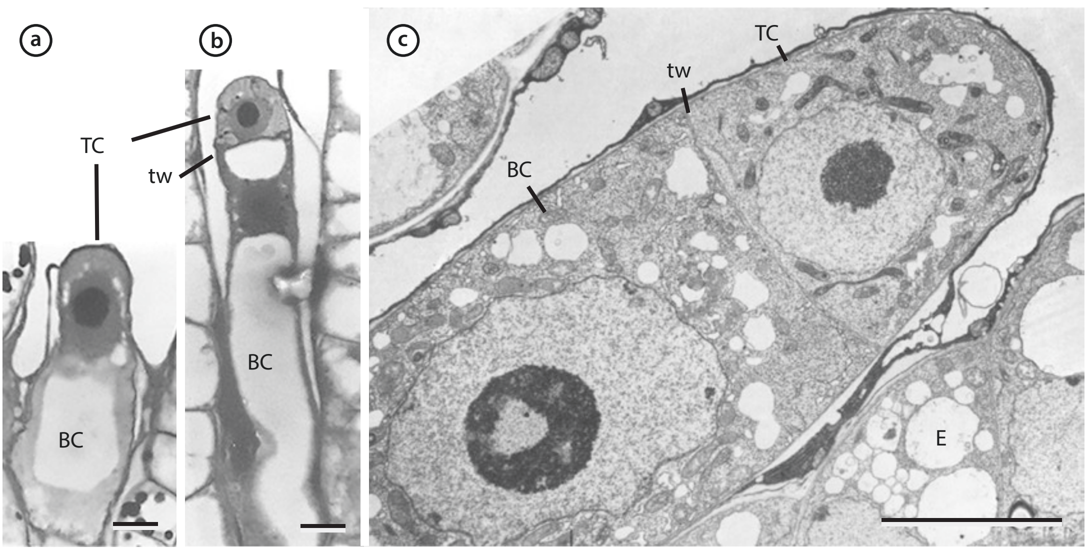


Fig. 18.6 **b** Double fertilization in Lily (*Lilium* sp.). The two polar nuclei are indicated with arrows. **c** The resulting tetraploid nucleus proceeds to divide to produce the endosperm. Scale bar in **c** = 50 µm and applies to both panels. (**b**, **c** RR Wise)

18.7 Postfertilization-to-Proembryo Phase Leads to the Formation of an Eight-Celled Embryo and Suspensor Whose Development Is Controlled by Circuit Elements

The postfertilization-proembryo phase of embryogenesis begins with the zygote and continues on to the eight-celled embryo. Embryogenesis starts with the unequal transverse division of the zygote that gives rise to a two-celled proembryo that consists of a large basal cell and a small terminal cell (◘ Fig. 18.7a). These cells differ in their ultrastructure as the terminal cell is rich in polymorphic electron-dense leucoplasts, and the basal cell is poorly vacuolated and contains electron-transparent ellipsoid plastids (◘ Fig. 18.7b, c). The proembryo protrudes into the highly vacuolated endosperm. In *Capsella*, the terminal cell undergoes longitudinal division to give rise to the embryo proper. The basal cell divides twice transversely, and the linear **suspensor** is initiated. Its cells also divide transversely. As a result, the embryo is pushed into the endosperm. During the eight-celled stage of the embryo or "octant," the suspensor completes cell divisions, and the nuclei, with their prominent and active nucleoli, occupy a large portion of the cells (◘ Fig. 18.7d–f). Thus, at the end of the first phase, we see the differentiation of the terminal and basal cells, as well as the formation of the embryo and suspensor.



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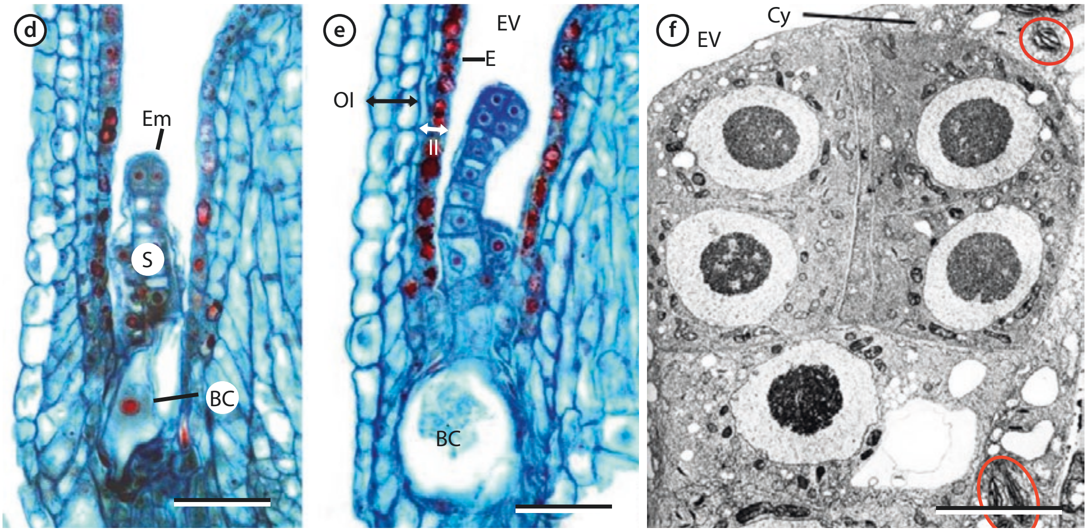
◘ **Fig. 18.7** **a**–**c** Early proembryo phase in shepherd's purse (*Capsella bursa*). **a** Longitudinal section through the polarized zygote within a large micropylar vacuole. **b** The two-celled proembryo. Look for the small densely cytoplasmic terminal cell (TC), the large vacuolated basal cell (BC) of the suspensor, and the transverse wall (tw) between them. **c** Transmission electron micrograph of a two-celled proembryo showing the terminal cell, the apical portion of the basal cell, and endosperm (E). Scale bars = 10 μm in **a** and **b** and 5 μm in **c**. (**a**–**c** R Schulz and WA Jensen 1968a)



◘ **Fig. 18.7** **d**–**f** Proembryo to octant transition in *Capsella*. **d** A two-celled embryo (Em), a five-celled suspensor (S), and a large basal cell (BC) during *Capsella* embryogenesis. **e** The eight-celled or octant stage of development of embryo. Only four cells can be seen in this view since the other four are in another section of the embryo. The suspensor has grown into a long filament of ten cells. Note outer (OI) and inner (II) integuments, precursors of seed coat, endothelium (E), and basal cell (BC). **f** The axile portion of an octant embryo seen with electron microscopy. Note how the embryo protrudes deeply in the endosperm vacuole and is separated from it by very thin layer of endosperm cytoplasm (Cy). The endosperm contains chloroplasts (red ellipses) and is green. Scale bars = 20 µm in **d** and **e** and 10 µm in **f**. (**d**–**f** R Schulz and WA Jensen 1968b)

18.8 Early Embryo-to-Heart Transition Leads to the Specification of the Basic Body Plan Within the Embryo

The globular-heart transition begins with the 16-celled embryo and continues to the cordate (heart-shaped) embryo. At the 16-celled embryo stage, the outer cells of the embryo are formed from ordered divisions, both periclinal and anticlinal. These cells constitute the beginning of the protoderm (a.k.a. embryoderm), the precursor of the epidermis (◘ Fig. 18.8a). At the globular stage of development, the embryo is surrounded by endosperm cytoplasm, the **protoderm** is clearly demarcated and, in the central region of the embryo, vertical divisions have delineated the procambium. The upper suspensor cell divides and produces a hypophysis, the uppermost cell protruding into the embryo. The **hypophysis** is the only cell of the suspensor that later becomes part of the embryo. Its derivatives take part in the formation of the radicle and root cap of the mature embryo (◘ Fig. 18.8b, c).

The cordate embryo stage is identified by a characteristic heart shape. During this stage, the formation of organs within the embryo begins with the cotyledons that appear as two protrusions in the

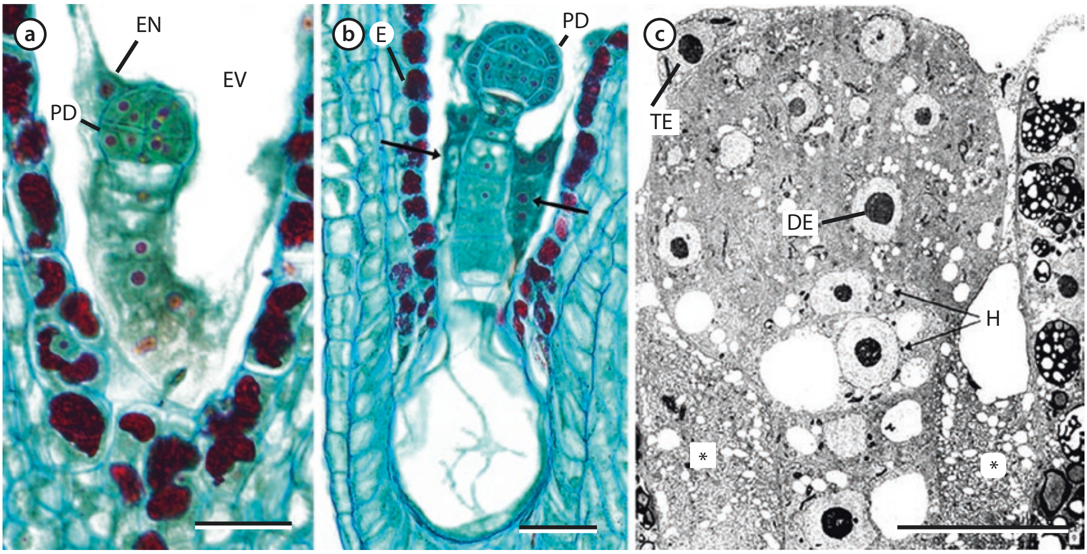
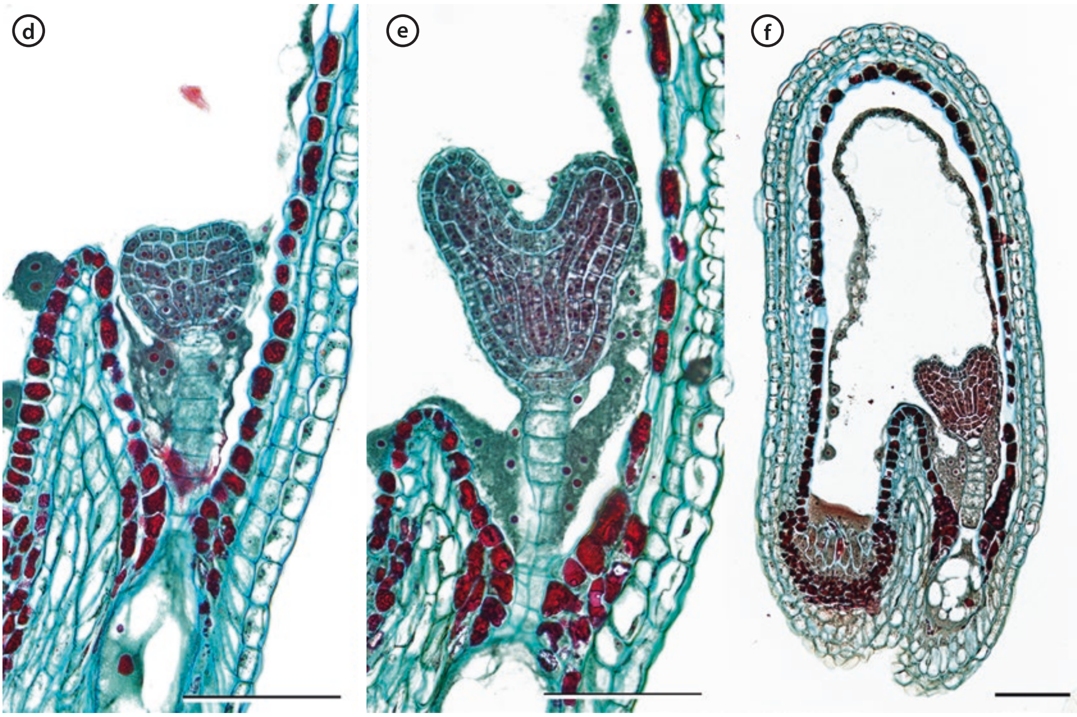


Fig. 18.8 **a**–**c** Early embryo-to-globular stage transition in *Capsella*. **a** At the 16-celled embryo stage, demarcation of the protoderm (PD) occurs. The endosperm vacuole (EV) and an endosperm-free nucleus (EN) are marked. **b**. *Capsella* has a characteristic nuclear type of endosperm development where the nuclei accumulate at two ends of the coenocytic multinucleate endosperm. In the micropylar end, they (together with the cytoplasm) form a "sheath" around the suspensor as shown here (*arrows*). Also visible are a portion of endosperm central vacuole (EV), endothelium of the inner integument (E), and several endosperm-free nuclei (at *arrows*). **c**. A transmission electron micrograph of the globular stage of the embryo. The cells of the protoderm, the future procambium, and ground meristem all show structural similarity. The two suspensor cells next to the embryo are derived from an unequal division of the hypophysis (H). The endosperm (*) closely envelopes the embryo. TE triploid endosperm nucleus; DE diploid embryo nucleus. Scale bars = 10 µm in **a** and **b** and 5 µm in **c**. (**a**–**c** R Schulz and WA Jensen 1968b)

apical part of the embryo. These protrusions give an embryo the cordate shape and are the result of preferential cell divisions in two areas of the embryo. Since cotyledons do not originate from the shoot apical meristem as do leaves, some anatomists do not consider them to be modified leaves. At this stage, both the endosperm and the embryo appear green in fresh specimens due to the differentiation of chloroplasts. In this stage, the basic body plan is established (Fig. 18.8d–f).

18.9 The Last Phase of Embryogenesis Involves Organ Expansion and Maturation

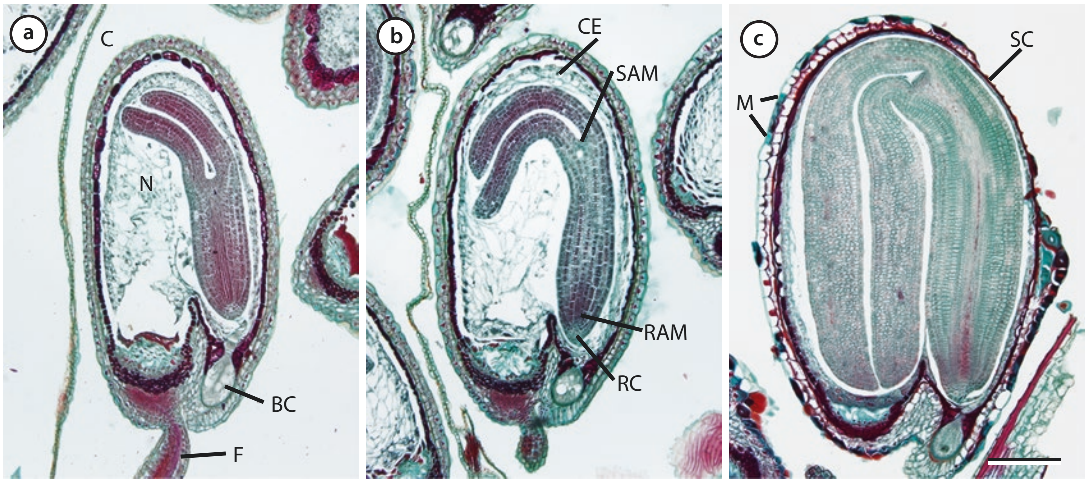
The last phase of embryogenesis involves three stages: the torpedo, walking-stick, and mature embryo. During this last phase, the embryo is named for what it resembles. Thus, the "torpedo embryo" resembles a torpedo. This stage marks the beginning of hypocotyl elongation where the hypocotyl becomes discernible and the cotyledons continue to elongate. The procambium extends from the hypocotyl into young cotyledons.



◻ **Fig. 18.8** **d**–**f** Organ specification during the globular-to-cordate shape transition in *Capsella*. **d** The cordate (heart-shaped) stage of the embryo. Identify two integuments, endothelium (inner layer of the inner integument), endosperm cytoplasm with nuclei, cotyledonary buttresses, procambium, hypophysis, and suspensor and its basal cell. **e**. A higher magnification of the heart-shaped (cordate) embryo which clearly shows its parts. **f** A low-magnification view of a longitudinal section of an ovule showing further growth of cotyledonary primordia. The bilaterally curved type of ovules in which the ovular cavity has a horse-shoe shape is characteristic of *Capsella*. Scale bars = 50 µm in all three panels. (**d**–**f** RR Wise)

More primitive plants tend to have abundant endosperm and small embryos; however, more evolutionary developed seed plants ten to have more mature and larger embryos with less endosperm. Early on, in species with abundant endosperm, the nuclei divide without cell wall formation, but later the walls are formed around the nuclei and contained protoplasmic materials. Within the developing endosperm, cell walls are formed around each nucleus so that the endosperm becomes transformed from nuclear into cellular (◻ Fig. 18.9a).

As the embryo and cotyledons continue to develop, the cotyledons bend, taking on the appearance of a walking-stick. The embryo fills a large portion of the endosperm cavity and displays cotyledon curvature, which is conditioned by the growth of the embryo in the curved ovule and embryo sac. The shoot apical meristem is recognizable between the cotyledons, and root (radicle) apical meristem is clearly demarcated from the root cap. The cells of the integuments (developing seed coat) are stretched considerably parallel with elongation of the ovule (developing seed; ◻ Fig. 18.9b).



◘ **Fig. 18.9** **a**–**c** Embryo maturation. **a** The "torpedo embryo" stage when the hypocotyl becomes discernible and cotyledons elongate. The embryo is approximately 350 µm long. **b** This walking-stick embryo (~500 µm long) is at an early-bending cotyledon stage. **c** Mature embryo within the fully formed seed. The embryo now fully fills the space and is about 900 µm long. Integuments have transformed into the seed coat. The outer layer of cells has filled with mucilage (stained blue). BC = basal cell of suspensor, C = cotyledons, CE = cellular endosperm, F = funiculus, M = mucilage, N = remnants of nucellus, RAM = root apical meristem, RC = root cap, SAM = shoot apical meristem, SC = seed coat. Scale bar in **c** = 100 µm and applies to all panels. (**a**–**c** RR Wise)

When the embryo matures, it fills the space within the seed coat. Still, the basal cell and some other cells of the suspensor are still discernible, and the funiculus can be clearly seen. In living tissue, the embryo has lost its green color. The cells of the inner integument, including the endothelium, are broken down, and the seed coat (**testa**) is formed entirely by only the dead derivatives of the two-layered outer integument. The outer layer now consists of cells filled with mucilage, and the inner layer is sclerified (◘ Fig. 18.9c). A summary of the process of eudicot embryogenesis can be seen in ◘ Fig. 18.9d.

Box 18.2 Plant Embryogenesis from Zygote to Seed

Plant embryos must establish a postembryonic structural differentiation in the shoot and root meristems of sporophytic plants as well as overcoming often severe environmental conditions during germination. The events begin within the fertilized egg cell and the early embryo. Thus, specific molecular markers are necessary in order to trace the developmental events that initiate in the early embryo but which continue into the regulatory networks with plant growth and differentiation. Auxins, such as indoleacetic acid, are involved in many plant development and transition activities and can block the transition from the globular to heart stage of the embryo and indicate that auxin asymmetries are established within the embryo-proper region of the globular stage but continue to contribute to the bilateral symmetry at the heart stage. Studies in *Arabidopsis* have identified genes that provide insight into plant development and embryogenesis.
Reference: Goldberg RB et al. (1994)

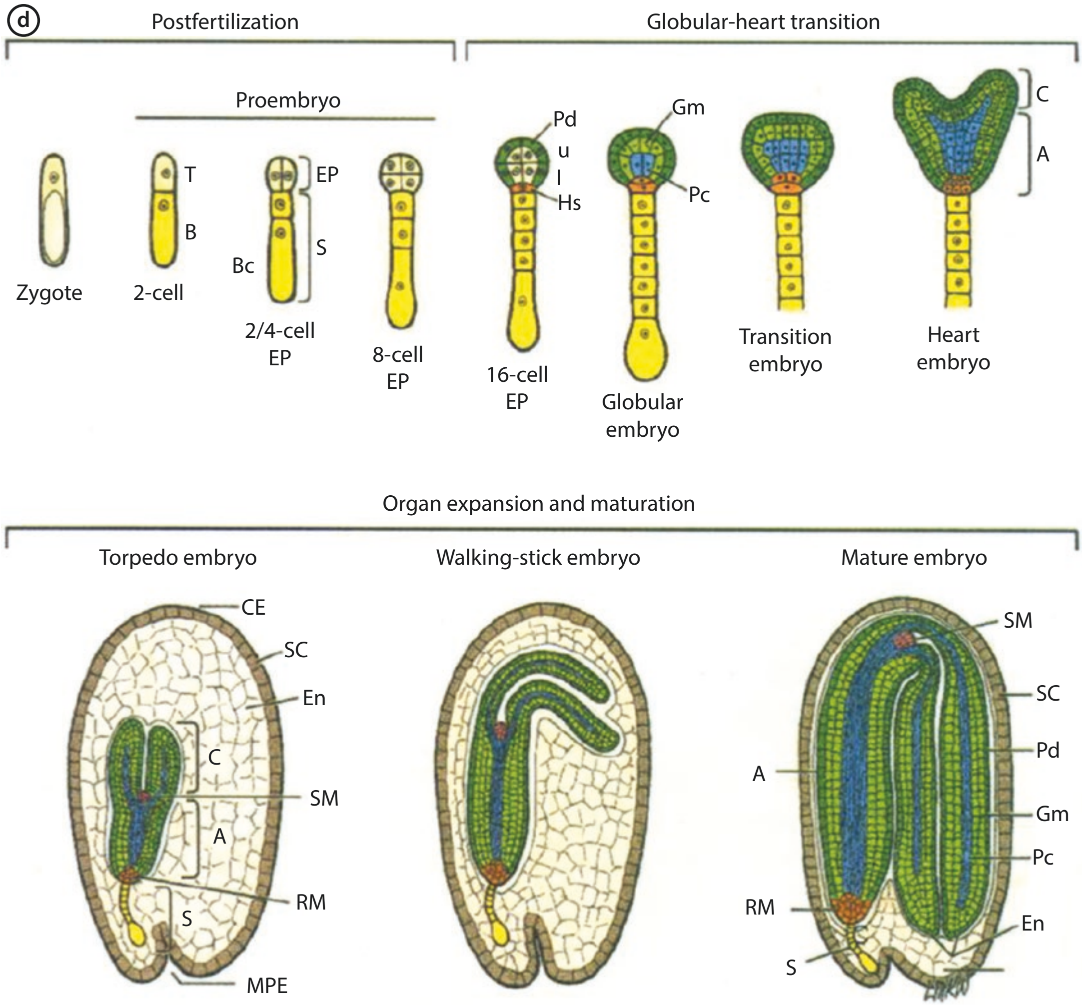


Fig. 18.9 **d** Summary of embryogenesis from zygote to mature embryo within an angiosperm such as *Capsella* or *Arabidopsis*. T terminal cell, B basal cell, EP embryo proper, S suspensor, Bc suspensor basal cell, Pd protoderm, u upper tier, Hs hypophysis, Pc procambium, Gm ground meristem, C cotyledon, A axis, MPE micropylar end, CE chalazal end, SC seed coat, En endosperm, SM shoot meristem, RM root meristem. (From Goldberg et al. 1994)

18.10 The General Pattern of Embryogenesis Differs Between Eudicots and Monocots

In monocots, early stages of embryogenesis are similar to those in eudicots, but further developmental stages are distinctly different. In monocots, the model organism for the study of embryogenesis is maize (*Zea mays*). The general pattern of monocot embryogenesis includes the zygote, proembryo, transition, coleoptile, stage 1, and succeeding mature stages. The monocot shoot apex is found, not between the bases of the two cotyledons, but occupies a lateral position to the single cotyledon as its niche. Monocots also differ from eudicots in only having one cotyledon rather than two.

Embryogenesis in maize differs from eudicots in several ways. First, the early cellular divisions in monocots are not equal. Second,

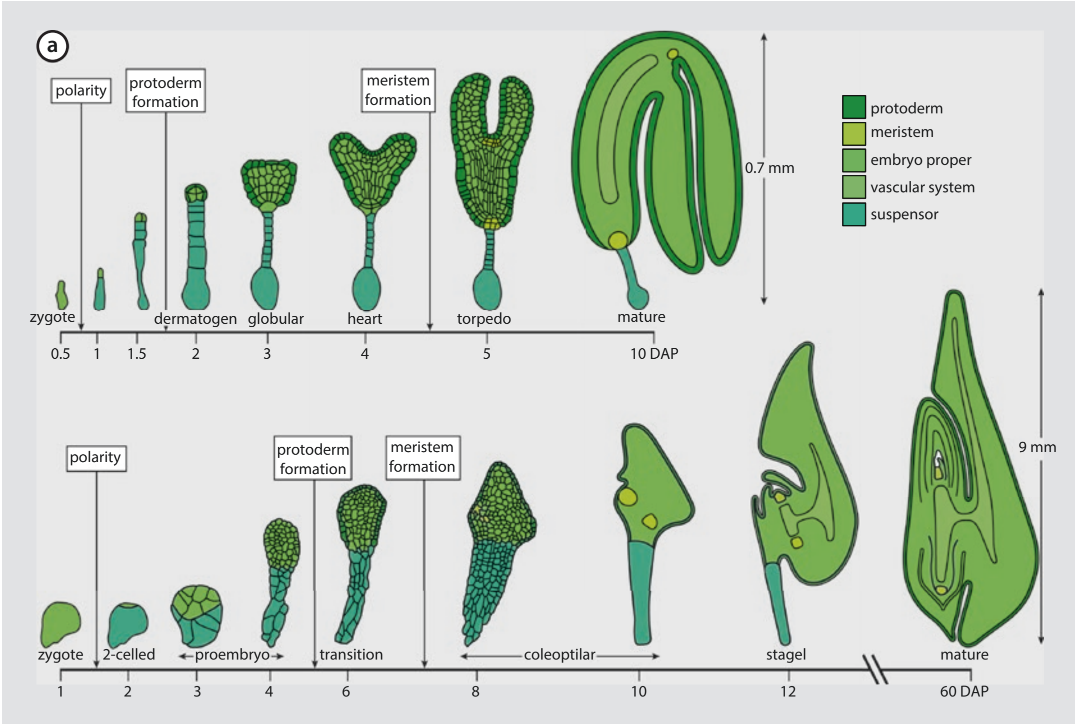


Fig. 18.10 **a** Comparison of dicot (*Arabidopsis thaliana*) and monocot (*Zea mays*) embryo development. Developmental time scale is days after pollination and will be influenced by genetics and the environment. (From Vernoud et al. 2005, open source)

the leaf primordia develop earlier in monocots in comparison to eudicots, as these structures have been noted to develop in *Arabidopsis* after entering dormancy (Vernoud et al. 2005, pg. 471). Because monocots have only one cotyledon, the axis between that apical and basal portions of the developing embryo is not as well defined in monocots as in eudicots. Third, the scutellum within the embryo of maize is functionally analogous to cotyledons of eudicots.

Differences within the environment of the developing seed exist between monocots and eudicots (Fig. 18.10a). The endosperm in *Arabidopsis* (a eudicot) is gone at seed maturity, in contrast to *Zea* (a monocot) where endosperm makes up a large part of the kernel. Both species have nuclear endosperm which is formed due to repeated nuclear divisions that are not immediately followed by cytokinesis (Fig. 18.10b).

18

18.11 Alternation of Generations Is Unique to Plants

Upon the formation of a zygote, a new generation begins that is diploid and considered to be the sporophyte since it produces haploid spores through the process of meiosis (megaspores and microspores). In all higher plants, the obvious organism seen is the sporophyte. The stages immediately following meiosis and leading up to the formation of the zygote represent the haploid gameto-

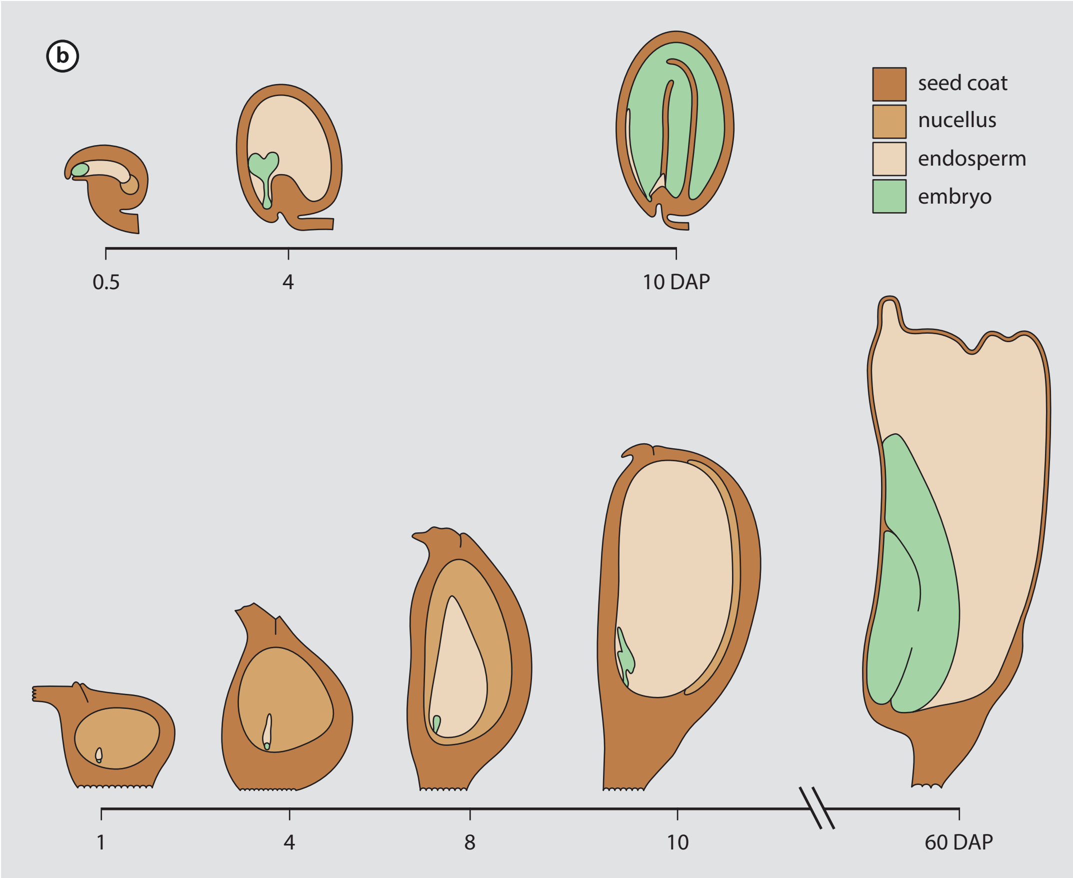


Fig. 18.10 **b** Comparison of dicot (*Arabidopsis thaliana*) and monocot (*Zea mays*) seed development. Developmental time scale is days after pollination and will be influenced by genetics and the environment. Compare relative sizes of embryos as well as endosperm during development. (From Vernoud et al. 2005, open source)

phyte stage that produces gametes by mitosis and is typically microscopic in higher plants. This shift from one phase to another in the lifetime of plants is termed the alternation of generations and is unique to plants (refer to ► Sect. 1.5).

18.12 Chapter Review

Concept Review

18.1 *The innermost whorl of the flower is typically composed of female floral parts*. The pistil (or carpel) has a terminal stigma, an elongated style, and a basal ovary, which in turn houses an egg cell, central cells, and related cells within an enclosed ovule.

18.2 *Ovaries are classified based upon their position within a flower and may contain nectaries*. Three types of ovaries are recognized according to their positions with respect to the lateral organs of the flower, superior, inferior, and half inferior. The ovaries of many monocots contain septal nectaries which represent the glandular epidermis. Gymnosperms, as opposed to angiosperms, are generally regarded as bearing "naked" seeds; the ovules are generally borne on stalks or flattened structures that cluster together to form cones.

18.3 *Ovules can be arranged within an ovary in a variety of ways*. The partitions dividing the ovaries into locules are formed by the lateral fusion of carpels along their margins, and the placentae are formed in the angles of locules. They can be represented by basal, free-central, and marginal placentation.

18.4 *Megasporogenesis begins with the differentiation of the megaspore mother cell and ends with the formation of the megagametophyte (embryo sac)*. Female gametophyte development in *Lilium* (a commonly-used example) starts with microsporogenesis. A single megasporocyte undergoes meiosis to produce four haploid megaspore nuclei. Megagametogenesis follows and involves fusion, mitosis, and cytokinesis to produce a seven-cell egg sac with a tetraploid endosperm. The egg sac is the mature female gametophyte.

18.5 *Pollination is followed by germination of the pollen grain and pollen tube growth*. Once transfer of pollen to a receptive pistil occurs, growth of a pollen tube occurs and delivers two haploid sperm to the egg cell apparatus.

18.6 *Double fertilization results in a triploid endosperm and a diploid zygote*. One sperm cell fertilizes the egg cell to generate a diploid zygote, and the other sperm cell fertilizes the two-central cell polar nuclei to generate the endosperm.

18.7 *Postfertilization-to-embryo phase leads to the formation of an eight-celled embryo and suspensor*. The eight-celled embryo is pushed into the endosperm by growth of the linear suspensor.

18.8 *Early embryo-to-heart transition leads to the specification of the basic body plan within the embryo*. At the 16-celled embryo stage, the outer cells of the embryo are formed from ordered divisions that produce the protoderm, and at a globular stage, the procambium is delineated. An upper suspensor cell, the hypophysis, forms the root cap and radicle.

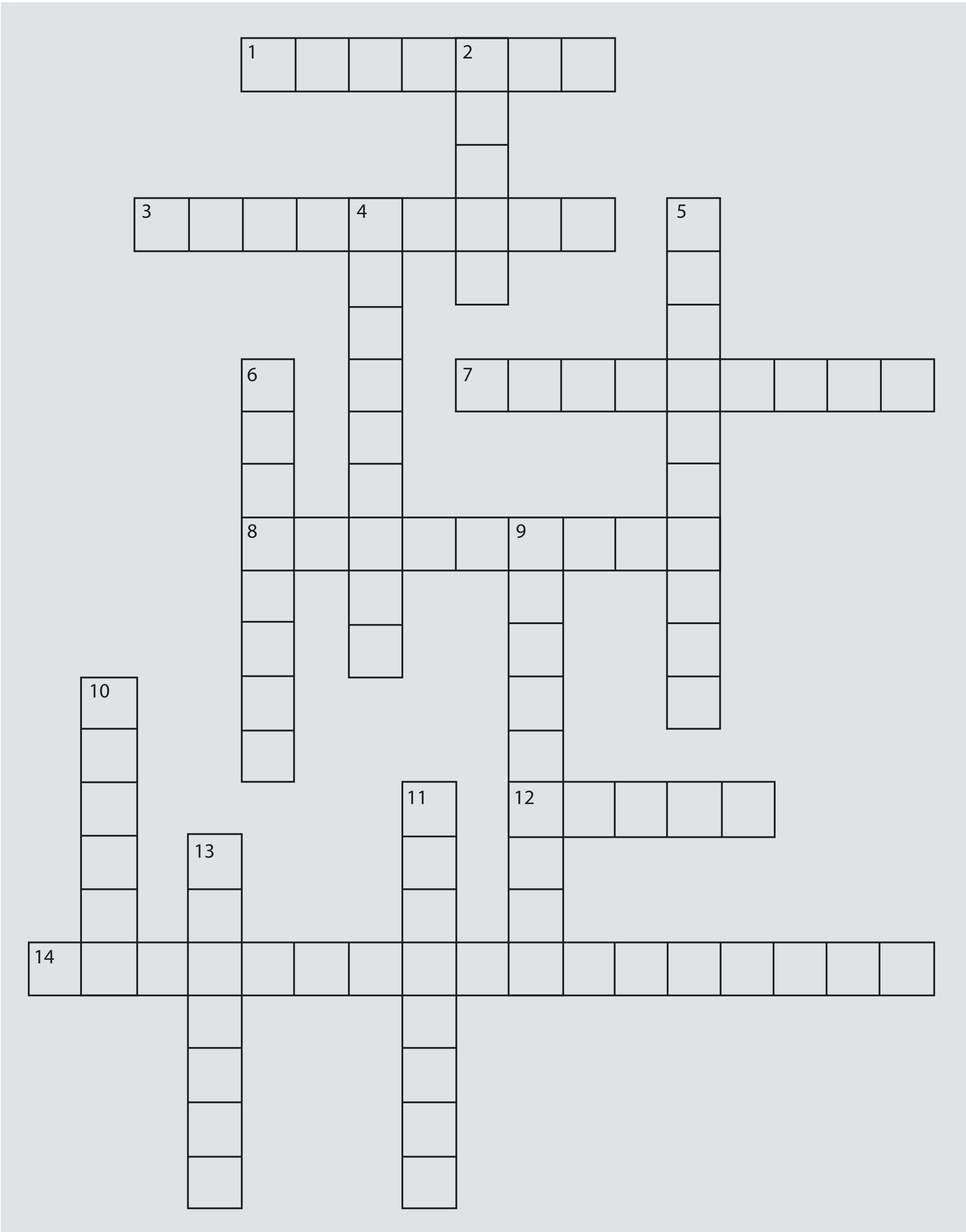
18.9 *The last phase of embryogenesis involves organ expansion and maturation*. More evolutionary developed seed plants tend to have more mature and larger embryos with less endosperm.

18.10 *The general pattern of embryogenesis differs between eudicots and monocots*. Cellular divisions in monocots are not equal, leaf primordia develop sooner in monocots, and the one cotyledon of monocots is modified as a scutellum.

18.11 *Alternation of generations is unique to plants*. Plants have a haploid phase of their life cycle, the gametophyte, and a diploid phase, the sporophyte.

Concept Connections

1. Complete the crossword puzzle with the most appropriate term:



Across

1. Heart-shaped developmental stage of the embryo
3. Stalk connecting an ovule to ovary wall
7. Uppermost cell protruding into the embryo
8. Triploid tissue that provides nutrition for the embryo
12. Placentation type where ovules are attached at base and point upright
14. Process of forming a female gamete via mitosis

Down

2. Placentation type in angiosperms with multilocular ovaries
4. Seed leaves within an embryo
5. Layers of cells around the nucleus
6. Type of ovary that has sepals, petals, and stamens attached above it
9. Consists of a large basal cell and a small terminal cell
10. Fertilization that is characteristic of angiosperms
11. Type of ovary with petals, sepals and stamens attached below it
13. Region where integuments merge with the nucellus

Concept Assessment

2. Which ovary type is characterized by having the hypanthium fusing with a portion of the ovary?
   a. inferior ovary.
   b. superior ovary.
   c. half-inferior ovary.
   d. half-superior ovary.
   e. ovary type isn't important in floral anatomy and morphology.

3. True/false: pollination is essentially the same as fertilization, and thus, these terms can be used interchangeable.
   a. true.
   b. false.

4. The antipodals play no role in egg sac development.
   a. true.
   b. false.

5. Parietal placentation within the ovary is identified when
   a. ovules are located within the center of the ovary.
   b. ovules are found within the center of the ovary, at the junction where many locules have fused.
   c. ovules are located along the edge of ovaries with several locules.
   d. ovaries are located within the center of one-locular ovaries.
   e. ovaries are located along the periphery of one-locular ovaries.

6. Megasporogenesis ends with the formation of
   a. the ovule.
   b. the nucellus.

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c. the embryo sac.
d. the micropyle.
e. the megaspore mother cell.

7. The formation of the embryo sac marks the end of
a. megagametogenesis.
b. microsporogenesis.
c. megasporogenesis.
d. microgametogenesis.
e. embryogenesis.

8. What structure is thought to be involved with directing the growth of the pollen tube toward the embryo sac?
a. chalaza.
b. micropyle.
c. filiform apparatus.
d. hypocotyl.
e. synergids.

9. The formation of the endosperm in angiosperms is important because it
a. allows the plant to supply offspring with nutrients.
b. is essential for attracting pollinators to disperse pollen.
c. provides nectar rewards to potential pollinators.
d. provides compounds to the seed important for defending against predation.
e. allows for water and other nutrients to move from within the ovary to the embryo.

10. Body plan specification in *Capsella* happens during
a. fertilization.
b. the proembryo to 8-cell embryo transition.
c. the early embryo to heart transition.
d. the torpedo to walking stick transition.
e. germination.

11. Which suspensor cell will become a part of the embryo during embryogenesis?
a. hypophysis.
b. terminal cell.
c. inner integument.
d. nucellus.
e. nuclear endosperm.

Concept Applications

12. What is the evolutionary significance of double fertilization?

13. What is the evolutionary significance of pollination?

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Fruits, Seeds, and Seedlings

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R. Crang et al., *Plant Anatomy*, https://doi.org/10.1007/978-3-319-77315-5_19

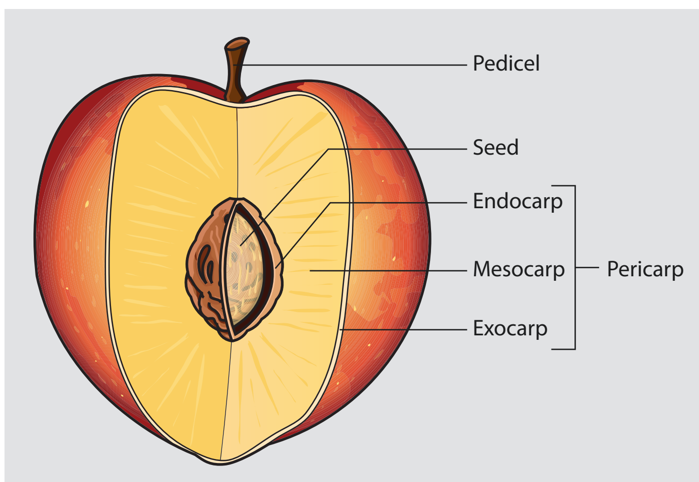
Introduction

The responsibility of the flower is to ensure fertilization; the responsibility of the fruit is seed dispersal. This chapter focuses on the anatomy and morphology of fruits, seeds, and seedlings. Like flowers, **fruits** occur only in angiosperms, not in gymnosperms; "angio" means vessel and "sperm" means seed. Therefore, angiosperms produce seeds inside a vessel (fruit). Gymnosperms (literally "naked seed") do not produce a fruit, although many such as Japanese yew (*Taxus cuspidata*) do have fleshy cones that may resemble a berry. As the angiosperm embryo and endosperm develop following double fertilization, the ovary wall increases in size and thickness and is gradually transformed into a fruit, in some cases along with the ripening of the receptacle. If the receptacle becomes a part of the mature fruit, such a fruit can be called an **accessory fruit**. The ovule enlarges into a seed, and tissues of the inner (if present) and outer integuments of the ovule become the seed coat.

19.1 Fruits Are Highly Modified Ovaries

The ovary wall typically develops into an expanded structure termed the **pericarp**. Three zones are often seen in the pericarp, an outer **exocarp**, a central **mesocarp**, and an inner **endocarp** (◘ Fig. 19.1). However, in many plants, the endocarp, the mesocarp, or both may be missing or fused with each other. In some fruit types like berries and in many dry fruits, these zones are difficult to distinguish in the mature fruit and can only be identified by carefully studying fruit development.

Following double fertilization (refer to ► Chap. 18), the ovary wall increases in size and gradually becomes a fruit. The ovule enlarges into a seed (refer to ► Chap. 18), and the tissues of the inner (if present) and outer integuments become the seed coat. The stalk of



◘ **Fig. 19.1** The three-dimensional structure of a drupe in peach (*Prunus persica*). The stony (i.e., heavily sclerified) endocarp encloses a single seed. The extensive mesocarp is fleshy and is covered by a thin skin (exocarp) comprised of epidermis and collenchyma. (Redrawn from Crang and Vassilyev 2003) the flower (termed a **pedicel**) remains present through the developmental process. In fruits derived from an inferior ovary, a hypanthium (a cuplike expansion of the receptacle bearing basal portions of sepals, petals, and stamens) participates in the pericarp formation.

With the exception of **parthenocarpy** (the development of fruit without seeds), fruits are developed only after double fertilization. As the embryo develops, parenchymatous extraembryonic tissues of a flower undergo complex taxon-specific modifications designed for embryo protection and seed dispersal. The other floral parts, i.e., style, perianth, and androecium, usually dry up and fall off. At the same time, both the cells of the pericarp and those of the seed coat divide and grow. The cells often contain chloroplasts capable of photosynthesis, which can provide a significant source of assimilates for the growing heterotrophic embryo.

19.2 Fruit Classification Is Based on Characters, Not Necessarily Species Relatedness

Fruits vary considerably by taxon, by means of specific dispersal and by germination strategies. Unlike taxonomic classification which is based on phylogenetic relationships, the classification of fruits is an artificial system that does not strictly recognize species relatedness. Indeed, some fruit types are restricted to a particular family or group of related plants; other fruit types are found across multiple, diverse taxa. Fruit taxonomy is based on morphological features such as the consistency of the pericarp—dry and hard or soft and fleshy (◘ Fig. 19.2a, b). Fruits may also be classified on the basis of whether they dehisce (i.e., release their seeds) or not when ripe and whether they contain a single carpel or multiple carpels. Overall, the type of fruit is important in understanding how seeds are dispersed. Not every fruit type can be discussed here, but one of several available fruit classification schemes is shown in ◘ Table 19.1, along with detail regarding the fate of the three pericarp layers (exocarp, mesocarp, and endocarp) and some information on the uses to which the fruit may be put.

◘ **Fig. 19.2** **a** Dry fruit of burdock (*Arctium* sp.) and **b** fleshy fruit of prickly pear cactus (*Opuntia* sp.). Both fruits contain the seeds of the plant. Scale bars = 1 cm in **a** and 3 cm in **b**. (**a** diablos, CC0 Creative Commons; **b** Bluesnap CC0 Creative Commons)

Table 19.1 Fruit type based on fruit characteristics and carpel number

Fruit characteristics		Number of carpels	Fruit type	Pericarp (fruit wall) layers			Examples
				Exocarp	Mesocarp	Endocarp	
Dry fruits	Indehiscent	Single carpel	Achene	All three fused together but not fused to seed			*Sunflower*—discard entire pericarp, eat seed
							Strawberry—eat receptacle (floral base) of the aggregate-accessory fruit and the fruits (achenes)
			Caryopsis	All three fused together, along with the seed coat and seed			*Wheat*—discard entire pericarp and eat seed—flour is endosperm of seed, wheat germ is embryo, bran is seed coat, whole wheat is entire seed
							Corn—yellow skin is entire pericarp; eat it and seed inside
			Samara	Papery, wing-shaped		Fused to exocarp	*Maple*, *ash*, *elm*—not eaten (maple syrup is concentrated xylem sap)
		Multiple carpels	Nut	All three thickened, highly lignified, and fused to form "shell"			*Walnut*—discard entire pericarp (nut shell); eat seed
	Dehiscent	Single carpel	Follicle	Exocarp splits open on one side only			*Milkweed*—not eaten
			Legume	Exocarp splits on both sides			*Beans*, *peas*, *peanuts*—eat seed (as in peas) or entire fruit and seed (as in pea pods, green beans)
		Multiple carpels	Capsule	Exocarp opens via holes, or a lid pops off			*Lily*, *poppy*—not eaten (heroin is extracted from the sap of the immature poppy seed capsule)

Fleshy fruits	Single carpel	Drupe	Papery	Fleshy or stringy	Hard and thick	*Peach*, *nectarine*, *cherry*, *plum*—eat exocarp and mesocarp; discard endocarp ("stone") and seed inside
						Almond—discard exo- and mesocarp, crack endocarp, and eat seed
						Coconut—endocarp is papery outer, mesocarp is thick stringy husk, and endocarp is "shell"; eat the endosperm (either liquid or solid)
	Multiple carpels	Berry	Papery	Fleshy	Fleshy	*Grape*, *eggplant*, *kiwifruit*, *tomato*—eat exo-, meso-, and endocarp
						Banana—discard exocarp (peel); eat meso- (very thick) and endocarp
						Pineapple—individual berries fused into a multiple fruit
						Blackberry, *raspberry*—individual berries fused into aggregate fruit
		Pepo	Papery	Fleshy	Fleshy or stringy	*Pumpkin*, *squash*, *cucumber*—eat mesocarp; endocarp is the stringy mass that holds the seeds
		Hesper-idium	Leathery exocarp (flavedo) fused to spongy mesocarp (albedo)		Papery	*Citrus*—each section is surrounded by the endocarp. Eat the juice-filled vesicles that fill inside of endocarp
		Pome	Papery	Fleshy	Hard or papery	*Apple*, *pear*—eat hypanthium (accessory fruit) which is derived from fusion of sepals and petals. Discard all of the fruit (core)

19.3 Dry Fruits Are Often Hard, Containing Fused Pericarp Layers and Dead Cells

At maturity, the pericarp of dry fruits consists mostly of dead, sclerified, and desiccated cells. In regions of the growing pericarp, some cells die earlier than others, and, as a result, they become crushed. Upon final maturation, one or more layers of cells undergo sclerification, giving the fruit a characteristic hardness. Dry fruits include two main groups: **indehiscent** and **dehiscent**. Dehisce (from the Latin, meaning to "split open" or "gape") means the fruit splits open and releases the seeds upon maturation of the fruit. A **schizocarp** is a dry fruit with multiple carpels that separates into individual one- or two-seeded carpels (each called a **mericarp**) upon maturity. The resulting mericarps may be indehiscent (as in carrot and mallow) or dehiscent (*Geranium* sp.).

19.3.1 Indehiscent Dry Fruits

Indehiscent fruits do not release their seeds upon maturity and are typically single-seeded. The pericarp of indehiscent fruits often resembles the seed coat in structure, and the fruits themselves are commonly called "seeds" even though this terminology is botanically incorrect. Indehiscent fruits include achenes, caryopsis, samaras, and nuts.

An **achene** is a fruit derived from superior or inferior ovaries and composed of one or more carpels. The pericarp has a leathery consistence and may be easily separated from the seed coat (◘ Fig. 19.3a, b). Examples of plants with achenes include buckwheat (Polygonaceae) and sunflowers (Asteraceae).

A **caryopsis** is similar to an achene but is derived from a superior ovary composed of a carpel in which the pericarp and the

◘ **Fig. 19.3** **a** Photograph of achenes from sunflower (*Helianthus annuus*). When mature, the entire ovary (fruit) is dried out and has a seedlike appearance. It is actually a fruit with the seed inside. **b** Sunflower seeds are contained within the achene fruit. Scale bars = 1 cm in **a** and 0.5 cm in **b**. (**a** Hans, CO0 Creative Commons; **b** F_A, CO0 Creative Commons)

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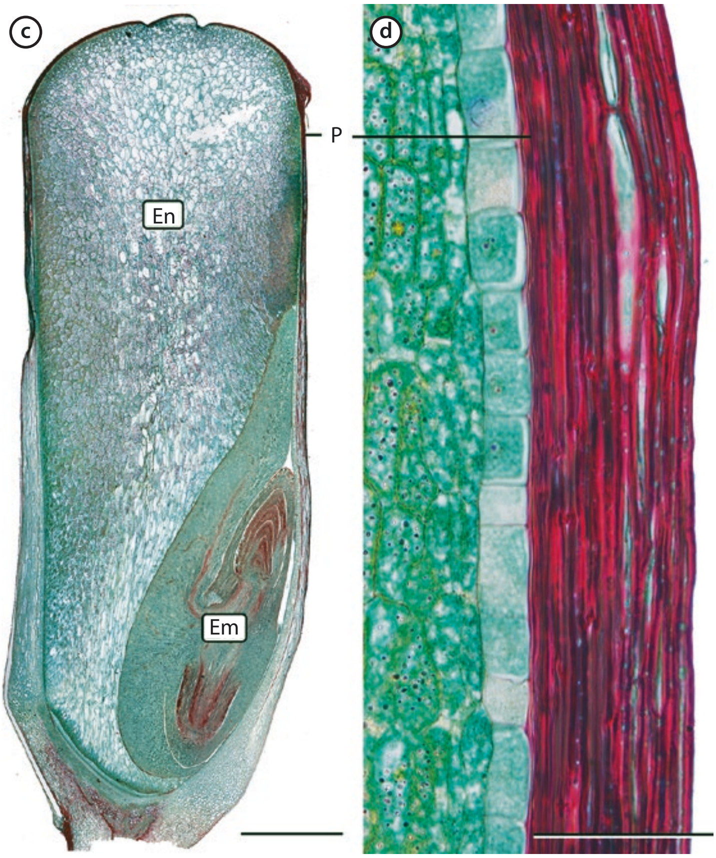


◘ **Fig. 19.3** **c** A longitudinal section of a mature maize (*Zea mays*) seed at low and **d** high magnification. The pericarp (P) is a fusion of the true pericarp tissues (exocarp, mesocarp, and endocarp) with the seed coat. The endosperm (En) and embryo (Em) are the two main parts of the seed. Scale bars = 2 mm in **c** and 50 µm in **d**. (**c**, **d** RR Wise)

remains of the integuments are completely fused (◘ Fig. 19.3c, d). The caryopsis of grasses is in reality not a seed as it is commonly designated but a special type of a single-seeded fruit because its covering is a pericarp rather than seed coat. Examples of plants with a caryopsis-type fruit are grasses such as corn, wheat, barley, rye, and rice (Poaceae). The maize fruit is frequently referred to as a "hull" which gets lodged in the teeth of people eating popcorn.

A **samara** is similar to an achene in its basic anatomy but has a winglike outgrowth(s) of the pericarp that assists in wind-borne seed dispersal (◘ Fig. 19.3e, f). Examples of samaras can be found in maples and box elders (Sapindaceae), tree of heaven (Simaroubaceae), and the bush willows (Combretaceae) (◘ Fig. 19.3e, f).

A **nut** is similar to an achene, but parts or all of the pericarp is hard and stony, commonly called the "shell." In the walnuts (◘ Fig. 19.3g, h) and hickories (Juglandaceae), the endocarp and mesocarp are shed, and the heavily sclerified endocarp is the shell. Oaks (Fagaceae) produce nuts in which all three layers of the pericarp are fused and sclerified to form the shell.

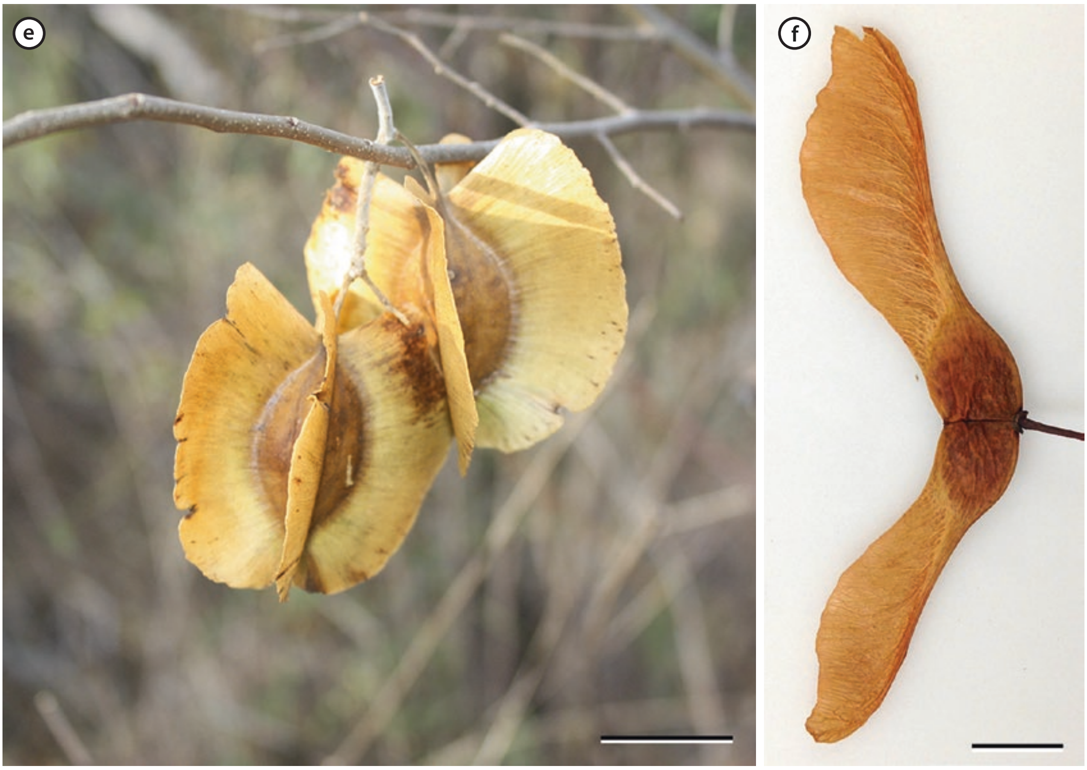


Fig. 19.3 **e**, **f** Samara fruit of **e** Zeyher's bush willow (*Combretum zeyheri*) (Marco Schmidt, CC-BY SA 3.0) and **f** silver maple (*Acer platanoides*) showing the outgrowths of the pericarp called "helicopters" that are important for seed dispersal. Scale bars = 5 cm in **e** and 1 cm in **f**. (**e** Marco Schmidt, CC-BY SA 3.0, **f** RR Wise)

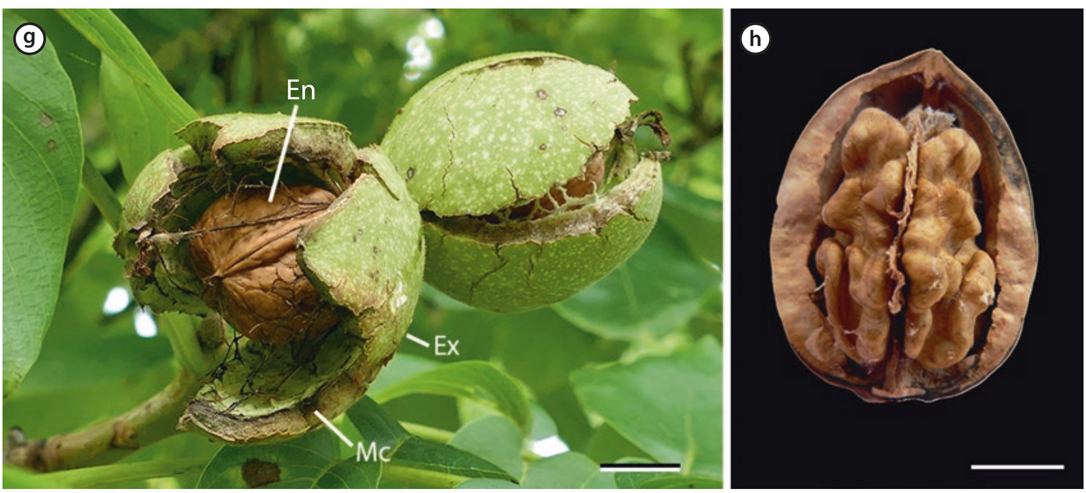


Fig. 19.3 **g**, **h** Fruit of the eastern black walnut (*Juglans nigra*). **g** The exocarp and mesocarp are shed after development of the nut. **h** The endocarp is heavily sclerified and hard. Scale bars = 1 cm in both panels. (**g** HelgaKA, CO0 Creative Commons; **h** public domain)

19.3.2 Dehiscent Dry Fruits

Dehiscent fruits are dry at maturity and usually contain several—to numerous—seeds. **Dehiscence** results in the release of seeds from the fruit and may occur in various ways from falling below mater-

Fig. 19.3 **i** Milkweed (*Asclepias syriaca*) is named for its milky sap and also contains podlike follicles at the terminal part of the shoot. The seeds within the fruit are densely packed and bearded with plumes for wind dissemination. **j** Follicle of a milkweed plant splitting and exposing seeds with plumes aiding in anemochory (wind dispersal). Scale bars = 5 cm in both panels. (**i** Marco Schmidt, CC BY-SA 3.0; **j** RR Wise)

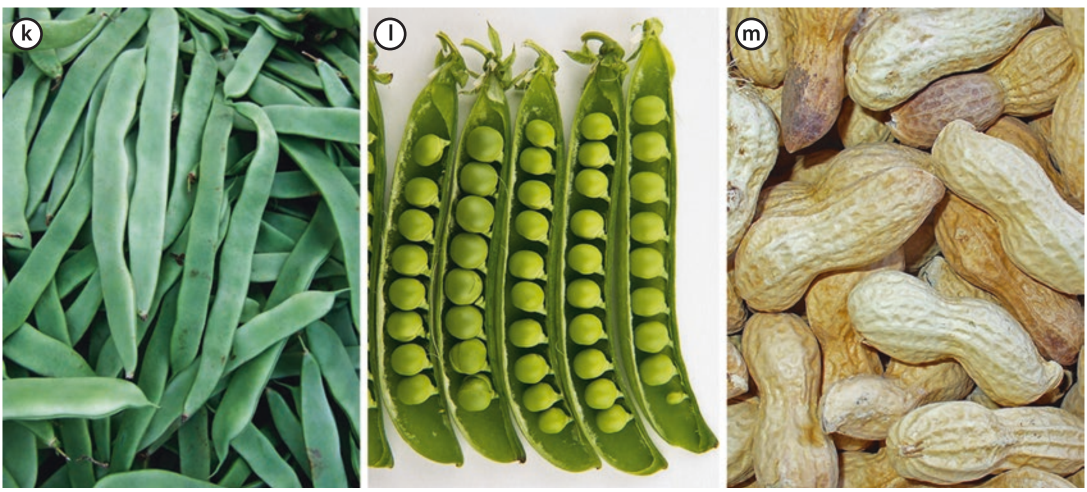


Fig. 19.3 **k–m** Legumes of **k** green bean (*Phaseolus vulgaris*) (Zyance – Own work, CC BY-SA 2.5), **l** sweet pea (*Pisum sativum*) (Bill Ebbesen – Own work, CC BY-SA 3.0), and **m** peanut (*Arachis hypogaea*). (H. Zell – Own work, CC BY-SA 3.0)

nal plants to wind dispersal and even ballistic dispersal. The dehiscent fruits include follicles, legumes, and capsules.

A **follicle** is a dry fruit derived from a superior ovary of a single carpel. It splits down the ventral side of the carpel. Examples of plants with follicular fruits include *Magnolia*, Christmas rose (*Helleborus niger*), and plants in the Apocynaceae—the milkweed family (Fig. 19.3i, k).

The **legume** fruit is only found in the legume family, Fabaceae. Thus, it is an exception to the rule that fruit taxonomy does not recognize species relatedness. A legume develops from a superior ovary that contains a single carpel. It splits open along both the ventral side and midrib of the carpel. At maturity, the fruit wall (pericarp) is dry and

Fig. 19.3 **n** Tulip (*Tulipa* sp.) capsule is loculicidal. **o** The campion (*Silene* sp.) capsule is denticulate. **p** Seeds dehisce from the poricidal poppy (*Papaver* sp.) capsule via pores at the top. **q** The lily (*Lilium* sp.) capsule is septicidal; it sheds its seeds by forming a split down the side, between two carpels. Lily has three carpels, thus three septal splits. Scale bars = 1 cm in all panels. (**n**–**q** RR Wise)

brown, and the seeds are dehisced. However, most of us are more familiar with the immature fruit. Green beans are picked at a very early stage, before the seeds have developed. The pod/pericarp/fruit/legume wall is eaten either fresh or cooked (Fig. 19.3k). Snow pea pods are likewise consumed when immature. Sweet peas are picked at a slightly later developmental stage, when the seeds have developed and the pod wall, which is discarded, has dried considerably, although it is still green (Fig. 19.3l). Peanuts are picked at maturity after the pericarp has sclerified (Fig. 19.3m). The pericarp is split open and the seeds are eaten. The peanut seed has hundreds of uses (Carver 1917).

A **capsule** fruit is derived from either superior or inferior ovaries and composed of two or more carpels. The capsule wall is dry and sclerified. Tulips, lilies, irises, jimsonweed, poppies, and *Amaryllis* are all examples of plants with capsules. Capsules may be divided into different types based on where the locule splits to release the seeds. **Loculicidal** capsules split along a seam in the locule. Tulips are a common example (◘ Fig. 19.3n). **Denticulate** capsules have a large opening at the top ring by teeth, or denticles, as found in campion (◘ Fig. 19.3o). Capsules that release their seeds via pores on the top of each carpel, such as poppy, are termed **poricidal** (◘ Fig. 19.3p). Those that dehisce by a split between locules are called **septicidal**, because the split is along a septum (boundary) between the locules (◘ Fig. 19.3q).

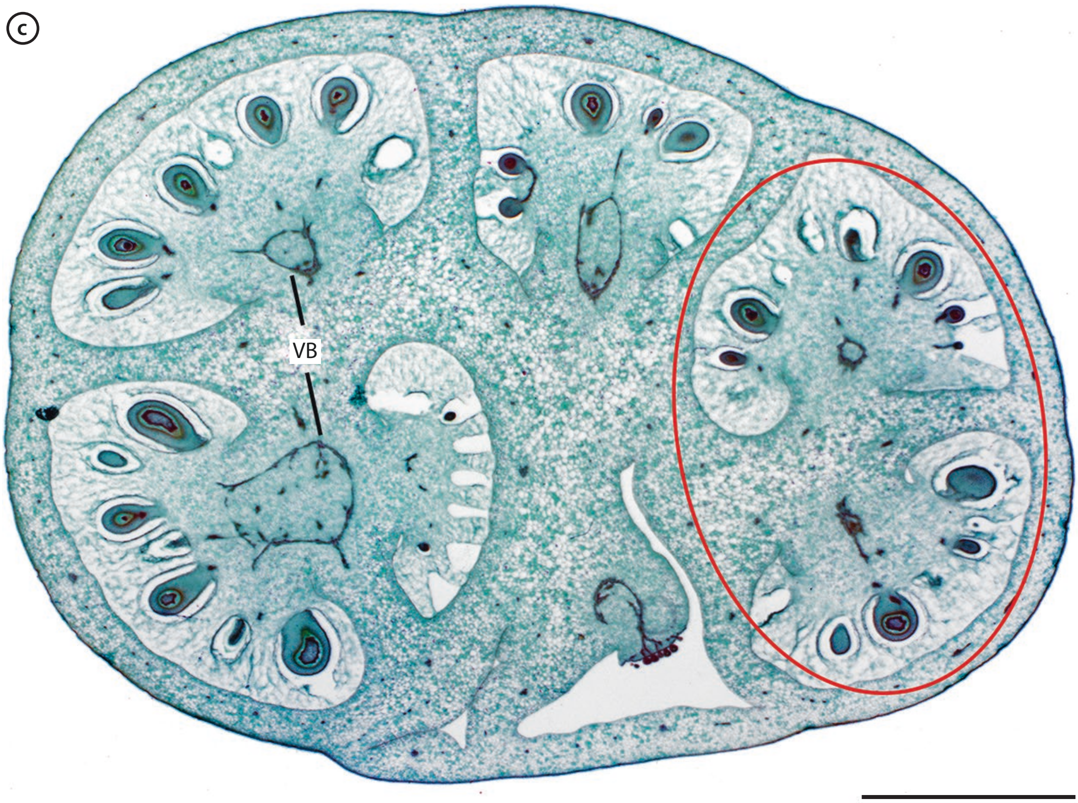
19.4 Fleshy Fruits Are Characterized by an Enlarged, Juicy Pericarp

Fleshy fruits represent what most nonbotanists mean when they use the term "fruit." Fleshy fruits are characterized by the expansion of parenchyma cells in the pericarp during fruit development and their differentiation into photosynthetic or storage tissue. Thin-walled and highly vacuolated parenchyma cells predominate in the pericarp of fleshy fruits. They are all indehiscent and do not release seeds upon fruit maturation. Many green fleshy fruits are capable of significant rates of photosynthesis. These cells remain intact and active, in one form or another, long after fruit maturation, hence the "fleshy" designation. The fleshy portion of the fruit attracts frugivores, animals that eat fruit and serve solely in seed dispersal. Fleshy fruits include the drupe, berry, pepo, hesperidium, and pome, as described below.

A **drupe** is a single-seeded fruit derived from a single carpel (◘ Fig. 19.4a, b). The drupe may also be called a stone fruit because it has a thick and hard endocarp consisting of stone cells, a fleshy mesocarp, and a thin "skin" or **exocarp** (refer to ◘ Fig. 19.1). Examples include olives, coconuts, as well as many fruits in the *Prunus* genera including peaches, cherries, nectarines, and plums.

A **berry** is a multiple-seeded fruit derived from the superior or inferior ovaries with one or more carpels (◘ Fig. 19.4c). All the ground tissue (mesocarp and endocarp) of the ovary wall expands into a fleshy or juicy tissue, and the outer layer or skin is usually the

◘ **Fig. 19.4** **a**, **b** Drupes. Cherry (*Prunus avium*) and olive (*Olea europaea*) are both drupes because they have a thin exocarp, thick mesocarp, and heavily sclerified endocarp or stone. A single seed is found within the endocarp. Scale bars = xx mm. (**a** Hans, CO0 Creative Commons, **b** ulleo, CC0 Creative Commons)



◘ Fig. 19.4 **c** Cross-section of a developing tomato (*Solanum lycopersicum*) fruit. The tomato has axile placentation, a single example of which can be seen within the red ellipse. Vascular bundles (VB) supply each seed with nutrients. Thousands of years of breeding has produced "meaty" tomato fruit with multiple, fused carpels such that the simple axile arrangement can be difficult to see. Scale bar = 500 µm. (RR Wise)

exocarp. Examples of berries include the blueberry, tomato, and peppers (*Capsicum annuum*). A developing tomato fruit is shown in ◘ Fig. 19.4c. At this early stage, the fruit would green due to active chloroplasts in the exocarp. In each locule, the axial placenta bearing seeds is enlarged and contains vascular bundles. As the fruit ripens, the chloroplasts of the cells in the pericarp and placenta undergo transformation into chromoplasts, which accumulate the red carotenoid, lycopene. The seeds become mucilaginous due to slime secreted by their epidermal layers as well as from the placenta.

A **pepo** fruit typically develops from an inferior ovary with three carpels. Pepo fruits bear some resemblance to pome fruit, but they do not contain a sclerified endocarp. One of the distinguishing features of a pepo is the occlusion of its locules by the ingrowths of carpels (◘ Fig. 19.4d, e). The pepo also has accessory tissue, i.e., an enlarged hypanthium, and the placentation is parietal. Examples of pepos are found in the Cucurbitaceae and include the cucumber (*Cucumis sativus*), watermelon (*Citrullus lanatus* var. *lanatus*), as well as various squashes and pumpkins (*Cucurbita pepo*).

A **hesperidium** is a multiple-seeded fruit derived from a superior ovary of about ten carpels with central-angular placentation (◘ Fig. 19.4f). The exocarp, sometimes called the **flavedo**, is a brightly colored rind that consists of compact parenchyma with oil

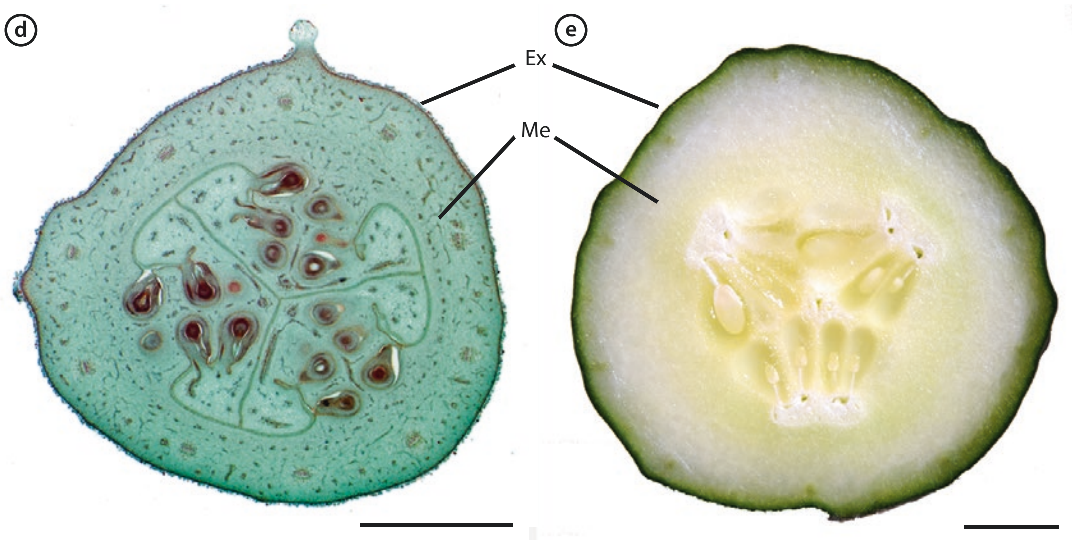


Fig. 19.4 **d**, **e** As seen here in cucumber (*Cucumis sativus*), a pepo, numerous seeds are connected to the parietal placentae and enclosed in a pulpy tissue. The pericarp consists of the green exocarp (Ex) that is composed of the epidermis, several layers of supporting tissue, and fleshy parenchymatous mesocarp (Me). No well-defined endocarp is present. Scale bars = 1 mm in **d** and 1 cm in **e**. (**d** RR Wise; **e** S Lyons-Sobaski)

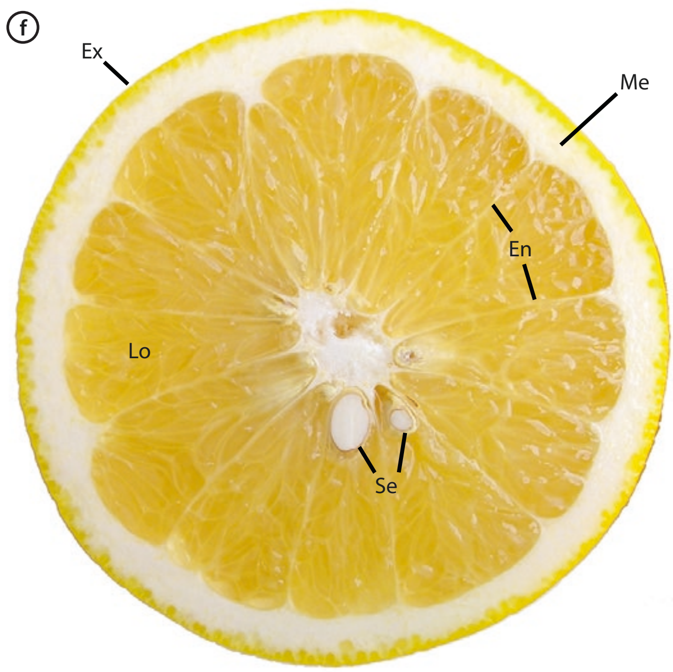


Fig. 19.4 **f** A hesperidium of a lemon (*Citrus limon*) fruit. The thick exocarp and white, spongy mesocarp are characteristic of this fruit type. The locules (Lo) are formed by the radial partitions of the endocarp (En) that represent fused and invaginated margins of adjacent carpels. The locules are filled with stalked, spindle-shaped multicellular juice sacs. Seeds (Se) are also present in the locules. Scale bar = 2 cm. (CO0 Creative Commons)

Fig. 19.4 **g**, **h** Photographs of a **g** longitudinal and **h** cross-section of an apple pome. In the pome of cultivated varieties of apple (*Malus pumila*), the border between the accessory part of the fruit and pericarp proper is not clearly demarcated. A boundary line may be drawn along vascular bundles (VB) that have supplied five petals. The "membranes" that line the five unoccluded locules (L) with seeds are morphologically a cartilaginous-like endocarp. Note the pedicel (P) and, on the opposite side, the withered remains of sepals (S). Scale bar = 2 cm. (**g**, **h** RR Wise)

cavities. The white spongy tissue underneath the rind is the mesocarp (a.k.a. **albedo**). It consists of loosely arranged colorless cells. This tissue appears white because of numerous air spaces. The locules are formed by the radial partitions that represent fused and invaginated margins of adjacent carpels. The locules are occluded with juice sacs that are modified trichomes and are the derivatives of the inner epidermis and subepidermis (collectively known as endocarp). Examples of plants with hesperidium fruit can be found in the Rutaceae, the citrus family.

A **pome** is a multiple-seeded fruit derived from an inferior ovary of five carpels. The fruit includes carpellary tissue from the hypanthium (floral tube). The flesh is mainly derived from an enlarged hypanthium rather than from the ovary wall. The hypanthium in the pome is the enlarged basal portion of the perianth and stamens, which are fused to the ovary (Fig. 19.4g, h). The endocarp is thin and sclerified and covered with a waxy cuticle. Sepals are often preserved on the top of the fruit, confirming that it originated from an inferior ovary. Examples of pome fruits include apples and pears. The hypanthium is the portion eaten, and the true fruit (the layers of the pericarp) is discarded as the "core."

19

19.5 Fruit Structure Can Include Aggregations of Flowers into One Fruit or Many Small Fruits Within a Larger Assembly

Aggregate and multiple fruits are complicated combinations of one of the fruit types described above. **Aggregate fruits** are derived from the ovaries of numerous free carpels of one individual flower.

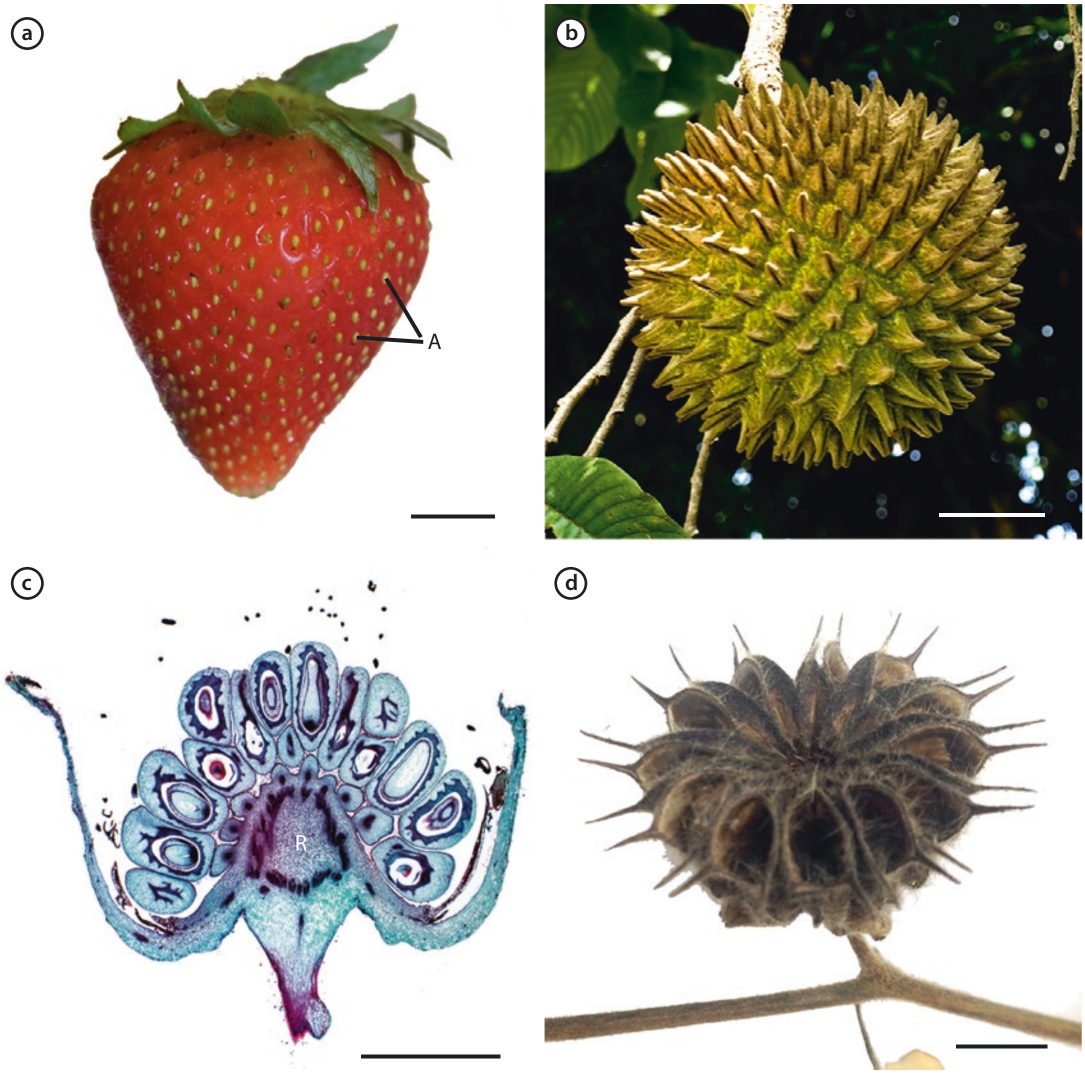


Fig. 19.5 **a**–**d** Four examples of aggregate fruit representing achenes, berries, drupes, and follicles. They all develop from the numerous ovaries of a single flower, with each superior ovary containing a single ovule. **a** The strawberry (*Fragaria* sp.) fruit is an aggregate of many achenes (dry, indehiscent fruits), attached to an enlarged and fleshy receptacle. The receptacle is the floral part that is selected for eating, with the accompanying achenes (A). (S Lyons-Sobaski) **b** The custard apple (*Annona purpurea*) fruit is an aggregate of berries (fleshy fruits). (Ll1324, CC0) **c** Raspberries (*Rubus* sp.) are aggregates of drupes (fleshy fruits). The receptacle (R) is a small, tasteless knob that remains on the plant when the fruits are picked. The individual fruits are called drupelets. **d** Velvetleaf (*Abutilon theophrasti*) fruits represent an aggregate of follicles (dry, dehiscent fruits). Scale bars = 1 cm in **a**, 5 cm in **b**, 2 mm in **c**, and 1 cm in **d.** (**a** S Lyons-Sobaski; **b** Ll1324, CC0, Creative Commons; **c**, **d** RR Wise)

The receptacle enlarges and becomes fleshy. Examples of aggregate fruits include strawberries (achene), magnolia (follicles, samaras, or berries), blackberry and raspberry (drupelets) (Fig. 19.5a–d). Such fruits may be aggregates of dry indehiscent, dry dehiscent, or fleshy fruits. In contrast, **multiple fruits** differ from aggregate fruits because each multiple fruit is derived from individual ovaries of multiple flowers. The classic example of a multiple fruit is the berries of the pineapple (Fig. 19.5e). Another example includes plants within the mulberry family, the Moraceae, where the multiple

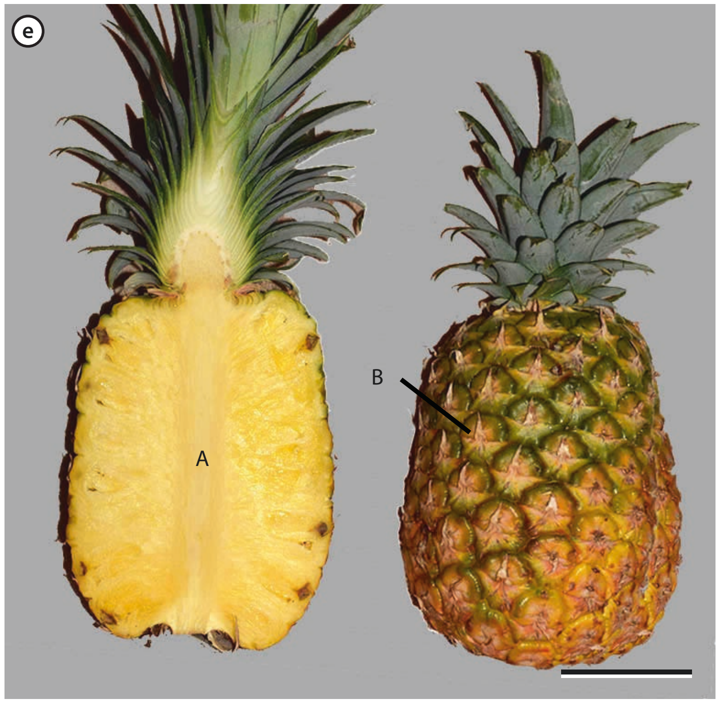


Fig. 19.5 **e** The multiple fruit of pineapple (*Ananas comosus*) develops from a compact inflorescence. In the internal view, the fleshy inflorescence axis (A) is shown cut lengthwise, and numerous swollen and coalesced fruits arise laterally from it. In cultivated varieties, each fruit develops parthenocarpically (without fertilization) from an inferior ovary. In the external view, numerous spirally arranged fruits, specifically berries (B), are visible. After flower production, the inflorescence apex reverts to vegetative growth. The leafy crown is used to propagate this crop by vegetative means. Scale bar = 5 cm. (S Lyons-Sobaski)

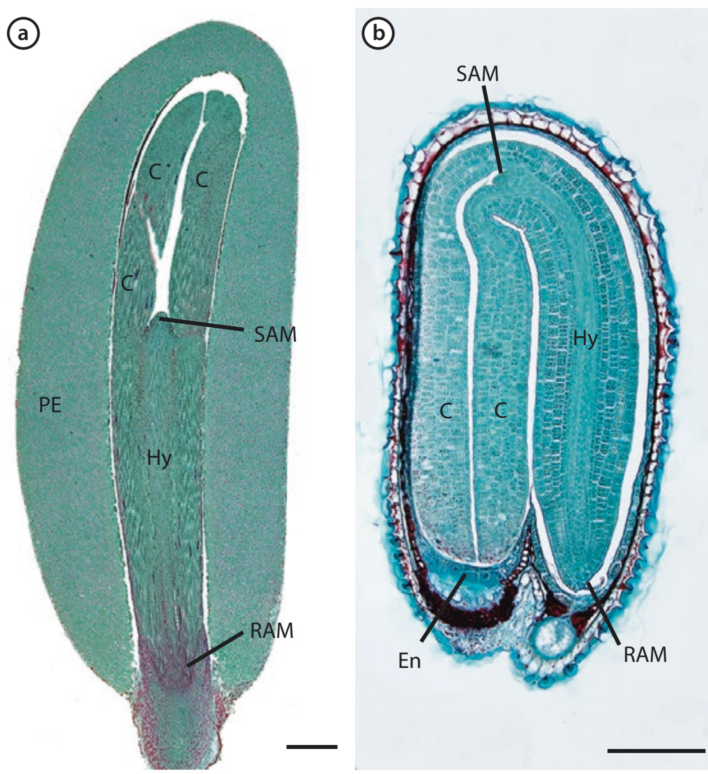
fruit often contains many drupelets or achenes that are united with a common receptacle. Fig trees (*Ficus*) produce another type of multiple fruit called a **synconium**. Fig fruits differ from all others discussed thus far, as the flowers are located within the developing fruit structure, with each flower potentially giving rise to a drupelet. Some species of fig must be pollinated by fig wasps that enter the fruit structure.

19.6 The Seed Is an Individual Plant Containing Nutrition for the Embryo

The **seed** is the main reproductive unit in both angiosperms and gymnosperms and provides continuity between the successive generations. Seeds are the means of plant dissemination (dispersal) through space. Dormancy (refer to ► Sect. 1.7) allows plants to disperse through time. Seeds help the tender embryo survive under cold, dry, and other unfavorable conditions and supply the embryo with nutritive materials for germination and prior to autotrophic growth. Plants that possess seeds are called spermatophytes (a.k.a.

also known as phanerogams). They include the four taxa of gymnosperms (cycads, *Ginkgo*, conifers, and gnetophytes) and the angiosperms. The spermatophyte seed is composed of three main parts: (1) the embryo, (2) a source of stored nutrients (endosperm or pseudoendosperm), and (3) a protective seed coat. The conifer, eudicot, and monocot seed will be discussed in this section.

The embryo (the incipient sporophyte) is the most important part of the seed (◘ Fig. 19.6a–c). It consists of many (gymnosperms), two (eudicotyledons), or one (monocotyledons) leaflike cotyledons and a **hypocotyl** ("below cotyledons")—the stemlike axis between the cotyledons and the root crown. The hypocotyl forms two apical meristems at its poles, the root apical meristem (RAM) at the lower pole and the shoot apical meristem (SAM) at the upper pole. If a short stem or embryonic leaves are present, they are called the **epicotyl** ("above cotyledons") or **plumule**. However, not all spermatophyte species, have seeds that contain well-developed plumule. The RAM and SAM give rise to all postembryonic structures in the primary growth of the plant. In conifers and eudicotyledons, the SAM is situated between the cotyledons at their



◘ **Fig. 19.6** **a** Longitudinal section of a pine (*Pinus* sp.) seed. Multiple cotyledons (C, three are marked) surround the shoot apex (SA) of the embryo (E). Food reserves are stored in the large pseudoendosperm (PE). The shoot apical meristem (SAM) and root apical meristem (RAM) represent the top and bottom of the hypocotyl (Hy). **b** Longitudinal section of a non-endospermic shepherd's purse (*Capsella bursa-pastoris*) seed. Most of food reserves in the endosperm (En) have been broken down and moved into the large cotyledons (C). Scale bars = 500 µm in **a** and 100 µm in **b**. (**a**, **b** RR Wise)

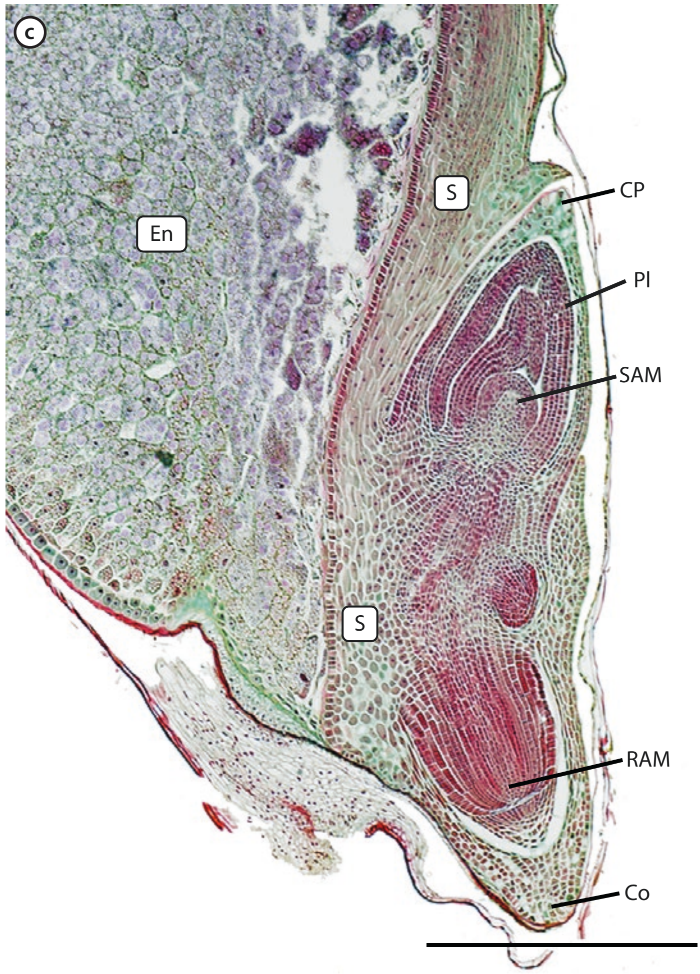


Fig. 19.6 **c** Longitudinal section of an endospermic caryopsis (or grain) of oats (*Avena sativa*). The lateral position of the embryo in the fruit is characteristic of the caryopsis, with the endosperm (En) occupying the majority of the seed volume. The scutellum (Sc) is almost twice as large as the remainder of the embryo (called the embryonic *axis*). The embryo contains a well-differentiated plumule (Pu) arising from the shoot apical meristem (SAM) with the primordium of the first leaf, termed a coleoptile (CP), protecting the plumule. The root apical meristem (RAM) is enclosed in a specific multilayered sheath, the coleorhiza (Co). Scale bar = 0.5 mm. (RR Wise)

bases, whereas in monocotyledons, it occupies a lateral position with respect to the vertically oriented cotyledon (scutellum).

Conifers lack double fertilization and therefore do not produce a true endosperm. The seeds do, however, have a seed coat, contain a developing diploid embryo, and possess a food storage tissue derived from haploid cells of the female gametophyte (Fig. 19.6a). In spite of its different ontogenetic origin but in keeping with its common function, this storage tissue is typically called a pseudoendosperm.

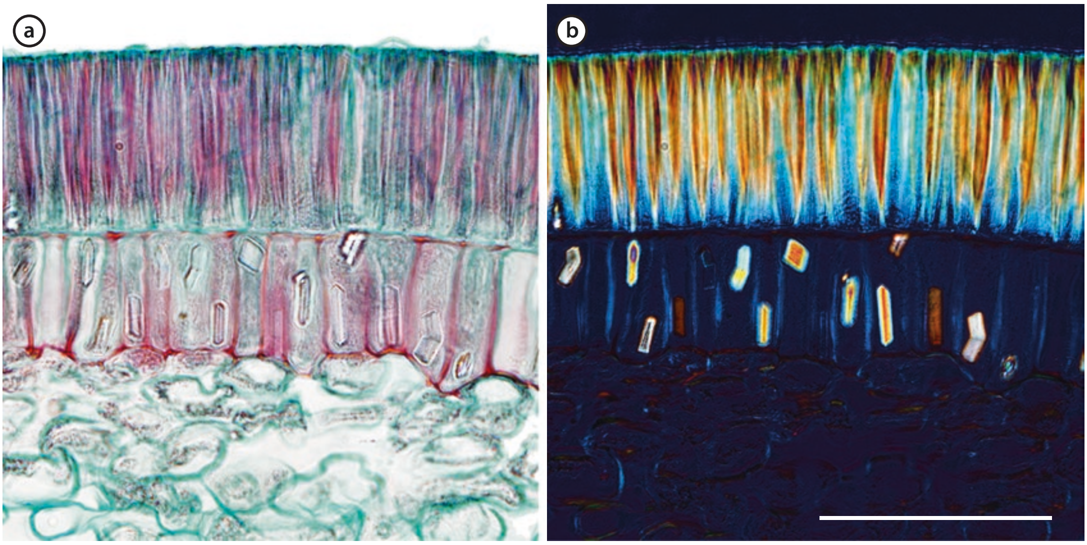
Eudicot and monocot seeds are more complex because the angiosperm embryo and food-storing endosperm are separate products of double fertilization. The seed coat has a maternal (ovular) origin. Although all angiosperms produce an endosperm, that tissue may not persist to the mature seed stage. In seeds with **non-endospermic storage**, the food reserves are synthesized within the endosperm but are soon transported into the cotyledons of the embryo (a.k.a. an **exalbuminous seed**). This can be seen in the eudicot seed shown in ◘ Fig. 19.6b in which little endosperm remains and the cotyledons are enlarged. But in most flowering plants, the endosperm tends to remain; such seeds are said to have endospermic storage (◘ Fig. 19.6c). The ratio of volumes occupied by the embryo and endosperm in the mature seed varies greatly among different plants.

In monocotyledons, the large, single cotyledon is termed the scutellum (◘ Fig. 19.6c; refer also to ◘ Fig. 19.3c). The scutellum is an absorptive organ. As food monomers are liberated from the stored reserves in the endosperm, they are loaded into the scutellum which has a direct vascular connection (mostly phloem) to the developing shoot and root on the embryonic axis. The immature leaves of the plumule are protected by a **coleoptile** that will grow in length and protect the juvenile leaves as they push through the soil. In a similar fashion, the **coleorhiza** will protect the young root tip until a proper root cap matures. In the **aleurone layer** (refer to ◘ Fig. 19.3c), the cell walls are thickened due to the deposition of hemicellulose reserves. During germination, cells of the aleurone layer secrete starch-degrading enzymes that are released into the endosperm. There, the enzymes break down the starch reserves and mobilize simple sugars for absorption by the scutellum. The scutellum then delivers the sugars to the germinating embryo.

19.7 The Seed Coat Surrounds the Embryo and Storage Tissues

The seed coat (or testa) is derived from the integument(s) of the ovule. It is the sole protective layer for the embryo in seeds released from dehiscent fruit but may be lost from or heavily modified on seeds in indehiscent dry fruits or in fleshy fruits. The frequent brown or black color of seeds is due to pigments accumulated in the cells of the seed coat. In single-seeded, indehiscent fruits where the embryo is protected by the pericarp, the seed coat is often obliterated or appears as a very thin, structureless membrane between the embryo and the pericarp, as in the sunflower seeds shown in ◘ Fig. 19.3b.

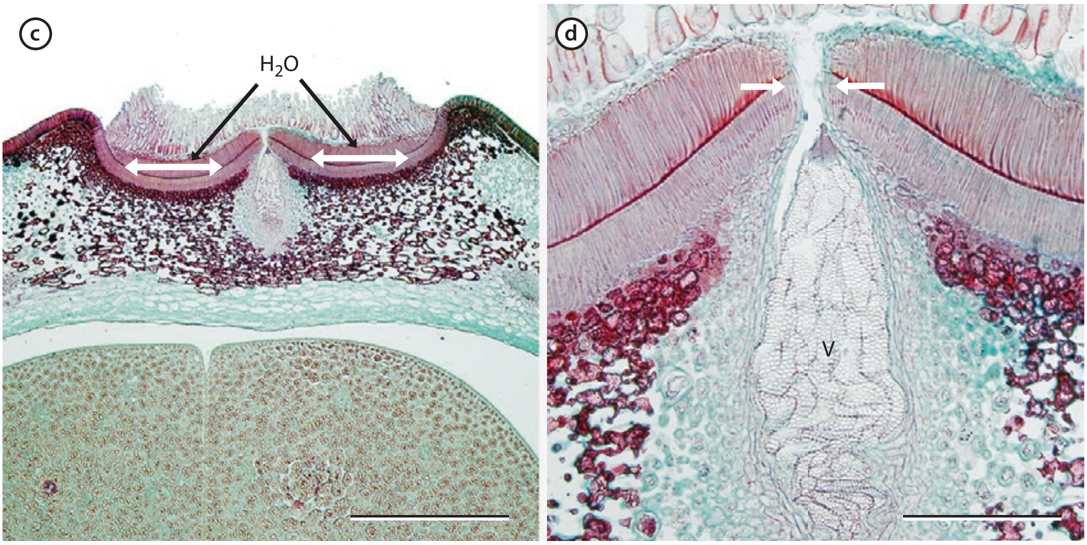
Most commonly, the seed coat in mature seeds is dry and usually consists of dead cells. The withering away of different layers of the seed coat occurs asynchronously in a developing seed. One or several cell layers may become nonliving when the cell walls are thin and the seed is still enlarging. Such layer or layers become crushed and may eventually disappear. But other layers remain alive and grow in pace with the seed expansion. Their cells may undergo sclerification and lignification after the cessation of seed growth. The pattern of secondary thickenings in the sclereids and the shape



■ **Fig. 19.7** **a**, **b** Bean (*Phaseolus vulgaris*) seed coat. **a** The seed coat is composed of an outer layer of columnar macrosclereids and an inner layer of osteosclereids. **b** Polarized light reveals the lignin of the outer layer and prismatic calcium oxalate crystals within the cells of the inner layer. Scale bar = 50 µm. (**a**, **b** RR Wise)

of sclereids themselves in the supporting layers of the seed coat vary greatly and are taxon-specific. In different plants, the transformation of the integumentary parenchyma into seed coat sclerenchyma may occur in different cell layers. The presence of one or more layers of calcium oxalate crystal-containing cells is also a frequent phenomenon (■ Fig. 19.7a, b).

One of the roles for the seed coat is to keep water out and prevent premature germination. But it must be able to allow the seed to dry down upon maturity and enter the desiccated, dormant stage. Thus, water must have a path to exit the seed and not reenter. The **hilum** serves that function in legumes. The hilum is the scar left by the attachment of the seed to the **funiculus**, the strand of vasculature that supplies the seed with water and food reserves for storage. It is typically dark colored and is represented by the "eye" of black-eyed peas. In legumes, the hilum is also a one-way valve that opens in dry air and shuts in the presence of water thus letting the seed dry down when conditions allow, but not reabsorb water upon hydration. When the seed is exposed to dry air, the thick-walled cells of the hilum shrink and open the pore of the hilum (■ Fig. 19.7c). Water within the seed collects in patch of vasculature just underneath the hilum pore (■ Fig. 19.7d) and exits the seed. If the air is humid, the thick-walled cells swell and close the pore so that no water can enter. Thus, water is lost from the seed in dry air, but no water can enter the seed in humid air. Constant exposure to water, such as in wet spring soils, combined with overwintering breakdown of the seed coat in other areas allows water to enter the seed and initiate germination.



◘ **Fig. 19.7** **c**, **d** The bean (*Phaseolus vulgaris*) hilum is composed of a ring of thick-walled cells with an underlying patch of conducting vessel elements. **c** Upon exposure to water or high humidity, the cells of the ring swell and expand in the lateral direction (double-headed white arrows). This expansion closes the pore in the hilum and water cannot enter the seed. **d** Water from the seed collects in the vasculature (V) just inside the hilum pore and readily escapes when the pore is open. Scale bars = 500 µm in **c** and 100 µm in **d**. (**c**, **d** RR Wise)

In some species, the cells of the outer layer of the seed coat may become heavily modified in other ways. The seed coat of lily secretes a conspicuous amount of slime at the terminal stage of seed development. When moistened, the slime becomes sticky and adheres to the soil. It may also facilitate seed dispersal by protecting the embryo as the seed passes through the gut of animals. The mucilaginous seed coat of mistletoe, a hemiparasitic plant, serves two purposes. It protects the seed during passage through a bird digestive system, and it adheres the seed to a tree branch when it is passed by the bird. The seed can then germinate directly on a potential host. The seed coat of cotton (*Gossypium* sp.) is covered with long trichomes composed of almost pure cellulose, a valuable fiber used for textiles for over 8000 years. Other seed coats may have hooks or grapples to attach to animal dispersers.

During desiccation of seeds at the final stage of their ripening, the seed surface relief, or micromorphology, acquires a characteristic pattern that is stable and taxon-specific (◘ Fig. 19.5e–j). Therefore, scanning electron microscope studies of seed surface have proved to be of great importance in solving taxonomic problems. Among the characters that may determine taxon-specific seed surface patterns are the cellular arrangement, the shape of cells, the outline (straight, lobed, or irregularly curved) of their anticlinal walls, the surface relief of their outer periclinal walls, the sculptures of the cuticle and epicuticular waxes, etc.

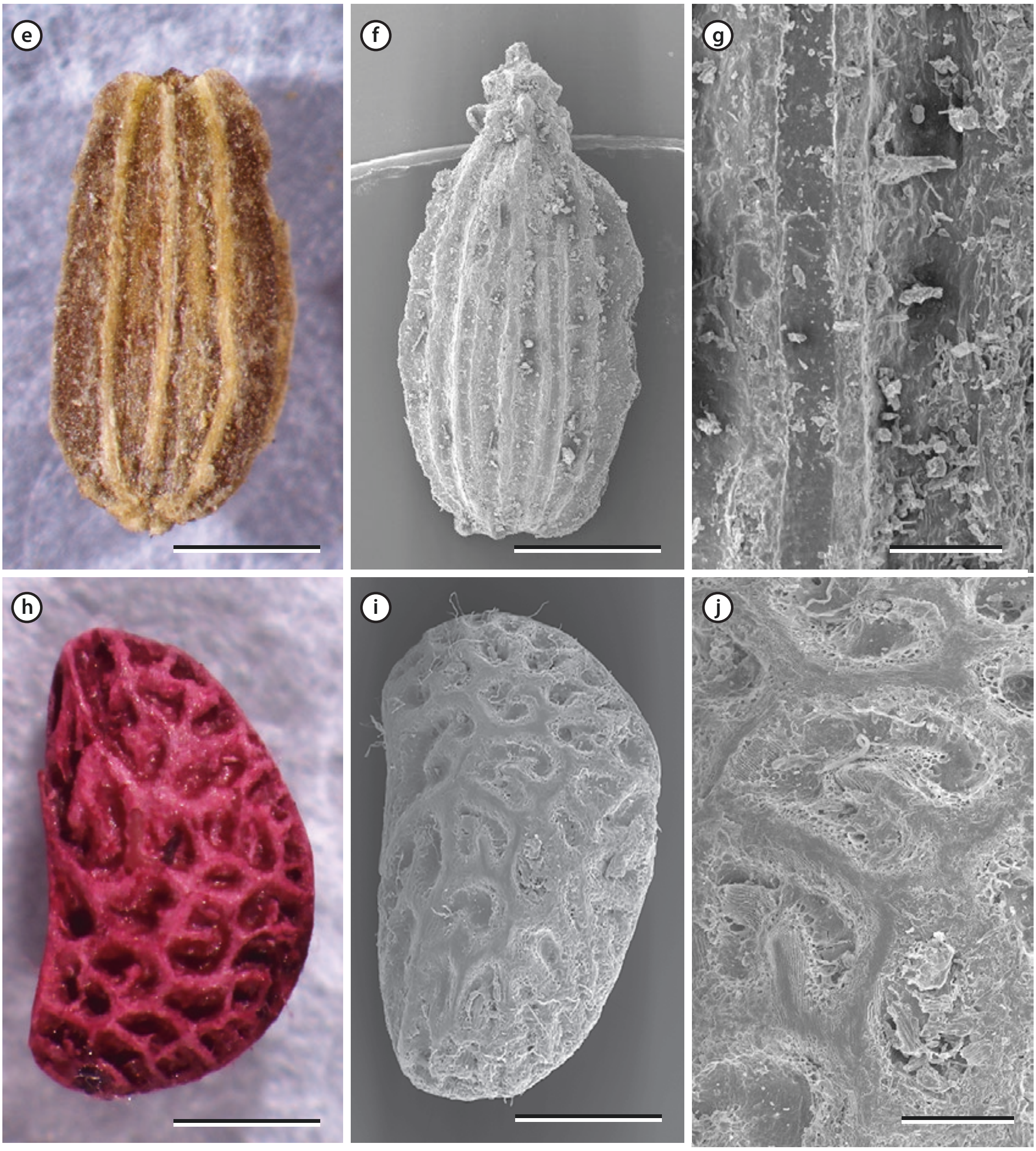


Fig. 19.7 **e**–**j** Mature seeds of carrot (*Daucus carota*—top row) and black raspberry (*Rubus occidentalis*, bottom row). Scale bars = 1 mm in **e**, **f**, **h**, and **i** and 250 μm in **g** and **j**. (**e**–**j** RR Wise)

Box 19.1 Insights from Nature—Adhesive Fruits and Hook and Loop Fasteners

Plants have inspired technological advances in some surprising ways. Perhaps the one that impacts most of us is "hook and loop" or Velcro-like fasteners that were invented in 1941. These fasteners are used in clothing, shoes, and hanging pictures, just to name a few. The inspiration for these fasteners is linked with burdock, an angiosperm with adhesive fruits (Saunders 2015). The hooklike structures on fruits assist in seed dispersal, to move the embryo away from conspecifics to limit competition and disease transmission, but also tend to get caught on clothing when walking through the woods and other habitats.

The physical structure of adhesive fruits can vary in terms of density of hooks as well as in physical characteristics such as length and width of hooks, leading to differences in the behavior of hooks. The force needed to remove fruits with hooks varies with sizes and shapes (Gorb and Gorb 2002). Further research reinforced the earlier discovery that the small hooks of *Galium aparine* had a larger load at contact separation than a larger hooked species, *Circaea lutetiana*. Thus, *G. aparine* could hold more force before separation from a substrate than *C. lutetiana*. Additional tests of hook behavior among several species showed that longer hook length and hook spans yielded more displacement of the hook from its initial position. These data may provide insight into new designs of hook and loop fasteners than what we currently use today (Chen et al. 2013).

References: Chen et al. (2013), Gorb and Gorb (2002), Saunders (2015)

19.8 Germination of the Seed Occurs when Environmental Conditions Are Appropriate and Marks the "Birth" of the Individual Plant

After the exposure of a desiccated dormant seed to favorable conditions, e.g., appropriate soil moisture, temperature, and aeration, it usually germinates. Germination is preceded by the absorption of large amounts of water. The imbibition of seeds is, as a rule, accompanied by the rupture of the seed coat usually at the micropylar end of the seed. The mobilization of food reserves coincides with water absorption. Water-soluble products of hydrolysis are transported to the activated apical meristems. First, the radicle elongates; the root appears out of the micropyle and starts its downward growth into the soil. The root develops root hairs and, frequently, lateral roots. Only after this do the other organs of the embryo start to emerge. The absorptional activity of the emerging root helps to assure the young seedling has an adequate supply of water and mineral nutrients when the shoot breaks through the surface of the soil.

During germination in some eudicots, the cotyledons, together with the incipient shoot apex, emerge above ground due to the intercalary growth of the hypocotyl, which pushes the first internode (to which the cotyledons are attached) above the soil surface. In such **epigeal** (above ground) germination, the cotyledons unfold, turn green, and become the first photosynthesizing organs of the seedling (◘ Fig. 19.8a). In other eudicots, the cotyledons, which are thick and rich in food reserves, remain within the seed coat under-

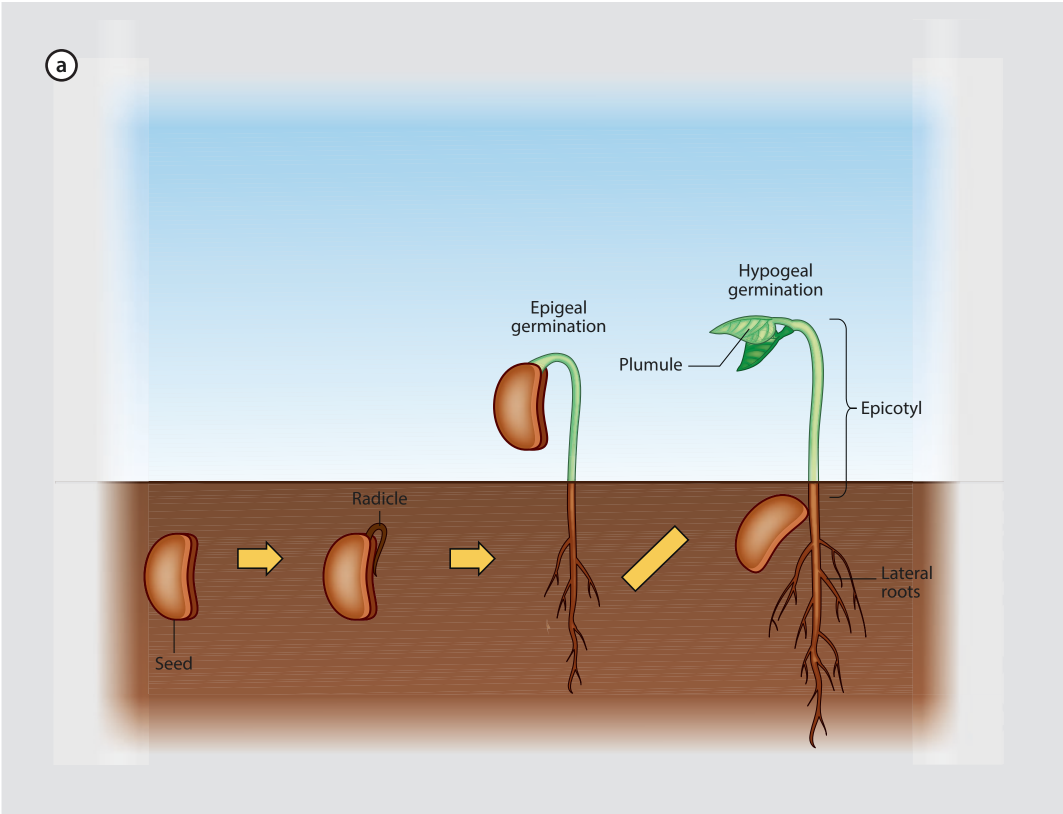
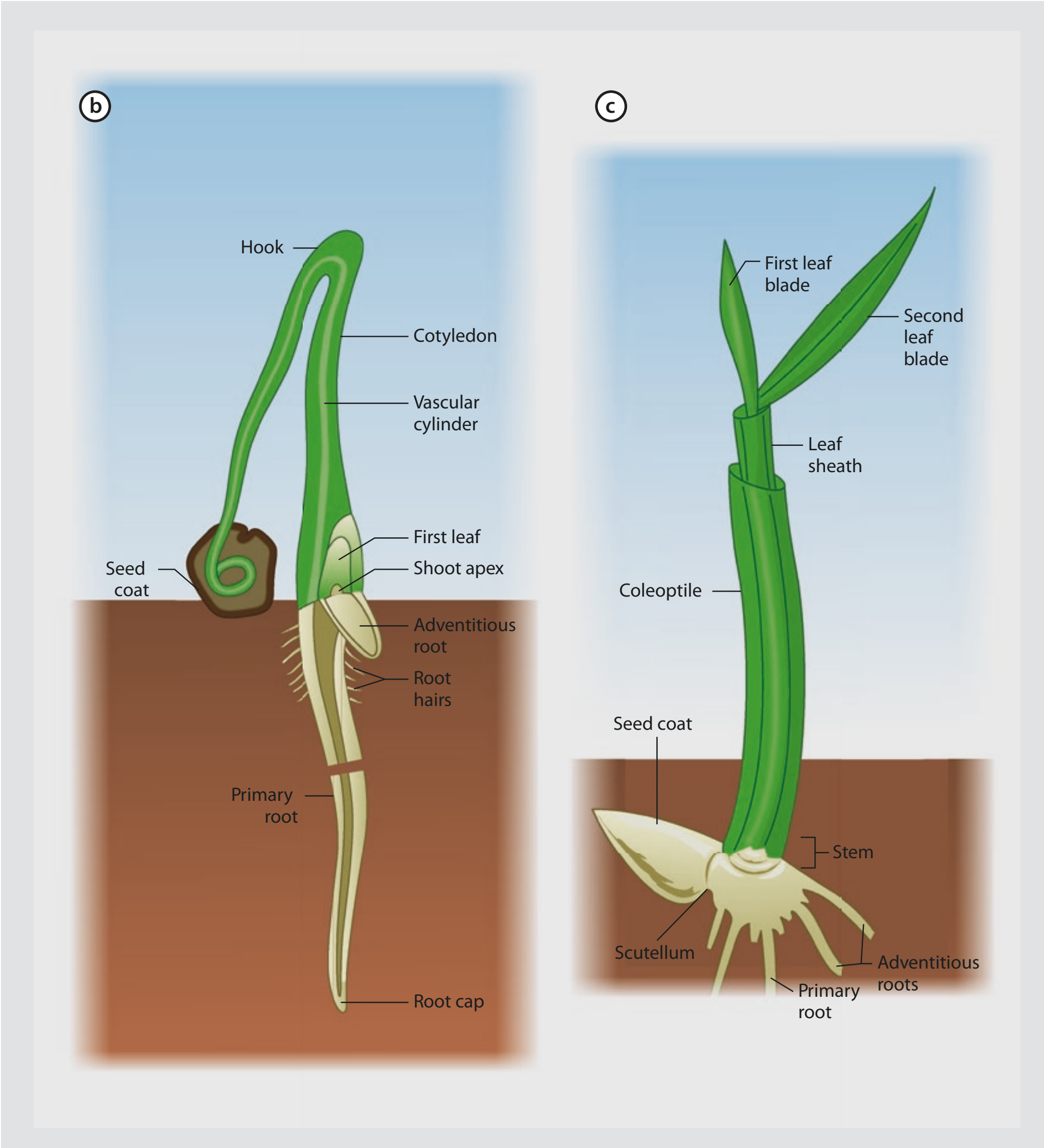


Fig. 19.8 **a** Epigeal and hypogeal germination. Both hypogeal and epigeal germination in eudicotyledons are shown in this figure. The first two images are the same for both processes. The embryo germinates and the radicle (immature root) emerges and grows downward. The third image shows epigeal germination in which the cotyledons are pushed out of the soil by growth of the hypocotyl. The fourth image shows hypogeal germination in which the cotyledons remain below the soil surface while growth of the epicotyl pushes the plumule out of the soil. (Redrawn from Begoon, CC BY-SA 3.0)

ground. In this **hypogeal** (below ground) germination, the shoot apical meristem is pushed through the soil surface by the elongating epicotyl (the internode between the cotyledons and the immature leaves) and the first photosynthesizing organs of the seedling are the leaves. This collection of immature leaves is called the plumule. As the leaves unfold, the stem portions between them elongate into internodes, new leaves emerge from each node, and, thus, the shoot system is established. The embryonic root develops into the primary root of the seedling. The primary root produces lateral (branch) roots that are called secondary roots. As a result, the root system is initiated, and the young sporophyte becomes established.

In contrast to eudicots, during epigeal germination in some monocots such as onion, the hypocotyl is not involved in breaking the seedling out of the soil. In onion, for example, this process occurs due to intercalary growth of the single cotyledon. The cotyledon expands unevenly and bends, forming a so-called hook that facilitates penetration through the soil surface. The apical portion of the cotyledon inside the seed coat does not grow, but the aboveground portion turns green and continues to elongate. This creates a force that causes the



■ **Fig. 19.8** **b**, **c** Epigeal germination and seedling structure in onion (*Allium cepa*), a monocot. Note that the seed will be above soil level as germination progresses. **c** Hypogeal germination in a typical grass. Note that the grain (seed) remains in the soil during germination. (Redrawn from Crang and Vassilyev 2003)

seed coat to be pulled out of the soil (■ Fig. 19.8b). In other monocots, such as grasses, germination is hypogeal since the grain with the enclosed cotyledon (scutellum) remains in the soil (■ Fig. 19.8c). At the onset of germination, the root and coleoptile elongate and break out of the grain. Intercalary growth pushes the coleoptile out from the soil and it subsequently becomes green. Adventitious roots then begin to emerge from the primary root. The first and subsequent leaves of the incipient shoot grow inside the coleoptile, and sheaths of the preceding leaves emerge into the light from the seedling by a type of telescopic intercalary growth.

Box 19.2 Trigger for Seed Germination in *Arabidopsis*

It is generally recognized that seeds need an appropriate temperature in order to germinate. However, breaking dormancy is not quite as simple as providing the proper temperature alone as has been documented by Topham et al. (2017). Studies at the University of Birmingham, UK, and the University of Toronto, Canada, reveal that in *Arabidopsis thaliana* seeds, plant growth regulators abscisic acid (ABA) and gibberellin (GA) together create a bistable developmental switch required to process temperature inputs to break dormancy. Of particular interest has been the fact that both ABA and GA were found to occur within distinct cell types. While alternating signals of temperature and light are recognized triggers to break dormancy, the sites of plant growth regulators appear to trigger phytochrome B to accept temperature induction for seed germination. Thus, the co-functioning of temperature and light may have ecological and adaptive consequences in seed plants.

Reference: Topham et al. (2017)

19.9 Chapter Review

Concept Review

19.1 *Fruits are highly modified ovaries*. The fruit is a specialized tissue found only in angiosperms. It is an expansion of the ovary wall called the pericarp. The fruit/pericarp has three layers—exocarp on the outside, mesocarp in the middle, and endocarp to the interior.

19.2 *Fruit classification is based on characters, not necessarily species relatedness*. Fruits are classified on the basis of pericarp texture, dry vs. fleshy, whether or not seeds are released upon maturation of the fruit (dehiscent vs. indehiscent), the number of carpels per fruit, and the nature of the individual pericarp layers (papery, hard, fleshy, stringy).

19.3 *Dry fruits are often hard, containing fused pericarp layers and dead cells*. Dry fruits have a hard or papery pericarp. Indehiscent fruits do not release seeds and include the achene, caryopsis, samara, and nut. Dehiscent fruits release seeds when mature. They include the follicle, legume, and capsule.

19.4 *Fleshy fruits are characterized by an enlarged, juicy pericarp*. Fleshy fruits have an enlarged, mostly parenchymatous pericarp used for photosynthesis or storage. Drupes have a papery exocarp, a fleshy or stringy mesocarp, and a thick, hard endocarp (peach, coconut). Berries are similar except that the endocarp is fleshy (grape, banana). Pepos are like berries (fleshy meso- and endocarp), except the exocarp is a hard, thick rind (cucumber, pumpkin). A hesperidium (typical of citrus) has an oily exocarp or rind, a spongy air-filled mesocarp, and a papery endocarp. The locules are full of juice sacs. The flesh of a pome (apple, pear) is composed mostly of an expanded and tasty hypanthium (floral tube).

19.5 *Fruit structure can include aggregations of flowers into one fruit or many small fruits within a larger assembly*. Aggregate fruits are a collection of individual fruits from a single, multi-carpel flower. The fruit may be achenes (as in strawberry), follicles (some magnolias), or drupes (blackberry). A multiple fruit is one in which the individual fruits of multiple flowers are fused together. Pineapple is a good example.

19.6 *The seed is an individual plant containing nutrition for the embryo*. The seed contains an embryo, food reserves, and a seed coat. Food reserves in gymnosperm seeds are derived from gametophytic tissue. Eudicots store reserves either in the endosperm or in the two cotyledons. Monocots store food in the endosperm and absorb the mobilized reserves through the single cotyledon (scutellum).

19.7 *The seed coat surrounds the embryo and storage tissues*. The seed coat is derived from the integument of the ovule. Its main functions are to allow desiccation of the developing seed yet prevent water uptake until the time is right for germination. The seed coat typically is composed of one to several layers of sclereids and is impregnated with tannins or calcium oxalate crystals.

19.8 *Germination of the seed occurs when environmental conditions are appropriate and marks the "birth" of the individual plant*. Upon germination, the seed imbibes water, and the embryo "wakes up," begins breaking down the food reserves, and begins growth of the radicle. In hypogeal germination, the cotyledons remain below ground, and only the primary leaves emerge from the soil. In epigeal germination, the cotyledons are pushed above the soil surface, expand, and become green and photosynthetic.

■ Concept Connections

1. In the picture below, identify
   - a–d. the seedling organs.
   - e. the type of germination.
   - f. whether it is a monocot or a eudicot.

- **Concept Assessment**

2. A pericarp is derived from
    a. integuments.
    b. endosperm.
    c. ovule wall.
    d. ovary wall.
    e. placenta.

3. What kind of plant would most likely have a hesperidium?
    a. oak.
    b. lime.
    c. maple.
    d. watermelon.
    e. strawberry.

4. In the classification of fruit, the primary division is based upon
    a. dry vs. fleshy.
    b. dehiscent vs. non-dehiscent.
    c. superior vs. inferior ovary.
    d. one carpel vs. multiple carpels.
    e. one seed vs. multiple seeds.

5. Which is true of hypogeal germination?
    a. a hypocotyl arch is formed.
    b. the cotyledons remain below the soil.
    c. a cotyledon arch is formed.

d. the primary shoot tip is first to emerge from soil.
e. it is characteristic of eudicots.

6. In a pome, a large part of the fruit is derived from the floral tube or hypanthium.
   a. true.
   b. false.

7. An example of a dry, dehiscent fruit is
   a. pome.
   b. nut.
   c. samara.
   d. berry.
   e. legume.

8. In monocots, the embryonic root is covered by a(n)
   a. hypodermis.
   b. scutellum.
   c. coleorhiza.
   d. endosperm.
   e. foliage leaf.

9. The fruit of a cucumber is termed a(n)
   a. hesperidium.
   b. drupe.
   c. achene.
   d. pepo.
   e. caryopsis.

10. In the formation of a fruit, the style, perianth, and androecium generally
    a. become the seed coat.
    b. are parts of the floral tube for fruit development.
    c. represent the pedicel.
    d. dry up and abscise.
    e. become part of the pericarp.

11. The "wing" of a maple seed is an outgrowth of the pericarp.
    a. true.
    b. false.

Concept Applications

12. Tomatoes (fruit type = berries) have a *very* interesting history. Research and write a minute paper on one of the following topics:
    a. In 1893, the US Supreme Court (Nix vs. Hedden) issued the decision that tomatoes are vegetables, in spite of the fact they are clearly fruits. What was the rationale behind this SCOTUS decision?
    b. Tomatoes were once considered by Europeans to be poisonous. Why?

c. For almost 200 years, the Latin binomial for the tomato was *Lycopersicon esculentum*. Recently, that name was changed to *Solanum lycopersicum*. Research and explain why the change was made.

13. Compare and contrast the following terms:
   a. Aggregate vs. multiple fruits
   b. Drupes vs. achenes
   c. Epigeal vs. hypogeal germination

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Supplementary Information

Appendix 1: Answers to End-of-Chapter Material – 680

Glossary – 696

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R. Crang et al., *Plant Anatomy*, https://doi.org/10.1007/978-3-319-77315-5

Appendix 1: Answers to End-of-Chapter Material

Chapter 1: The Nature of Plants

Concept Connections

1. Crossword puzzle answers:
   Across
   3. Megaphylls
   8. Eudicot
   10. Autotroph
   11. Primary
   12. Cenozoic
   14. Sporophyte
   15. Gametophyte
   16. Coevolution
   Down
   1. Meristems
   2. Fruits
   4. Secondary
   5. Pigment
   6. Monocot
   7. Cellulose
   9. Chlorophyll
   13. Heterotroph

Concept Assessment

2. e
3. c
4. c
5. e
6. c
7. a
8. c
9. a
10. d
11. e

Concept Applications

12. Many scenarios apply here. One could include a variety of plants to ensure a wide variety of types of foods would ensure a complete diet. One might include soybeans in the microcosm as they contain all nine essential amino acids needed by humans. Many plants in the legume (bean) family also help provide nitrogen in the soil with the help of microorganisms, Rhizobium, contained within root nodules. Recycling of human wastes as fertilizer will be necessary.

13. Spices are derived from plant secondary compounds, a broad class of molecules produced by plants mostly for defense.

Chapter 2: Microscopy and Imaging

Concept Connections

1. Crossword puzzle answers:
   Across
   2. Resolution
   4. Scanning
   6. Esau
   7. Grew
   9. Confocal
   10. Hooke
   11. Lens
   Down
   1. Brown
   3. Van Leeuwenhoek
   5. Compound
   6. Electron
   8. Transmission

Concept Assessment

2. a
3. d
4. c
5. a
6. a

7. c

8. c

9. e

10. d

11. d

- **Concept Applications**

12. Confocal laser scanning microscopy (CLSM) would be the method of choice. Start by isolating a tissue-specific promoter that is only expressed in roots. Ligate to it the gene for the green fluorescent protein (GFP). Transform an oak plant with the chimeric gene—stable transformation is a necessity. The gene should be expressed in the roots only, and GFP should be produced. Use CLSM to localize the GFP inside the root cells. CLSM is rarely used on leaf tissue because fluorescence from the abundant chlorophyll would overwhelm any signal from a fluorescent probe.

13. Scanning electron microscopy could be used to visualize surface structures such as stomata, trichomes, and waxes. Light microscopy could be used to visualize leaf internal structures such as cells, internal air spaces, and vascular strands. Transmission electron microscopy could be used to visualize cellular detail such as chloroplasts, mitochondria, and membranes.

Chapter 3: Plant Cell Structure and Ultrastructure

- **Concept Connections**

1. Answers:
proplastid: source of all other plastids, nitrogen fixation
elaioplast: oil storage in the tapetum
amyloplast: starch storage, graviperception
etioplast: plant growth regulator synthesis
chloroplast: photosynthesis, starch synthesis, amino acid synthesis, protein synthesis, lipid synthesis, pigment synthesis, photorespiration, sulfur assimilation, nitrogen assimilation
gerontoplast: resource recovery
chromoplast: seed dispersal

- **Concept Assessment**

2. d

3. a

4. b

5. c

6. d

7. e

8. e

9. e

10. e

11. a

- **Concept Applications**

12. Plastids are the primary anabolic organelles in cells, and they are all derived from germinal proplastids. They would need to be transplanted into the animal cells and then develop into the proper type of mature plastid needed by that host tissue.

13. A number of marine animals (mostly sea slugs) extract fully functional chloroplasts from algae and incorporate those chloroplasts into their cells. These stolen plastids are called “kleptoplasts,” and the process is known as kleptoplasty. The chloroplasts remain photosynthetically active for an extended period of time

and contribute to the carbon needs of their new host. However, they cannot enter the egg cells and are not passed on to the next generation during sexual reproduction. Newly hatched young must acquire their own set of kleptoplasts.

Chapter 4: Mitosis and Meristems

Concept Connections

1. Matching answers
   - c. Interphase
   - e. Prophase
   - d. Metaphase
   - a. Late anaphase
   - f. Telophase/cytokinesis
   - b. Late cytokinesis

Concept Assessment

2. a

3. a

4. e

5. a

6. d

7. b

8. a

9. e

10. b

11. e

Concept Applications

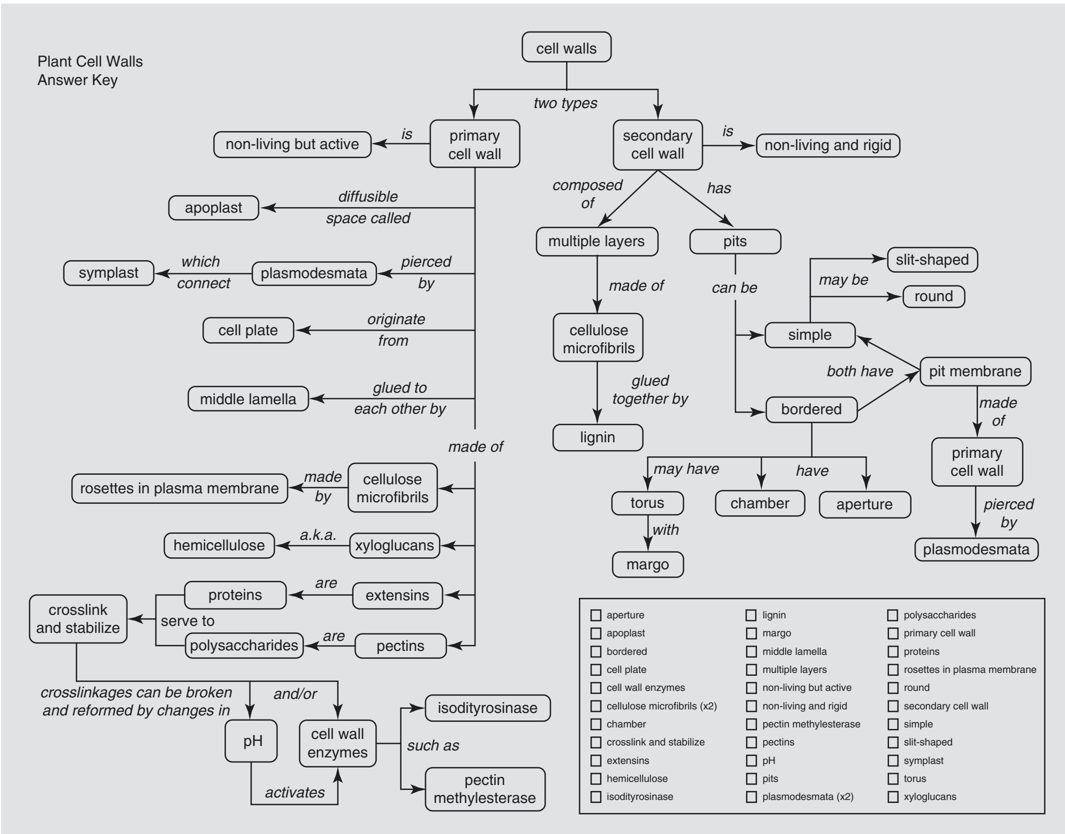
12. Amyloplasts (also called statoliths) in the root cap settle in response to the gravitational field, interact with the endoplasmic reticulum at the "bottom" of the cell, and indicate which direction is down. The root cap cells then send signals to the adjacent root tip cells to induce cellular division and elongation in a directional manner.

13. Shoot lateral organs originate exogenously, whereas lateral root organs must originate endogenously because the shoot is growing through air but the root is growing through soil. If a root produced a lateral root at the tip of a developing primary root, that young lateral root would be torn off as the primary root is pushed downward through the soil. Therefore, lateral roots develop further back on the root, where forward expansion has stopped. The only meristematic tissues available at that part of the root are the internal pericycle. Developing leaves, on the other hand, face no resistance as the shoot tip on which they are borne pushes through the air.

Chapter 5: Cell Walls

Concept Connections

1. Concept map answers



Concept Assessment

2. c
3. a
4. e
5. a
6. b
7. d
8. e
9. e
10. d
11. e

Concept Applications

12. Woody plants would be the plant of choice as they produce more biomass per year. In addition, woody plants keep the carbon sequestered for multiple years, whereas herbaceous plants typically have shorter life spans and their carbon is quickly returned to the atmosphere as they die and decompose.

13. Pectins form the basis of the glue that holds cells together. PMEs break down the pectin, cells detach from one another, and the fruit "softens."

Chapter 6: Parenchyma, Collenchyma, and Sclerenchyma

Concept Connections

1. Answers
   a. Angular collenchyma
   b. Annular collenchyma
   c. Astrosclereids
   d. Brachysclereids
   e. Fibers
   f. Lacunar collenchyma
   g. Lamellar collenchyma
   h. Sclereid (xylem vessel element)

Concept Assessment

2. d
3. b
4. d
5. e
6. a
7. c
8. b
9. d
10. b
11. e

Concept Applications

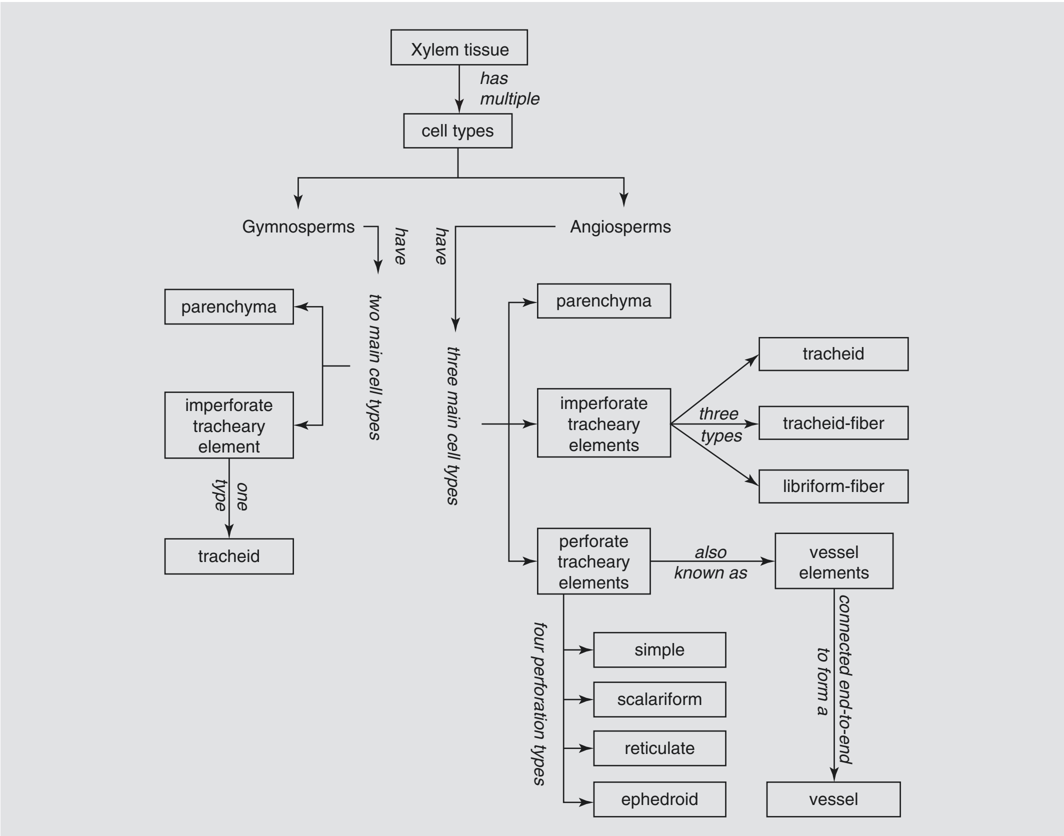
12. Animal body plans, and the names of the tissues, organs, and cells within those body plans, are arranged around "systems." Namely, there is a circulatory system, nervous system, digestive system, excretory system, etc. Each system may have multiple organs such as the esophagus, stomach, small intestine, and large intestine of the digestive system. Animal anatomy is taught from the system standpoint. Plant body plans, on the other hand, are arranged around organs—leaf, stem, root, flower, and fruit—and each organ is composed of a mixture of parenchyma, sclerenchyma, and collenchyma cells. Therefore, understanding plant anatomy is best approached by understanding the characteristics of those three cell types and then integrating them into tissues (dermal, ground, vascular) and then organ.

13. Totipotency is the ability of a cell to develop into multiple different cell types. In humans and other animals, these are typically called "stem cells" and are restricted, for the most part, to cells of the embryo. Once an embryonic stem cell heads down a developmental pathway, it is very difficult or impossible to revert to totipotency. The majority of plant cells are parenchyma, and many of those retain their totipotent ability into maturity. Meristematic cells, which are found in apical meristems, lateral meristems, and open vascular bundles, remain totipotent for the entire life of the plant.

Chapter 7: Xylem

Concept Connections

1. Concept map answers



Concept Assessment

2. e
3. b
4. c
5. d
6. e
7. a
8. b
9. d
10. a
11. b

Concept Applications

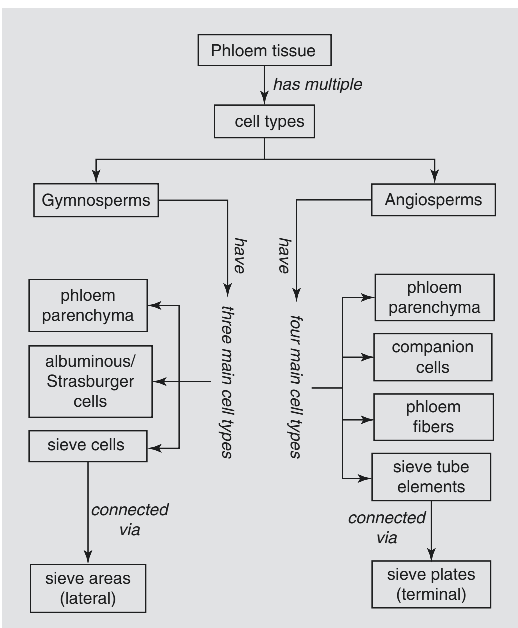
12. Angiosperm secondary xylem consists of three types of imperforate tracheary elements (tracheid, tracheid-fiber, libriform-fiber) and perforate tracheary elements (vessel elements) and xylem parenchyma. Gymnosperm secondary xylem has one type of imperforate tracheary element (tracheid) and xylem parenchyma. All of the tracheary elements function, to smaller or greater degrees, in water conduction and support. The parenchyma cells serve roles in storage and water balance. The cells perform similar functions in both angiosperms and gymnosperms, but the greater diversity of tracheary elements in angiosperms allows them to occupy a greater diversity of ecological niches.

13. Water is cohesive. Therefore, water exits the stoma via transpiration and in turn draws water from the leaf mesophyll, leaf vasculature, petiole, stem, root, and eventually soil. Because the water is being pulled, not pushed, it is always under tension during times of active transpiration (typically daytime). Water adheres to the inner surfaces of the tracheary elements and does not drain back to the roots when transpiration stops (typically nighttime). Cavitation is the formation of bubbles of water gas and occurs when the water column is pulled too hard (because the air or soil, or both, is dry). Cavitation events block water flow through that tracheary element and have been a powerful driver of tracheary element evolution.

Chapter 8: Phloem

Concept Connections

1. Concept map answers



Concept Assessment

2. e
3. c
4. d
5. a
6. e
7. c
8. d
9. b
10. e
11. a

Concept Applications

12. Angiosperm secondary phloem is composed of sieve tube elements (STE, responsible for translocation of photosynthate), companion cells (STE metabolic support, phloem loading/unloading), phloem parenchyma (storage and water balance), and phloem fibers (support). Gymnosperm secondary phloem contains sieve cells (SC, translocation) and albuminous/Strasburger cells (SC metabolic support, loading/unloading).

13. Phloem sap movement (translocation) as described by the Münch pressure flow hypothesis is osmotically driven. Osmotically active photosynthate molecules (sugars) are actively loaded into the STE in the source tissue, which decreases the water potential of the phloem sap. This causes an influx of water via osmosis (supplied by the adjacent xylem tissue) and a pressurization of the STE. The phloem sap is then forced toward the sink cells, where the sugars are actively unloaded, water follows the

osmolytes, and the pressure drops. A water potential gradient is established between the source tissues (higher pressure) and the sink tissues (lower pressure). Therefore, the sugar molecules being translocated are responsible for creating the water potential gradient that drives their own transport.

Chapter 9: Epidermis

Concept Connections

1. Matching answers:
    - i. (j) Anomocytic stomatal complex (*Betula papyifera* leaf)
    - ii. (i) Pavement cells (*Acer negundo* leaf)
    - iii. (e) Multicellular non-glandular trichome (*Solanum tuberosum* leaf)
    - iv. (f) Epidermal waxes (*Phaseolus vulgaris* leaf)
    - v. (h) Glandular trichome (*Juglans nigra* fruit)
    - vi. (g) Silica bodies (*Setaria* sp. leaf)
    - vii. (a) Hypostomatous leaf (*Epipactis* sp. leaf)
    - viii. (c) Paracytic stomatal complex (*Eichhornia crassipes* leaf)
    - ix. (b) Non-glandular trichomes (*Cucurbita* sp. leaf)
    - x. (d) Amphistomatous leaf (*Lactuca* sp. leaf)

Concept Assessment

2. d
3. a
4. c
5. a
6. e
7. c
8. e
9. a
10. e
11. a

Concept Applications

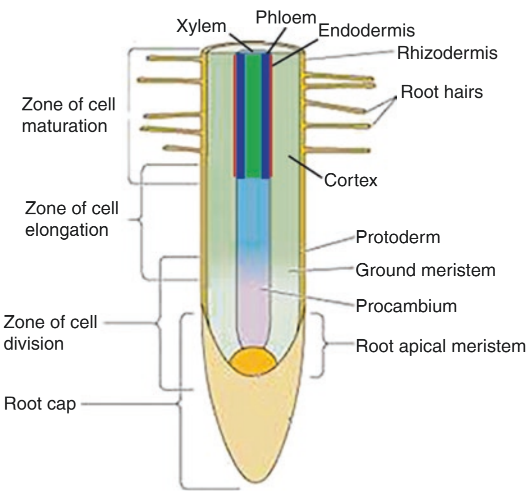
12. Chaparral is an ecosystem of shrubs and heaths found in the southwestern USA and the northern Baja of Mexico. It is characterized by a Mediterranean climate of hot, dry summers and cool, wet winters. Chaparral plants develop thick waxy cuticles to preserve moisture during the summer droughts. Many of the species are drought deciduous and shed their leaves in the summer. The chaparral ecosystem has evolved to withstand fires on a 10–20-year cycle. Fire repression by humans generates a multiyear accumulation of dry, wax-coated leaf litter which represents a significant "fuel load." In such areas, fires can be extremely severe and have devastating impacts.

13. Stomatal density is somewhat sensitive to the carbon dioxide concentration present during leaf development, with fewer stomata under high CO_2 levels. Scientists have quantified stomatal densities on fossil leaves and used those values as a proxy for the [CO_2] at the time the leaf was fossilized.

Chapter 10: Roots

Concept Connections

1. Labeled as Fig. 10.3 a. The procambium gives rise to the xylem, phloem, and pericycle. The ground meristem gives rise to the cortex and the endodermis. The protoderm gives rise to the rhizodermis which gives rise to the root hairs.



Concept Assessment

2. b
3. d
4. c
5. c
6. b
7. a
8. d
9. e
10. c
11. b

Concept Applications

12. Stem cuttings work because stems have nodes from which more stem, leaves, and adventitious roots can develop. Roots do not have nodes and cannot produce stems or leaves.

13. The roots respond normally; they grow downward. So do the shoots, they grow upward. However, because the roots are constrained by the bottom of the bucket, they are forced to grow laterally and, to a certain degree, up the insides of the container. The shoots are pulled down by their weight and the weight of the fruit, even though the shoot tips point upward. It is a completely artificial orientation, but as long as the roots can get water and the shoots can get light, the plant will survive.

Chapter 11: Stems

Concept Connections

1. Answers to matching:
   a. Rhizome = storage, perennation, and asexual reproduction
   b. Corm = perennation and storage
   c. Stolon = asexual reproduction
   d. Cladode = photosynthesis
   e. Tendril = attachment

Concept Assessment

2. d
3. d
4. e
5. a
6. b
7. a
8. e
9. c
10. a
11. d

- **Concept Applications**

12. Palms and bamboo take advantage of the ability of each vascular bundle to generate fibers to both the interior (adaxial) and exterior (abaxial). Each of the hundreds of vascular bundles in the stem ("trunk") becomes heavily sclerified which imparts great strength to the stem.

13. The primary thickening meristem covers the stem apex. At its center, the divisions are perpendicular to the stem axis and contribute to the length of the stem. As the apex grows in length, those meristematic cells are pushed and reoriented to the side where they divide in a plane parallel to the stem axis and contribute to the width (girth) of the stem.

Chapter 12: Leaves

- **Concept Connections**

1. Answers to matching:
   a. Foliage = ii. photosynthesis = f. *Rosa* sp.
   b. Leaf sheath = i. support = *c.* many grasses
   c. Cataphyll = v. protection = *h.* bud scales
   d. Frond = iv. photosynthesis = *g.* ferns and duckweeds
   e. Pseudostem = i. support = *k. Musa* sp.
   f. Scutellum = absorption = *d.* monocotyledon seed
   g. Needle = vi. photosynthesis = *i.* conifers
   h. Spine = iii. antiherbivory = *b.* cacti
   i. Cotyledon = vii. food storage = *a. eudicotyledon* seed
   j. Hypsophyll = viii. floral structures = *e.* flowering plants
   k. Tendril = x. attachment = *j. Clematis* sp.

- **Concept Assessment**

2. c
3. a
4. b
5. e
6. c
7. d
8. b
9. d
10. b
11. a

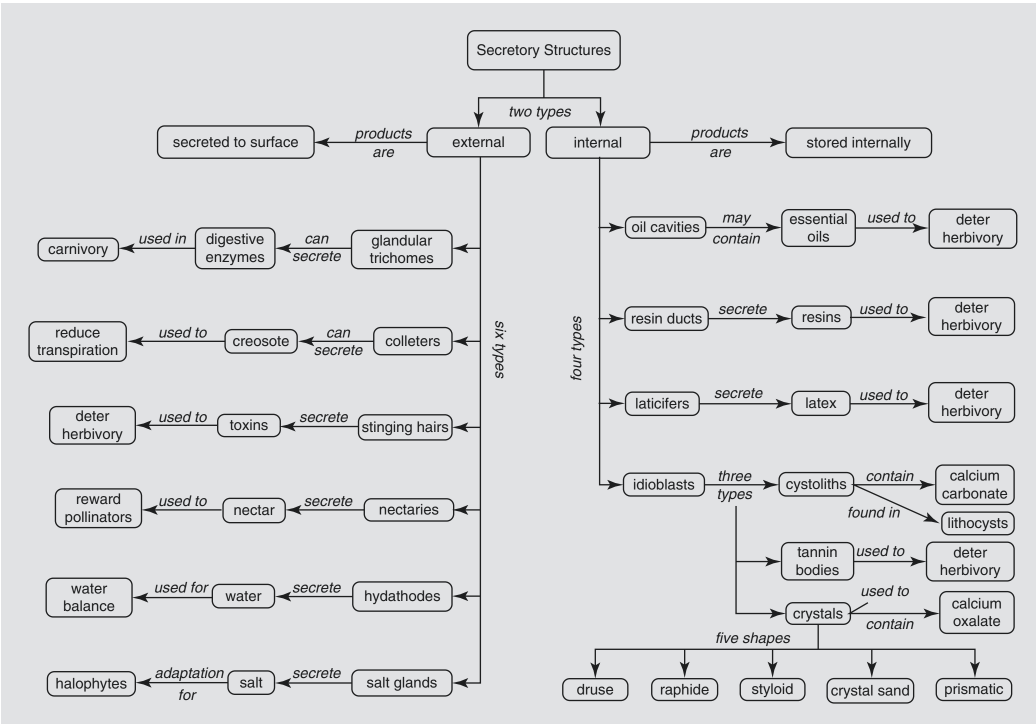
- **Concept Applications**

12. Leaves of the xeromorphic *Nerium oleander* leaf have a thick cuticle, stomatal crypts, and numerous trichomes extending into the crypt. All of these features are adaptations of the leaf epidermis. The cuticle prevents water loss through the epidermis. The stomatal crypts and trichomes create a dead-air space to which the stomata are exposed, thus reducing transpiration.
13. Most gymnosperms are "evergreen," meaning they retain their leaves for multiple growing seasons. The period of the year between the favorable growing seasons is usually cold and dry (ground water is frozen and in the solid state). Therefore, their leaves have xeromorphic adaptations as mechanisms for surviving the "drought" of winter.

Chapter 13: Secretory Structures

Concept Connections

1. Concept map answers



Concept Assessment

2. e
3. b
4. d
5. b
6. b
7. a
8. c
9. c
10. e
11. a

Concept Applications

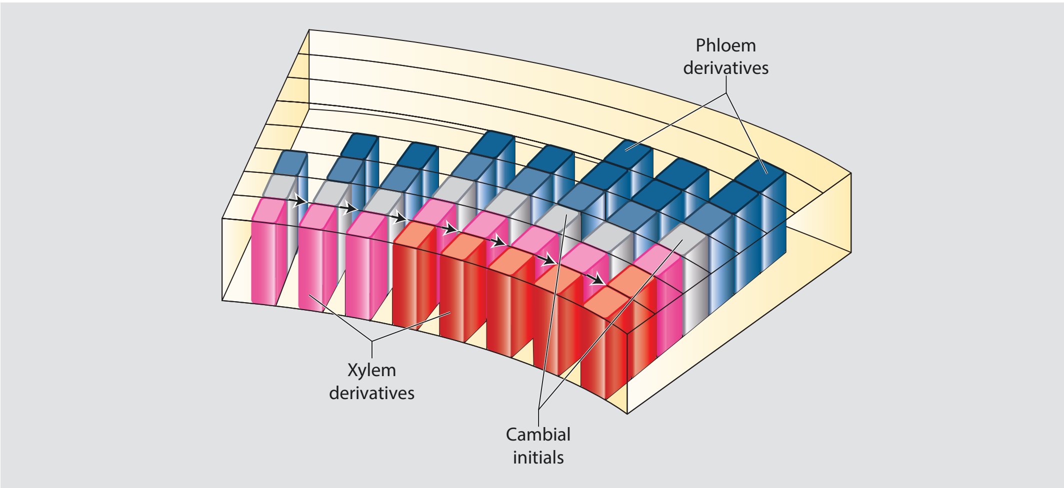
12. Antiherbivory structures include stinging hairs, laticifers, oil glands, resin ducts, crystal-containing idioblasts, and glandular trichomes. They all serve to deter feeding by stinging, trapping, or poisoning animals—mostly, but not exclusively, insects.

13. The connection between carnivory and high light has to do with competition. Noncarnivorous plants do not grow well in the low-nutrient environments to which carnivorous plants are adapted. Therefore, carnivory provides a competitive advantage and allows such plants to grow where others will not.

Chapter 14: Vascular Cambium

- **Concept Connections (Springer to Redraw)**

1. Labeled drawing



- **Concept Assessment**

2. c
3. b
4. d
5. b
6. b
7. a
8. c
9. c
10. e
11. a

- **Concept Applications**

12. Closed vascular bundles lack a vascular cambium and cannot generate new vascular tissues. That is to say, they cannot contribute to secondary growth, only primary growth. Open bundles have a vascular cambium and can contribute to secondary growth.
13. Holoparasites rely on the host plant for water (via a xylem connection) and photosynthate (via a phloem connection). They get all of their nutrition from the host and do not need to photosynthesize.

Chapter 15: Wood – Economics, Structure, and Composition

- **Concept Connections**

a. *Sassafras albidum*
b. *Quercus rubra*
c. *Carya illinoinensis*
d. *Diospyros virginiana*
e. *Juglans cinerea*
f. *Ilex opaca*
g. *Malus domesticus*
h. *Albania julibrissin*
i. *Cornus florida*
j. *Magnolia virginiana*

Concept Assessment

2. b
3. d
4. b
5. e
6. e
7. b
8. e
9. b
10. c
11. c

Concept Applications

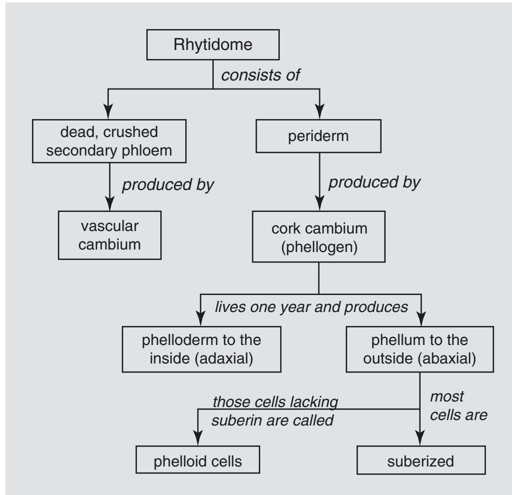
12. For the boat building industry engineer, select for slow growth (strength) and tyloses. For the furniture industry engineer, select for slow growth (strength), maximum heartwood (color), and different patterns of vessel element distribution (to generate figure). For the paper industry engineer, select for fast growth (maximum production, easier to chip) and minimal lignin (easier to digest or macerate).

13. Students might access the following websites for their minute paper:
    Forest Stewardship Council – ► https://ic.fsc.org
    Weyerhaeuser – ► https://www.weyerhaeuser.com/timberlands/forestry/sustainable-forestry/
    Georgia Pacific – ► https://www.gp.com/Company/Sustainability/Forestry
    World Resources Institute – ► http://sustainableforestproducts.org/

Chapter 16: Periderm

Concept Connections

1. Concept map



Concept Assessment

2. d
3. a
4. c
5. e
6. c
7. b
8. d
9. e
10. d
11. b

Concept Applications

12. The cork removed from the cork oak (*Quercus suber*) is only the dead outer bark. The living, inner bark is left intact. Overharvesting just the outer bark would do little damage, but the yield would be low and result in a lower quality of cork. Removing the vascular

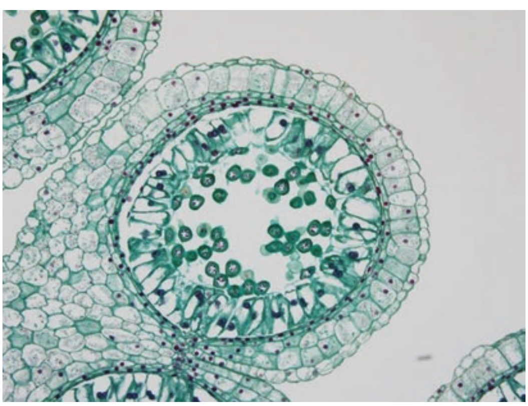
cambium, the living secondary phloem, or the inner bark (vascular cambium, living secondary phloem, and phellogen) would kill the tree.

13. Both the vascular cambium and the cork cambium generate cells that make up the rhytidome. The vascular cambium persists for the entire life of the tree. It produces secondary xylem to the interior and secondary phloem to the exterior. A growing season's worth of secondary xylem accumulates each year and forms annual tree rings. The secondary phloem, which consists of conducting cells and fibers, is crushed each year, and those dead cells intermingle with the periderm cells to form the rhytidome. The phellogen (usually) arises from the cells of the cortex, produces the periderm (phelloderm to the interior and phellem to the exterior), and ceases activity at the end of the growing season. A new phellogen arises the next year, or multiple phellogens may arise in a single growing season.

Chapter 17: Floral Development and Male Reproduction

Concept Connections

1. epidermis (1), connective (2), tapetum (3), and developing microspores (4).



Concept Assessment

2. c
3. a
4. e
5. c
6. a
7. e
8. c
9. e
10. e
11. b

Concept Applications

12. While both genera are within the same plant family (Asteraceae), the goldenrod pollen has evolved a sticky pollen to facilitate dispersal by insects. In contrast, ragweed has evolved to be buoyant in the air.
13. The evolution of exine structure appears to be related to how the pollen is physically dispersed between plants. For example, terrestrially dispersed pollen has a thicker exine than amphibiously dispersed pollen. Pollen from hypohydrophilous plants that are underwater has very thin exine and may be coated with remnants of the tapetum.

Chapter 18: Female Reproduction and Embryogenesis

Concept Connections

1. Crossword puzzle answers:
   1. Cordate
   2. Axile
   3. Funiculus
   4. Cotyledon
   5. Integument
   6. Inferior
   7. Suspensor
   8. Endosperm
   9. Proembryo

10. Double
11. Superior
12. Basal
13. Chalaza
14. Megagametogenesis

Concept Assessment

2. c
3. b
4. b
5. e
6. e
7. a
8. c
9. a
10. c
11. a

Concept Applications

12. The evolution of double fertilization was likely due to the efficiency of providing for offspring (producing endosperm) only when embryos were developing. Hence, less waste occurs as nutrients are only produced for offspring when needed.

13. Pollination is a process that occurs prior to fertilization. It takes time for sperm cells within the pollen tube of an angiosperm to get to the egg cells within the embryo sac. Given that the number of ovules within a flower is limited, the sperms must compete with those from other pollen grains in fertilizing egg cells, resulting in pollen tube competition. Thus, we see natural selection occurring at the level of the gametophyte.

Chapter 19: Fruit, Seeds, and Germination

Concept Connections

1. Identify
    a. Emerging leaves
    b. Hypocotyl hook
    c. Cotyledon
    d. Seed coat
    e. Hypogeal (even though a bit of the cotyledon is visible above the soil)
    f. Eudicot (mung bean—*Vicia faba*)

Concept Assessment

1. d
2. b
3. a
4. b
5. a
6. e
7. c
8. d
9. d
10. a

Concept Applications

11. a. The Tariff Act of March 3, 1883, declared that a tax be paid on vegetables imported to the USA. Fruits were excluded from the act. John Nix was an importer of fruits and vegetables in New York City. The tax collector of the Port of New York, Edward Hedden, had assessed taxes on Mr. Nix's imported tomatoes, claiming they were vegetables, and therefore subject to the Tariff Act. Nix sued Hedden to recover the tariffs paid on the basis that tomatoes are (botanically) fruit and should therefore be exempt from the act. Nix lost.

b. When tomatoes were introduced to Europe in the 1500s, they were seen as exotics and cultivated and eaten by aristocrats more so than the common person. Aristocrats could afford to use pewter plates, those of lesser classes could not. Pewter is an alloy of lead and tin. Tomatoes are naturally acidic. Serving a tomato dish on pewter plates extracts the lead from the pewter, which can lead to lead poisoning.

c. In 1753 Carolus Linnaeus applied the name *Solanum lycopersicum* to tomato, the same genus as potato. In 1768, Philip Miller moved the plant to a different taxon and changed the name in to *Lycopersicon esculentum*. It was not until the 1990s—over 200 years—before the error was corrected and the designation by Linnaeus was recognized as valid.

12. a. An aggregate fruit is a made of multiple individual carpels on a single flower, each of which generates an individual fruit. All of the individual fruits remain attached to the same receptacle. A multiple fruit is composed of the ovaries of multiple individual flowers fused together.

b. A drupe is a fleshy fruit derived from a single carpel. All three pericarp layers (exocarp, mesocarp, and endocarp) are fleshy. An achene is a dry, indehiscent fruit in which all the pericarp layers are sclerified and fused together.

c. In epigeal germination, the cotyledons (and the first internode to which they are attached) are pushed above the soil surface. In hypogeal germination, the cotyledons (and the first internode to which they are attached) remain below the soil surface.

Glossary

abaxial Facing away from the axis of stem or root (as opposed to adaxial). Also, typically the lower surface of leaves.

abscisic acid A plant growth regulator involved in abscission, germination, flowering, senescence, and other processes.

abscission The dropping of leaves, fruits, or floral structures upon maturation or at the end of a growing season.

abscission zone The layer of cells which transverses the structure (e.g., petiole) which is separated in the process of abscission.

accessory fruit A fruit composed primarily from tissues other than the ovary.

acicular crystal Typically, a calcium oxalate crystal which is elongated into a needle shape, such as raphides and styloids.

acropetal Directed toward the apex of an organ, e.g., the tip of a stem or root.

achene A dry, indehiscent fruit with a single carpel characterized by the fusion of the exocarp, mesocarp, and endocarp into a thin, hard layer which is not fused to the seed, for example, sunflower and strawberry.

actin A globular protein often organized into two filamentous strands wound around each other. An important component of the cell cytoskeleton.

actinostele A protostele that is star-shaped in cross-sectional view.

adaxial Facing toward the axis of stem or root (as opposed to abaxial). Used to describe the upper surface of leaves.

adnation Fusion of stamens, pistils, or petals in a flower involving different whorls.

adventitious Anomalous growth of tissues or organs as in the growth of roots directly from stems and/or leaves.

aerenchyma Parenchymatous tissue characterized by air spaces between cells.

aggregate fruit A fruit developing from a single flower but with multiple carpels.

albedo The white, air-filled mesocarp of a hesperidium. See flavedo.

albuminous cells Found in gymnosperm phloem where cells which are functionally and structurally similar to companion cells exist but do not originate from the same precursors as do the companion cells in angiosperms. Same as a **Strasburger cell**.

aleurone layer The outermost layer of the endosperm in grass seeds which are characterized by large protein deposits and enzymes which can degrade the endosperm.

alternation of generations A life cycle characteristic of higher plants that have both haploid and diploid phases.

aliform xylem parenchyma A pattern of xylem parenchyma in which the parenchyma forms winglike extensions around the vessels.

amphicribral vascular bundle A concentric vascular bundle in which the phloem surrounds the xylem tissue.

amphiphloic siphonostele A stele in which the vascular system appears as a tube with the phloem located on both the external and internal sides of the xylem.

amphistomatous leaves Having stomata on both adaxial and abaxial surfaces of a leaf.

amphivasal vascular bundle A vascular bundle in which the xylem surrounds the phloem.

amyloplast A colorless plastid containing starch grains, involved in starch storage and graviperception.

anabolism Utilizing energy to synthesize molecular structures. See catabolism.

anaphase That phase of mitosis or meiosis in which the separation of chromatids takes place in the opposite poles of the cell.

anatropous A configuration of an ovule in which it is bent downward with the micropyle adjacent to the funiculus.

androecium Collectively, all of the stamens in the flower of a seed plant.

anemophilous Pollinated by wind.

angiosperm Higher plants in which seeds are borne within a mature ovary.

angular collenchyma Collenchyma cells in which the primary wall is thickened at intercellular sites with adjacent cells.

anomalous vascular cambium Unusual growth (usually of secondary nature) from vascular cambium.

annual plant A plant that completes its life cycle in 1 year and then dies.

annual ring The growth of xylem tissues formed in a single growing season as observed in transectional view.

annular cell wall thickenings Secondary wall thickenings appearing as rings in xylem tracheary cells.

annular collenchyma Collenchyma cell in which the primary wall is uniformly thickened.

antechamber A recessed space beneath the stomatal opening.

anther The pollen sack typically at the terminus of a stamen.

anthesis The time period during which the flower is open and available to release and/or accept pollen.

anthocyanin A red, purple, or reddish-blue water-soluble pigment found in the cell vacuole.

anthropogenic Of human origin or cause.

anticlinal A plane of growth or development at right angles to the nearest surface.

antiherbivory compounds Any one of hundreds of secondary compounds produced by plant leaves, stems, or roots that serve to deter herbivory.

antipodals In angiosperms, the cells at the opposite end of the embryo sac from the site of the zygote.

aperture A thin plate of exine covering an opening through which the pollen tube may emerge (in pollen). May also be an opening into a pit from the interior of a cell.

apical cell A cell found at the apex which is typically the origin, or initial, of a meristem.

apical dominance Situation in which the central stem grows more vigorously than the lateral branches.

apical meristem A group of mitotically dividing cells found in the apical region of a root or shoot and which give rise to primary tissues.

apical tip growth Growth at the pollen tube tip.

apocarpy The lack of fusion between carpels in a flower (also free carpels).

apoplast Region of the plant body outside of the living cell contents, typically limited to the cell wall and intercellular spaces.

apoplastic loading The process of phloem loading seen in some plants in which the photosynthate is exported from the companion cell to the apoplast and then taken up by sieve tube elements. See symplastic loading.

apotracheal xylem parenchyma That parenchyma in wood which is not closely associated with vessel members.

apposition Growth of cell wall by successive deposition of layers of wall material.

areole A leaf mesophyll region limited by vascular tissues around it.

articulated laticifer Fusion of two or more cells in a laticifer in which the partitioning walls are partly or wholly lacking.

aspirated pit A bordered pit in gymnosperm wood in which the pit membrane is displaced to one side and the torus blocks the aperture.

astrosclereid A branched sclereid.

atactostele A stele with the vascular bundles scattered throughout the ground tissue.

atrichoblast A rhizodermal cell that does not give rise to a root hair.

autotroph An organism capable of making its own food substances from (usually) light energy and producing organic material from CO_2 as a raw material.

autumnal senescence In leaves, a genetically controlled process of resource recovery that takes place in the fall and ends in leaf abscission.

axial parenchyma That parenchyma found in the vertical axis of a plant, not associated with rays.

axial vascular system Secondary vascular cells derived from cambial initials and with their axis running parallel with the axis of the stem or root.

axial tracheid Tracheids in the axial system of secondary xylem, in contrast to ray tracheids.

axis The upper (and usually smaller) angle between a stem and the petiole of a leaf.

axile placentation A form of placentation in which ovules are attached at the center (the axis) of a compound ovary.

axillary bud A bud found in the axil of a leaf.

axillary meristem The meristematic region in the axil of a leaf that gives rise to an axillary bud.

banded xylem parenchyma A pattern of xylem parenchyma in which the parenchyma appears as large bands.

bark A general term for all tissues outside of the vascular cambium.

basal placentation A form of placentation in which ovules are attached at the base of the ovary.

bast fiber Any fibrous tissue outside of the xylem, primarily phloem fibers.

berry A fleshy fruit with multiple carpels characterized by a papery exocarp and fleshy mesocarp and endocarp, for example, tomato.

bicollateral vascular bundle A vascular bundle with phloem on two sides of the xylem.

biennial plant Higher plants that require 2 years to complete their growth cycle; the first year is vegetative growth and the second year reproduction and death.

bifacial initials Secondary growth at two sites, e.g., cork cambium is producing cork while vascular cambium is producing vascular tissues.

bifacial leaf Leaf with palisade mesophyll on one side of the leaf (within the epidermis) and spongy mesophyll on the other.

birefringence Having a refractive property to light that alters its pathway, often characteristic of crystals.

biforine cell An idioblast in the leaf or stem of plants in the Araceae containing a bundle of raphide crystals.

biseriate ray A vascular tissue ray that is two cells wide.

bordered pit A pit in the secondary wall which overarches the pit membrane.

bordered pit-pair The pairing of bordered pits from adjacent cells.

boundary layer resistance The resistance imposed on leaf gas exchange by still air on the leaf surface.

brachysclereid A thick-walled sclereid that is nearly isodiametric.

branch root A root arising from the pericycle of the primary root. Same as **lateral root**.

Brownian movement Microscopic random movement of small particles due to bombardment of surrounding molecules.

bulliform cell In grasses, it appears as a large epidermal cell arranged in a row that may regulate the rolling or unrolling of the leaf.

bundle sheath One or more layers of cells which enclose a vascular bundle in a leaf. While usually parenchyma cells comprise the bundle sheath, they may also be composed of sclerenchyma cells.

bundle sheath chloroplast In C_4 plants, chloroplasts in the bundle sheath are agranal and lack photosystem II activity.

bundle sheath extension An extension of the bundle sheath cells that extends to one or both of the epidermal layers in a leaf.

C_3 photosynthesis Plants that only use the Calvin cycle to produce carbohydrates but also undergo photorespiration.

C_4 photosynthesis Plants that convert CO_2 by means of a two-stage process into a four-carbon molecule and do not have photorespiration.

callose Depositions of ß-1,2 glucan (a carbohydrate which can be hydrolyzed to glucose residues) on sieve plates in phloem, as partitions in pollen tubes, and occasionally in parenchyma cells.

callosic wall A temporary cell wall, made of callose, that forms around developing pollen grains.

calyptrogen Meristematic cells (histogen) of the root tip which give rise to the root cap. Characteristic of monocots.

calyx Collectively, all the sepals of a flower.

cambial initials Cells of the vascular cambium which give rise through periclinal divisions to either phloem or xylem (fusiform initials) or to rays (ray initials).

cambial zone While technically only a single layer of cells that produces both xylem and phloem, it is a region of cells that may include both tissues due to inability to accurately distinguish the individual cells.

cambium Lateral meristematic cells of either vascular cambium or cork cambium.

candelabra trichome A highly branch trichome.

capsule A dry, dehiscent fruit type characterized by multiple capsules. See also poricidal, loculicidal, and septicidal fruit.

carotenoid Naturally occurring plant pigments appearing red, orange, and yellow for the most part.

carpel Highly modified leaflike organs in angiosperm flowers that produce one or more ovules.

caryopsis A dry, indehiscent fruit with a single carpel characterized by the fusion of the exocarp, mesocarp, and endocarp into a thin, hard layer which are fused to the seed and seed coat, for example, maize and wheat.

Casparian strip Deposits of suberin and lignin on the radial and transverse anticlinal walls of the root endodermis which limit the flow of water and solutes through the apoplast.

catabolism The breakdown of larger molecules to form smaller ones while releasing energy. See anabolism.

cataphyll A leaf modified to perform functions other than photosynthesis such as protection of an immature bud.

cavitation The process by which liquid water will undergo a phase change to gaseous water within the xylem of gymnosperms and angiosperms. Occurs most frequently under conditions of high transpirational demand (high tension).

cell cycle The process of cell division, typically mitosis, giving rise to daughter cells.

cell plate The partition of cell wall material that appears during the latter stages of mitosis and which becomes the new primary cell wall that separates the daughter cells.

cell wall The nonliving materials deposited outside of the plasmalemma which give rigidity, form, and protection to the cell. Typically composed of cellulose and other organic materials that may contain extracellular enzymes and other substances. See primary cell wall and secondary cell wall.

cellular endosperm An endosperm divided into multiple cells, due to cytokinesis following mitosis. See nuclear endosperm.

cellulose A polysaccharide component of primary cell walls consisting of a glucan polymer of indeterminate length, typically gathered into bundles forming microfilaments. A principal component of primary cell walls and the scaffolding for secondary walls.

cellulose synthase complex A transmembrane protein complex responsible for the production of cellulose microfibrils.

central cell A large binucleate cell of the megagametophyte that will develop into endosperm after double fertilization.

central mother cell Dominant cell that gives rise to meristematic initials in multiple directions; in root tip, it is covered by the root cap.

centrarch xylem A pattern of xylem development in which xylem is initiated in the center and matures in an outward direction. Only found in early (extinct) land plants.

centric Morphology of monocot leaves that are cylindrical in cross-sectional view.

centrifugal Refers to movement or development progressively away from the center.

centripetal Refers to movement or development progressively toward the center.

chalaza The site of an ovule opposite the micropyle and adjacent to the stalk region.

chemoautotrophic An autotrophic organism which uses energy from chemical degradation as opposed to light energy. Found among microorganisms.

chlorenchyma Any parenchyma tissue containing chloroplasts.

chlorophyll Any of several closely related green pigments that capture light energy used in the initial steps of photosynthesis.

chloroplast A photosynthetically active organelle with chlorophyll pigments organized into thylakoid membranes usually arranged in stacks. The organelle is typically bounded by two membranes and is found in eukaryotic plants.

chromatin DNA and associated protein of a cell which is (typically) not in a chromosomal state, i.e., in an interphase nucleus. May be euchromatin or heterochromatin.

chromoplast A plastid containing pigments other than chlorophyll, usually carotenoids.

chromosome Rodlike structure containing units of genetic information as DNA in association with histone proteins. Formed within the nucleus of eukaryotic cells.

circular bordered pit A bordered pit with a circular aperture.

cis face The forming face of a dictyosome.

cladode A stem whose primary function is photosynthesis. Those more stemlike may be called a "pad" (as in cactus). Those more leaflike are called a **cladophyll**, **phyllode**, or **phylloclade**.

cladogram A branching diagram depicting the successive point of species divergence from common ancestral lines.

cladophyll A flattened stem, functioning and appearing much as a leaf. Another name for **cladode, phyllode**, and **phylloclade**.

closed minor vein A minor leaf vein that does not have direct symplastic connections (via plasmodesmata) to the adjacent leaf mesophyll cells. Photosynthate is transferred apoplastically. See open minor vein.

closed vascular bundle A vascular bundle with no cambium tissue.

coenocyte Refers to usually large, multinucleate cells in plants.

coevolution A situation in which two or more species affect each other's structural evolution.

cohesion-adhesion-tension model The model that utilizes the properties of water to explain transpiration.

coleoptile In grasses, a leafy sheath which encloses the epicotyl of the embryo.

coleorhiza In grasses, a sheath that encloses the radicle of the embryo.

collateral vascular bundle A vascular bundle with phloem on the abaxial side of the xylem. The most common situation.

collenchyma Elongated cells with uneven primary cell walls and containing no lignin. Usually found in early development of stems and leaf petioles.

colleter A multicellular trichome of a leaf or bud scale that produces a sticky secretion.

columella The central part of a root cap in which the parenchyma cells are arranged in a series of columns. Involved in gravisensing.

commissural vein A small vascular bundle which connects the larger, parallel vascular bundle of grass leaves.

companion cell A living phloem parenchyma cell in angiosperms which is associated with a sieve tube member and was derived from the same mother cell.

compound light microscope An optical instrument designed for producing magnified images of objects using two or more glass lenses.

compound middle lamella A general term referring collectively to the middle lamella and the primary cell walls of two adjacent cells.

compound sieve plate A sieve plate composed of several patchy sieve areas.

compression wood A reaction wood in conifers characterized by dense structure at the lower side of limbs due to stress.

confluent xylem parenchyma A pattern of xylem parenchyma in which the parenchyma surrounding a vessel (called vasicentric parenchyma) extends to and coalesces with the parenchyma surrounding adjacent vessels.

confocal A type of light microscopy in which a point of illumination is projected or rastered over a specimen, and the reflected illumination is screened through an exit aperture in order to eliminate light from out-of-focus planes.

conjunctive tissue Secondary growth in which scattered vascular bundles are found within a parenchyma tissue.

connective A band of parenchyma cells that unites the lobes of an anther.

cork Nonliving cells with suberized walls and formed from cork cambium (phellogen). Also known as phellem.

cork cambium A lateral meristem producing cork centripetally in stems and sometimes roots.

corky layer In leaf abscission, a layer of cork cells formed where the petiole attaches to the stem. Also called separation layer.

corm A round, underground perennating organ. Commonly known as a bulb.

corolla Refers to all the petals of a single flower.

corpus A mass of meristematic cells in the apical meristem of roots and shoots which is covered by a less meristematically active tunica and in which divisions occur in various planes.

cortex Region found between the epidermis and the vascular system in roots and stems.

cotyledon The first leaf/leaves generated from a plant embryo. Function in food storage or absorption. See **scutellum**.

crassulae Ridgelike thickenings of the compound middle lamellae in tracheids of certain conifers. Appear near bordered pits, normally.

crista(e) The infolding(s) of the inner mitochondrial membrane possessing the electron transport mechanism.

cross-linking glycans Polysaccharides found in the primary cell wall that cross-link the cellulose fibrils. Formerly known as hemicelluloses

cross section Same as a transverse section.

cryptochrome Flavoprotein sensitive to blue light and functional in attracting pollinators as well as in regulating circadian rhythms.

crystal An accumulation of almost pure calcium oxalate formed in the vacuoles of idioblasts. Several shape variants are found; all are birefringent.

crystal sand Calcium oxalate crystals shaped like sand grains.

cuticular ledge The ending of the cuticle covering guard cells that provides an opening to the stoma.

cuticular membrane A layer of water-impervious material (cutin) deposited on the outer surfaces of epidermal cell walls, particularly in leaves. Often referred to as the cuticle.

cuticular transpiration The movement of gasses across the epidermal cuticle.

cutan A hydrophobic hydrocarbon polymer that makes up a minor portion of the cuticle. It differs chemically from cutin.

cutin A hydrophobic polyester polymer that is the primary material of the cuticle.

cystolith Inorganic deposits (usually calcium carbonate) on the inner surface of the cell walls of lithocysts.

cytokinesis The division of the remaining cytoplasmic substances in a cell aside from the nuclear events of mitosis.

cytoplasm All the living contents of a cell aside from the nucleus. Does not include vacuole or cell wall substances.

cytoplasmic sleeve Cytoplasmic content of a plasmodesma surrounding the desmotubule.

cytoplasmic streaming The movement of cytoplasm around the plant cell carrying a variety of substances and organelles.

cytoskeleton A network of protein filaments (microfibrils and microtubules) that give eukaryotic cells shape and movement. Are involved in directing chromosome movement, cell plate formation, orientation of chloroplasts, etc.

deciduous Plants with a loss of foliage at the end of a growing season.

decussate A leaf arrangement on stems in which alternating leaves are at right angles to one another.

deep-seated phellogen A phellogen that develops inside the organ, such as in the pericycle of a root. See superficial phellogen.

dehiscence The process of splitting open to release enclosed spores, seeds, or other reproductive structures.

dehiscent fruit Fruits which open spontaneously upon maturity and drying.

dendritic wood Vessel distribution in wood that appears to have a branched pattern when viewed in cross section.

dendrochronology The use of annual tree rings to reconstruct past climatological and meteorological conditions and date archeological artifacts.

denticulate fruit A dry, dehiscent, capsule-type fruit with a single carpel. Characterized by a large opening at the top ring by teeth at the top of the capsule. Ex: campion.

derivative A cell which comes from a meristem and undergoes differentiation into a specialized tissue. The sister cell from the mitosis in the meristem may or may not also become a derivative.

desmotubule A cylindrical membrane within a plasmodesma that connects the endoplasmic reticulum system of adjacent cells.

determinate growth Development to a point characterized by a fixed number of leaves or other lateral organs.

diarch Primary xylem of the root showing two strands or poles of protoxylem in cross-sectional view.

dichotomous venation Branching of veins within a leaf blade resulting in two new veins from each existing one. Found in ferns and in Ginkgo. See also dichotomous venation and reticulate venation.

dictyosome A functional unit of a Golgi apparatus. Characterized by a stack of membranes involved with secretory activities.

dictyostele Vascular system in which the phloem surrounds the xylem in anastomosing strands defined by a series of leaf gaps.

diffuse porous wood Wood characterized by a relatively uniform distribution of xylem vessels in the annual rings, so that the change from 1 year to the next is not easily distinguished.

diffuse secondary growth The differentiation of parenchyma cells scattered through the trunk into xylem and phloem in palm trees.

diffuse xylem parenchyma A pattern of xylem parenchyma in which the parenchyma is spread throughout the xylem in no apparent pattern.

dimorphic chloroplasts In C_4 plants, the mesophyll and bundle sheath chloroplasts vary in appearance and functionality.

dissected siphonostele A variant of stele architecture in which multiple leaf gaps result in a netlike arrangement. Also called a dictyostele.

distal The position of an object farthest away from the site of attachment or origin.

distichous The arrangement of leaves in two vertical rows on a stem.

discontinuous growth ring A temporary, but perhaps multiyear, cessation of the activity of the vascular cambium. No annual growth rings are produced during that time but the vascular cambium remains alive.

dormancy A period of growth and development is stopped.

dorsiventral A leaf characterized by having palisade mesophyll on one side and spongy mesophyll on the opposite side.

double fertilization The process of two sets of nuclear fusions in an embryo sac occurring at the same time, involving the fusion of egg and sperm as well as the fusion of a second male gamete with the two polar nuclei.

drought deciduous plant A plant that drops (abscises) its leaves during the dry season.

drupe A fleshy, single-carpel fruit characterized by a papery exodermis, fleshy or stringy mesocarp, and a hard, thick endocarp. Also called a stone fruit, for example, almond and peach.

druse Calcium oxalate crystals with a globular shape, usually with many spikelike processes on the surface.

early wood The same as springwood, which is formed first in the growing season and is often characteristically distinctive from the late (or summer) wood.

ectophloic siphonostele A stele characterized by xylem enclosing a pith region and with phloem outside of the xylem.

egg apparatus A group of three cells in the angiosperm egg sac consisting of one egg cell and two synergids.

elaioplast An oil-containing plastid found most prominently in the tapetum and involved in pollen maturation.

embryo A small, multicellular individual plant, enclosed in a seed, that upon germination will develop into a mature plant.

embryo sac In angiosperms, the female gametophyte which is multinucleate/multicellular. Also known as the **egg sac**.

enation Outgrowths of the stem in simple, primitive land plants. May be called microphylls to distinguish them from megaphylls which are true primitive leaves derived from a system of branches.

endarch xylem A xylem system in which the progression of development occurs to a direction away from the axial center. Typical of most seed plants.

endocarp The innermost layer(s) of the pericarp.

endodermis The innermost layer of ground tissue in a root representing modified cortex and possessing a Casparian strip on its anticlinal walls.

endogenous Arising from a deep tissue in the plant's organization, such as the development of branch roots from the pericycle of a primary root.

endoplasmic reticulum A series of (usually) flattened saclike membranes that extend throughout the cytoplasm of cells. Site of lipid and lipoprotein production. May be rough (with ribosomes attached) or smooth (with no ribosomes).

endosperm Typically a 3n tissue in the seeds of angiosperms formed by the fusion of a sperm nucleus with the two polar nuclei in an embryo sac. The endosperm is rich in proteins and carbohydrates that serve as a food substance for the early growing embryo.

endosymbiosis The concept of evolution from invasion of prokaryote cells into eukaryotic ones.

endothecium In anthers, it is a wall layer adjacent to the tapetum that lines the locules (or pollen sacs) and is characterized by secondary wall thickenings.

endothelium The innermost layer of the integument lining an embryo sac.

entomophylous Pollinated by insects.

epiblem The "epidermis" of a root, also called rhizodermis.

epicotyl The shoot of an embryo above the cotyledons.

epicuticular wax Wax deposits on the outer surface of epidermal cuticle in stems and leaves.

epidermis The outer layer of cells of a plant body derived from protoderm.

epigeal Growth of an embryo plant characterized by having the cotyledon(s) raised above the level of the ground.

epigyny A flower structure organized with the petals, sepals, and stamens above the ovary. In this case, the ovary is said to be inferior.

epiluminescence Illumination for microscopy in which the light source is above the specimen. Commonly used in confocal microscopy.

epistomatal cavity In gymnosperms, a cavity to the exterior of the guard cells and overarched by epidermal subsidiary cells.

epistomatic leaves Possessing stomata only on the upper (adaxial) surface of a leaf.

epithelium Parenchyma cells lining a duct or cavity, which are typically secretory in nature.

epithem Modified leaf mesophyll cells between minor vein endings and a hydathode pore. Cells may form a structure as transfer cells.

erect ray cell A cell at the periphery of a ray that is elongated in the axial direction.

etioplast A plastid developed in the dark or under very low light levels and having a prolamellar body with no chlorophyll.

eudicotyledonous plants Members derived from the Magnoliopsida that possess two cotyledons. Believed to be ancestral to monocotyledonous plants.

eumetazoan The major clade of animals, based on having a tissue level of organisms. Includes all multicellular animals except sponges.

eustele A stele in which the primary vascular tissues are arranged in strands around the pith.

exalbuminous seed A mature seed lacking endosperm.

exarch xylem A xylem in which the oldest members are located away from the axis, as in most roots.

exine The outer, rather rigid and resistant wall of pollen grains, primarily composed of sporopollenin.

exocarp The outer layer of pericarp.

exocytosis The release of vesicular materials to the outside of a cell. The opposite of endocytosis.

exodermis The outer layer of root cortex cells functioning as a hypodermis.

exogenous Developing from superficial tissue, as in the development of leaves and flowers at the shoot apical meristem.

external phloem Primary phloem located outside, or external to, the primary xylem.

extrafloral nectary A nectary occurring outside of a flower. Compare to floral nectary.

extraxylary fibers Fibers found in regions outside of the xylem.

fascicle A bundle, usually vascular.

fascicular cambium That vascular cambium derived from a vascular bundle.

fertilization The fusion of male and female gametes to produce a 2n (diploid) zygote.

fiber An elongated narrowly tapered sclerenchyma cell with thickened cell wall and typically no living cytoplasm at maturity.

fiber tracheid A cell intermediate between a fiber and a tracheid, with characteristics of both.

fibrillin Proteins in chloroplasts that help maintain plastoglobuli structure.

fibrous roots Roots characterized by many similar branching roots of common length and thickness. Generally not highly adapted for food storage.

fibrovascular bundle Another name for a vascular bundle and accompanying fibers.

filament The stalk of a stamen which supports the anther.

filiform apparatus Threadlike extensions of the synergid cell walls thought to play a role in increasing the rate of transport of molecules into and out of the synergids.

filling tissue Loose tissue formed by a lenticel phellogen toward the outside.

flavedo The colored exocarp of a hesperidium fruit. See albedo.

floral nectary A nectary situated within the flower. Compare to extrafloral nectary.

follicle A dry, dehiscent, fruit derived from a single carpel, dehiscent along a single axis.

free central placentation A form of placentation similar to axile placentation in which ovules are attached at the center (the axis) of a compound ovary. However, the placenta is not attached to the ovary wall.

frond A large divided leaf, typically associated with ferns and palms. May also be used to describe the photosynthetic body found in the Lemnaceae.

fruit A mature ripened ovary containing seeds in angiosperms. May also include associated floral tube.

funiculus The stalk of an ovule.

fusiform initial A cambial cell which is characteristically elongated with tapering end walls.

gamete Haploid reproductive cells (egg or sperm) produced in plants by mitosis from a gametophyte.

gametophyte That plant generation which gives rise to the gametes by means of mitosis. Typically haploid.

gap In a siphonostele, the parenchymatous region in the vascular cylinder above the position where the leaf trace (or branch trace) enters a leaf (or branch).

gelatinous fiber/layer A non-lignified fiber which appears gelatinous-like with light microscopy. Layers of such fibers comprise reaction wood.

generative cell The smaller haploid cell in a pollen grain that divides (most often in the pollen tube) to form two sperm cells.

gerontoplast A type of chromoplast typically found in senescent cells.

gibberellic acid A plant growth regulator active in fruit set and seed germination.

girdling The removal of a ring of live bark around a tree trunk that includes all tissues down to the secondary xylem (wood).

glandular trichome A trichome with an enlarged unicellular or multicellular secretory cells, at the terminus. May be stalked or unstalked.

glaucous A gray or gray-blue surface color on fruits such as grapes caused by epidermal waxes.

glyoxisome A type of microbody largely found in the cells of germinating seeds and containing enzymes that convert stored lipids to carbohydrates.

Golgi apparatus A system of interconnected dictyosomes of similar function in a cell.

grafting Joining two or more related plants together by fitting one or more scions onto a rootstock.

granum(a) Stack(s) of chloroplast thylakoids.

gravitropism A directional growth response to the influence of gravity. Induced by mechanical and hormonal (plant growth regulator) influences.

gravisensing The process of growth toward or away from the direction of gravity. Mostly used in root response, but some responses are noted in shoots.

ground cell(s) Cells other than vascular, epidermal, or periderm.

ground meristem Primary meristem derived from the apical meristem.

growth ring A circular layer of secondary xylem (or, in some cases, secondary phloem) which is the result of seasonal growth in perennial stems or roots. Typically observed in cross-sectional view.

guard cells A specialized pair of epidermal cells surrounding and adjusting the size of a stomatal pore.

guttation The exudation of liquid water from hydathodes fed by vascular xylem traces.

gynoecium All of the carpels in a flower or that part of the flower in which megasporogenesis occurs.

half-bordered Referring to pit-pairs in which one is bordered and the adjacent one is simple.

halophyte A plant adapted to living in salty or brackish conditions.

haplostele A variant of stele architecture in which a central core of xylem is surrounded by phloem.

hardwood General non-specific term for the wood of eudicotyledons.

Hartig net In ectomycorrhizae, hyphae which penetrate between the outermost root cells where they form a mycelium

haustorium A modified root that penetrates host tissues for the purpose of absorbing nutrient materials.

heartwood Inner, non-functional wood characterized by a darker color than the surrounding sapwood. Often becomes prone to decay or degradation by biotic agents.

helical cell wall thickening A helical pattern of secondary cell wall thickening found in xylem vessel elements.

hemicelluloses Soluble and loosely organized polysaccharides in the cell wall matrix.

hemiparasite A photosynthetic plant parasite that only gets water and minerals from the host. See holoparasite.

hemitropous A half-inverted ovule.

herbaceous A plant with only primary growth. Non-woody.

hesperidium A fleshy fruit with multiple carpels, a leathery exocarp (flavedo), spongy mesocarp (albedo), and papery endocarp, for example, all citrus.

heterobaric leaf A leaf in which vascular bundle extensions segregate the internal air spaces into separate compartments.

heterocellular ray A vascular ray composed of more than one type of cell.

heterotrophic An organism incapable of producing organic compound from inorganic materials and thus must rely on other living or dead organisms for its food supply.

hilum Seed scar where the funiculus was once attached. Serves as a one-way water valve in some species. Also may designate the central part of a starch grain.

histogen An older term for root or shoot apical meristems, which are initials that form definite tissue systems in the plant body. See also primary meristem.

holoparasite A parasite that cannot complete its life cycle without a suitable host. Usually non-photosynthetic.

homobaric leaf A leaf in which all of the air spaces are internally connected (see heterobaric leaf).

homocellular ray A vascular ray composed of only one type of cell.

hydathode Pore in the margin of a leaf through which the exudation of water in liquid form takes place, usually by the process of guttation.

hydrophyte A plant adapted to growing in or under the surface of water.

hypanthium A ringlike, cup-shaped, or tubular structure of a flower on which the sepals, petals, and stamens are borne, as in the flowers of the rose or cherry.

hypocotyl That part of the embryo or seedling located below the site of cotyledon attachment.

hypodermis One or more layers of cells beneath the epidermis of the leaf, root, or stem and distinctly different from the cortex or other ground tissues.

hypogeal Type of germination in which the cotyledons remain beneath the surface of the ground.

hypogyny Floral structure in which the sepals, petals, and stamens are attached below the ovary (which is said to be superior).

hypophysis The top cell of a suspensor which gives rise to the development of the root in the embryo of angiosperms.

hypsophylls Leaves located at high levels on the stem resembling floral bracts.

hypostomatous Having stomata only on the abaxial surface of a leaf.

idioblast An unusual cell in a tissue which is distinctly different in form, size, or content from the surrounding cells.

included phloem Phloem tissue that is completely surrounded by secondary xylem or wood.

imperfect flower Flower lacking in either stamens or carpels.

imperforate tracheary element A tracheary element lacking perforations. Typically referred to as a tracheid. Found in both gymnosperms and angiosperms.

indehiscent fruit Fruits which do not open spontaneously and release their seeds upon maturity and drying.

indoleacetic acid (IAA) A plant growth regulator that stimulates growth in stem and roots. Often used in the development of asexual cuttings.

inferior ovary Floral structure in which the sepals, petals, and stamens are attached above the ovary.

initial cell A cell which normally gives rise to two cells, one of which remains in the meristem and the other is added to the plant body.

inner bark Region in stems or roots from vascular cambium through cork cambium. Includes living tissues.

integument Cell layers enveloping the nucellus of an ovule and which will become the seed coat.

intercalary meristem Meristematic tissue located at some distance away from the meristem that gave rise to it.

interfascicular cambium Vascular cambium that develops between the sites of vascular bundles and in the ground tissue.

intermediate filament A non-force-generating, structural, proteinaceous component of the plant cell cytoskeleton.

interphase The non-divisional stages of the cell cycle. Although mitotic activity and cytokinesis do not occur in interphase, replication of DNA does.

internal cuticle A layer of cuticle on the interior periclinal walls that border substomatal cavities.

internal phloem Primary phloem located internally from the primary xylem.

internode Regions of a stem between nodes.

intine The inner wall of a pollen grain which does not contain sporopollenin.

intrusive growth Growth of cells which invade between existing ones by interpositioning themselves.

isobilateral leaf Leaf in which the palisade mesophyll occurs on both adaxial and abaxial sides.

isodiametric Essentially uniform in diameter.

isolateral see isobilateral

kinesin Motor proteins that move along microtubule filaments and powered by ATP.

Kranz anatomy Radially oriented mesophyll cells which surround the vascular bundles in plants with C_4 pathway of photosynthesis (Kranz = wreath).

lacuna A hole or space.

lacunar collenchyma Collenchyma cells with intercellular spaces adjacent to cell wall thickenings.

lamellar collenchyma Collenchyma cells with cell wall thickenings on the tangential surfaces. Also sometimes designated as “plate collenchyma.”

lamina The flattened portion of a leaf blade.

late wood Secondary xylem that forms late in the growing season. Sometimes called summer wood.

lateral meristem Those meristems, such as vascular cambium or cork cambium, which are located in a cylinder around the periphery or parallel to it.

latex Milky-like fluid produced in laticifers.

laticifer(s) One or more cells containing latex.

laticiferous cell A non-articulated laticifer.

laticiferous vessel An articulated laticifer in which the cell walls between cells are partially or wholly lacking.

leaf buttress The initial formation of a leaf primordium characterized by a protrusion of tissues below the shoot apical meristem.

leaf gap A region where a portion of the vascular materials connecting the stem to the leaf is interrupted.

leaf scar The scar left on a stem after leaf abscission.

leaf sheath The base of a monocot leaf that wraps completely around the stem.

leaf trace The vascular bundle connecting the vasculature of the stem with that of the leaf. There may be multiple leaf traces per leaf.

leaves The most transient and variable vegetative organ of higher plants. Typically adapted for photosynthesis, they also include cotyledons.

legume A dry, dehiscent, single-carpel fruit, for example, beans and peas.

lenticel An opening, usually characterized as an eruption of the periderm through which gaseous exchange may occur in stems.

liana A woody climbing plant, usually tropical, that hangs from trees.

libriform fiber A very long xylem fiber with thick walls and simple pits.

lignification The process of depositing lignin in cell walls, primary or secondary.

lignin Mixed organic polymers of complex structure with units derived from phenylpropane and other complex phenolics. A component of many plant cell walls—especially in secondary wall structure.

lithocyst A cell, usually epidermal, that contains a calcium carbonate and cell wall accretion known as a **cystolith**.

locule An opening or cavity within a sporangium, as in anthers and ovules.

loculicidal fruit A dry, dehiscent, capsule-type fruit with multiple carpels. Characterized by the release of seeds via splitting of the locules. See poricidal and septicidal fruit.

maceration The breakdown of a tissue into individual cells through the digestion, or hydrolysis, of the middle lamella with chemical or enzymatic agents.

macrosclereid An elongated sclereid with randomly thickened secondary walls.

marginal placentation A form of placentation in which ovules are attached to the margin of the ovary.

margo The pit membrane around the torus in bordered pits of conifers.

medulla Pith.

medullary bundles Vascular bundles distributed in the pith.

medullary ray An extension of the medulla (pith) that reaches from the center of the stem to the cortex, through the vascular region. Same as a pith ray.

megagametogenesis The process of forming a female gamete, and egg, through mitotic division.

megagametophyte The female gametophyte which is the embryo sac in angiosperms.

megaphyll A foliage leaf in ferns and seed plants that has branched or parallel vascular bundles within the lamina and is associated with a leaf gap.

megasporangium The plant structure that produces megaspores.

megaspore A haploid cell that develops into a female gametophyte.

megaspore mother cell Same as a megasporocyte

megasporocyte The diploid cell that gives rise by meiosis to four haploid megaspores, of which only one survives to become a megaspore. Also called the megaspore mother cell.

megasporogenesis Process of forming the female megaspore as a consequence of meiosis.

meiosis Cell division in which the number of chromosomes is reduced to half the number and four cells are produced.

membranes Partitional structures limiting the surface of cells and comprising the structural organization of most organelles of cells. Typically comprised of a bilayer of lipids with various protein and glycoprotein components.

mericarp A fruit. One portion (carpel) of a schizocarp.

meristem Region of actively dividing cells giving rise to new tissues.

mesarch xylem Xylem strand in which the protoxylem is in the center and metaxylem differentiates from the center.

mesocarp The central layer of a pericarp.

mesogenous Ontogeny in stomatal complexes where there is a common developmental origin between subsidiary cells and guard cells of the epidermis.

mesoperigenous Ontogeny in stomatal complexes where there is a partial common origin of subsidiary cells and neighboring guard cells in epidermis.

mesophyll Leaf parenchyma cells active in photosynthesis and located within the two epidermal layers.

mesophyte A plant living in a temperate environment and receiving average amounts of moisture.

mestome sheath An inner layer of cells around vascular bundles of grass leaves characterized by sclerenchyma cells.

metaphase That phase of mitosis or meiosis in which the chromosomes are aligned on an equatorial plane prior to separation of the chromatids. Chromosomes are at their shortest length during this phase.

metaphloem That phloem which matures after the establishment of the protophloem and before the secondary phloem.

metaxylem That xylem which matures after the establishment of the protoxylem and before the secondary xylem.

microbody A small subcellular organelle, enclosed with a single membrane, and containing a variety of non-hydrolytic enzymes. See glyoxisome and peroxisome.

microfibril A grouping of cellulose molecules in the cell wall.

microfilament Long, thin proteinaceous fibers in the cytoplasm which serve multiple structural roles in the cell. Other proteins use the microfilaments to generate force.

microgametogenesis The formation of male gametes (sperm) through mitosis.

microgametophyte The male gametophyte—pollen grains in seed plants.

micrometer Same as micron, 1000 of a millimeter.

microphyll A type of leaf in which there is one single unbranched leaf vein.

micropyle The opening in the integument of an ovule through which the pollen tube may pass and enter the embryo sac.

microscope An optical instrument capable of producing a magnified image of an object. Also adapted as electron, X-ray, and sonic microscopes, among others.

microsporangium A sporangium in which microspores are formed—the anther in angiosperms.

microspore A haploid spore that develops into the male gametophyte, e.g., the first stage of a pollen grain.

microspore mother cell Same as a microsporocyte.

microsporocyte Diploid cell that undergoes meiosis and forms four haploid microspores. Same as microspore mother cell.

microsporogenesis Process of forming haploid male microspores through meiosis.

microtubules Proteinaceous tubules in the cytoplasm of cells which appear hollow and are approx. 25 nm in diameter. These structures form to guide chromosomes in nuclear divisions, establish the cell plate, and provide a framework for the cell prior to cell wall establishment.

middle lamella A "cementing" layer of pectic materials holding together the primary cell walls of adjacent cells.

mitochondrion Double-membrane-limited subcellular organelle actively involved in functions of aerobic respiration.

mitosis Division of the cell's nucleus into two daughter nuclei—each with the same number of chromosomes as the original parent nucleus.

monocarpic A plant that dies soon after setting seed. May be an annual or a perennial plant.

mucigel A mucopolysaccharide produced by the root cap. Functions to lubricate the root tip as it is pushed through the soil and serves as a medium to support the growth of microbes beneficial to the plant.

mucilage Gums and other carbohydrates which swell in water.

multiple epidermis Two or more layers of epidermal tissue derived from protoderm.

multiple fruit Fruit composed of several matured ovaries, each from a separate flower.

multiseriate ray A phloem or xylem ray which is several cell layers in width.

mycorrhiza The symbiotic association of fungi with roots of higher plants.

nectary A glandular structure in flowers (floral nectary) or on vegetative structures (extrafloral nectary) that secretes insect-attracting substances, usually containing sugars.

nitrogen fixation A process carried out by free-living or symbiotic bacteria in which atmospheric N_2 gas is reduced to the level of ammonia.

node The position on a stem at which one or more leaves are attached.

non-articulated laticifer A single, often multinucleate cell that may be branched and transport latex.

non-endospermic storage A form of seed storage in which the food reserves are stored in the cotyledons. Also called cotyledonary storage.

non-storied Typically, secondary growth in which the cells and rays are not found to be synchronously developed in tiers.

non-stratified Same as non-storied (see above).

nucellus The internal region of an ovule in which the embryo sac develops.

nuclear endosperm A multinucleate endosperm not divided into multiple cells, due to lack of cytokinesis following mitosis. See cellular endosperm.

nuclear envelope The double membranes limiting the boundary of a nucleus in eukaryotic cells.

nucleolus An irregularly dense region of a nucleus responsible for the development of ribosomes.

nucleus The double-membrane-limited organelle of eukaryotic cells which contains the hereditary materials.

numerical aperture Measure of a microscope objective lens to gather light and to resolve fine detail at a fixed distance.

obturator A growth in the style or its canal that brings the pollen tubes and conducting tissue near to the micropyle.

oil cavity A cavity, usually in the leaf or stem, in which oils produced by the epithelium accumulate.

ontogeny The development of an individual from embryo to maturity.

open minor vein A minor leaf vein that has direct symplastic connections (via plasmodesmata) to the adjacent leaf mesophyll cells. See closed minor vein.

open vascular bundle Vascular bundles found in eudicots in which fascicular cambium is found between the xylem and phloem.

operculum A portion of the pollen wall that covers the aperture through which the pollen tube will grow.

organ A unique structure composed of tissues which possess common functions, e.g., leaves, stems, and roots are vegetative organs.

organelle Characteristic subcellular structures, usually membrane-limited, that have a specific function within the cell.

orthic tetrakaidecahedron A 14-sided geometric three-dimensional figure often considered to represent the average cell form of closely compacted parenchyma cells.

orthotropous An ovule that is upright or not bent over.

osteosclereid A bone-shaped sclereid, swollen at the ends.

outer bark The "dead" bark lying outside of the phellogen or cork cambium.

ovary Basal region of a carpel or simple pistil containing ovules and developing into a fruit.

ovule Structure in the flower which contains the female gametophyte and which develops into a seed.

P-protein A network of protein filaments found in sieve tube elements. Formerly called "slime." Palmate radiating from a point, as fingers radiating from the palm of a hand.

palisade mesophyll Columnar, photosynthetic cells found toward the adaxial surface in many eudicot leaves.

palynology The study of plant pollen, both living and fossilized.

papilla A non-lignified modified trichome appearing as a protuberance on an epidermal (usually leaf or petal) cell.

paradermal Refers to a plane of sectioning that is parallel to the epidermal layer (or surface of the leaf).

parallel venation A pattern of leaf venation in which the vascular bundles run parallel to each other. Most often seen in monocot leaves. See dichotomous venation and reticulate venation.

parasitic plant A plant deriving some or all of its nutrients from a host plant. Incapable of surviving without the host and often lacking sufficient chlorophyll to produce sugars through photosynthesis.

paratracheal xylem parenchyma Wood parenchyma associated in some form with vessel members.

parenchyma cell An unspecialized plant cell which usually has thin walls with no secondary wall development.

parietal placentation A form of placentation in which ovules are attached to the outer wall of a compound ovary.

parthenocarpy Development of a fruit (typically seedless) without fertilization.

passage cell Endodermis cell that remains thin-walled when others in the tissue are thick-walled. Still has Casparian strip.

pavement cells Ground cells of an epidermis, not a part of a stomatal complex or trichome.

pectic substances Carbohydrate compounds which are an important part of the middle lamella and which are derived from polygalacturonic acid.

pedicel The stalk of an individual flower.

peduncle The stem of an inflorescence.

peltate trichome A flattened disc-shaped plate of cells that may or may not have a stalk for attachment to an epidermal layer.

pentarch A pattern of root vascular in which the xylem is arranged in a star-shaped arrangement with five arms or poles

pepo A fleshy fruit with multiple carpels with a papery exocarp, fleshy mesocarp, and a fleshy or stringy endocarp, for example, cucumber and squash.

perennating organ A plant part—usually rhizome or corm—that is used to survive unfavorable growing conditions.

perennation The process of persisting for multiple growing seasons.

perennial A species that persists for multiple growing seasons.

perfect flower Flower containing both stamens and carpels.

perforate tracheary element A tracheary element with large holes (perforations) at the end walls and, occasionally, side walls. Commonly known as vessel elements. Only found in angiosperms, not present in gymnosperms.

perforation plate That region of a cell wall which is perforated and found in a vessel member.

perianth Collectively, the petals and sepals (or tepals) of a flower.

pericarp The wall of a fruit which was derived from an ovary wall.

periclinal A plane of division or cell wall establishment which is parallel with the surface of the organ.

pericycle A tissue of roots which is found between the endodermis and the phloem and which gives rise to branch roots.

periderm A secondary tissue that replaces epidermis in roots and stems and which consists of phellem, phellogen, and phelloderm.

perigenous Ontogeny in stomatal complexes where there is no common origin of guard and subsidiary cells.

perigyny Floral structure in which the sepals, petals, and stamens are attached at the level of the ovary (which is said to be half inferior).

perimedullary region The outer layer of the stem pith, in which those cells are distinctly different than the inner pith cells.

periplasmodial tapetum A form of tapetum in which the cell walls break down, generating a multinucleate plasmodium that secretes the components needed for pollen maturation. See secretory tapetum.

perivascular fiber A fiber, not of phloem origin, which is located at the outer periphery of a vascular cylinder or even toward the margin of a stem.

peroxisome An organelle enclosed by a single membrane and contained large amounts of catalase and peroxidase to degrade long-chain fatty acids and complex molecules.

petal A nonreproductive modified leaf which is a component of the corolla of a flower.

petiole Stalk of a leaf which is the attachment to a stem.

phellem Corky tissues characterized by nonliving suberized cells produced in a centrifugal manner by the cork cambium (phellogen).

phelloderm Parenchyma-like cells produced in a centripetal manner (to the inside) by the cork cambium (phellogen).

phelloid Idioblasts of the phellem that may be sclerified or contain other wall materials than suberin.

phellogen The cork cambium which produces cork to the outside (centrifugal manner) and phelloderm to the inside (centripetal manner).

phloem Food-conducting tissue of a plant composed of sieve elements, companion cells, and various parenchyma and fibers

phloem ray A vascular ray found in the secondary phloem.

phloem sap The aqueous sap of the phloem. Contains photosynthate, amino acids, hormones, and, occasionally, viruses.

photoautotrophic Capable of synthesizing food products (based on molecules of carbon) using light energy.

photoinhibition Light-induced damage to photosystem II.

photorespiration The production of glycolic acid in chloroplasts in the light. The glycolic acid may be oxidized by enzymes of peroxisomes.

photosynthate Reduced carbon compounds that are the product of photosynthesis.

phragmoplast A disk or platelike structure composed of microtubules and microfilaments which define the site of new wall formation following mitosis or meiosis.

phylloclade A flattened stem that resembles a leaf and performs photosynthesis. Another name for **phyllode**, **cladode**, and **cladophyll**.

phyllode A flattened stem that resembles a leaf and performs photosynthesis. Another name for **phylloclade**, **cladode**, and **cladophyll**.

phyllotaxy The pattern of leaf arrangement on a stem.

phylogeny The sequence of evolutionary changes that have occurred in the development of a species or taxonomic group.

phytochrome A light-sensitive blue-green pigment responding to red and far-red light that regulates plant development such as seed germination, stem growth, etc.

pigment Natural coloring of chemical agents in plant tissues, many of which are significant in growth, photosynthesis, and other processes.

pinna (pinnae) One extension of a frond.

pistil A gynoecium composed of ovary, style, and stigma.

pistillate flower Referring to having pistil(s). A female flower.

pit A small region of the cell wall in which the primary wall is not covered with secondary wall material. See simple pit and bordered pit.

pit aperture Opening into a pit from the interior of a cell.

pit membrane The compound middle lamella separating two pits.

pit-pair Two adjacent pits from opposing cells sharing a common pit membrane.

pith Ground tissue in the center of a root or stem originating from ground meristem.

pith ray An extension of the pith (medulla) that reaches from the center of the stem to the cortex, through the vascular region. Same as a medullary ray.

placenta Site of attachment of the ovule to the ovary wall.

plasma membrane The outer limiting membrane of a cell.

plasmalemma Synonymous with cell membrane or plasma membrane.

plasmodesma The connecting strands of protoplasm between the cytoplasm of adjacent cells which form canals through the cell walls. It may contain a desmotubule which links the endoplasmic reticulum of the adjacent cells.

plastid A family of developmentally and ontogenetically related cellular organelles containing photosynthetic and/or ancillary pigments in internal membranes and limited by a pair of membranes.

plastoglobule Oil-containing droplets in the stroma of a plastid, often associated with senescence.

plectostele A variant of stele architecture in which interconnected platelike regions of xylem surrounded by and immersed in phloem tissue.

plumule The immature leaves on an angiosperm embryo.

pluripotency Cells that can give rise to all functional cells in a plant. Often considered to be plant stem cells.

polar nuclei The two central nuclei which migrated from the opposite poles of an embryo sac.

pollen grain A mature microspore in a seed plant with a distinctive cell wall exine and containing sperm.

pollen sac The locule in an anther containing pollen grains.

pollen tube A hypha-like germination tube from a pollen grain that transmits the male (micro)gametophytes to an embryo sac in an ovule.

pollenkitt An adhesive molecule on the surface of pollen grains. See also tryphine.

pollination The transfer of pollen from an anther to the stigma of the same species.

polyarch The primary xylem of a root with many protoxylem strands.

polyderm A multilayered protective tissue found in the roots and rhizomes of some plants and consisting of alternating layers of suberized and non-suberized cells.

pome A fleshy fruit with multiple carpels, a papery exocarp, a thick mesocarp, and a papery endocarp, for example, apple and pear.

poricidal fruit A dry, dehiscent, capsule-type fruit with multiple carpels. Characterized by release of seeds via pores that form at the top of the capsule, for example, poppy. See loculicidal and septicidal fruit.

pre-prophase band An array of microtubules that form a band in plant cells prior to prophase of mitosis.

primary cell wall Cell wall developing during the growth of a cell in which the wall microfibrils are layered in various, often random, orientations.

primary endosymbiosis A situation in which a prokaryotic organism is engulfed by a eukaryote that may then become an autotrophic organism.

primary growth Plant growth derived from the tissues of apical meristems.

primary meristems Root or shoot apical meristems which form definite tissue systems in the plant body. See histogens (older term).

primary phloem Phloem derived from procambium and divided into the earlier protophloem and the latter metaphloem.

primary pit field A thin area of a primary wall in which a number of pits develop as the secondary wall is deposited.

primary thickening meristem A meristem that increases the girth of a monocot stem.

primary xylem Xylem derived from procambium and divided into the earlier protoxylem and the latter metaxylem.

primexine An early exine wall stage in which sporopollenin is deposited over the stretching wall.

prismatic crystal Calcium oxalate crystals with a prismatic shape. Often found in cells of the bundle sheath.

procambium That primary meristem which develops into primary vascular tissue.

procumbent ray cell A secondary vascular ray cell with its long axis in the horizontal (ray) direction.

proembryo A very early stage of plant embryo development, before protoderm and suspensor are formed.

prophase The first recognizable stage of mitosis or meiosis when the structural organization of chromosomes becomes visually evident with light microscopy.

prokaryotic Organisms whose cells have no membrane-limited nucleus or organelles. Mostly, bacteria and cyanobacteria.

prop roots Aerial adventitious roots which usually provide support.

proplastid The early stage of plastid development.

protoderm The primary meristem that gives rise to epidermis.

protophloem Initial phloem elements produced in primary growth.

protoplasm All of the living contents of a cell, including the cytoplasm and nucleus.

protoplast All cell components but lacking the cell wall.

protostele A simple stele with phloem outside of a solid column of xylem.

protoxylem The first formed primary xylem.

pseudostem A false stem made of a series of concentric leaf sheaths, as in banana.

pubescence A hairy or downy plant surface.

quiescent center That region of apical meristems, particularly in roots, in which there is relatively little (or no) mitotic activity.

radial micellation A pattern of primary cell wall thickening seen in guard cells that causes the cells to bend upon the uptake of water.

radial section A longitudinal section along a radial plane directly through the plant axis.

radicle An embryonic root.

ramiform pit A pit that is branched due to two or more simple pits being fused.

raphides Calcium oxalate crystals with a slender, needle-like shape.

ray Tissue extending radially in the secondary xylem and phloem.

ray initial A small isodiametric cell in the vascular cambium that gives rise to a radial file of cells forming a ray.

ray parenchyma Parenchyma cells of a ray.

reaction wood Wood showing stress formations due to leaning or uneven growth of a stem. See **compression wood** and **tension wood**.

receptacle A modified stem upon which the floral organs are borne.

refractive index The speed of light in a vacuum as opposed to its speed in a medium. Also measured as the sine of the angle of bending from one medium to another.

resin canal A duct formed by the breakdown of cell walls of end members, lined with epithelial cells, and transporting resin in wood.

resin duct A duct formed by the breakdown of cell walls of end members, lined with epithelial cells, and transporting resin. Also referred to as a resin canal in wood.

resolution The finest detail observable with an optical device. Often defined as the ability to observe two object points very close to one another. The measure of the finest distance between the points is referred to as the resolution of an instrument.

resolving power The ability of a microscope to see fine detail, often measured by the narrowest distance between two small objects.

reticulate venation A pattern of leaf venation having the appearance of a net. Most often seen in eudicot leaves. See dichotomous venation and parallel venation.

reticulate cell wall thickenings Secondary wall thickenings having a netlike pattern in xylem tracheary cells.

rhizodermis Primary surface layer of the root, similar to epidermis but of different origin and function. Also called the epiblem.

rhizome A stem that grows underground. Often used for storage.

rhytidome Outer bark.

ribosome A very small non-membranous cell organelle composed of protein and RNA that is the site of protein synthesis and is found in the nucleus, cytoplasm, mitochondria, and plastids of a cell.

ring porous wood Secondary wood of hardwood species which have large diameter vessel elements located primarily in the early wood.

root apical meristem A region of actively dividing cells just behind the root cap that give rise to future growth.

root hair An extension of cells of the rhizodermis, increasing surface area for absorption.

root cap The mass of cells covering and protecting the root apical meristem.

rootstock An underground stem or rhizome. In grafting, the rootstock is the lower portion of the stem or trunk onto which the apical portion (scion) is mounted.

root(s) The (typically) underground vegetative organ of plants derived from the root apical meristem. Capable of storage, support, mutualistic associations with microorganisms, and secondary growth in many cases.

rough endoplasmic reticulum Endoplasmic reticulum with membrane-bound ribosomes that may assemble a variety of protein molecules.

Rubisco Ribulose *bis*phosphate carboxylase/oxygenase. The primary carbon-fixing enzyme in the C_3 photosynthetic pathway and the most abundant protein on Earth.

salt gland A gland on the surface of the leaves of some halophytes that excretes salts taken up via the transpiration stream.

samara A dry, indehiscent, single-carpel fruit characterized by the development of large flat wings that aid in wind dispersal. Sometimes called "helicopters," for example, maple.

sapwood The outer part of the secondary xylem which still contains some living cells and in which water conduction takes place.

scalariform Having a ladderlike organizational pattern.

scalariform xylem parenchyma A pattern of xylem parenchyma that appears as bands (or ladder rungs) spanning between xylem rays.

scion In grafting, the upper part of the graft that is mounted on the rootstock.

schizocarp A dry fruit found in the Apiaceae (celery and parsnip family) that, upon maturity, splits into individual mericarps.

sclereid A relatively short sclerenchyma cell characterized by thick lignified secondary walls with many simple pits.

sclerenchyma A tissue composed of sclerenchyma cells which have thick, lignified cell walls and may or may not have living contents.

sclerophyllous leaf A heavily sclerified, "leathery" leaf.

scutellum A modified cotyledon found in monocots that absorbs nutrients from the endosperm during germination.

secondary cell wall Cell wall material formed after the cell ceases to enlarge and in which the wall microfibrils have one or more sets of parallel orientation.

secondary endosymbiosis A case in which a living eukaryotic cell engulfs another living eukaryotic cell that becomes dependent upon the larger cell and cannot live independently.

secondary growth Growth originating from a vascular cambium and/or phellogen that gives rise to an increase in girth.

secondary phloem Phloem derived from vascular cambium.

secondary thickening meristem A meristem that increases the girth of a root or stem.

secondary xylem Xylem derived from vascular cambium.

secretory cell A cell that produces and exports various types of secretions and may be an idioblast or a part of a specific morphological and anatomical structure.

secretory tapetum A tapetum in which the cells remain intact and cooperate in a coenocytic fashion to secrete the components needed for pollen maturation. See periplasmodial tapetum.

seed A ripened ovule containing a multicellular embryo plant, an endosperm, and a protective seed coat.

seed coat The outer coat, or testa, of a seed that is derived from the integument.

semi-ring porous wood Secondary wood of hardwood species which has large diameter vessel elements located mostly, but not exclusively, in the early wood.

sepals Outermost vegetative organs of a flower, collectively called a calyx.

separation layer In leaf abscission, a layer of weak cells formed where the petiole attaches to the stem. Also called corky layer.

septicidal fruit A dry, dehiscent, capsule-type fruit with multiple carpels. Characterized by the release of seeds via splitting of the septa separating the locules, for example, lily. See also poricidal and loculicidal fruit.

sessile A leaf lacking a petiole or a flower lacking a pedicel.

shade chloroplast Chloroplasts from leaves in the shade. They typically have larger grana than sun chloroplasts.

shade leaf Leaves that develop in the shade that are larger in area, are thinner, and have a thin cuticle. See sun leaf.

shoot The aboveground portion of a plant which typically includes stem and leaves and later flowers.

shoot apical meristem (SAM) Region of actively dividing cells at the apex of a stem which give rise to stem tissues as well as regenerating itself.

sieve area A pitlike area in the wall of a sieve element whose pores are lined with callose.

sieve cell A type of sieve element with undifferentiated sieve areas and no sieve plates. Common in gymnosperms.

sieve plate Wall of a sieve element with sieve areas.

sieve pores Openings in a sieve plate or sieve area.

sieve tube A series of sieve elements arranged end to end and interconnected with sieve plates.

sieve tube element A phloem cell involved with food conduction, a.k.a. a sieve tube member.

sieve tube member A cell component of a sieve tube, a.k.a. sieve tube element.

silica body Inorganic silicon structures of various shapes and sizes that may add to plant rigidity, strength, and fungal resistance. Also known as phytoliths.

silica cell An epidermal cell containing silica bodies.

silvichemicals A class of chemicals derived from wood or wood products.

simple pit A pit in which the cavity remains uniform in width or gradually becomes either wider or narrower during growth in thickness of the secondary wall.

siphonostele A stele in which the vascular cylinder has a core of pith.

slime A viscous secretion of various composition, mostly rich in protein.

smooth endoplasmic reticulum Cytoplasmic membranes devoid of ribosomes that function largely in the synthesis of lipids.

softwood That wood lacking vessel members and fibers, typically used to refer to gymnosperm wood.

solenostele A variant of stele architecture in which the vascular cylinder forms a more or less continuous ring around the pith.

sperm Male gametes formed by mitosis in plants.

spindle apparatus/fibers An aggregation of microtubules that aid in the movement of chromosomes during mitosis or meiosis.

spiral cell wall thickening A spiral pattern of secondary cell wall thickening found in xylem vessel elements.

spongy mesophyll Leaf parenchyma cells of irregular shape and with large air spaces surrounding it. Primary function is in gaseous exchange.

sporophyte The diploid phase of the life cycle of plants that gives rise to the production of spores by means of meiosis. In higher plants, it is the dominant phase of the life cycle.

sporopollenin The highly resistant material comprising the exine of a pollen grain.

springwood Same as early wood.

stamen Floral organ producing pollen and typically composed of a filament and an anther.

staminate flower Referring to having stamens. A male flower.

statocyte A term sometimes applied to the cells of the endodermis and root cap that are involved in gravisensing.

statolith Starch or carbonate-containing structure (often plastids) in a root cap cell believed to be involved in sensing gravitational pull.

stele The vascular system of a plant body and its associated ground tissues.

stellate trichome Star-shaped trichome.

stigma The terminal portion of a style morphologically adapted to holding and germinating pollen.

stigmatoid tissue Tissue of the style which provides a pathway and nutrition for growing pollen tubes.

stinging hairs Secretory cells on the surface of leaves, petioles, and stems, usually with silica-rich walls, that act like hypodermic needles to inject an irritant into the soft parts of herbivores.

stipule A small, leaflike appendage typically found in pairs at the base of the petiole.

stolon A stem that grows across the soil surface. May generate adventitious roots at the nodes.

stoma/stomata An opening in an epidermal layer (usually in leaves and stems) which is bordered by two guard cells.

stomatal complex The arrangement of stoma and epidermal cells that form any of several patterns on leaf surfaces.

stomatal crypt A leaf depression in which the stoma(ta) and guard cells are found.

stomography The study of stomata.

stomium An opening, often slit-like, in an anther that dehisces upon drying to release pollen.

stone cell See brachysclereid.

storied Stratified (often found in cambium, wood, and rays).

Strasburger cell Found in gymnosperm phloem where cells which are functionally and structurally similar to companion cells exist but do not originate from the same precursors as do the companion cells in angiosperms. Same as **albuminous cell**.

style A filamentous portion of the ovary through which pollen tubes may grow.

styloid crystal Calcium oxalate crystals with a slender, pointed shape.

suberin A fatty substance found in the cell wall of cork cells and the Casparian strip of endodermis tissue.

subsidiary cell A morphologically distinguishable cell associated with a stoma and its guard cells. A part of the stomatal complex.

substomatal cavity The space immediately proximal to the stoma.

successive cambium An anomalous situation in which successive layers of cambium are organized concentrically. Also called supernumerary cambium.

succulence A characteristic of mostly xerophytic plants in which leave or stem cells have large central vacuoles for water storage.

summer wood That secondary xylem formed late in the growth season for temperate plants. Also called "late wood." Suspensor A cellular filament that anchors the embryo into the endosperm.

sun chloroplast Chloroplasts from leaves in the sun. They typically have smaller grana than shade chloroplasts.

sun leaf Leaves that develop in direct sunlight that are smaller in area, are thicker, and have a thick cuticle. See shade leaf.

sunken stomata Stomata that are sunken a few micrometers to aid in the preservation of water. Found in desert plants and in many gymnosperms, such as pine.

superficial phellogen A phellogen that develops near the organ surface. See deep-seated phellogen.

superior ovary Floral structure in which the sepals, petals, and stamens are attached below the ovary.

supernumerary cambium An anomalous situation in which successive layers of cambium are organized concentrically. Also called successive cambium.

suspensor A short column of cells that connect the developing embryo to surrounding tissues.

symplast The living cell contents of tissues (which may be connected from cell to cell by plasmodesmata).

symplastic loading The process of phloem loading seen in some plants in which the photosynthate moves from companion cell to sieve tube elements via plasmodesmatal connections. See apoplastic loading.

syncarpy A floral arrangement in which all the carpels are fused into one.

synconium A floral arrangement in which the carpels are fused but remain separated by a thin septum.

syncytium A single cell containing multiple nuclei.

synergids A pair of "sister" cells associated with the egg at the micropylar end of an embryo sac.

tabular cells Early cells of an abscission zone in a leaf petiole which possess a rectangular outline.

tangential section A plane of sectioning at right angles to the radial plane or parallel to the surface of a flattened structure (as a leaf or stem).

tannin Any of a group of polyphenolic compounds used in tanning and dyeing. Typically makes a strong preservative solution in water.

tannosome Tiny organelles that are formed in chloroplasts but in development filled with tannins.

tapetum A layer of (often binucleate) cells lining the locules of anthers and which provide nutrition to the developing pollen. May become coenocytic (see **secretory tapetum**) or plasmodial (see **periplasmodial tapetum**) in later stages of development. Also see elaioplast.

taproot A root that is not highly branched and may be adapted for food storages.

telophase The divisional stage when chromosomes have moved to opposite poles of the cell and have begun to decondense.

tendril A modified stem or leaf used for attachment primarily by twining.

tension wood A type of reaction wood formed on the upper side of limbs in eudicotyledons in which there is less lignification and more gelatinous fibers.

tepal Units of calyx and corolla that cannot be differentiated from each other.

terminal xylem parenchyma Parenchyma at the end of a xylem vessel.

terpene Volatile unsaturated hydrocarbons found in essential oils of plants.

testa Seed coat.

tetracytic stoma A stoma with four subsidiary cells.

tetrarch Primary xylem of a root with four protoxylem poles.

thylakoid A membrane element, usually in stacked orientation, within the stroma of a plastid, usually a chloroplast.

tissue Groups of cells associated in large numbers and of common origin, common structure, and common function.

tissue culture The growth of living cells in an artificial medium.

tonoplast The limiting membrane surrounding a vacuole.

torus A central thickened portion of a pit membrane in a bordered pit of gymnosperms.

totipotency The growth and development of an entire plant from a single cell containing all necessary genomics.

tracheary elements Cells of the xylem involved with water conduction. May be tracheids or vessel members.

tracheid A tracheary element with no perforations and often intermediate between a vessel member and a fiber.

trans face The secretory side of the cisternae in a dictyosome.

transfer cell Parenchyma cell with primary cell wall invaginations that aid in the transfer of solutes.

transfusion tissue Tracheids and parenchyma cells that surround the vascular tissues in leaf veins of gymnosperms.

translocation The method by which photosynthate and other solutes move through the phloem from the source tissues to sink tissues.

transpiration The evaporation of water from plant leaves.

transport protein A membrane-bound protein that assists the movement of specific solutes across the membrane.

triarch Primary xylem of a root in which there are three protoxylem poles.

trichoblast A rhizodermal cell that develops a root hair.

trichome A hair or scale, usually multicellular, of a leaf or stem epidermis that may be glandular.

tryphin An adhesive molecule on the surface of pollen grains. Found exclusively in the Brassicaceae. See also pollenkitt.

tubulin A globular polypeptide which, in the dimer form, represents the building block of microtubules.

tunica In stem apices, it is a layer (or sheath) of cells that divide perpendicular to the stem axis.

tunica-corpus Concept of the two-layered structural organization of a shoot tip in angiosperms.

tylosis An outgrowth of a parenchyma cell extending through a pit cavity into a tracheary cell. It usually blocks the lumen of the vessel and therefore the movement of materials.

unifacial leaf A leaf in which one face, typically the adaxial face, has fused, so that both faces are abaxial, as in the *iris*.

uniseriate ray A ray (xylem and/or phloem) that is only one cell in thickness (width).

upright ray cell A cell at the periphery of a ray that is elongated in the axial dimension. Also called an erect ray cell.

vacuole Nonliving region within a cell that is membrane-bound and is filled with water, storage, and waste products. Bound by the tonoplast.

vasicentric xylem parenchyma Xylem parenchyma that surrounds a vessel in wood.

vascular bundle A strand of xylem and phloem originating from primary meristems. See open vascular bundle and closed vascular bundle.

vascular cambium Lateral meristem which gives rise to secondary vascular tissues in stems and roots.

vascular cylinder Same as stele but excluding associated ground tissues.

vegetative cell The larger haploid cell of a pollen grain that forms the pollen tube.

vein A strand of vascular tissue in a flat organ such as a leaf.

velamen Multiple epidermises found on aerial roots of tropical orchids.

vesicles Small membrane-limited bodies often derived from dictyosomes and carrying structural or enzymatic materials for deposition at a more remote location, such as the cell surface or cell plate.

vessel A tubelike series of vessel members which have perforations in their common end walls.

vessel member (element) A single cellular component of a vessel.

vestured pit A pit in the secondary cell wall that has multiple, small ingrowths into the pit chamber.

warty layer Small deposits on the inner walls of the S3 layer in secondary walls. Believed to be derived from final decomposition of the protoplast.

wax Long-chain hydrocarbons containing alkanes, fatty acids, alcohols, and aldehydes. They are typically epicuticular.

wood The secondary xylem of seed plants.

woody A type of plant with secondary growth.

X-ray elemental microanalysis An analytical method that uses a beam of electrons to cause a sample to emit characteristic X-rays. The energy of the X-rays is used to identify and map the elements on the surface of the specimen.

xeromorphic leaves Leaves with special structural adaptations to living in a dry environment.

xerophyte A plant adapted to growth and survival in a dry environment.

xylary fiber A fiber cell associated with the xylem. See extraxylary fiber.

xylem The tissue in vascular plants that conducts water and dissolved nutrients upward from the root to the stem and leaves. Also provides support and comprises the woody portions of the stem and root.

xylem initial A cambial cell that provides one or more xylem cells through periclinal divisions. Also known as a xylem mother cell.

xylem ray That portion of a vascular ray which is found in the xylem.

xylem ray initial A cell of the vascular cambium that will produce a xylem derivative.

zygote The diploid cell produced after an egg cell is fertilized. Beginning of the new sporophyte plant.

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