The Nature of Plants

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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 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 (eukaryotes).

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.

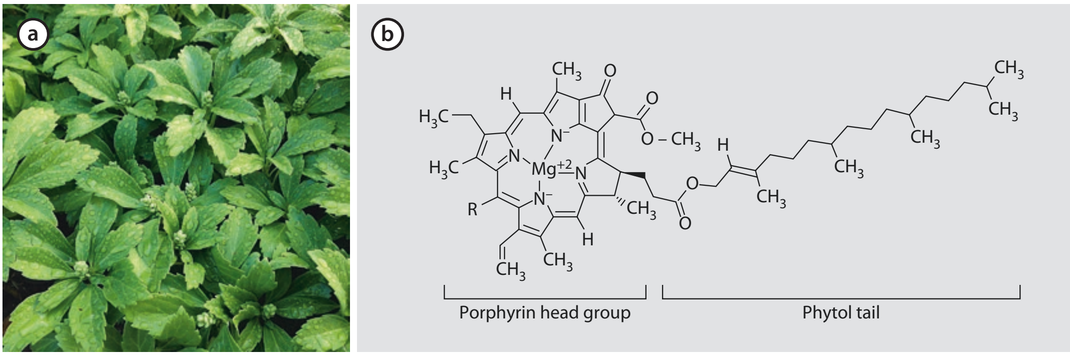

Fig. 1.1 **a** A dew-covered pachysandra (*Pachysandra* sp.) leaf exhibits a typical green of photosynthetic tissues. **b** Both chlorophyll *a* and *b* are present in the leaf, in a ratio of about 3:1. Chlorophyll *a* has a methyl group (-CH_3) in the R position; chlorophyll *b* has an aldehyde (-CHO). 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** RR Wise; **b** public domain)

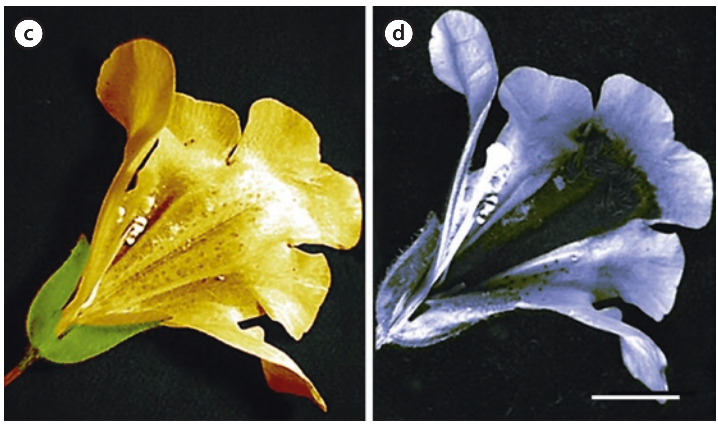

Fig. 1.1 Monkey flower (*Mimulus* sp.) photographed in visible light **c** and ltraviolet light **d** showing a dark nectar guide visible to bees but not to humans. The nectar guide facilitates visitation to flowers by pollinators that can see in the UV (usually insects or birds). Scale bar = 1 cm (**c** 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

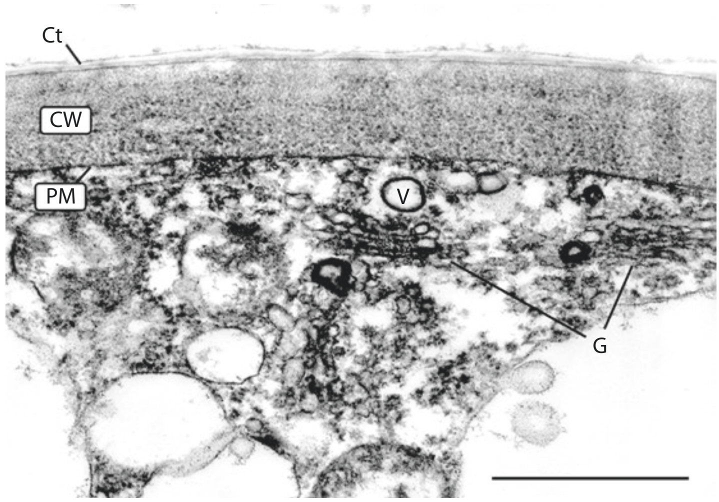

Fig. 1.4 Primary cell wall synthesis in an epidermal cell of a blackjack oak (*Quercus marilandica*) leaf. Golgi bodies (G) produce vesicles (V) that deliver precursors to the developing cell wall (CW). Note also cuticle (Ct) to the exterior and plasma membrane (PM) to the interior or of the cell wall.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

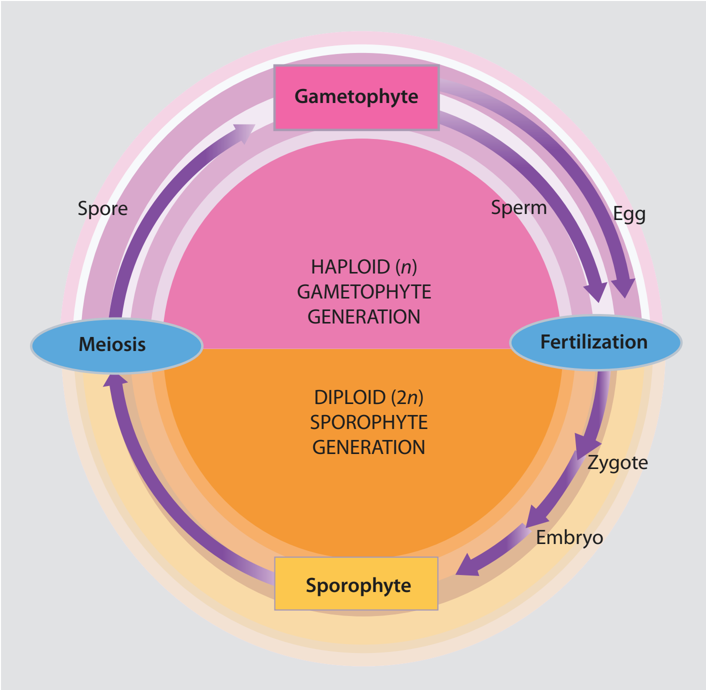

Fig. 1.5 Events (in a clockwise manner) that define an alternation of generations (Redrawn from Crang and Vassilyev 2003)

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.

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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)

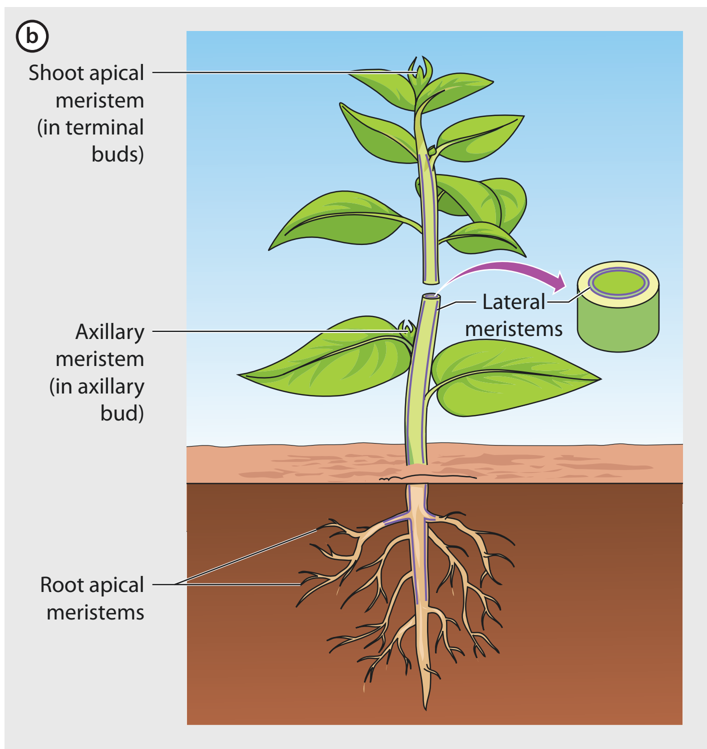


Fig. 1.6 **b** Meristems are found at the shoot and root tips and within the cylinder of the stem and root (Redrawn from Crang and Vassilyev 2003)

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)

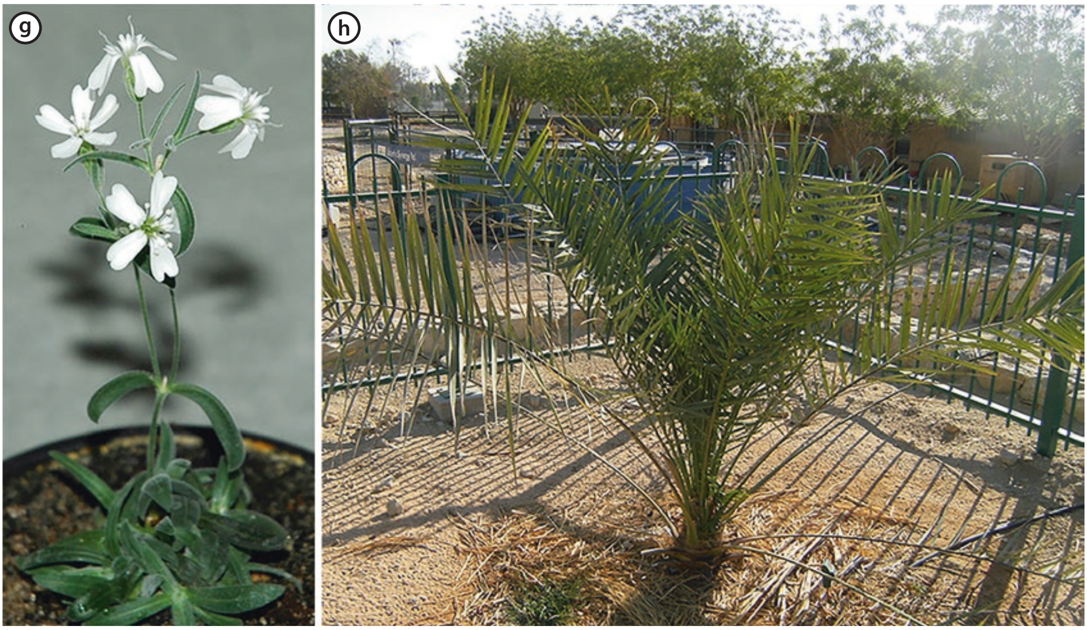


Fig. 1.7 Two plants germinated from long-dormant seeds. **g** Campion (*Silene stenophylla*) and **h** King Herod's palm (*Phoenix dactylifera*). **g** (Image **g** from Yasina, S. et al. 2012, with permission. Image **h** by Benjitheijneb, CC BY-SA 3.0; via Wikimedia Commons)

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.

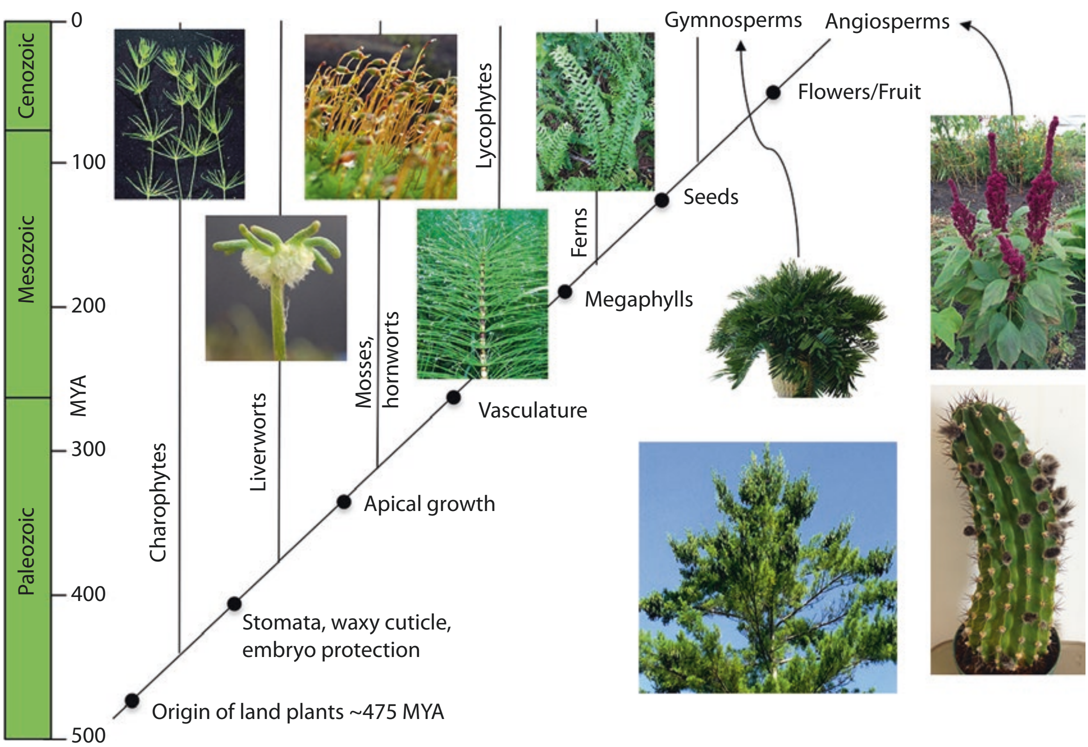
1.8.1 The Precambrian: 4550 to 542 mya

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).

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

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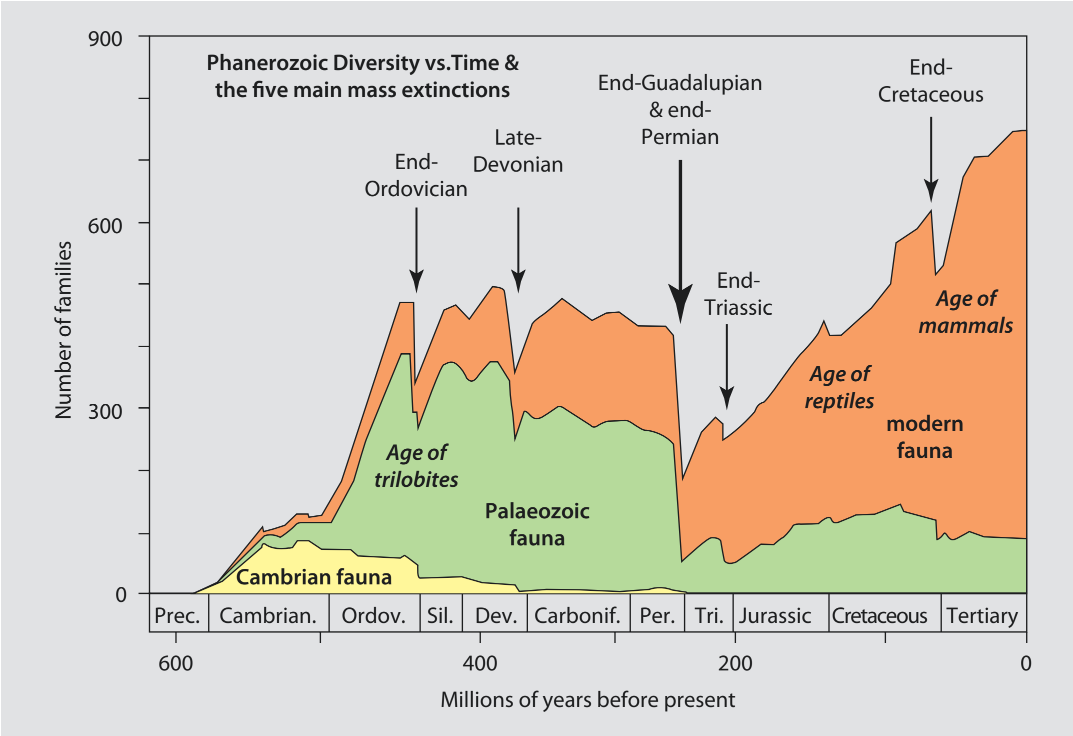


Fig. 1.9 An illustration of the geological periods, mass extinctions, and the relative numbers of animal families before and after the times of mass extinctions. Fossil spores indicate that land plants may have arisen as early as 470 mya, during the Ordovician Period. (Redrawn from Sepkoski (1984))

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

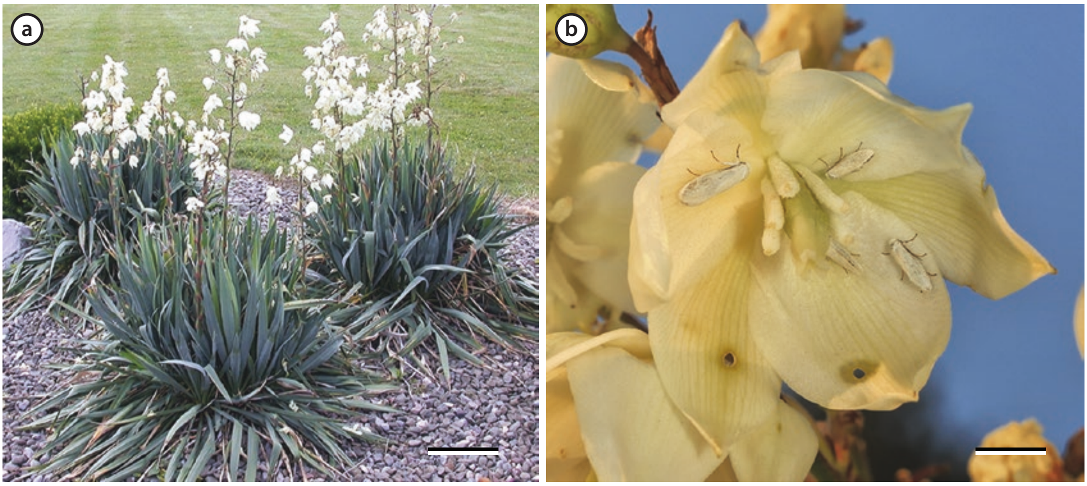


Fig. 1.10 **a**, **b** Species-specific coevolution. **a** The Spanish bayonet (*Yucca filamentosa*) is pollinated by only one species of **b** Yucca moth (*Tegeticula yuccasella*). Scale bars = 10 cm in **a** and 1 cm in **b**. (**a** Image courtesy of Kevin Nixon (Copyright © 2004 by Kevin C. Nixon,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

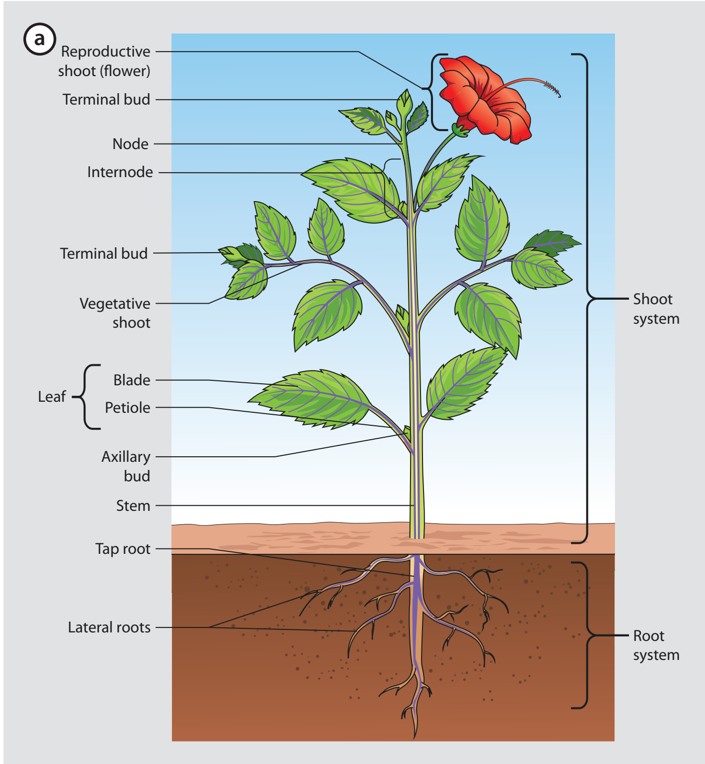
the yucca moth (genus *Tegeticula*; Fig. 1.10). The female moth lays her eggs in the ovules of yucca flowers and then scrapes up pollen from the flower's anthers into a ball. The pollen ball is then carried to another yucca plant where it is placed on the stigma of a flower and where another batch of 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,

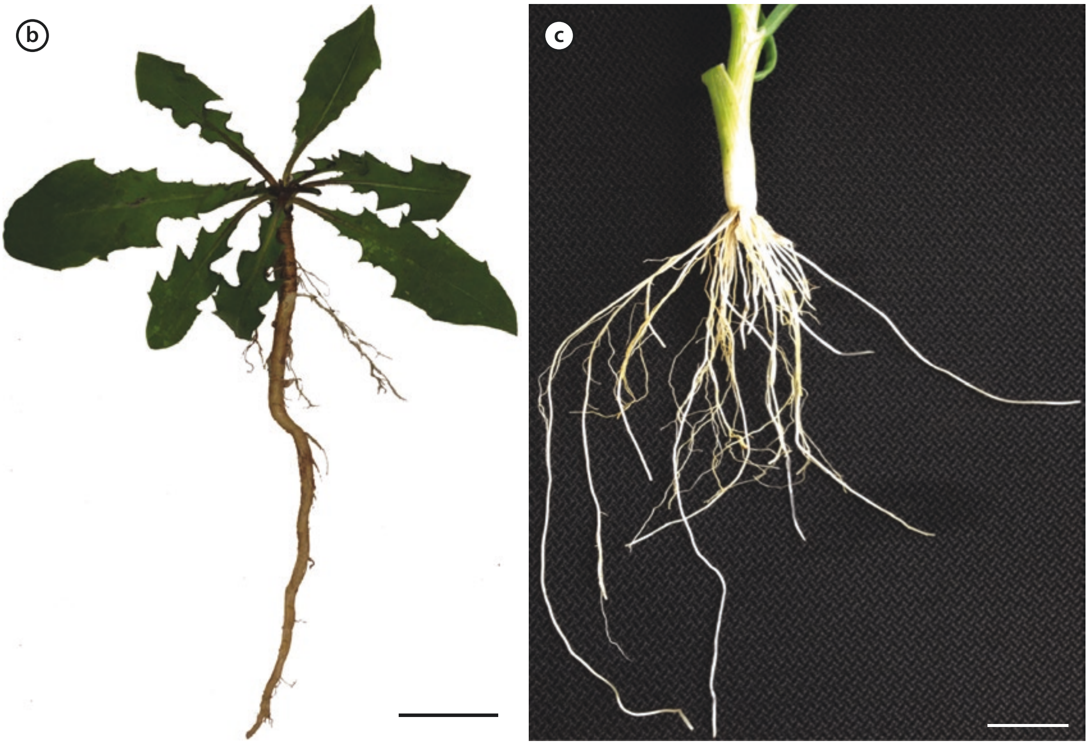


Fig. 1.11 **b** Taproot system of a typical eudicot (dandelion, *Taraxacum officinale*). **c** Fibrous, adventitious roots on a monocot (green onion, *Allium cepa*). Scale bar in (**c**) = 2 cm and applies to both panels (**b**, **c** RR Wise)

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.

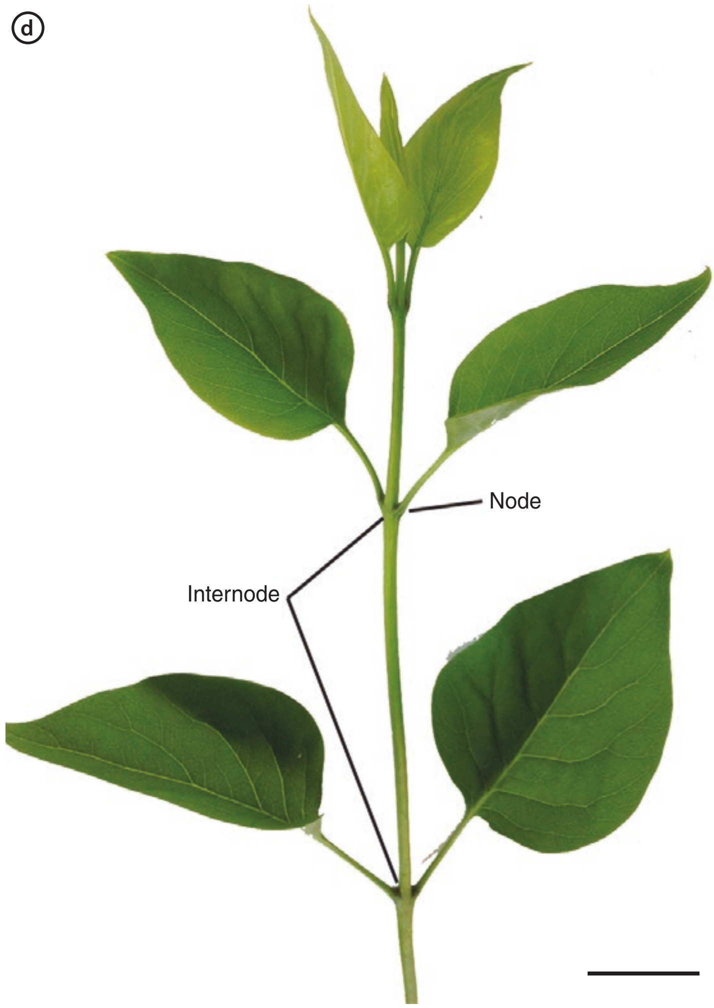


Fig. 1.11 **d** Stem from a lilac bush (*Syringa* sp.). Scale bar = 5 mm (RR Wise)

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

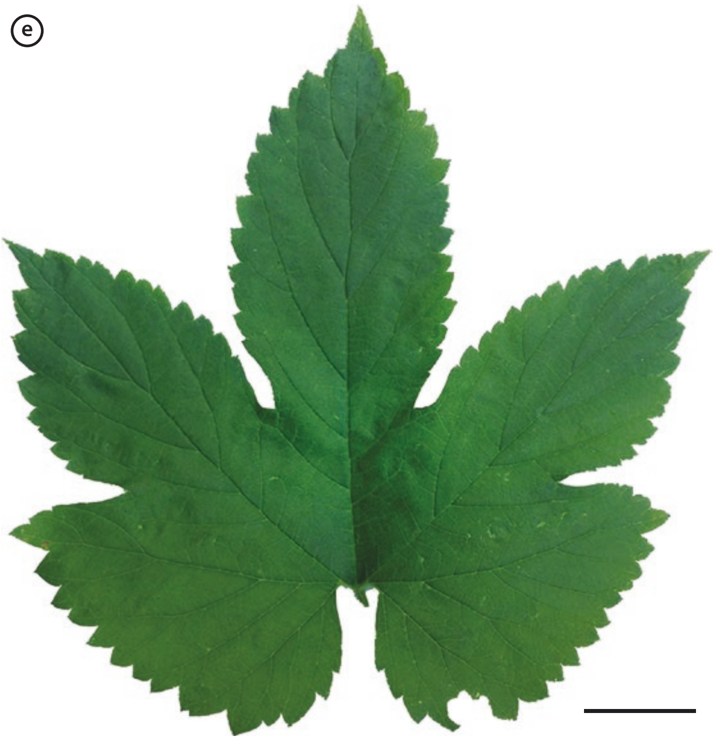


Fig. 1.11 **e** Leaf of hops (*Humulus lupulus*). Scale bar = 5 cm (RR Wise)

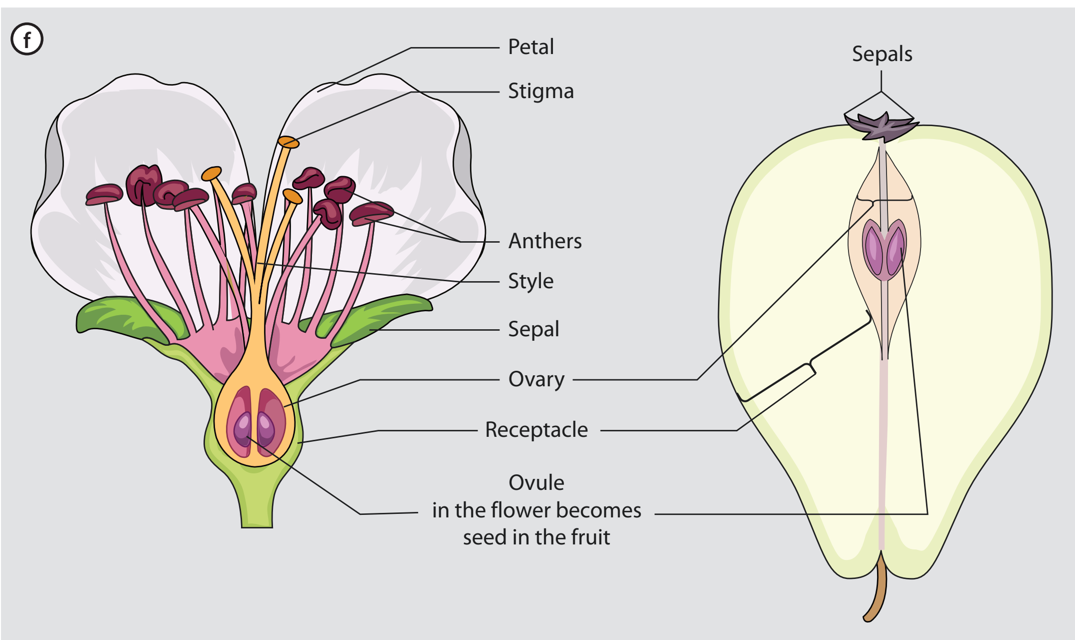


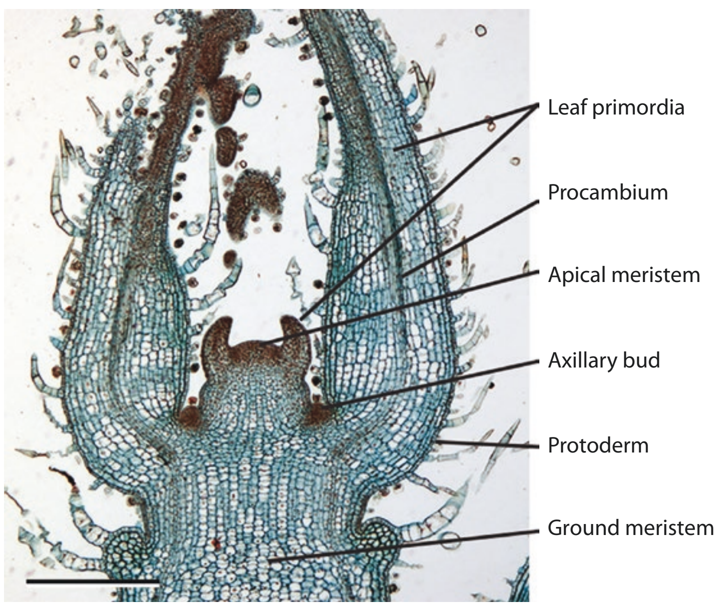
Fig. 1.11 **f** Cutaway drawings of a pear flower and the fruit that develops from the receptacle and ovary wall (Redrawn from Crang and Vassilyev 2003)

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

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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	Vascu-lature	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 (2*n*)	Yes	No	No
Gymno-sperms and allies	Ginkgophyta – *Ginkgo* Gnetophyta – gnetophytes Cycadophyta – cycads Coniferophyta – conifers	1 70 130 630	Sporophyte (2*n*)	Yes	Yes	No
Basal angiosperms	*Amborella* Nymphaeales Austrobaileyales	1 70 100	Sporophyte (2*n*)	Yes	Yes	Yes
Angiosperms	*Ceratophyllum* Chloranthales Magnoliids Monocotyledonae – monocots Eudicotyledonae – eudicots	6 70 9000 70,000 175,000	Sporophyte (2*n*)	Yes	Yes	Yes
Total		364,300				

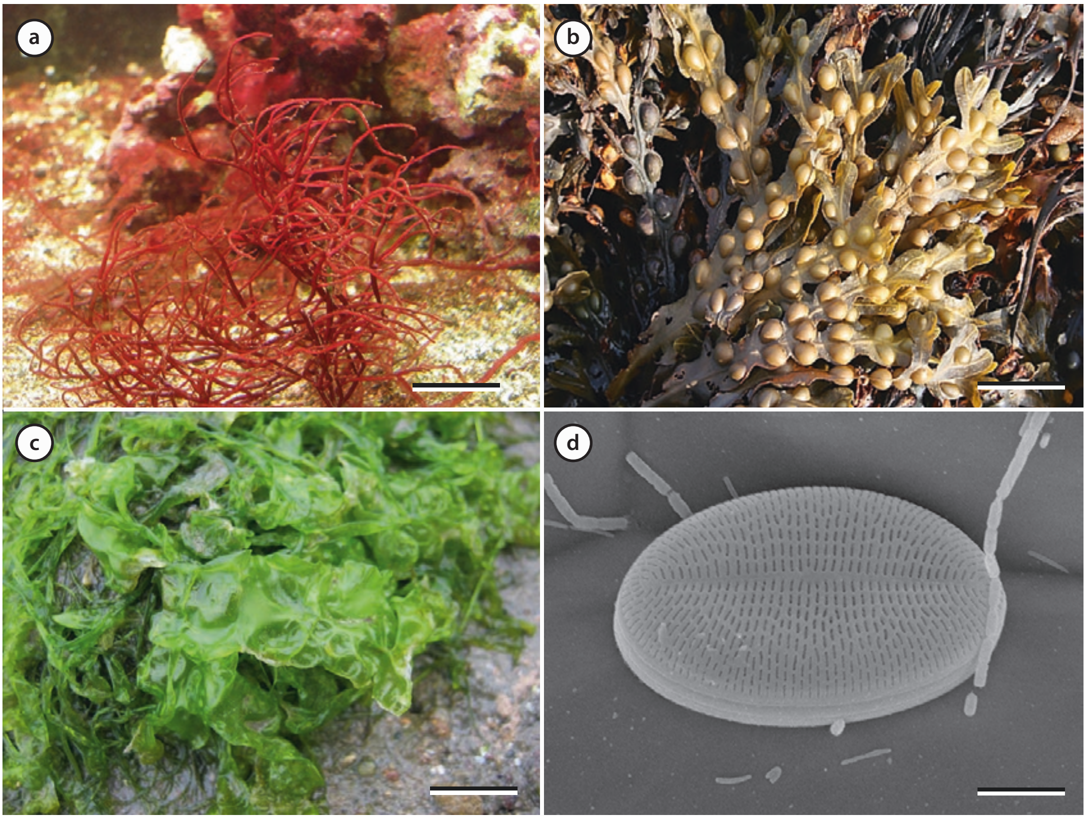


Fig. 1.13 **a**–**d** Representatives of four major algal groups: **a** red algae (*Gracilaria* sp.), **b** brown algae (*Fucus vesiculosus*), **c** green algae (*Ulva lactuca*) and **d** an unidentified freshwater diatom. Scale bars = 2 cm in a and b, 1 cm in c and 2 µm in d. (**a** Eric Moody CC BY 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.

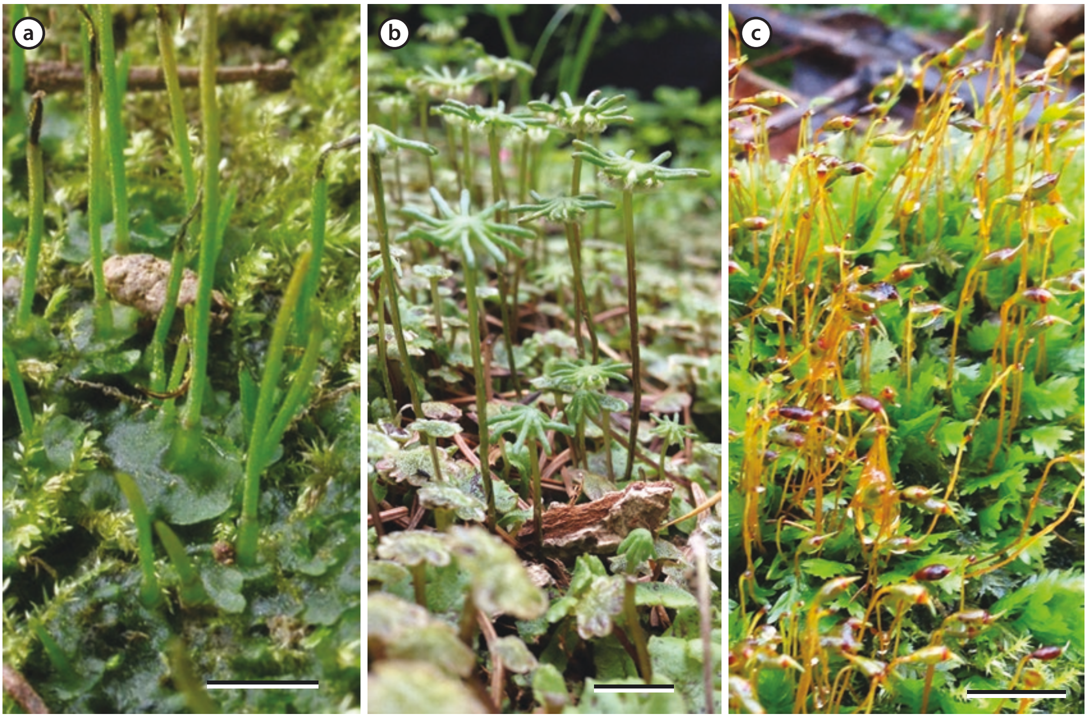
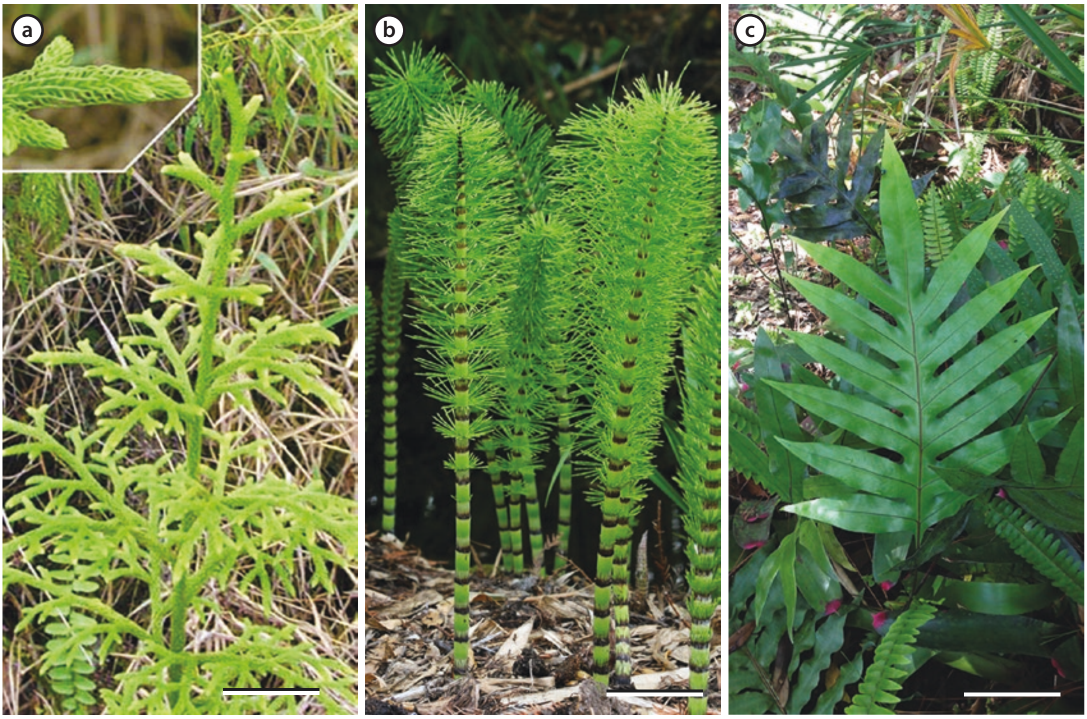


Fig. 1.14 Representative bryophytes. **a** The hornwort (*Phaeoceros laevis*) is so-named because of the horn-like sporophytes arising from the flattened thalli of the gametophyte. **b** The liverwort (*Marchantia* sp.) has male and female sporophytes. The flattened thalli lay on the ground while the 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).

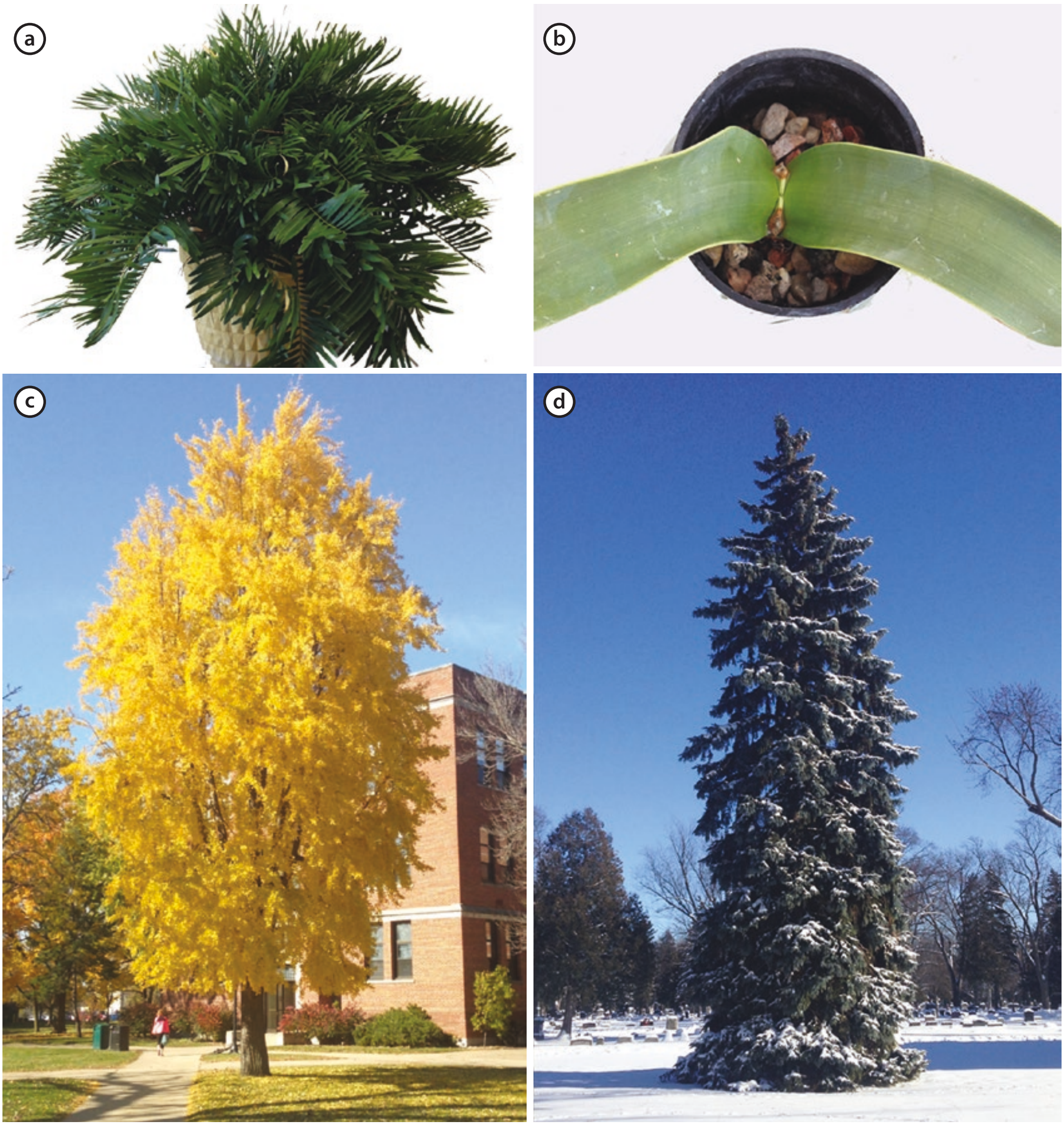


Fig. 1.16 Representative gymnosperms: **a** coontie (*Zamia pumila,* Cycadophyta) **b** welwitschia (*Welwitschia mirabilis*, Gnetophyta), **c** maidenhair tree (*Ginkgo biloba*, Ginkgophyta) in fall foliage, and **d** white spruce (*Picea glauca*, Coniferophyta) (RR Wise)

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.

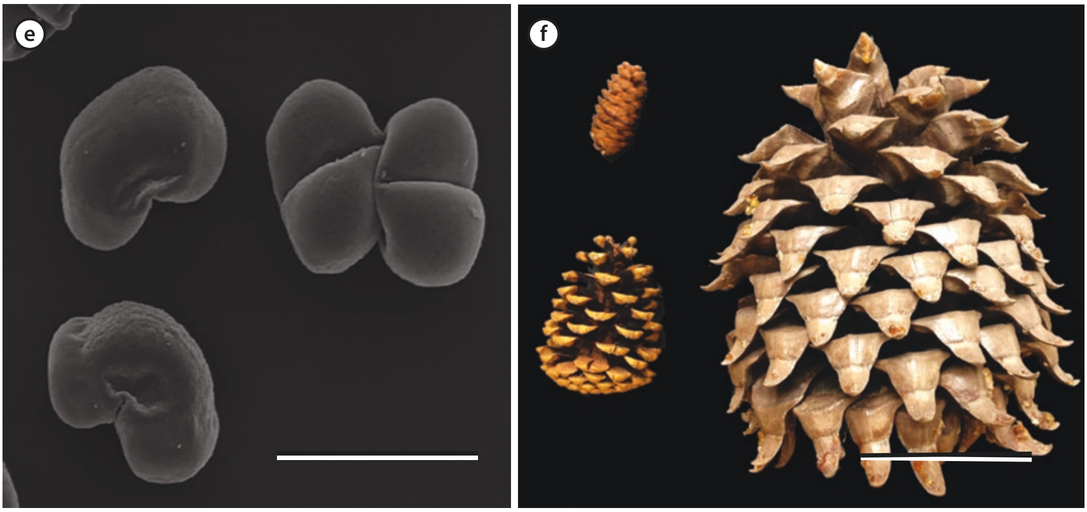


Fig. 1.16 **e** Pollen grains from blue spruce (*Picea pungens*) male cones and **f** several gymnosperm female cones, each of which bears exposed seeds. In pine, there are two seeds with papery wings on the upper surface of each scale of the female cone. Scale bars: (**e**) = 100 µm, (**f**) = 5 cm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

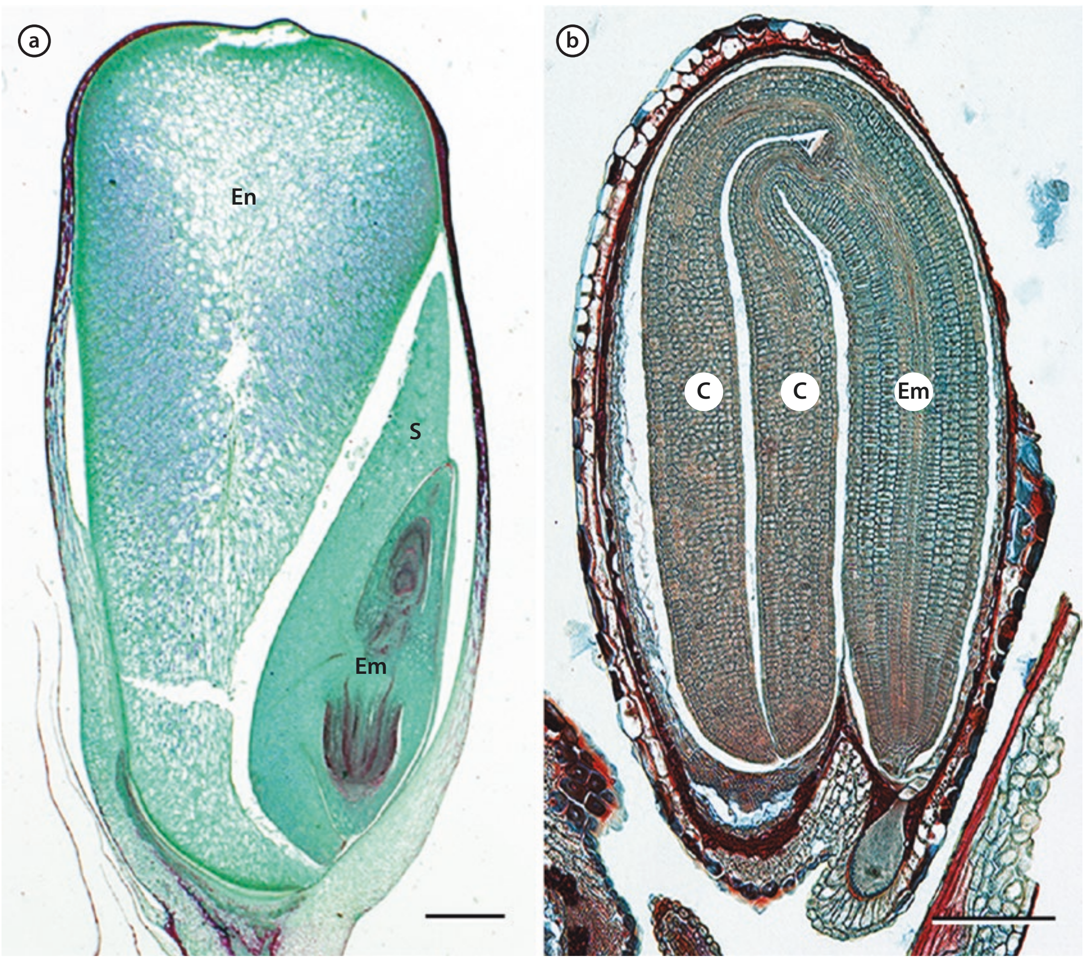
The needle-shaped leaves are also resistant to drought. Conifer woods contain tracheids to conduct water. Tracheids are long tapered cells with overlapping ends. They are believed to be ancestors of elongated cells that became modified for water transport at the center of the stem. In an evolutionary 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)

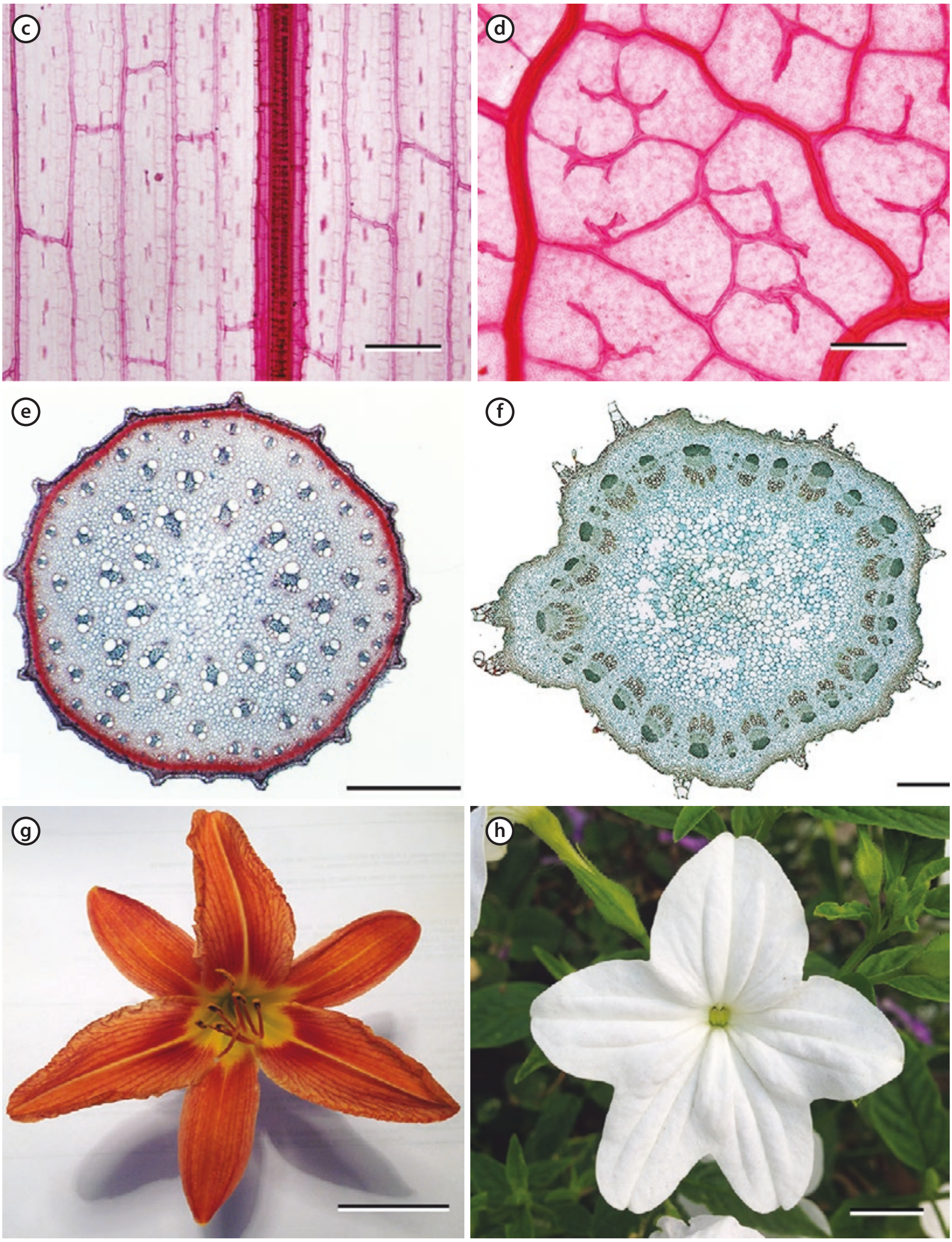


Fig. 1.17 **c–h** (continued)

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

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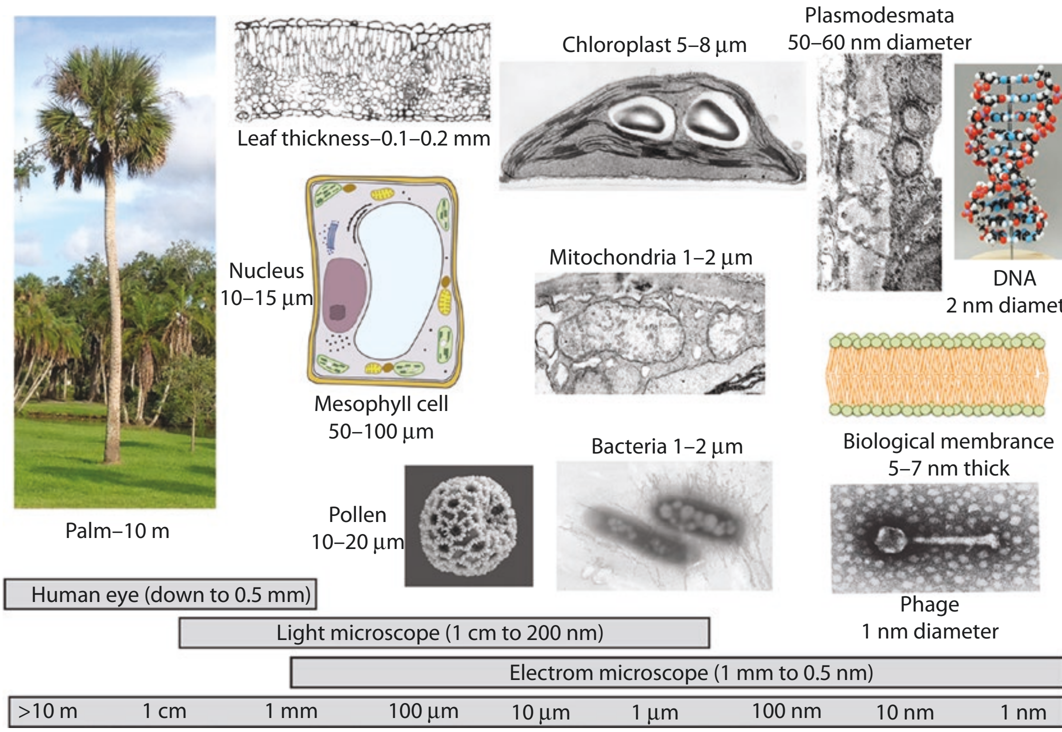


Fig. 1.18 A pictorial depiction of various plant structures and their sizes. The ability to visualize the size of each component is given by the bars across the bottom of the figure (Palm tree courtesy of J.F. Wise, DNA model courtesy of Molecular Models Corporation, Beloit, WI, phage courtesy of RV 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, $1\text{x}10^{-1}$ 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.

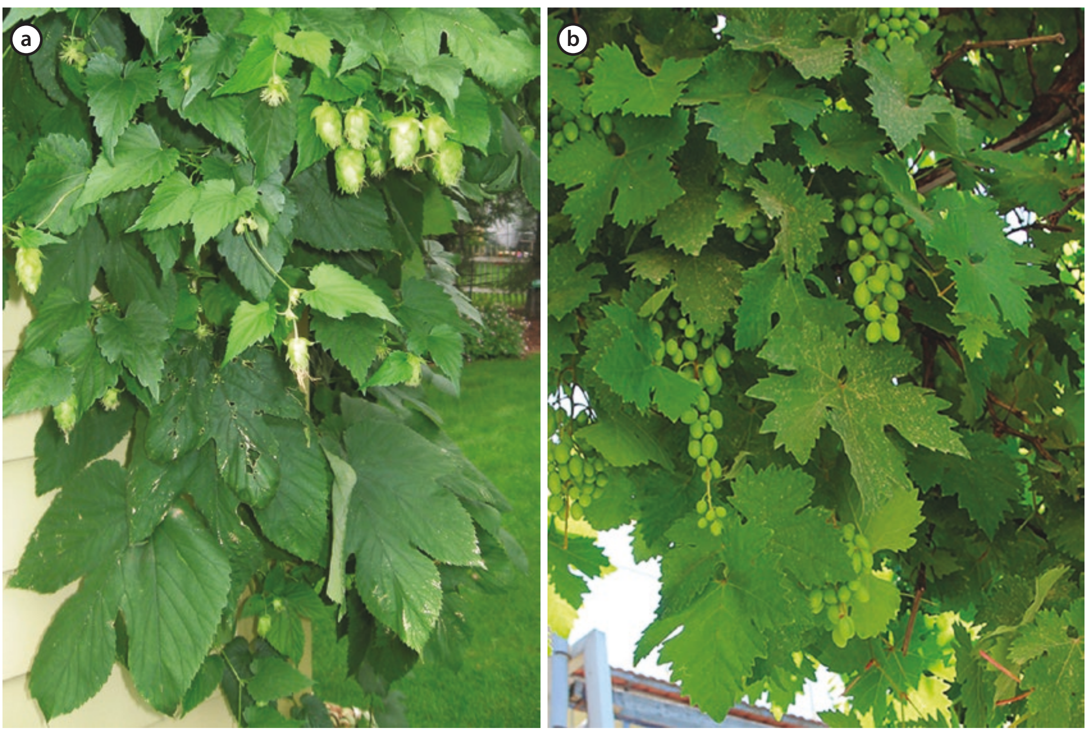
1.19.1 Primary Versus Secondary Growth and Meristems

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

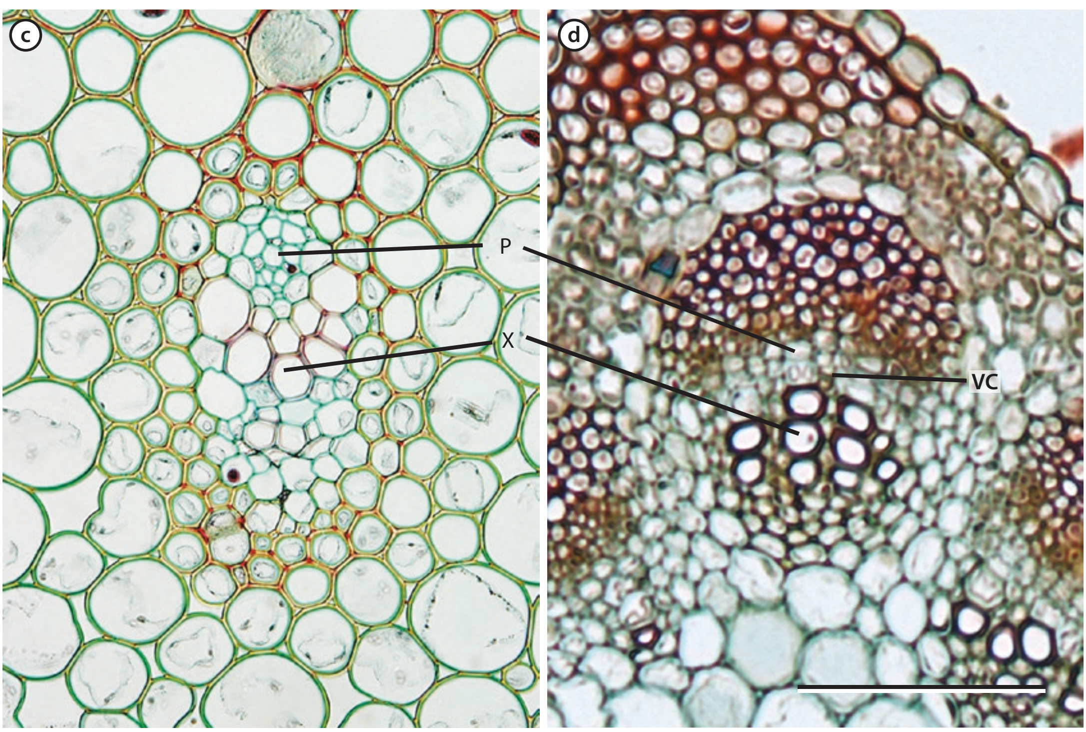


◘ **Fig. 1.19** **a** Although hops (*Humulus lupulus*) stems may grow 10 m or more in a growing season, they are herbaceous, annual organs displaying only primary growth. They die back to the ground in the autumn and grow anew from underground rhizomes in the spring. **b** Grapes (*Vitis riparia*) produce 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	

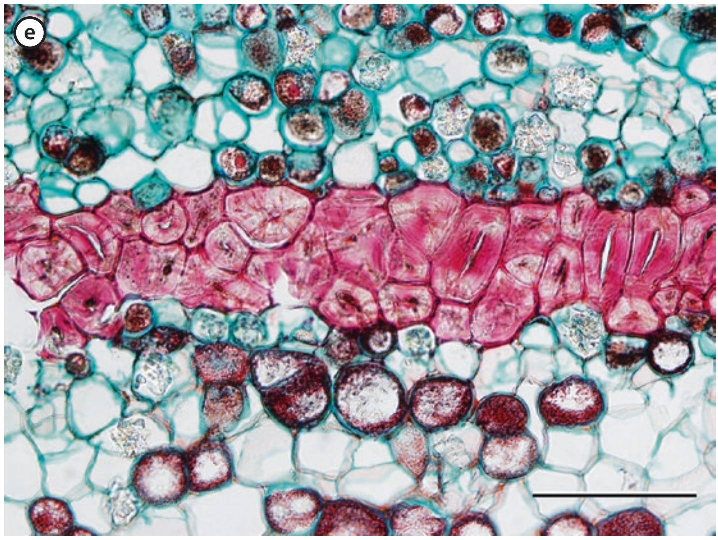


Fig. 1.19 **e** Primary and secondary cell walls in a young black walnut (*Juglans nigra*) stem. Parenchyma cells with thin primary walls (*green*) lie to either side of a band of brachysclereids with thick secondary walls (*red*). Many of the parenchyma cells contain reddish-brown tannin deposits. Scale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

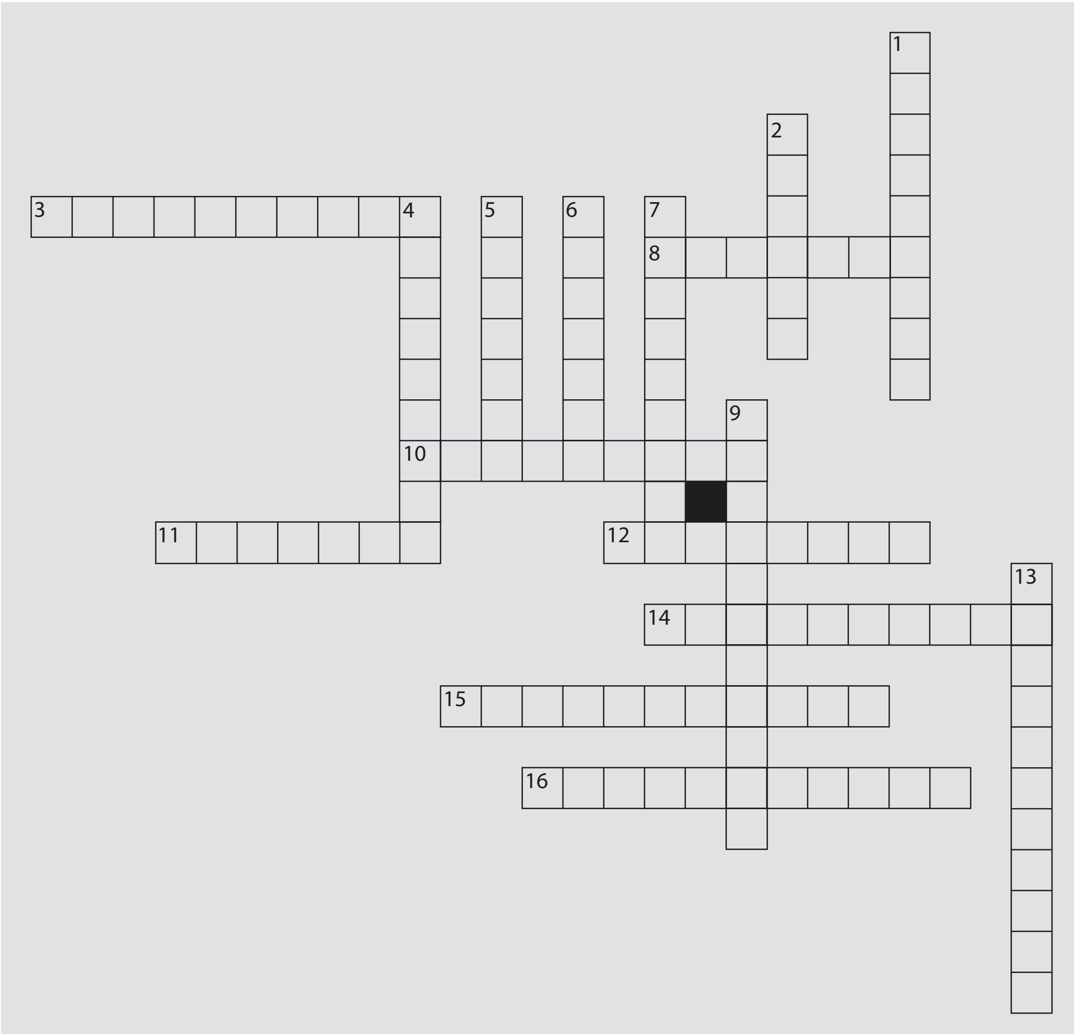
1.17 *Monocots and eudicots are the two largest groups of angiosperms*. Angiosperms, roughly divided into the monocots and the eudicots, are the dominant and most diverse group of modern plants. Monocots and eudicots have vasculature, flowers, seeds, and fruit but differ from each other in many ways 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?

References and Additional Readings

Brocks JJ, Jarrett AJM, Sirantoine E, Hallmann C, Hoshino Y, Liyanage T (2017) The rise of algae in Cryogenian oceans and the emergence of animals. Nature. https://doi.org/10.1038/nature23457

Conway S (2013) Beyond pine cones: an introduction to gymnosperms. Arnoldia 70:2–14

Crang RFE, Vassilyev AE (2003) Electronic plant anatomy. McGraw-Hill, New York

Cutler DF, Botha T, Stevenson D (2008) Plant anatomy: an applied approach. Blackwell Publishing, Malden

Dickinson WC (2000) Integrative plant anatomy. Hardcourt, Inc., Orlando

Esau K (1953) Plant anatomy. Wiley, New York

Esau K (1977) Anatomy of seed plants. Wiley, New York

Evert RF (2006) Esau's plant anatomy: meristems, cells and tissues of the plant body – their structure, function and development, 3rd edn. Wiley, Hoboken

Fahn A (1990) Plant Anatomy, 4th edn. Pergamon Press, New York

Gensel PG (2008) The earliest land plants. Ann Rev Ecol Evol Syst 39:459–477

Hirano T, Tanidokoro K, Shimizu Y, Kawarabayasi Y, Ohshima T, Sato M, Tadano S, Ishikawa H, Takio S, Takechi K, Takano H (2016) Moss chloroplasts are surrounded by a peptidoglycan wall containing d-amino acids. Plant Cell 28:1521–1532

Knoll AH, Summons RE, Waldbauer JR, Zumberge J (2007) The geological succession of primary producers in the oceans. In: Falkwoski P, Knoll AH (eds) The evolution of photosynthetic organisms in the oceans. Elsevier, Boston, pp 133–163

Mauseth JD (1988) Plant anatomy. Benjamin/Cummings, Menlo Park

Metcalfe CR, Chalk L (1979) Anatomy of the Dicotyledons: Vol 1, Systematic anatomy of the leaf and stem, 2nd edn. Oxford University Press, New York

Metcalfe CR, Chalk L (1983) Anatomy of the Dicotyledons: Vol 2, Wood structure and conclusion of the general introduction, 2nd edn. Oxford University Press, New York

Morgan JV, Gulick SPS, Bralower T et al (2016) The formation of peak rings in large impact craters. Science 354:878–882

Nichols DJ, Johnson KR (2008) Plants and the K–T boundary. Cambridge University Press, Cambridge, England, 280 pp

Reynolds C, Cumming GS (2016) Seed dispersal by water birds in southern Africa: comparing the roles of ectozoochory and endozoochory. Freshw Biol 61:349–361

Royer DL, Miller IM, Peppe DJ, Hickey LJ (2010) Leaf economic traits from fossils support a weedy habit for early angiosperms. Amer J Bot 97:438–445

Ryberg PE, Stockey RA, Hilton J, Mapes G, Riding JB, Rothwell GW (2012) Reconsidering relationships among stem and crown group Pinaceae: oldest record of the genus *Pinus* from the early cretaceous of Yorkshire, UK. Intl J Plant Sci 173:917–932

Solereder H (1908a) Systematic anatomy of the Dicotyledons: a handbook for laboratories of pure and applied botany, vol 1. Clarendon Press, Oxford

Solereder H (1908b) Systematic anatomy of the Dicotyledons: a handbook for laboratories of pure and applied botany. Vol. 2, Monochlamydeae, addenda, and concluding remarks. Clarendon Press, Oxford

Sørensen I, Domozych D, Willats WGT (2010) How have plant cell walls evolved? Plant Physiol 153:366–372

Sepkoski JJ Jr (1984) A kinetic model of phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. Paleobiology 10:246–226

Vajda V, Bercovici A (2014) The global vegetation pattern across the cretaceous-Paleogene mass-extinction interval – an integrated global perspective. Glob Planet Chang 12:29–49

Wise RR, Hoober JK (eds) (2016) The structure and function of plastids. In: Govindjee (ed) Advances in photosynthesis and respiration series, vol 23. Springer, Amsterdam

Yasina S et al. (2012) Regeneration of whole fertile plants from 30,000-year-old fruit tissue buried in Siberian permafrost. Natl Acad Sci Proc 109:4008–4013

Zhang L, Takanori T, Hasegawa I, Tadano T, Ohta T (2015) Furanonaphthoquinones from *Tabebuia avellanedae* induce cell cycle arrest and apoptosis in human non-small cell lung cancer cell line A549. Phytochem Lett 11:9–17