

A temperate forest with representatives of three major groups of land plants—mosses (bryophytes), conifers (gymnosperms), and flowering plants (angiosperms).

## STUDY PLAN

### 27.1 The Transition to Life on Land

Early biochemical and structural adaptations enhanced plant survival on land

Vascular tissue was an innovation for transporting substances within a large plant body

Root and shoot systems were adaptations for nutrition and support

In the plant life cycle, the diploid phase became dominant

Some vascular plants evolved separate male and female gametophytes

### 27.2 Bryophytes: Nonvascular Land Plants

Liverworts may have been the first land plants

Hornworts have both plantlike and algalike features

Mosses most closely resemble vascular plants

### 27.3 Seedless Vascular Plants

Early seedless vascular plants flourished in moist environments

Modern lycophytes are small and have simple vascular tissues

Ferns, whisk ferns, horsetails, and their relatives make up the diverse phylum Pterophyta

### 27.4 Gymnosperms: The First Seed Plants

Major reproductive adaptations occurred as gymnosperms evolved

Modern gymnosperms include conifers and a few other groups

Cycads are restricted to warmer climates

Ginkgos are limited to a single living species

Gnetophytes include simple seed plants with intriguing features

Conifers are the most common gymnosperms

### 27.5 Angiosperms: Flowering Plants

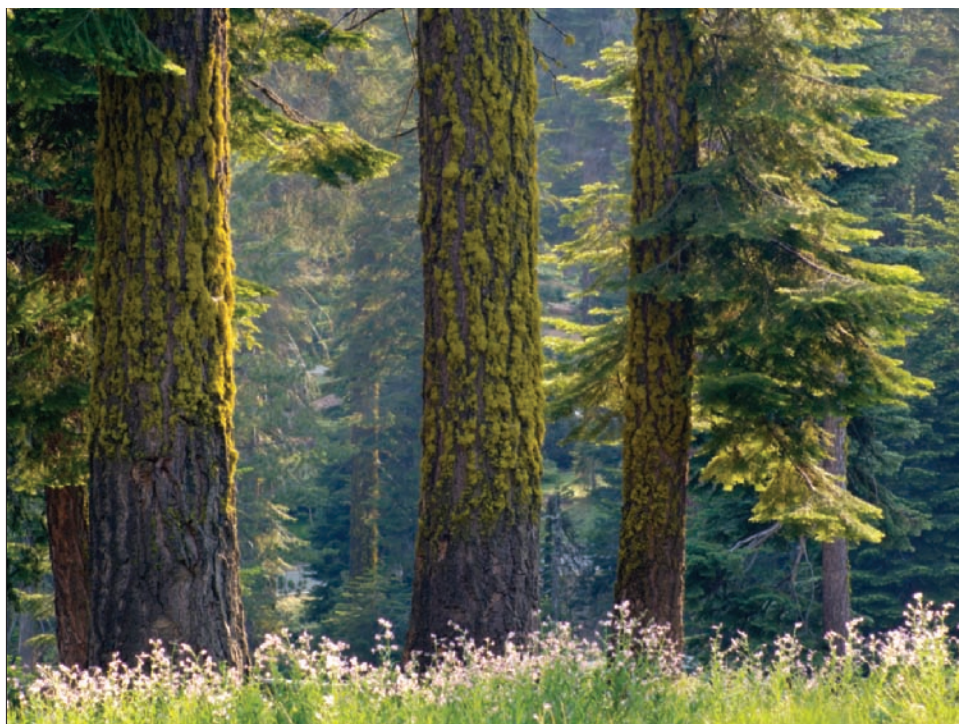
The fossil record provides little information about the origin of flowering plants

Angiosperms are subdivided into several clades, including monocots and eudicots

Many factors contributed to the adaptive success of angiosperms

Angiosperms coevolved with animal pollinators

Current research focuses on genes underlying transitions in plant traits



Animals, Animals—Earth Scenes

## 27 Plants

### WHY IT MATTERS

Ages ago, along the edges of the ancient supercontinent Laurentia, the only sound was the rhythmic muffled crash of waves breaking in the distance. There were no birds or other animals, no plants with leaves rustling in the breeze. In the preceding eons, oxygen-producing photosynthetic cells had come into being and had gradually changed the atmosphere. Solar radiation had converted much of the oxygen into a dense ozone layer—a shield against lethal doses of ultraviolet radiation, which had kept early organisms below the water's surface. Now, they could populate the land.

Cyanobacteria were probably the first to adapt to intertidal zones and then to spread into shallow, coastal streams. Later, green algae and fungi made the same journey. Seven to eight hundred million years ago, green algae living near the water's edge, or perhaps in a moist terrestrial environment, became the ancestors of modern plants. Several lines of evidence indicate that these algae were charophytes, a group discussed in Chapter 26. Today the **Kingdom Plantae** encompasses more than 300,000 living species, organized in this textbook into 10 phyla. These modern plants range from mosses, horse-tails, and ferns to conifers and flowering plants (**Figure 27.1**). Most

a. Mosses growing on rocks



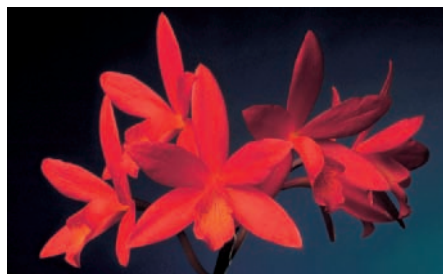
Craig Wood/Visuals Unlimited

b. A ponderosa pine



Robert Potts, California Academy of Sciences

c. An orchid



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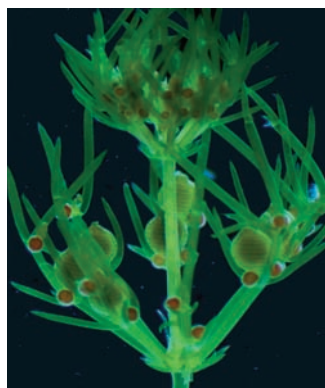
Figure 27.1

Representatives of the Kingdom Plantae. (a) Mosses growing on rocks. Mosses evolved relatively soon after plants made the transition to land. (b) A ponderosa pine, *Pinus ponderosa*. This species and other conifers belonging to the phylum Coniferophyta represent the gymnosperms. (c) An orchid, *Cattalya rojo*, a showy example of a flowering plant.

plants living today are terrestrial, and nearly all plants are multicellular autotrophs that use sunlight energy, water, carbon dioxide, and dissolved minerals to produce their own food. Together with photosynthetic bacteria and protists, plant tissues provide the nutritional foundation for nearly all communities of life.

Humans also use plants as sources of medicinal drugs, wood for building, fibers used in paper and clothing, and a wealth of other products.

While the ancestors of land plants were making the transition to a fully terrestrial life, some remarkable adaptive changes unfolded. Eons of natural selection sorted out solutions to fundamental problems, among them avoiding desiccation, physically supporting the plant body in air, obtaining nutrients from soil, and reproducing sexually in environments where water would not be available for dispersal of eggs and sperm. With time, plants evolved features that not only addressed these problems but also provided access to a wide range of terrestrial environments. Those ecological opportunities opened the way for a dramatic radiation of varied plant species—and for the survival of plant-dependent organisms such as ourselves.



Courtesy Microbial Culture Collection, National Institute for Environmental Studies, Japan

Figure 27.2

*Chara*, a stone-wort. This representative of the charophyte lineage is known commonly as muskweed because of its skunky odor.

## 27.1 The Transition to Life on Land

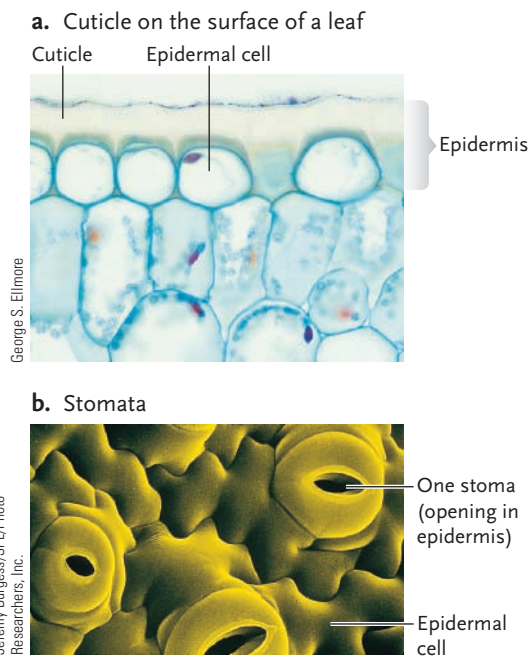
Land plants and green algae share several fundamental traits: they have cellulose in their cell walls, they store energy captured during photosynthesis as starch, and their light-absorbing pigments include both chlorophyll *a* and chlorophyll *b*. Like other green algae, the charophyte lineage that produced the ancestor of land plants arose in water and has aquatic descendants today (Figure 27.2). Yet because terrestrial environments pose very different challenges than aquatic environments, evolution in land plants produced a range of adaptations crucial to survival on dry land.

The algal ancestors of plants probably invaded land between 425 and 490 million years ago (mya). We say “probably” because the fossil record is sketchy in pinpointing when the first truly terrestrial plants appeared. A British and Arab research team working in the Middle East found fossilized tissue and spores from what appears to be a land plant in rocks dated to 475 mya. If the remains indeed are from a plant, they represent the earliest known plant fossils. Even in more recent deposits the most common finds of possible plant parts are microscopic bits and pieces. Obvious leaves, stems, roots, and reproductive parts seldom occur together, or if they do, it can be difficult to determine if the fossilized bits all belong to the same individual. Whole plants are extremely rare. Adding to the challenge, some chemical and structural adaptations to life on land arose independently in several plant lineages. Consequently, a fossil may have some but not all the features of modern land plants, leaving the puzzled paleobotanist to guess whether a given specimen was aquatic, terrestrial, or a transitional form. Despite these problems, botanists have been able to gain insight into several innovations and overall trends in plant evolution.

### Early Biochemical and Structural Adaptations Enhanced Plant Survival on Land

To survive on land, plants had to have protection against drying out, a demand that had not been a problem for algae in their aquatic habitats. The earliest land plants may have benefited from an inherited ability to make **sporopollenin**, a resistant polymer that surrounds the zygotes of modern charophytes. In land plants, sporopollenin is a major component of the thick wall that protects reproductive spores from drying and other damage. Some of the first land plants also evolved an outer waxy layer called a **cuticle**, which slows water loss, helping to prevent desiccation (Figure 27.3a). Another multifaceted adaptation was the presence of **stomata**, tiny passageways through the cuticle-covered surfaces (Figure 27.3b). Stomata (singular, *stoma*; *stoma* = mouth), which can open and close, became the main route for plants to take up carbon di-





**Figure 27.3**  
 Land plant adaptations for limiting water loss. **(a)** A waxy cuticle, which covers the epidermis of land plants and helps reduce water loss. **(b)** Surface view of stomata in the epidermis (surface layer of cells) of a leaf. Stomata allow carbon dioxide and water to enter plant tissues and oxygen to leave.

oxide and control water loss by evaporation. The next unit describes these tissue specializations more fully.

By about 470 million years ago, land plants had split into two major groups, the **nonvascular plants**, or **bryophytes**, such as mosses, which lack internal trans-

port vessels, and the **vascular plants**, or **tracheophytes**. This split correlates with the appearance of several fundamental adaptations in the vascular plant lineage (**Table 27.1**). Transport vessels, which we describe shortly, was one adaptation. Another was **lignin**, a tough, rather inert polymer that strengthens the secondary walls of various plant cells and thus helps vascular plants to grow taller and stay erect on land, giving photosynthetic tissues better access to sunlight. Another was the **apical meristem**, a region of unspecialized dividing cells near the tips of shoots and roots. Descendants of such unspecialized cells differentiate and form all mature plant tissues. Meristem tissue is the foundation for a vascular plant's extensively branching stem parts, and is a central topic of Chapter 31.

Other land plant adaptations were related to the demands of reproduction in a dry environment. As described in more detail shortly, they included multicellular chambers that protect developing gametes, and a dependent, multicellular embryo that is sheltered inside tissues of a parent plant. Botanists use the term **embryophyte** (*phyton* = plant) as a synonym for land plants because all land plants produce an embryo during their reproductive cycle.

### Vascular Tissue Was an Innovation for Transporting Substances within a Large Plant Body

The Latin *vas* means duct or vessel, and vascular plants have specialized tissues made up of cells arranged in lignified, tubelike structures that branch throughout the plant body, conducting water and solutes. One type

**Table 27.1** Trends in Plant Evolution

Traits derived from algal ancestor: cell walls with cellulose, energy stored in starch, two forms of chlorophyll ( <i>a</i> and <i>b</i> ); possibly, sporopollenin in spore wall				
Bryophytes	Ferns and Their Relatives	Gymnosperms	Angiosperms	Functions in Land Plants
Cuticle				Protection against water loss, pathogens
Stomata				Regulation of water loss and gas exchange (CO <sub>2</sub> in, O <sub>2</sub> out)
Nonvascular	Vascular			Internal tubes that transport water, nutrients
	Lignin			Mechanical support for vertical growth
	Apical meristem			Branching shoot system
	Roots, stems, leaves			Enhanced uptake, transport of nutrients and enhanced photosynthesis
Haploid phase dominant	Diploid phase dominant			Genetic diversity
One spore type (homospory)	Two spore types (heterospory)			Promotion of genetic diversity
Motile gametes		Nonmotile gametes		Protection of gametes within parent body
Seedless		Seeds		Protection of embryo

**Figure 27.4**

Fossil of one of the earliest vascular plants, *Cooksonia*, which dates to about 420 mya.

*Cooksonia* was small and, as this image shows, its stems lacked leaves and probably were less than 3 cm long. The cup-shaped structures at the top of the stems produced reproductive spores.



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of vascular tissue, called **xylem**, distributes water and dissolved mineral ions through plant parts. Another vascular tissue, **phloem**, distributes sugars manufactured during photosynthesis. Chapter 32 explains how xylem and phloem perform these key internal transport functions.

Ferns, conifers, and flowering plants—most of the plants you are familiar with—are vascular plants. Supported by lignin and with a well-developed vascular system, the body of a plant can grow large. Extreme examples are the giant redwood trees of the northern California coast, some of which are more than 300 feet tall. By contrast, nonvascular plants lack lignin, and have very simple internal transport systems, or none at all. As a result, modern nonvascular plants generally are small, as are the examples you will read about shortly.

### Root and Shoot Systems Were Adaptations for Nutrition and Support

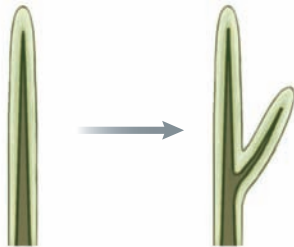
The body of a bryophyte is not differentiated into true roots and stems—structures that are fundamental adaptations for absorbing nutrients from soil and for sup-

port of an erect plant body. The evolution of sturdy stems—the basis of an aerial *shoot system*—went hand in hand with the capacity to synthesize lignin. To become large, land plants would also require a means of anchoring aerial parts in the soil, as well as effective strategies for obtaining soil nutrients. **Roots**—anchoring structures that also absorb water and nutrients—were the eventual solution to these problems. The earliest fossils showing clear evidence of roots are from vascular plants, although the exact timing of this change is uncertain. The first unquestioned fossils of a vascular plant, a small plant called *Cooksonia* (**Figure 27.4**), were found in deposits that date to about 420 mya. *Cooksonia* fossils have been unearthed in various locales but, frustratingly, none has ever included the lower portion of the plant—only its leafless, branching upper stems. *Cooksonia* probably was supported physically only by a **rhizome**—a horizontal, modified stem that can penetrate a substrate and anchor the plant. At some point, however, ancestral forms of vascular plants did come to have true roots. Ultimately, vascular plants developed specialized **root systems**, which generally consist of underground, cylindrical absorptive structures with a large surface area that favors the rapid uptake of soil water and dissolved mineral ions.

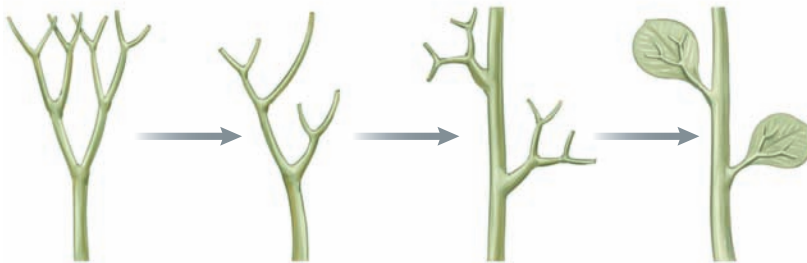
Above ground, the simple stems of early land plants also became more specialized, evolving into **shoot systems** in vascular plants. Shoot systems have stems and leaves that arise from apical meristems and that function in the absorption of light energy from the sun and carbon dioxide from the air. Stems grew larger and branched extensively after the evolution of lignin. The mechanical strength of lignified tissues almost certainly provided plants with several adaptive advantages. For instance, a strong, internal scaffold could support upright stems bearing leaves and other photosynthetic structures—and so help increase the surface area for intercepting sunlight. Also, reproductive structures borne on aerial stems might serve as platforms for more efficient launching of spores from the parent plant.

Structures we think of as “leaves” arose several times during plant evolution. In general, leaves represent modifications of stems, and **Figure 27.5** illustrates the basic steps of two main evolutionary pathways. In at least one early group of plants, the club mosses described in Section 27.3, leaflike parts evolved as outgrowths of the plant’s main vertical axis (see Figure 27.5a). In other groups, leaves arose when small, neighboring stem branches became joined by thin, weblike tissue containing cells that had chloroplasts (see Figure 27.5b).

**a.** Leaf development as an offshoot of the main vertical axis



**b.** Development of leaves in a branching pattern



**Figure 27.5**

**Evolution of leaves.** **(a)** One type of early leaflike structure may have evolved as offshoots of the plant’s main vertical axis; there was only one vein (transport vessel) in each leaf. Today, the seedless vascular plants known as lycophytes (club mosses) have this type of leaf. **(b)** In other groups of seedless vascular plants, leaves arose in a series of steps that began when the main stem evolved a branching growth pattern. Small side branches then fanned out and photosynthetic tissue filled the space between them, becoming the leaf blade. With time the small branches became modified into veins.

### In the Plant Life Cycle, the Diploid Phase Became Dominant

As early plants moved into drier habitats, their life cycles also were modified considerably. You may recall that in sexually reproducing organisms, meiosis in

diploid cells produces haploid ( $n$ ) reproductive cells (see Chapter 11). These cells may be gametes—sperm or eggs—or they may be **spores**, which can give rise to a new haploid individual asexually, without mating.

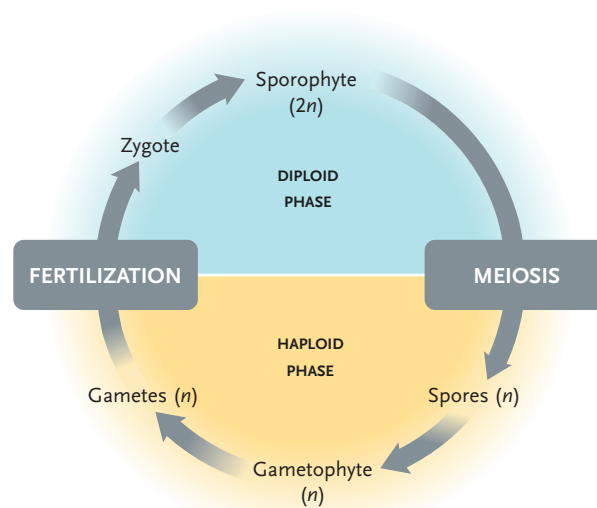
As noted in Chapter 26, in green algae the haploid phase that starts at meiosis is usually the greater part of the life cycle, and the haploid alga spends much of its life producing and releasing gametes into the surrounding water. A much shorter diploid ( $2n$ ) phase starts when gametes fuse at fertilization. Plants also cycle between haploid and diploid life phases, a phenomenon called **alternation of generations** (Figure 27.6). The diploid generation produces haploid spores and is called a **sporophyte** (“spore grower”). The haploid generation produces gametes and is called a **gametophyte** (“gamete grower”). As plants evolved on land, the haploid gametophyte phase became physically smaller and less complex and had a shorter life span while just the opposite occurred with the diploid sporophyte phase. In mosses and other nonvascular plants the sporophyte is a little larger and long-lived than in green algae, and in vascular plants the sporophyte clearly is larger and more complex and lives much longer than the gametophyte (Figure 27.7). When you look at a pine tree, for example, you see a large, long-lived sporophyte.

The sporophyte generation begins after fertilization, when the resulting zygote grows mitotically into a multicellular, diploid organism. Its body will eventually develop capsules called **sporangia** (“spore chambers”; singular, *sporangium*), which produce spores. Many botanists hypothesize that the trend toward “diploid dominance” in vascular plants reflects the advantages conferred by genetic diversity in land environments, where the supply of water and nutrients is inconsistent. Whereas haploid organisms are genetically identical to the parent, in a changeable environment the new combinations of parental alleles in a diploid organism may provide the genetic basis for adaptations to varying circumstances.

The haploid phase of the plant life cycle begins in the reproductive parts of the sporophyte. There, meiosis produces haploid spores in the sporangia. The spores then divide by mitosis and give rise to multicellular haploid gametophytes. A gametophyte’s function is to nourish and protect the forthcoming generation. Unlike nonvascular plants, most groups of vascular plants retain spores and gametophytes until environmental conditions favor fertilization.

### Some Vascular Plants Evolved Separate Male and Female Gametophytes

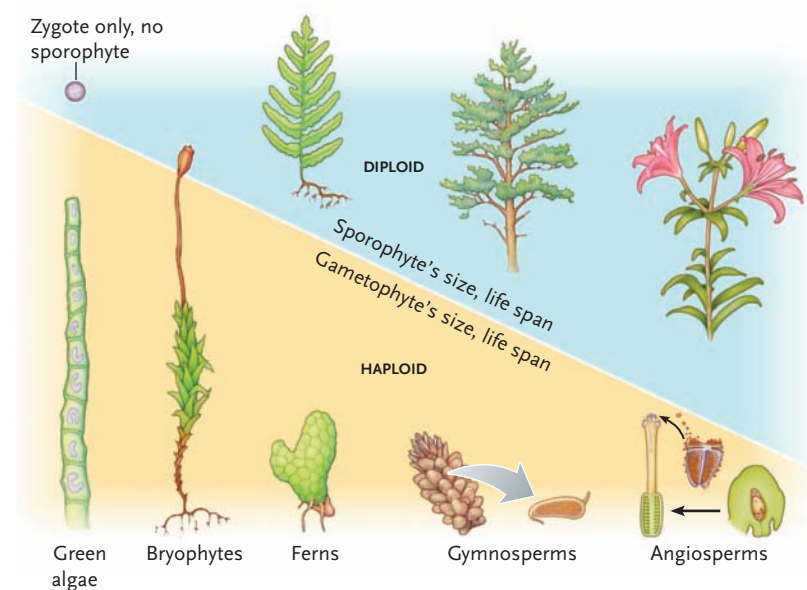
As already noted, during sexual reproduction in plants, meiosis produces spores. When a plant makes only one type of spore it is said to be **homosporous** (“same spore”). A gametophyte that develops from such a spore is bisexual—it can produce both sperm and eggs.



**Figure 27.6**

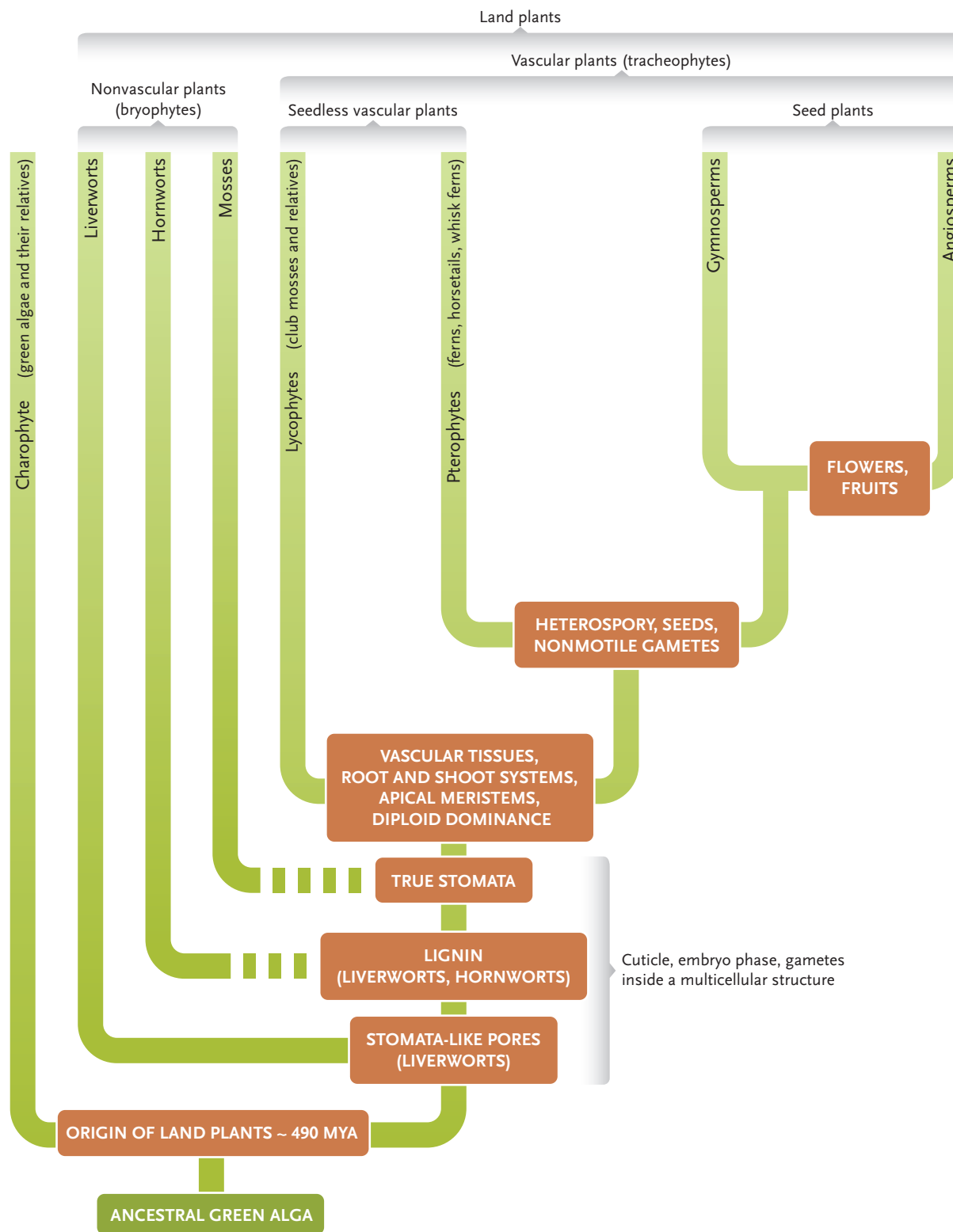
Overview of the alternation of generations, the basic pattern of the plant life cycle. The relative dominance of haploid and diploid phases is different for different plant groups (compare with Figure 27.7).

The sperm have flagella and are motile, for they must swim through liquid water in order to encounter female gametes. Other vascular plants, including gymnosperms and angiosperms, are **heterosporous**. They produce two types of spores in two different types of sporangia, and those spores develop into small, sexually different gametophytes. The smaller spore type develops into a male gametophyte—a *pollen grain*. The larger one develops into a female gametophyte, in which eggs form and fertilization occurs. The pollen grains of most vascular plants produce nonmotile sperm and also the structures required to deliver them to the egg.



**Figure 27.7**

Evolutionary trend from dominance of the gametophyte (haploid) generation to dominance of the sporophyte (diploid) generation, represented here by existing species ranging from a green alga (*Ulothrix*) to a flowering plant. This trend developed as early plants were colonizing habitats on land. In general, the sporophytes of vascular plants are larger and more complex than those of bryophytes, and their gametophytes are reduced in size and complexity. In this diagram the fern represents seedless vascular plants.



**Figure 27.8**

Overview of the possible phylogenetic relationships between major groups of land plants. Plant systematists do not agree on the relative place of bryophytes in this evolutionary history, hence the dashed lines. This diagram provides only a general picture of the points in land plant evolution where major adaptations took hold. For example, heterospory and seeds are shown as adaptations common to all seed plants, but some living fern species also are heterosporous. Fossil evidence indicates that certain ancient lycophytes and horsetails also produced two types of spores and some had seeds as well. Cycads and ginkgoes are unlike other gymnosperms in that they have motile sperm.

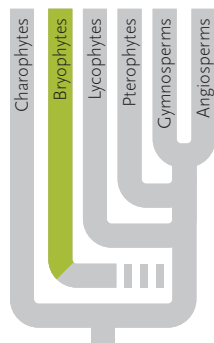


As you will read in a later section, the evolution of pollen grains and pollination helped spark the rapid diversification of plants in the Devonian period, 408–360 mya. During this time another innovation, the seed, contributed to this diversification. In fact, so many new fossils appear in Devonian rocks that paleobotanists—scientists who specialize in the study of fossil plants—have thus far been unable to determine which fossil lineages gave rise to the modern plant phyla. Clearly, however, as each major lineage came into being, its characteristic adaptations included major modifications of existing structures and functions (**Figure 27.8**). The next sections fill out this general picture, beginning with the plants that most clearly resemble the plant kingdom’s algal ancestors.

## STUDY BREAK

1. How did plant adaptations such as a root system, a shoot system, and a vascular system collectively influence the transition to terrestrial life?
2. Describe the difference between homosporous and heterosporous, and explain how heterosporous paved the way for other reproductive adaptations in land plants.

## 27.2 Bryophytes: Nonvascular Land Plants



The **bryophytes** (*bryon* = moss)—liverworts, hornworts, and mosses—have a curious combination of traits that allow them to bridge aquatic and land environments. Because bryophytes lack a well-developed system for conducting water, it is not surprising that they commonly grow on wet sites along creek banks or on rocks just above running water;

in bogs, swamps, or the dense shade of damp forests; and on moist tree trunks or rooftops. Some species are **epiphytes** (*epi* = upon)—they grow independently (that is, not as a parasite) on another organism and in a host of other moist places, ranging from the splash zone just above high tide on rocky shores, to edges of snowbanks, to coastal salt marshes.

In general, bryophytes are strikingly algalike. They produce flagellated sperm that must swim through water to reach eggs, and as noted they do not have a complex vascular system (although some have a primitive type of conducting tissue). Bryophytes have parts that are rootlike, stemlike, and leaflike. However, the

“roots” are rhizoids (slender rootlike structures), and bryophyte “stems” and “leaves” did not evolve from the same structures as vascular plant stems and leaves did. (Said another way, stems and leaves are not homologous in the two groups.) Also, as already mentioned, bryophyte tissues do not contain lignin. The absence of this strengthening material and the lack of internal pipelines for efficient nutrient transport partly account for bryophytes’ small size—typically less than 20 cm long—and for their tendency to grow sprawled along surfaces instead of upright.

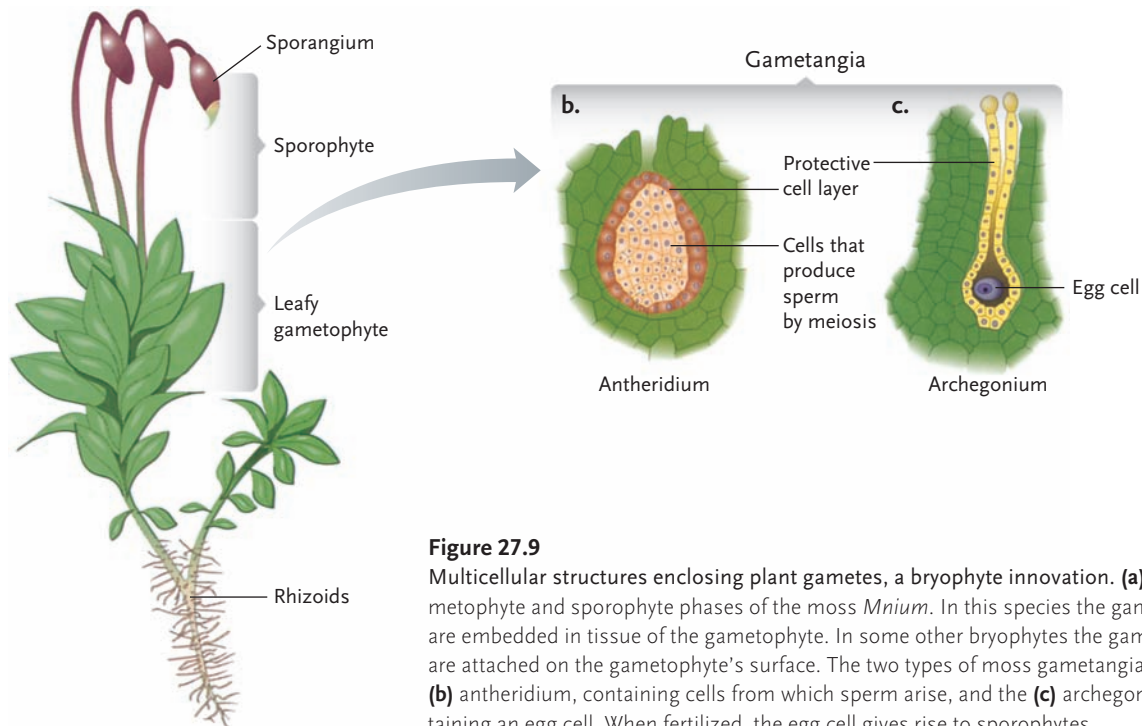
In other ways, bryophytes are clearly adapted to land. Along with their leaflike, stemlike, and fibrous, rootlike organs, sporophytes of some species have a water-conserving cuticle and stomata. Like most plants, bryophytes also have both sexual and asexual reproductive modes. And as is true of all plants, the life cycle has both gametophyte ( $n$ ) and sporophyte ( $2n$ ) phases, though the sporophyte is tiny and lives only a short time. **Figure 27.9** shows the green, leafy gametophyte of a moss plant, with miniscule diploid sporophytes attached to it by slender stalks. Bryophyte gametophytes produce gametes sheltered within a layer of protective cells called a **gametangium** (plural, *gametangia*). The gametangia in which bryophyte eggs form are flask-shaped structures called **archegonia** (*archi* = first, *gonos* = seed). Flagellated sperm form in rounded gametangia called **antheridia** (*antheros* = flowerlike). The sperm swim through a film of water to the archegonia and fertilize eggs. Each fertilized egg gives rise to a diploid embryo sporophyte, which stays attached to the gametophyte, produces spores—and the cycle repeats.

Despite these similarities with more complex plants, bryophytes are unique in several ways. Unlike in vascular species, the gametophyte is much larger than the sporophyte and obtains its nutrition independently of the sporophyte body. In fact, the comparatively tiny sporophyte remains attached to the gametophyte and depends on the gametophyte for much of its nutrition.

Because of bryophytes’ mix of characteristics, their position in plant evolution is still an open question. The basic bryophyte body plan may be similar to the ancestral condition from which higher plants evolved, but it is also possible that bryophytes represent structurally simplified vascular plant lineages that evolved after vascular plants had already appeared. In another view, they are a side shoot of evolution, completely separate from the path that led to vascular plants. The fossil record provides little help in resolving the issue, because the first undisputed bryophyte fossils appear in late-Devonian rocks 350 mya, after vascular plants were already on the scene. (Fossil remains that may resemble liverworts, however, have recently been discovered in rocks that are 50 to 100 million years older.)

Despite questions raised by recent fossil finds, most current molecular, biochemical, cellular, and

a. Moss gametophyte with attached sporophytes



**Figure 27.9**

Multicellular structures enclosing plant gametes, a bryophyte innovation. **(a)** The gametophyte and sporophyte phases of the moss *Mnium*. In this species the gametangia are embedded in tissue of the gametophyte. In some other bryophytes the gametangia are attached on the gametophyte's surface. The two types of moss gametangia are the **(b)** antheridium, containing cells from which sperm arise, and the **(c)** archegonium, containing an egg cell. When fertilized, the egg cell gives rise to sporophytes.

morphological evidence supports the view that bryophytes are not a monophyletic group. Instead, the various bryophytes evolved as separate lineages, in parallel with vascular plants. The relationships are far from resolved, however. For example, molecular evidence can be interpreted to mean that liverworts diverged early on from the lineage that led to all other land plants, with hornworts diverging later and mosses later still. Until new discoveries and interpretive work clarify this picture, the classification scheme in this chapter places liverworts, hornworts, and mosses in separate phyla. Our survey of nonvascular plants begins with the liverworts and hornworts, the simplest of the group, and concludes with mosses—plants that not only are more familiar to most of us, but whose structure and physiology more closely resemble that of vascular plants.

### Liverworts May Have Been the First Land Plants

Liverworts make up the phylum **Hepatophyta**, and early herbalists thought that these small plants were shaped like the lobes of the human liver (*hepat* = liver; *wort* = herb). The resemblance might be a little vague to modern eyes: many of the 6000 species of liverworts consist of a flat, branching, ribbonlike plate of tissue closely pressed against damp soil. This simple body, called a **thallus** (plural, *thalli*) is the gametophyte generation. Threadlike rhizoids anchor the gametophytes to their substrate. About two-thirds of liverwort species have leaflike structures and some have stemlike parts.

None have true stomata, the openings that regulate gas exchange in most other land plants, although some species do have pores that open and close. Mitochondrial gene sequence data show that liverworts lack a few features (three introns) that are present in other bryophytes and in vascular plants. Taken together with liverwort morphology, this finding has led many researchers to conclude that liverworts were probably the first land plants.

In species of the liverwort genus *Marchantia* (**Figure 27.10**), male and female gametophytes are separate plants. Male plants produce antheridia and female plants produce archegonia on specialized stalked organs (see **Figure 27.10a–b**). The motile sperm released from an antheridium swim through surface water, and some eventually encounter an egg inside an archegonium of a female gametophyte. After fertilization, a small, diploid sporophyte develops inside the archegonium, matures there, and produces haploid spores by meiosis. During meiosis, *Marchantia* sex chromosomes segregate, so some spores have the male genotype and others the female genotype. As in other liverworts, the spores develop inside jacketed sporangia that split open to release the spores. The capsules contain elongated cells twisted into a corkscrew shape. When certain regions of the cell wall absorb water and swell, the “corkscrews” rapidly unwind, helping to eject spores to the outside. A spore that is carried by air currents to a suitable location germinates and gives rise to a haploid gametophyte, which is either male or female. *Marchantia* also can reproduce asexually by way of **gemmae** (*gem* = bud), small cell masses that form



in cuplike growths on a thallus (see Figure 27.10c). Gemmae can grow into new thalli when rainwater splashes them out of the cups and onto an appropriately moist substrate.

### Hornworts Have Both Plantlike and Algalike Features

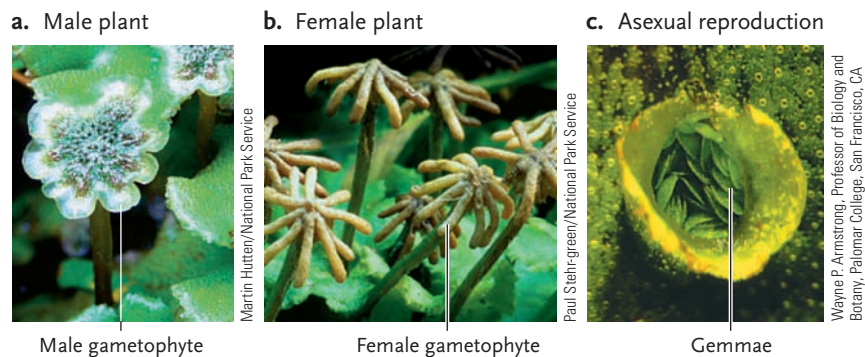
Roughly 100 species of hornworts make up the phylum **Anthoceroophyta**. Many of them have cell features in common with green algae, including the presence in each cell of a single large chloroplast that contains algal-like protein bodies called pyrenoids. No other group of land plants has this feature, and some biologists have speculated that the distinction of “first land plant” should be assigned not to liverworts but to hornworts instead. Like some liverworts, a hornwort gametophyte has a flat thallus, but the sporangium of the sporophyte phase is long and pointed, like a horn (**Figure 27.11**). The sporangia split into two or three ribbonlike sections when they release spores. Sexual reproduction occurs in basically the same way as in liverworts: free-swimming sperm fertilize eggs, which give rise to the sporophytes. Hornworts sometimes reproduce asexually by fragmentation as pieces of a thallus break off, form rhizoids, and develop into new individuals.

### Mosses Most Closely Resemble Vascular Plants

Chances are that you have seen, touched, or sat upon at least several of the approximately 10,000 species of mosses, and the use of the name **Bryophyta** for this phylum underscores the fact that mosses are the best-known bryophytes. They also are structurally and functionally most similar to the vascular plants we will consider in following sections. Their spores, produced by the tens of millions in sporangia, give rise to threadlike, haploid gametophytes that grow into the familiar moss plants, which often form tufts or carpets of vegetation on the surface of rocks, soil, or bark.

The moss life cycle, diagrammed in **Figure 27.12**, begins when a haploid ( $n$ ) spore lands on a wet soil surface. After the spore germinates it elongates and branches into a filamentous web of tissue called a **protonema** (“first thread”), which can become dense enough to color the surface of soil, rocks, or bark visibly green. After several weeks of growth, the bud-like cell masses on a protonema develop into leafy, green gametophytes anchored by rhizoids. A single protonema can be extremely prolific, producing bud after bud—and in this way giving rise to a dense clone of genetically identical gametophytes. Leafy mosses also may reproduce asexually by gemmae produced at the surface of rhizoids as well as on above-ground parts.

When a leafy moss is sexually mature, gametangia develop on its gametophytes and gametes form in

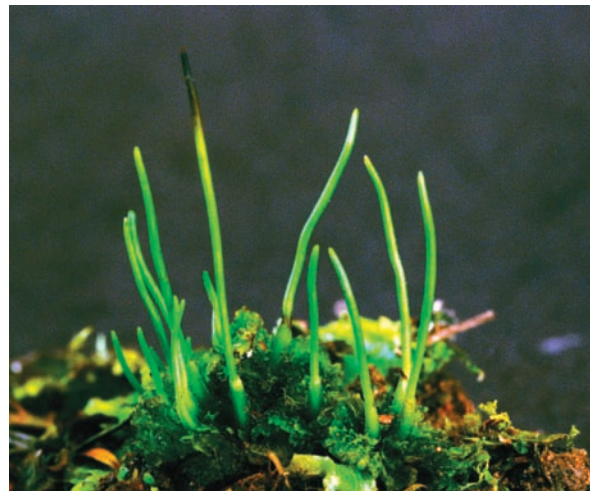


**Figure 27.10**

The bryophyte *Marchantia*, the only liverwort to produce (a) male and (b) female gametophytes on separate plants. *Marchantia* also reproduces asexually by way of (c) gemmae, multicellular vegetative bodies that develop in tiny cups on the plant body. Gemmae can grow into new plants when splashing raindrops transport them to suitable sites.

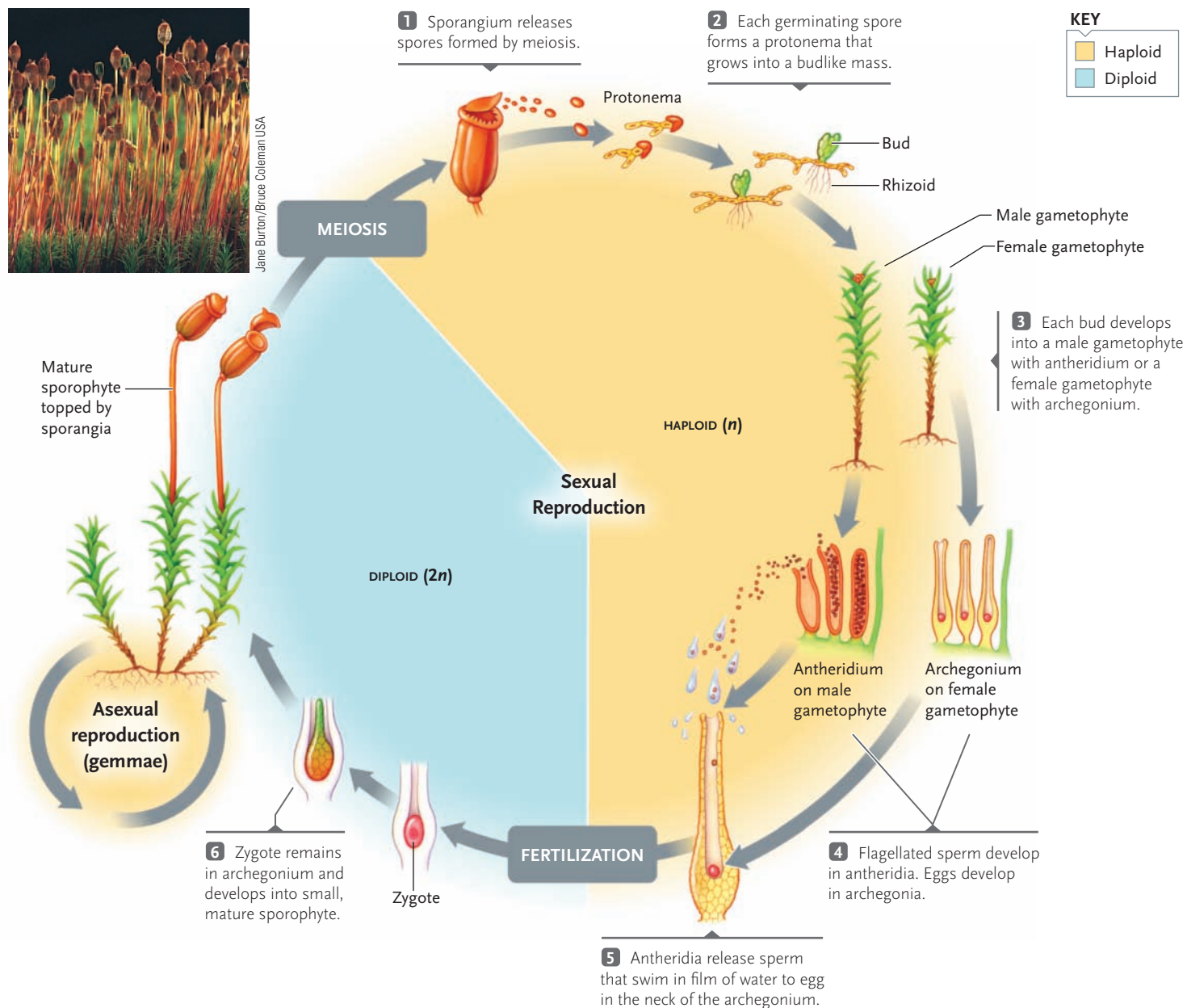
them. In some moss genera, plants are unisexual and produce male *or* female gametangia—antheridia at the tips of male gametophytes and archegonia at the tips of female gametophytes. In other genera, plants are bisexual and produce both antheridia and archegonia. Propelled by a pair of flagella, sperm released from antheridia swim through a film of dew or rainwater and down a channel in the neck of the archegonium, attracted by a chemical gradient secreted by each egg. Fertilization produces the new sporophyte generation inside the archegonium, in the form of diploid zygotes that develop into small, mature sporophytes, each consisting of a sporangium on a stalk. Moss sporophytes may eventually develop chloroplasts and nourish themselves photosynthetically, but initially they depend on the gametophytes for food. And even after a moss sporophyte begins photosynthesis, it still must obtain water, carbohydrates, and some other nutrients from the gametophyte.

Certain moss gametophytes are structurally complex, with features similar to those of higher plants. For example, some species have a central strand of primitive conducting tissue. One kind of tissue is made up of elongated, thin-walled, dead and empty cells that



**Figure 27.11**

The hornwort *Anthoceros*. The base of each long, slender sporophyte is embedded in the flattened, leafy gametophyte.



**Figure 27.12**  
Life cycle of a moss, *Polytrichum*.

conduct water. These specialized cells, called hydroids, have oblique end walls that sometimes are partly dissolved or perforated with pores. Experiments with dyes show that water moves through them, as it does in similar xylemlike arrangements in vascular plants (see Chapters 31 and 32). In a few mosses, the water-conducting cells are surrounded by sugar-conducting tissue resembling the phloem of vascular plants.

Mosses and other bryophytes are important both ecologically and economically. As colonizers of bare land, their small bodies trap particles of organic and inorganic matter, helping to build soil on bare rock and stabilizing soil surfaces with a biological crust in harsh places like coastal dunes, inland deserts, and embankments created by road construction. Some hornworts harbor mutualistic nitrogen-fixing cyanobacteria, and so increase the amount of nitrogen available to other plants. In arctic tundras, bryophytes constitute as

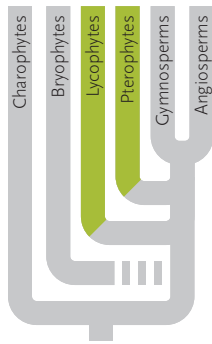
much as half the biomass, and they are crucial components of the food web that supports animals in that ecosystem. People have long used *Sphagnum* and other absorbent “peat” mosses (which typically grow in bogs) for everything from diapering babies and filtering whiskey to increasing the water-holding capacity of garden soil. Peat moss also has found use as a fuel; each day the Rhode generating station in Ireland, one of several in that nation, burns 2000 metric tons of peat to produce electricity.

In the next section we turn to the vascular plants, which have specialized tissues that can transport water, minerals, and sugars. Without the capacity to move these substances efficiently throughout the plant body, large sporophytes could not have survived on land. Unlike bryophytes, modern vascular plants are monophyletic—all groups are descended from a common ancestor.

## STUDY BREAK

1. Give some examples of bryophyte features that bridge aquatic and terrestrial environments.
2. How do specific aspects of a moss plant's anatomy resemble those of vascular plants?

## 27.3 Seedless Vascular Plants



The first vascular plants, which did not “package” their embryos inside protective seeds, were the dominant plants on Earth for almost 200 million years, until seed plants became abundant. The fossil record shows that seedless vascular plants were well established by the late Silurian, some 428 mya, and they flourished until the end of the Carboniferous, about 250 mya. Some living seedless vascular plants have certain bryophyte-like traits, whereas others have some characteristics of seed plants. On one hand, like bryophytes, seedless vascular plants reproduce sexually by releasing spores, and they have swimming sperm that require free water to reach eggs. On the other hand, as in seed plants, the sporophyte of a seedless vascular plant separates from the gametophyte at a certain point in its development and has well-developed vascular tissues (xylem and phloem). Also, the sporophyte is the larger, longer-lived stage of the life cycle and the gametophytes are very small. Some bryophytes even lack chlorophyll. **Table 27.2** summarizes these characteristics and gives an overview of seedless vascular plant features within the larger context of modern plant phyla.

Seedless vascular plants once encompassed a huge number of diverse species of trees, shrubs, and herbs. In the late Paleozoic era, they were Earth's dominant vegetation. Some lineages have endured to the present, but collectively these survivors total fewer than 14,000 species. The taxonomic relationships between various lines are still under active investigation, and comparisons of gene sequences from the genomes in plastids, cell nuclei, and sometimes mitochondria are revealing previously unsuspected links between some of them. In this book we assign seedless vascular plants to two phyla, the Lycophyta (club mosses and their close relatives) and the Pterophyta (ferns, whisk ferns, and horsetails).

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### Early Seedless Vascular Plants Flourished in Moist Environments

The extinct plant genus *Cooksonia* (see Figure 27.4) probably was one of the earliest ancestors of modern seedless vascular plants. Like other members of its

extinct phylum (Rhyniophyta) *Cooksonia* was small, rootless, and leafless, but its simple stems had a central core of xylem, an arrangement seen in many existing vascular plants. Mudflats and swamps of the damp Devonian period were dominated by plants like *Cooksonia* and *Rhynia* (**Figure 27.13**). While these and other now-extinct phyla came and went, ancestral forms of both modern phyla of seedless vascular plants appeared. In botanical terms, the earliest seedless vascular plants were “herbs”—that is, they did not have woody, lignified tissue. By the start of the Carboniferous period, however, the small herbaceous Devonian plants had given rise to larger shrubby species and to trees with some woody tissue, bark, roots, leaves, and even seeds.

Carboniferous forests were swampy places dominated by members of the phylum **Lycophyta**, and fascinating fossil specimens of this group have been unearthed in North America and Europe. One example is *Lepidodendron*, which had broad, straplike leaves and sporangia near the ends of the branches (**Figure 27.14a**). It also had xylem and several other types of tissues that are typical of all modern vascular plants (although probably not in the same proportions as seen today). Like trees growing in modern year-round tropical climates, the fossils do not exhibit growth rings. This observation implies that the continents of Europe and North America lay along the equator during the Carboniferous period. Also abundant at the time were representatives of the phylum **Pterophyta**, including ferns such as *Medullosa* and giants such as *Calamites*—huge horsetails that could have a trunk diameter of 30 cm. The sturdy, upright stems were attached to a system of rhizomes—horizontal underground stems. Ferns populated the forest understory. Some early seed plants also were present, including now-extinct fern-like plants, called seed ferns, which bore seeds at the tips of leaves (**Figure 27.14b**).

*Lepidodendron* and *Calamites* dominated lush swamp forests in a subtropical climate. After leaves, branches, and old trees fell to the ground, they became buried in anaerobic sediments. Over geologic time, these buried remains became compressed and fossilized, and today they form much of the world's coal reserves. This is why coal is called a “fossil fuel,” and the Carboniferous period is called the Coal Age. Characterized by a moist climate over much of the planet, and by the dominance of seedless vascular plants, the Carboniferous period continued for 150 million years, ending when climate patterns changed during the Paleozoic era.

Most modern seedless vascular plants are ferns, and like their ancestors they also are confined largely to wet or humid environments because they require external water for reproduction. Except for whisk ferns, their gametophytes have no vascular tissues for water transport, and male gametes must swim through water to reach eggs. The few vascular seedless plants that are



Table 27.2

Plant Phyla and Major Characteristics

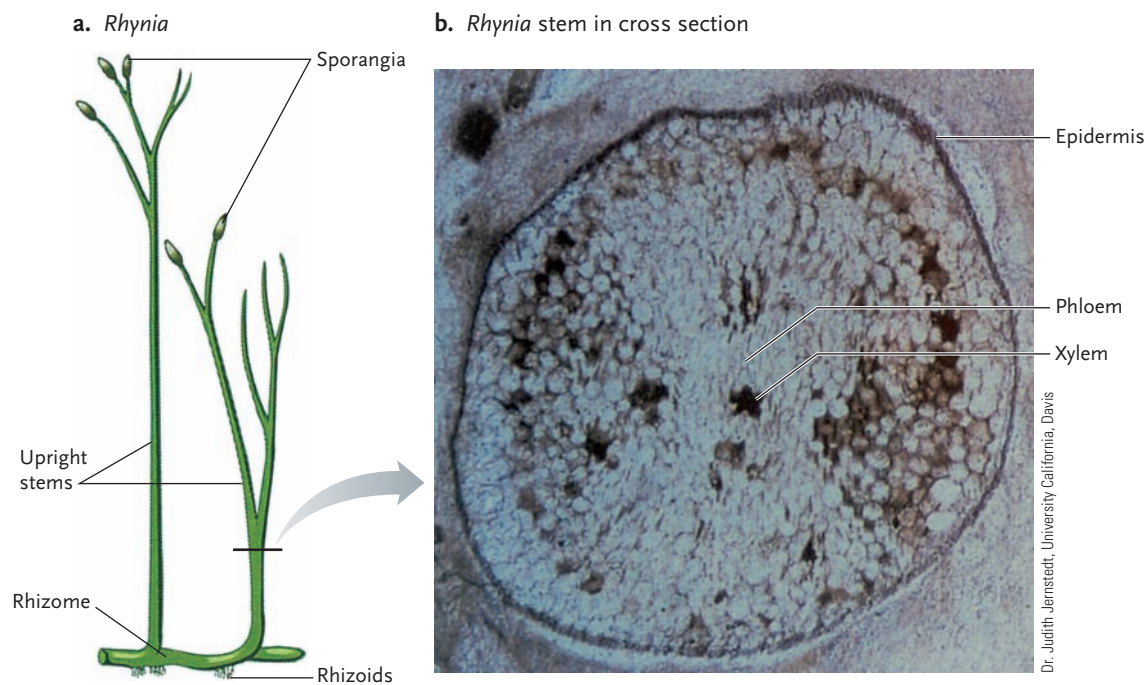
Phylum	Common Name	Number of Species	Common General Characteristics
<b>Bryophytes: Nonvascular plants. Gametophyte dominant, free water required for fertilization, cuticle and stomata present in some.</b>			
Hepatophyta	Liverworts	6000	Leafy or simple flattened thallus, rhizoids; spores in capsules. Moist, humid habitats.
Anthoceroophyta	Hornworts	100	Simple flattened thallus, rhizoids; hornlike sporangia. Moist, humid habitats.
Bryophyta	Mosses	10,000	Feathery or cushiony thallus, some have hydroids; spores in capsules. Moist, humid habitats; colonizes bare rock, soil, or bark.
<b>Seedless vascular plants: Sporophyte dominant, free water required for fertilization, cuticle and stomata present.</b>			
Lycophyta	Club mosses	1000	Simple leaves, true roots; most species have sporangia on sporophylls. Mostly wet or shady habitats.
Pterophyta	Ferns, whisk ferns, horsetails	13,000	<i>Ferns</i> : Finely divided leaves, woody stems in tree ferns; sporangia in sori. Habitats from wet to arid. <i>Whisk ferns</i> : Branching stem from rhizomes; sporangia on stem scales. Tropical to subtropical habitats. <i>Horsetails</i> : Hollow photosynthetic stem, scalelike leaves, sporangia in strobili. Swamps, disturbed habitats.
<b>Gymnosperms: Vascular plants with “naked” seeds. Sporophyte dominant, fertilization by pollination, cuticle and stomata present.</b>			
Cycadophyta	Cycads	185	Shrubby or treelike with palmlike leaves, pithy stems; male and female strobili on separate plants. Widespread distribution.
Ginkgophyta	Ginkgo	1	Woody-stemmed tree, deciduous fan-shaped leaves. Male, female structures on separate plants. Temperate areas of China.
Gnetophyta	Gnetophytes	70	Shrubs or woody vines; one has strappy leaves. Male and female strobili on separate plants. Limited to deserts, tropics.
Coniferophyta	Conifers	550	Mostly evergreen, woody trees and shrubs with needlelike or scalelike leaves; male and female cones usually on same plant.
<b>Angiosperms: Plants with flowers and seeds protected inside fruits. Sporophyte dominant, fertilization by pollination, cuticle and stomata present.</b>			
Major groups: Monocots, eudicots.			
Anthophyta	Flowering plants	268,500+ (including magnoliids, other basal angiosperms)	Wood and herbaceous plants. Nearly all land habitats, some aquatic.
Monocots	Grasses, palms, lilies, orchids, and others	60,000	Pollen grains have a single groove; one cotyledon. Parallel-veined leaves common.
Eudicots	Most fruit trees, roses, cabbages, melons, beans, potatoes, and others	200,000	Pollen grains have three grooves. Most species have two cotyledons; net-veined leaves common.

adapted to dry environments such as deserts can reproduce sexually only when adequate water is available, as during seasonal rains.

### Modern Lycophytes Are Small and Have Simple Vascular Tissues

Lycophytes such as club mosses were highly diverse 350 mya, when some tree-sized forms inhabited lush swamp forests. Today, however, such giants are no more. The most familiar of the 1000 or so living species of lycophytes are club mosses, including members of genera such as *Lycopodium* and *Selaginella*, which grow on forest floors (Figure 27.15a). Other groups include

the spike mosses and quillworts. The sporophyte of a club moss has upright or horizontal stems that contain a small amount of xylem and bear small green leaves and roots—both of which have vascular tissue. Sporangia are clustered at the bases of specialized leaves, called **sporophylls**, that occur near stem tips. A cluster of sporophylls forms a **cone** or **strobilus** (plural, *strobili*). In some species the sporangia release haploid spores produced by meiosis (Figure 27.15b). If a spore eventually germinates (which can occur even several years after it is released), it forms a free-living gametophyte, but one that differs markedly from the sporophyte. Ranging in size from nearly invisible to several centimeters, the gametophyte easily becomes buried under decompos-



**Figure 27.13**

*Rhynia*, an early seedless vascular plant. **(a)** Fossil-based reconstruction of the entire plant, about 30 cm tall. **(b)** Cross section of the stem, approximately 3 mm in diameter. This fossil was embedded in chert approximately 400 million years ago. Still visible in it are traces of the transport tissues xylem and phloem, along with other specialized tissues.

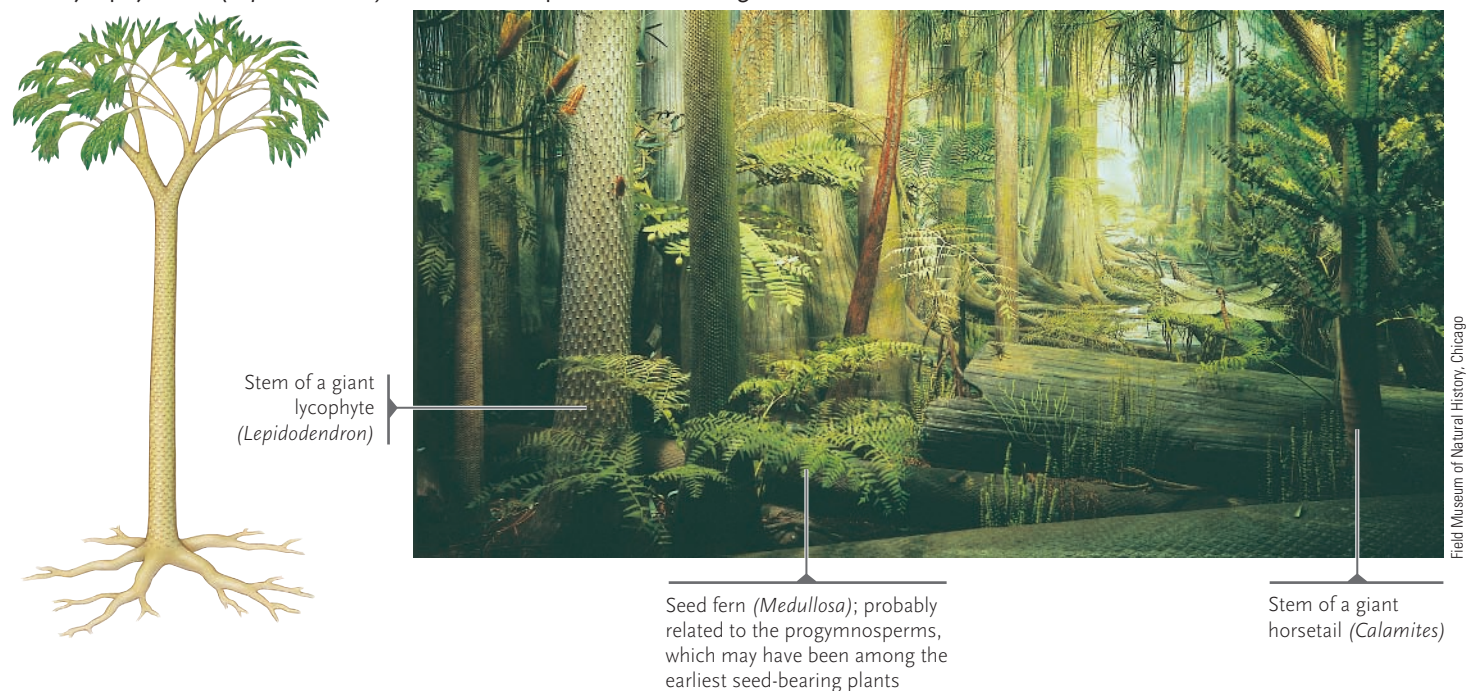
ing plant litter. There rhizoids attach it to its substrate. It cannot photosynthesize, and instead obtains nutrients by way of mycorrhizae. Although all species of *Lycopodium* are homosporous—that is, one bisexual gametophyte produces both eggs and sperm—those of

other genera are heterosporous. Regardless, as with ancestral lycophytes, the sperm require water in which they can swim to the eggs. After fertilization, the life cycle comes full circle as the zygote develops into a diploid embryo that grows into a sporophyte.

**Figure 27.14**

Reconstruction of the lycophyte tree (*Lepidodendron*) and its environment. **(a)** Fossil evidence suggests that *Lepidodendron* grew to be about 35 m tall with a trunk 1 m in diameter. **(b)** Artist's depiction of a Coal Age forest.

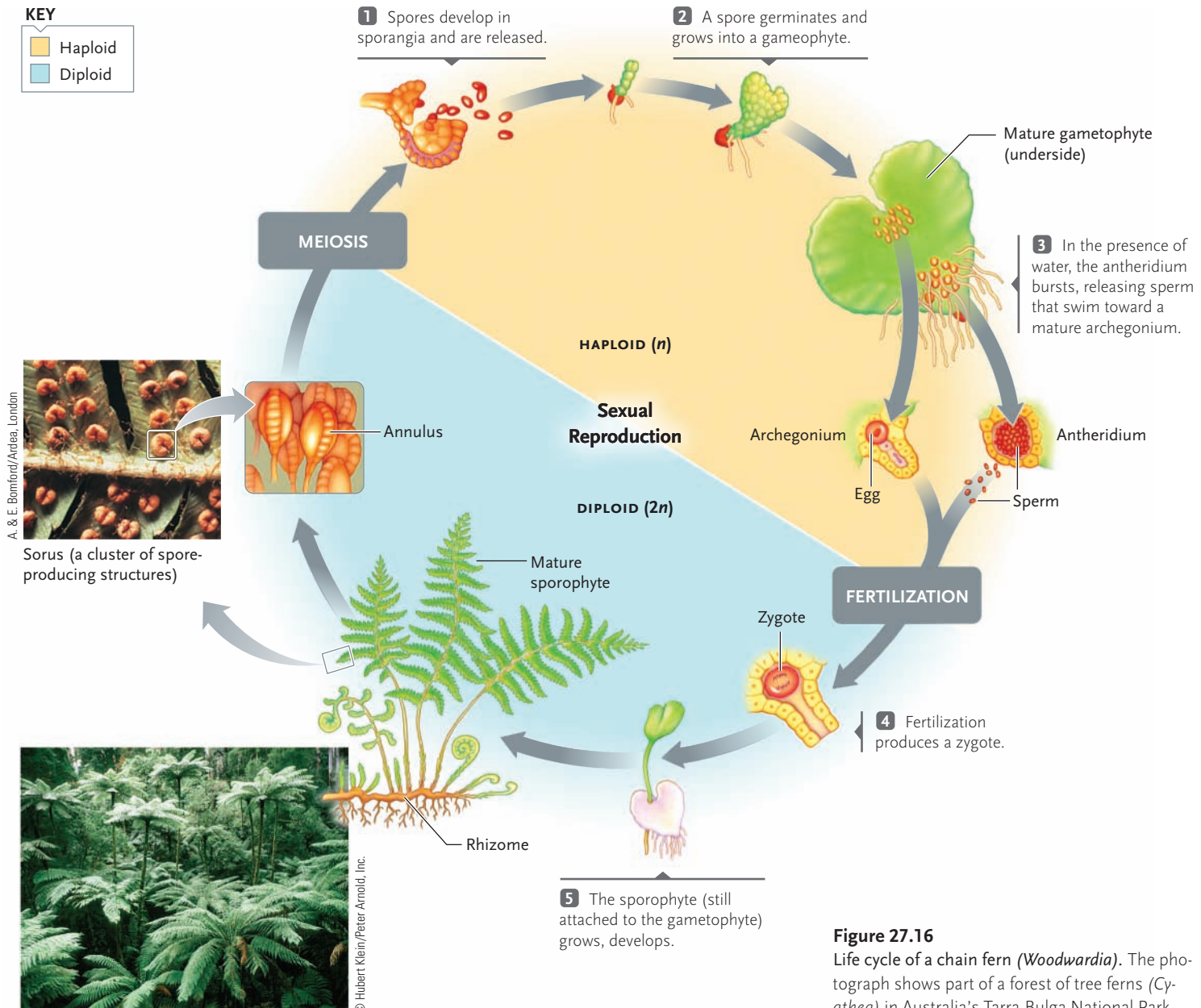
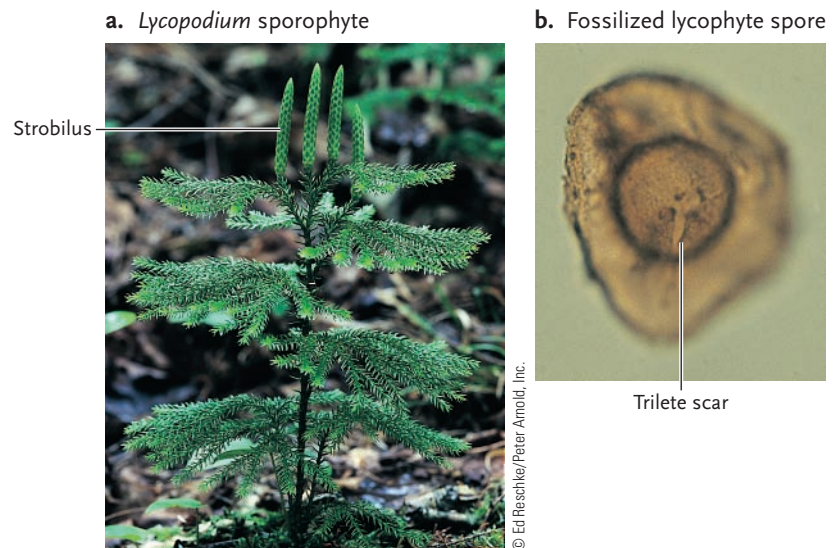
**a. The lycophyte tree (*Lepidodendron*)** **b. Artist's depiction of a Coal Age forest**





**Figure 27.15**

Lycophytes. **(a)** *Lycopodium* sporophyte, showing the conelike strobili in which spores are produced. **(b)** A fossilized lycophyte spore bearing a characteristic Y-shaped mark (arrow) called a trilete scar.



**Figure 27.16**  
Life cycle of a chain fern (*Woodwardia*). The photograph shows part of a forest of tree ferns (*Cyathea*) in Australia's Tarra-Bulga National Park.



## Ferns, Whisk Ferns, Horsetails, and Their Relatives Make Up the Diverse Phylum Pterophyta

Second only to the flowering plants, the phylum Pterophyta (*pteron* = wing) contains a large and diverse group of vascular plants—the 13,000 or so species of ferns, whisk ferns, and horsetails. Most ferns, including some that are popular houseplants, are native to tropical and temperate regions. Some floating species are less than 1 cm across, while some tropical tree ferns grow to 25 m tall. Other species are adapted to life in arctic and alpine tundras, salty mangrove swamps, and semi-arid deserts.

**Complex Anatomical Features in Ferns.** The familiar plant body of a fern is the sporophyte phase (**Figure 27.16**). It produces an above-ground clump of fern leaves, called fronds. Often finely divided and feathery-like, and containing multiple strands of vascular tissue, fronds are the most complex leaves of the plant kingdom. Young fronds are tightly coiled, and as they emerge above the soil these “fiddleheads” (so named because they resemble the scrolled pegheads of violins) unroll and expand. Before they unfurl, fiddleheads may be gathered by people who relish them as a gastronomic treat (albeit with care—the fiddleheads of some species contain a carcinogen). Leaves of some species last for only a single growing season, while in others they grow for several years. A typical frond has a well-developed epidermis with chloroplasts in the epidermal cells and stomata on the lower surface.

Except for tropical tree ferns, the stems of most ferns are underground rhizomes. The stem’s vascular system is organized into a complex, interconnecting network of bundles, each having a central core of xylem surrounded by phloem. Roots descend along the length of the rhizomes. A rhizome can live for centuries, growing at its tip and extending outward horizontally through the soil, sometimes over a considerable area. In most ferns, the fronds arise from nodes positioned along the rhizome. A **node** is the point on a stem where one or more leaves are attached.

A fern sporophyte produces sporangia on the lower surface or margin of some leaves. Often, several sporangia are clustered into a rust-colored **sorus** (plural, *sori*). Sori may be exposed or they may be protected with a flap of tissue. Each sporangium is a delicate case, shaped rather like an old-fashioned pocket watch and covered by a layer of epidermal cells. In the layer, a row of thick-walled cells called the **annulus** (“ring”) nearly encircles the sporangium.

Inside the sporangium, haploid spores arise by meiosis. Meanwhile, the sporangium slowly dries out, and as it does so the annulus steadily contracts. Eventually the force of the contracting annulus rips open the sporangium, which snaps back on itself, flinging out the mature spores. In this way fern spores can be dis-

persed up to 2 m away from the parent plant. Wind may carry them much farther: on board the *Beagle*, Charles Darwin collected fern spores hundreds of miles from shore.

A germinating spore develops into a gametophyte, which is typically a small, heart-shaped plant anchored to the soil by rhizoids. Both antheridia and archegonia are present on the lower surface of each gametophyte, where moisture is trapped. Inside an antheridium is a globular packet of haploid cells, each of which develops into a helical sperm with many flagella. When water is present, the antheridium bursts, releasing the sperm. If mature archegonia are nearby, the sperm swim toward them, drawn by a chemical attractant that diffuses from the neck of the archegonium, which is open when free water is present.

After a sperm fertilizes an egg, the diploid zygote begins dividing and developing into an embryo, which at this stage obtains nutrients from the gametophyte. In a short time, however, the embryo develops into a young sporophyte that is larger than the gametophyte and has its own green leaf and a root system. The sporophyte now is nutritionally independent and the parent gametophyte degenerates and dies.

**Features of Early Vascular Plants in Whisk Ferns.** The whisk ferns and their relatives are represented by two genera, *Psilotum* (pronounced si-lo'-tum) and *Tmesipteris* (may-sip'-ter-is), with only about 10 species in all. These rather uncommon plants grow in tropical and subtropical regions, often as epiphytes. In the United States the range for *Psilotum* species (**Figure 27.17**) includes Hawaii, Gulf Coast states such as Florida and Louisiana, and parts of the West.

The sporophytes of whisk ferns are up to 60 cm tall and resemble the extinct *Cooksonia* and *Rhynia*. Like those early vascular plants, they lack true roots and leaves. Instead, small leaflike scales adorn an upright, green, branching stem, which arises from a horizontal rhizome system anchored by rhizoids. The absorptive rhizoids have mycorrhizal fungi associated with them, which provide enhanced access to some nutrients.

A whisk fern’s stem is structurally and functionally multifaceted. The stem’s epidermal cells carry out photosynthesis, while its core has the transport tissues xylem and phloem and other anatomical features of more complex vascular plants. Sporangia rest atop some of the stem scales. Inside them, meiotic divisions of specialized cells produce haploid spores.

**Horsetails, Possibly the Most Ancient Living Plant Species.** The ancient relatives of modern-day horsetails included treelike forms taller than a two-story building. Only fifteen species in a single genus,



**Figure 27.17** Sporophytes of a whisk fern (*Psilotum*), a seedless vascular plant. Three-lobed sporangia occur at the ends of stubby branchlets; inside the sporangia, meiosis gives rise to haploid spores.

a. Sporophyte stem



William Ferguson

b. Sporangia



Strobilus, an aggregation of sporangia at the tip of the horsetail sporophyte



Kratz/Zeta

c. Each petal shaped sporangium of a strobilus contains spores that formed by meiosis.

W. H. Hoediges

**Figure 27.18**

A species of *Equisetum*, the horsetails. (a) Vegetative stem. (b) Strobili, which bear sporangia. (c) Close-up of sporangia and associated structures on a strobilus.

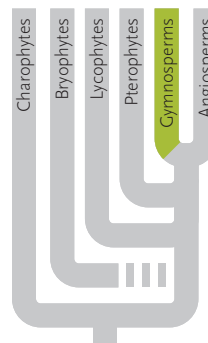
*Equisetum*, have survived to the present (Figure 27.18). Horsetails grow in moist soil along streams and in disturbed habitats, such as roadsides and beds of railroad tracks. Their sporophytes typically have underground rhizomes and roots that anchor the rhizome to the soil. The scalelike leaves are arranged in whorls about a photosynthetic stem that is stiff and gritty because horsetails accumulate silica in their tissues. American pioneers used them to scrub out pots and pans, hence their other common name, “scouring rushes.”

*Equisetum* sporangia are borne in strobili on highly specialized stem structures quite different from the sporophylls of club mosses. In most horsetails the strobili occur on ordinary vegetative shoots, but in a few species they occur only on special fertile shoots. Each stalked spore-bearing structure in a strobilus resembles an umbrella and is attached at right angles to a main axis. Haploid spores develop in sporangia attached near the edge of the “umbrella’s” underside, and air currents disperse them. They must germinate within a few days to produce gametophytes, which are free-living plants about the size of a small pea.

### STUDY BREAK

1. Compare and contrast the lycophyte and bryophyte life cycles with respect to the sizes and longevity of gametophyte and sporophyte phases.
2. In ferns, whisk ferns, and horsetails, what kinds of structures fulfill the roles of roots and leaves?
3. How does the life cycle of a horsetail differ from that of a fern?

## 27.4 Gymnosperms: The First Seed Plants



**Gymnosperms** are the conifers and their relatives. The earliest fossils identified as gymnosperms are found in Devonian rocks. By the Carboniferous, when nonvascular plants were dominant, many lines of gymnosperms had also evolved, and the first true conifers appeared. These radiated during the Permian period; the Mesozoic era that

followed, 248 to 65 mya, was the age not only of the dinosaurs but of the gymnosperms as well.

The evolution of gymnosperms involved sweeping changes in plant structures related to reproduction. As a prelude to our survey of modern gymnosperms, we begin by considering some of these innovations, which opened new adaptive options for land plants.

### Major Reproductive Adaptations Occurred as Gymnosperms Evolved

The word *gymnosperm* is derived from the Greek *gymnos*, meaning naked, and *sperma*, meaning seed. The evolution of gymnosperms included important reproductive adaptations—pollen and pollination, the ovule, and the seed. The fossil record has not revealed the sequence in which these changes arose, but all of them contributed to the radiation of gymnosperms into land environments. Figure 27.19 shows an artist’s rendering of *Archaeopteris*, which may have been one of the first true trees. Called a *progymnosperm*, it belonged to an evolutionary line that is thought to have given rise to modern seed plants.

**Pollen and Ovules: Shelter for Spores.** Unlike bryophytes and seedless vascular plants, gymnosperm sporophytes do not disperse their spores. The sporophyte produces haploid spores by meiosis, but it retains these spores inside reproductive structures where they give rise to multicellular haploid gametophytes. As noted briefly earlier, sperm arise inside a **pollen grain**, a male gametophyte that typically has walls reinforced with the polymer sporopollenin. All but a few gymnosperms have nonmotile sperm. Usually, two of these nonswimming sperm develop inside each pollen grain—very different from the flagellated, swimming sperm of algae and plants that do not produce seeds.

An **ovule** is a structure in a sporophyte in which a female gametophyte develops, complete with an egg. Physically connected to the sporophyte and surrounded by the ovule’s protective layers, a female gametophyte no longer faces the same risks of predation or environmental assault that can threaten a free-living gametophyte.

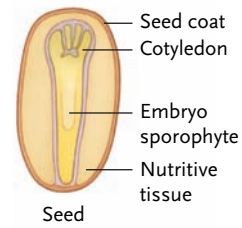


**Figure 27.19**  
Fossil-based reconstruction of *Archaeopteris*, a large Devonian progymnosperm. It could grow 25 m tall and may have been a seed-forming ancestor of modern gymnosperms.

**Pollination** is the transfer of pollen to female reproductive parts via air currents or on the bodies of animal pollinators. Pollen and pollination were enormously important adaptations for gymnosperms, because the shift to nonswimming sperm along with a means for delivering them to female gametes meant that reproduction no longer required liquid water. The only gymnosperms that have retained swimming sperm are the cycads and ginkgoes, described shortly, which have relatively few living species and are restricted to just a few native habitats.

**Seeds: Protecting and Nourishing Plant Embryos.** A **seed** is the structure that forms when an ovule matures after a pollen grain reaches it and a sperm fertilizes the egg. It consists of three basic parts: (1) the embryo sporophyte, (2) tissues around it containing carbohydrates, proteins, and lipids that nourish the embryo until it becomes established as a plantlet with leaves and roots, and (3) a tough, protective outer seed coat (**Figure 27.20**). This complex structure makes seeds ideal packages for sheltering an embryo from drought, cold, or other adverse conditions. As a result, seed-making plants enjoy a tremendous survival advantage over species that simply release spores to the environment. Encased in a seed, the embryo also can be transported far from its

parent, as when ocean currents carry coconut seeds (“coconuts” protected in large, buoyant fruits) hundreds of kilometers across the sea. As discussed in Chapter 34, some plant embryos housed in seeds can remain dormant for months or years before environmental conditions finally prompt them to germinate and grow.



**Figure 27.20**  
Generalized view of a seed—in this case, the seed of a pine, a gymnosperm.

### Modern Gymnosperms Include Conifers and a Few Other Groups

Today there are about 800 gymnosperm species. The sporophytes of nearly all are large trees or shrubs, although a few are woody vines. The most widespread and familiar gymnosperms are the conifers (Coniferophyta). Others are the cycads (Cycadophyta), ginkgoes (Ginkgophyta), and gnetophytes (Gnetophyta).

Economically, gymnosperms, particularly conifers, are vital to human societies. They are sources of lumber, paper pulp, turpentine, and resins, among other products. They also have huge ecological importance. Their habitats range from tropical forests to deserts, but gymnosperms are most dominant in the cool-temperate zones of the northern and southern hemispheres. They flourish in poor soils where flowering plants don’t compete as well. In North America, for example, gymnosperm forests cover more than one-third of the continent’s landmass—although in some areas, logging has significantly reduced the once-lush forest cover. Our survey of gymnosperms begins, however, with the cycads, ginkgoes, and gnetophytes—the latter two groups remnants of lineages that have all but vanished from the modern scene.

### Cycads Are Restricted to Warmer Climates

During the Mesozoic era, the **Cycadophyta** (*kykas* = palm), or cycads, flourished along with the dinosaurs. About 185 species have survived to the present, but they are confined to the tropics and subtropics.

At first glance, you might mistake a cycad for a small palm tree (**Figure 27.21**). Some cycads have massive, cone-shaped strobili (clusters of sporophylls) that bear either pollen or ovules. Air currents or crawling insects transfer pollen from male plants to the developing gametophyte on female plants. Poisonous alkaloids that may help deter insect predators occur in various cycad tissues. In tropical Asia, some people consume cycad seeds and flour made from cycad trunks, but only after the toxic compounds have been rinsed away. Much in demand from fanciers of unusual plants, cycads in some countries are uprooted and sold in what amounts to a black-market trade—greatly diminishing their numbers in the wild.





Carlton Hay/Science Photo Library/Photo Researchers, Inc.

**Figure 27.21**  
The cycad *Zamia*. Note the large, terminal female cone and fernlike leaves.

### Ginkgoes Are Limited to a Single Living Species

The phylum **Ginkgophyta** has only one living species, the ginkgo (or maiden-hair) tree (*Ginkgo biloba*), which grows wild today only in warm-temperate forests of central China. Ginkgo trees are large, diffusely branching trees with characteristic fan-shaped leaves (**Figure 27.22**) that turn a brilliant yellow in autumn. Nursery-propagated male trees often are planted in cities because they are resistant to insects, disease, and air pollutants. The female trees are equally pollution-resistant, but gardeners shy away from them—their fleshy fruits produce a notoriously foul odor.

### Gnetophytes Include Simple Seed Plants with Intriguing Features

The phylum Gnetophyta contains three genera—*Gnetum*, *Ephedra*, and *Welwitschia*—that together include about 70 species. Moist, tropical regions are home to about 30 species of *Gnetum*, which includes both trees and leathery leafed vines (lianas). About 35 species of *Ephedra* grow in desert regions of the world (**Figure 27.23a–c**).

Of all the gymnosperms, *Welwitschia* is the most bizarre. This seed-producing plant grows in the hot deserts of south and west Africa. The bulk of the plant is a deep-reaching taproot. The only exposed part is a woody disk-shaped stem that bears cone-shaped strobili and leaves. The plant never produces more than two strap-shaped leaves, which split lengthwise repeatedly as the plant grows older, producing a rather scraggly pile (**Figure 27.23d**).

Although gnetophytes are structurally and functionally simpler than most other seed plants, recent studies of sexual reproduction mechanisms in *Gnetum* and *Ephedra* species uncovered a two-step process of fertilization—which is a hallmark of angiosperms, the most advanced seed plants. This discovery raised some provocative evolutionary questions, even leading some investigators to propose that ancient gnetophytes may have given rise to flowering plants. Complicating this picture, however, are molecular findings, such as those arrived at by a research team at the Academia Sinica in

**a.** Ginkgo tree



© Joyce Photographics/Photo Researchers, Inc.

**b.** Fossil and modern ginkgo leaves



Runk/Schoenberger/Grant Heilman

**c.** Male cone



William Ferguson

**d.** Ginkgo seeds



Kingsley R. Stern

**Figure 27.22**

*Ginkgo biloba*. **(a)** A ginkgo tree. **(b)** Fossilized ginkgo leaf compared with a leaf from a living tree. The fossil formed at the Cretaceous–Tertiary boundary. Even though 65 million years have passed, the leaf structure has not changed much. **(c)** Pollen-bearing cones and **(d)** fleshy-coated seeds of the *Ginkgo*.

Taiwan, People's Republic of China. When the team compared 65 nuclear rRNA sequences from ferns, gymnosperms, and angiosperms, their analysis supported the hypothesis that cycads and ginkgoes represent the earliest gymnosperm lineage, with a divergent lineage of gnetophytes and conifers arising later. The team found no molecular evidence for a link between the Gnetophyta and angiosperms.

### Conifers Are the Most Common Gymnosperms

About 80% of all living gymnosperm species are members of one phylum, the **Coniferophyta**, or conifers (“cone-bearers”). Conifer trees and shrubs are longer-lived, and anatomically and morphologically more complex, than any sporophyte phase we have discussed so far. Characteristically, they form woody reproductive cones, and most of the 550 conifer species are woody trees or shrubs with needlelike or scalelike leaves, which are anatomically adapted to aridity. For instance, needles have a thick cuticle, sunken stomata, and a fibrous epidermis, all traits that reduce the loss of water vapor.

Most conifers are evergreens. That is, although they shed old leaves, often in autumn, they retain enough leaves so that they still look “green,” unlike deciduous species like maples, which shed *all* their leaves as winter approaches. Familiar conifer examples are the pines, spruces, firs, hemlocks, junipers, cypresses, and redwoods. Like other seed plants, conifers are heterosporous, producing pollen in clusters of small strobili and eggs in larger, woody ones. Both of these structures are often referred to as cones. Seeds develop on the shelflike scales of the female cones.

Pines and many other gymnosperms produce resins, a mix of organic compounds that are by-products of metabolism. Resin accumulates and flows in long resin ducts through the wood, inhibiting the activity of wood-boring insects and certain microbes. Pine resin extracts are the raw material of turpentine and (minus the volatile terpenes) the sticky rosin used to treat violin bows.

We know a great deal about the pine life cycle (**Figure 27.24**), so it is a convenient model for gymnosperms. All but 1 of the 93 pine species are trees (*Pinus mugo*, native to high elevations in Europe, is a shrub). The male cones (strobili) are relatively small and delicate, only about 1 cm long, and are borne on the lower branches. Each one consists of many small scales, which are specialized leaves (called sporophylls) attached to the cone's axis in a spiral. Two sporangia develop on the underside of each scale. Inside the sporangia, spore “mother cells” called microsporocytes undergo meiosis and give rise to haploid **microspores**. Each microspore then undergoes mitosis to develop into a winged pollen grain—an immature male gametophyte. At this stage the pollen grain consists of four



**Figure 27.23**

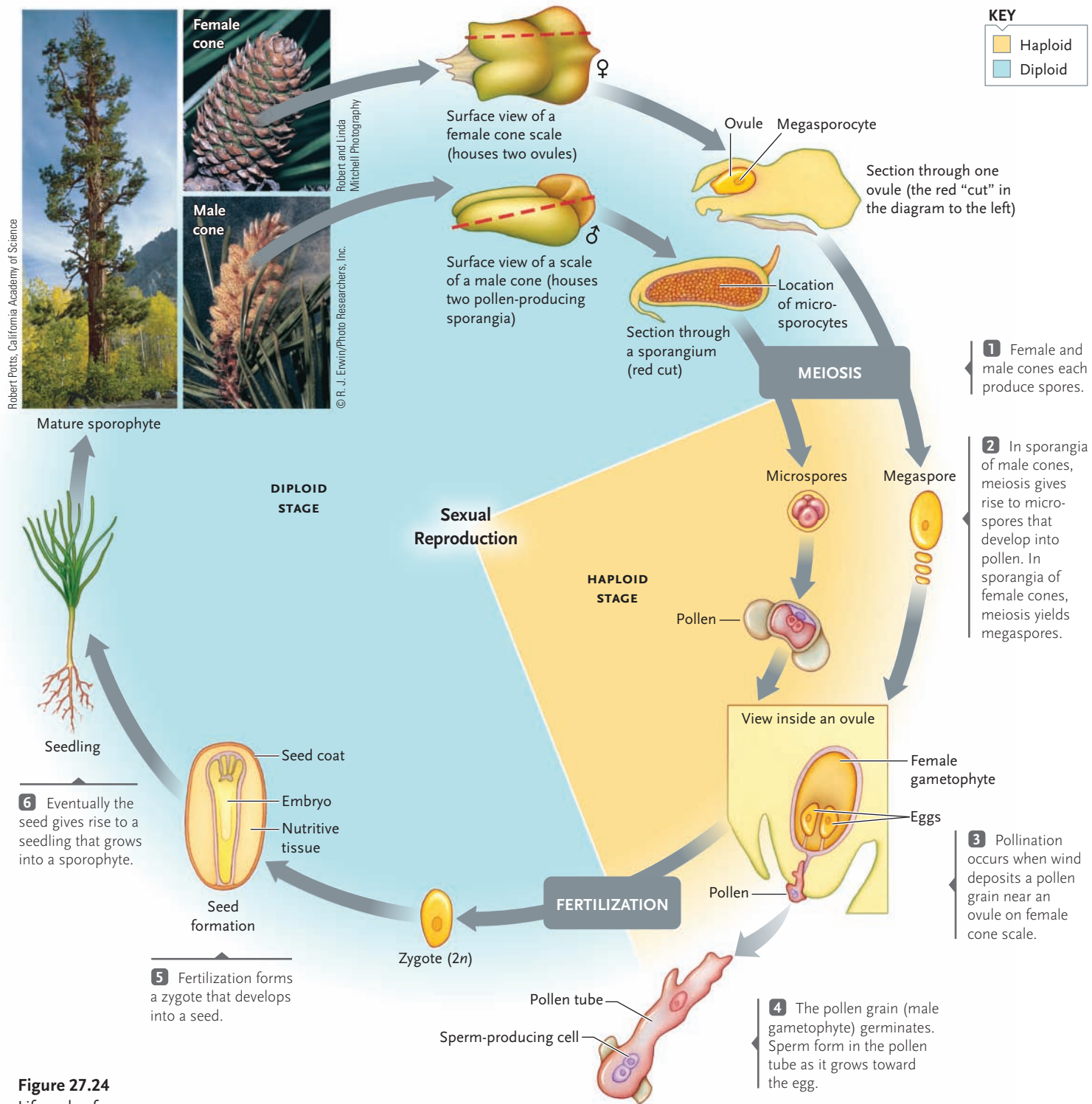
Gnetophytes. **(a)** Sporophyte of *Ephedra*, with close-ups of **(b)** its pollen-bearing cones and **(c)** a seed-bearing cone, which develop on separate plants. **(d)** Sporophyte of *Welwitschia mirabilis*, with seed-bearing cones.

cells, two that will degenerate and two that will function later in reproduction.

Young female cones develop higher in the tree, at the tips of upper branches. The cone scales bear ovules. Inside each ovule is a spore mother cell called a megasporocyte. Unlike microsporocytes, the megasporocyte in an ovule undergoes meiosis only when conditions are right and produces four haploid spores called **megaspores**. Only one megaspore survives, however, and it develops slowly, becoming a mature female gametophyte only when pollination is underway. In a pine, the process takes well over a year. The mature female gametophyte is a small oval mass of cells with several archegonia at one end, each containing an egg.

Each spring, air currents lift vast numbers of pollen grains off male cones—by some estimates, billions may be released from a single pine tree. The extravagant numbers assure that at least some pollen grains will land on female cones. The process is not as random as it might seem: studies have shown that the contours of female cones create air currents that





**Figure 27.24**

Life cycle of a representative conifer, a ponderosa pine (*Pinus ponderosa*). Pines are the dominant conifers in the Northern Hemisphere and their large sporophytes provide a heavily exploited source of wood.

can favor the “delivery” of pollen grains near the cone scales. After pollination, the pollen grain develops into a *pollen tube* that grows toward the female spore mother cell. As it does, sperm form in the tube and stimulate maturation of the female gametophyte and the production of eggs. When a pollen tube reaches an egg, the stage is set for fertilization, the formation of a zygote, and early development of the plant em-

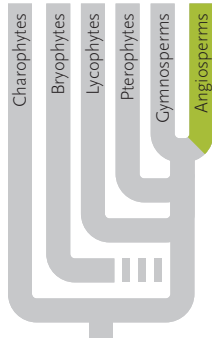
bryo. Often, fertilization occurs months to a year after pollination. Once an embryo forms, a pine seed—which, recall, includes the embryo, female gametophyte tissue, and seed coat—eventually is shed from the cone. The seed coat protects the embryo from drying out, and the female gametophyte tissue serves as its food reserve. This tissue makes up the bulk of a “pine nut.”



## STUDY BREAK

1. What are the four major reproductive adaptations that evolved in gymnosperms?
2. What are the basic parts of a seed, and how is each one adaptive?
3. Describe some features that make conifers structurally more complex than other gymnosperms.

## 27.5 Angiosperms: Flowering Plants



Of all plant phyla, the flowering plants, or **angiosperms**, are the most successful today. At least 260,000 species are known (**Figure 27.25** shows a few examples), and botanists regularly discover new ones in previously unexplored regions of the tropics. The word angiosperm is derived from the Greek *angeion* (meaning a case or vessel) and *sperma*

(seed). The “vessel” refers to the modified leaf, called a *carpel*, that surrounds and protects the ovules and later, the seeds of angiosperms. Carpels are **flowers**, reproductive structures that are a key defining feature of angiosperms. Another defining feature is the **fruit**—botanically speaking, a structure that surrounds the angiosperm embryo and aids seed dispersal.

In addition to having flowers and fruits, angiosperms are the most ecologically diverse plants on Earth, growing on dry land and in wetlands, fresh water, and the seas. They range in size from tiny duckweeds about 1 mm long to towering *Eucalyptus* trees more than 100 m tall. Most are free-living photosynthesizers. Others lack chloroplasts and feed on nonliving organic matter or are parasites that feed on living host organisms.

### The Fossil Record Provides Little Information about the Origin of Flowering Plants

The evolutionary origin of angiosperms has confounded plant biologists for well over a hundred years. Charles Darwin called it the “abominable mystery,” because

a. Flowering plants in a desert



George H. Huey/Corbis

b. Alpine angiosperms



Bill Coster/Peter Arnold, Inc.

c. Triticale, a grass



© John Mason/Ardea, London

d. A parasitic angiosperm



© Peter F. Zika/Visuals Unlimited

**Figure 27.25**

Flowering plants. Diverse photosynthetic species are adapted to nearly all environments, ranging from **(a)** deserts to **(b)** snowlines of high mountains. **(c)** Triticale, a hybrid grain derived from parental stocks of wheat (*Triticum*) and rye (*Secale*), is one example of the various grasses utilized by humans. **(d)** The parasitic flowering plant Indian pipe (*Monotropa uniflora*) having no chlorophyll of its own, obtains food by associating with mycorrhizae, which are in turn associated with the roots of photosynthetic plants.

*Archaeofructus sinensis*



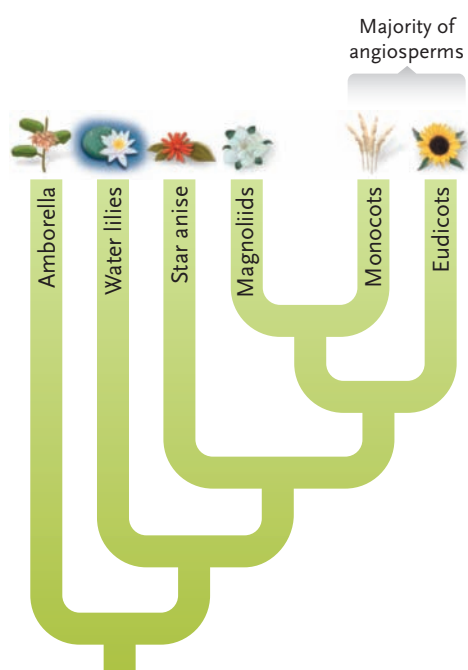
© David Dilcher, Florida Museum of Natural History/Paleobotany Laboratory

Sketch of *Archaeofructus sinensis*



**Figure 27.26**

Fossil of *Archaeofructus sinensis*, thought to have been an early flowering plant. The sketch shows what this small, possibly aquatic plant may have looked like.



**Figure 27.27**

A hypothetical phylogenetic tree for flowering plants.

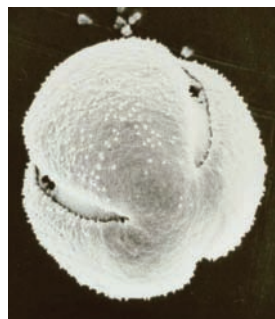
flowering plants appear suddenly in the fossil record, without a fossil sequence that links them to any other plant groups. The oldest well-documented fossil specimens date back 125 million years. Discovered in China, these remarkable fossils show complex and strikingly modern-looking plants that have leaves, stems, fruits, and seeds (**Figure 27.26**).

Two species have been unearthed and have been assigned to the genus *Archaeofructus*, representing a newly discovered, extinct angiosperm group.

The fossil record has yet to reveal obvious transitional organisms between flowering plants and either gymnosperms

**Figure 27.28**

Eudicot pollen grain. Eudicot pollen grains have three slitlike grooves, only two of which are visible here. Pollen made by all other seed plants, including monocots, have just one groove.



Electron micrograph courtesy of J. Ward

or seedless vascular plants. As with gymnosperms, attempts to reconstruct the earliest flowering plant lineages from morphological, developmental, and biochemical characteristics have produced several conflicting classifications and family trees. Some paleobotanists hypothesize that flowering plants arose in the Jurassic period; others propose they evolved in the Triassic from now-extinct gymnosperms or from seed ferns.

As the Mesozoic era ended and the modern Cenozoic era began, great extinctions occurred among both plant and animal kingdoms. Gymnosperms declined, and dinosaurs disappeared. Flowering plants, mammals, and social insects flourished, radiating into new environments. Today we live in what has been called “the age of flowering plants.”

### Angiosperms Are Subdivided into Several Clades, Including Monocots and Eudicots

Angiosperms are assigned to the phylum **Anthophyta**, a name that derives from the Greek *anthos*, meaning flower. **Figure 27.27** shows one current model of major clades within the phylum. The great majority of angiosperms are classified either as monocots or eudicots. **Monocots** are distinguished by the morphology of their embryos, which have a single seed leaf called a cotyledon (“cuplike hollow”). **Eudicots** (“true dicots”), which generally have two cotyledons, are set apart from other angiosperms by the structure of their pollen grains, which have three grooves (**Figure 27.28**). By contrast, the pollen of monocots and all other seed plants (including more than 8500 species once lumped with eudicots under the term “dicots”) have only a single groove. Paleobotanists use this clear structural difference not only to help establish the general type of plant that produced fossil pollen, but also what types of plants were present in fossil deposits of a particular age or geographic location.

While most angiosperms can fairly easily be categorized as either monocots or eudicots, figuring out the appropriate classification for other angiosperms is an ongoing challenge and an extremely active area of plant research. The diagram in **Figure 27.27** reflects a synthesis of evidence from both morphological and molecular studies, an approach examined in this chapter’s *Insights from the Molecular Revolution*. Along with eudicots and monocots, botanists currently recognize four other clades (**Figure 27.29**). The **magnoliids**, a group that includes magnolias (see **Figure 27.29a**), laurels, and avocados, are more closely related to monocots than to eudicots. Some researchers also place plants that are the sources of spices such as peppercorns, nutmeg, and cinnamon in the magnoliid clade. The other three clades are considered to be **basal angiosperms** representing the earliest branches of the flowering plant lineage. They include the star anise group (see **Figure 27.29b**), water lilies (see **Figure**



## INSIGHTS FROM THE MOLECULAR REVOLUTION

### The Powerful Genetic Toolkit for Studying Plant Evolution

Unlike animals and most other eukaryotic organisms, plants have three distinct sets of genes—in the cell nucleus, in mitochondria, and in chloroplasts. Chloroplast DNA, or cpDNA, has been especially useful for evolutionary studies, particularly the chloroplast *rbcL* gene. Mutations of the gene have occurred slowly, at about one-fourth to one-fifth the rate of genes in the nucleus. As a result, the DNA sequences of *rbcL* genes of different species diverge less than those of most other plant genes. Further, there are no introns—noncoding sequences—interrupting the coding sequence of the *rbcL* gene. Researchers can compare *rbcL* DNA from different species base by base, with no need to subtract introns. At the same time, the *rbcL* genes of different spe-

cies are different enough to allow researchers to assemble evolutionary trees based on the degree of sequence variation.

Studies using cpDNA have helped fuel several fundamental shifts in our understanding of branch points in plant evolution. For example, together with gene sequence data from nuclear DNA, analysis of *rbcL* genes provided the molecular foundation for the now widely accepted view that charophyte green algae were the evolutionary forerunners of land plants. Similarly, in the late 1990s an international research team led by Yin-Long Qiu at the University of Massachusetts at Amherst correlated the loss of introns from two mitochondrial genes with the hypothesis that the first land plants were liverworts. Qiu and his

colleagues carried out a genetic survey of more than 350 land plants representing all major lineages. They discovered that the noncoding sequences were present in all other bryophytes and all major lines of vascular plants, but were absent in liverworts, green algae, and all other eukaryotes. The findings are supported by analysis of *rbcL* sequences in various plant groups. Data from cpDNA and mtDNA analyses also underlies the hypothesis that, as land plants evolved, the ancient relatives of club mosses (lycophytes) were the forerunners of other vascular plants. Clearly, these varied molecular tools, and cpDNA in particular, are helping plant scientists explore evolutionary relationships across the whole spectrum of the Kingdom Plantae.

27.29c), and an intriguing ancient line represented by a single shrub, *Amborella trichopoda* (see Figure 27.29d). Found only in cloud forests of the South Pacific island of New Caledonia, *Amborella*'s small white flowers and vascular system are structurally simpler than those of other angiosperms, and its female gametophyte differs as well. These morphological differences and a comparison of the nucleotide sequences of genes encoding the two angiosperm phytochromes (photoreceptors discussed in Chapter 35) suggest that *Amborella* is the closest living relative of the first flowering plants.

Figure 27.30a gives some idea of the variety of living monocots, which include grasses, palms, lilies, and orchids. The world's major crop plants (wheat, corn, rice, rye, sugarcane, and barley) are domesticated grasses, and all are monocots. There are at least 60,000 species of monocots, including 10,000 grasses

and 20,000 orchids. Eudicots are even more diverse, with nearly 200,000 species (Figure 27.30b). They include flowering shrubs and trees, most nonwoody (herbaceous) plants, and cacti. Figure 27.31 shows the life cycle of a lily, a monocot. The life cycle of a typical eudicot is described in detail in the next unit, which focuses on the structure and function of flowering plants.

### Many Factors Contributed to the Adaptive Success of Angiosperms

At this writing, molecular studies place the origin of flowering plants at least 140 mya. It took only about 40 million years—a short span in geological time—for angiosperms to eclipse gymnosperms as the prevailing form of plant life on land (see Figure 22.19). Several

**Figure 27.29** Representatives of basal angiosperm clades. (a) Southern magnolia (*Magnolia grandiflora*), a magnoliid. (b) Star anise (*Illicium floridanum*). (c) Sacred lotus (*Nelumbo nucifera*), a water lily. (d) *Amborella trichopoda*.

a. Southern magnolia (*Magnolia grandiflora*), a magnoliid



D. Hams/Peter Arnold, Inc.

b. Star anise (*Illicium floridanum*)



Rob & Ann Simpson/Visuals Unlimited

c. Sacred lotus (*Nelumbo nucifera*), a water lily



© Gregory C. Dimijian/Photo Researchers, Inc.

d. *Amborella trichopoda*



© Sangtae Kim, University of Florida



a. Representative monocots



Wheat (*Triticum*)



Tulips (*Tulipa*)



Eastern prairie fringed orchid (*Platanthera leucophaea*)

b. Representative eudicots



Rose (*Rosa*)



Yellow bush lupine (*Lupinus arboreus*)



Cherry (*Prunus*)



Claret cup cactus (*Echinocereus triglochidatus*)

**Figure 27.30**  
Examples of  
monocots and  
eudicots.

factors fueled this adaptive success. As with other seed plants, the large, diploid sporophyte phase dominates a flowering plant's life cycle, and the sporophyte retains and nourishes the much smaller gametophytes. But flowering plants also show some evolutionary innovations not seen in gymnosperms.

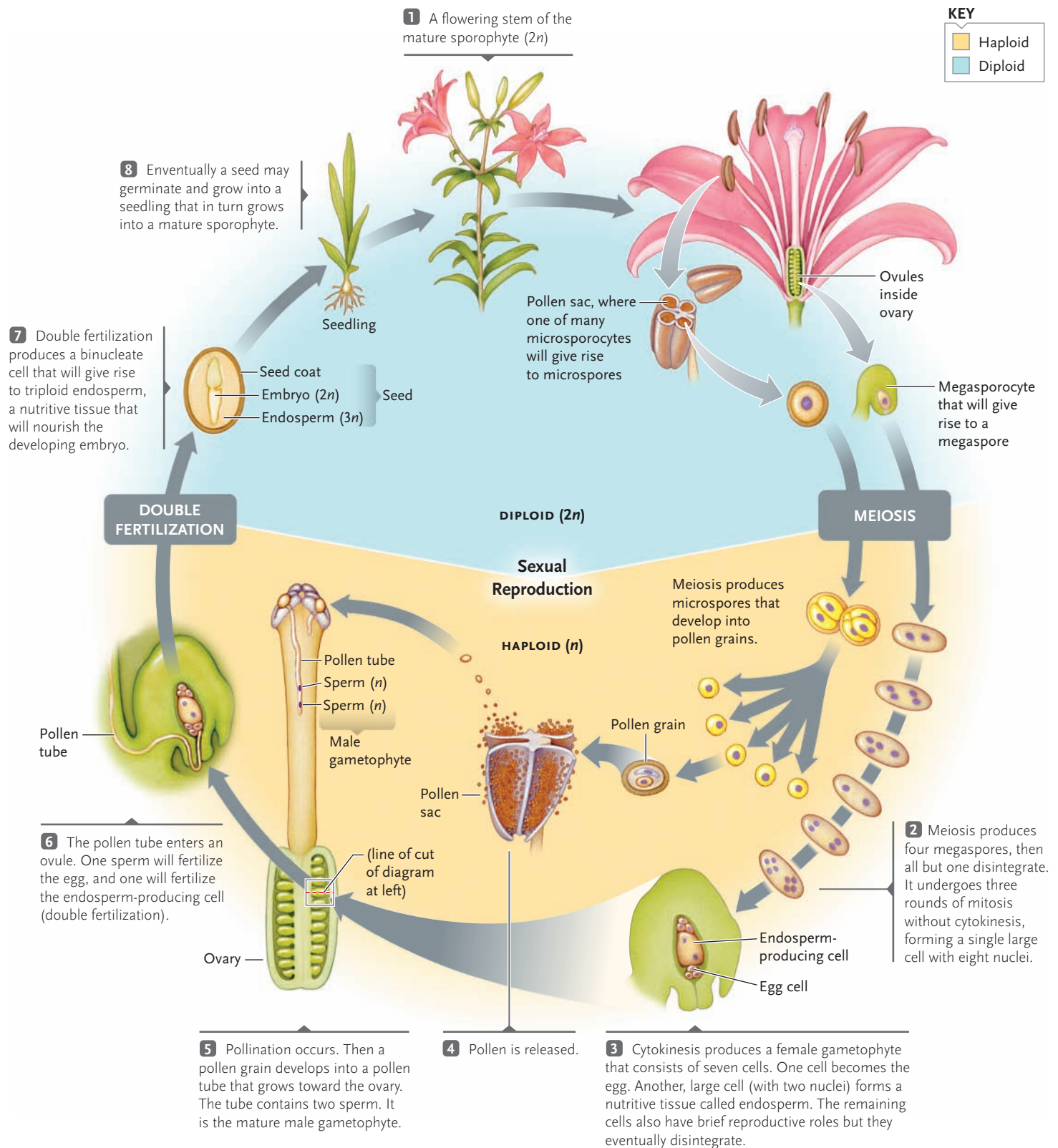
**More Efficient Transport of Water and Nutrients.** Where gymnosperms have only one type of water-conducting cell (tracheids), angiosperms have an additional, more specialized type (called vessel elements). As a result, an angiosperm's xylem vessels move water more rapidly from roots to shoot parts. Also, modifications in angiosperm phloem tissue allow it to more efficiently transport sugars produced in photosynthesis through the plant body.

**Enhanced Nutrition and Physical Protection for Embryos.** Other changes in angiosperms made it more likely that reproduction would succeed. For example, a two-step *double fertilization* process in the seeds of flowering plants gives rise to both an embryo and a unique nutritive tissue (called endosperm) that nour-

ishes the embryonic sporophyte. The ovule containing a female gametophyte is enclosed within an **ovary**, which develops from a carpel and shelters the ovule against desiccation and against attack by herbivores or pathogens. In turn, ovaries develop into the fruits that house angiosperm seeds. As noted earlier, a fruit not only protects seeds, but helps disperse them—for instance, when an animal eats a fruit, seeds may pass through the animal's gut none the worse for the journey and be released in a new location in the animal's feces. Above all, angiosperms have flowers, the unique reproductive organs that you will read much more about in the next unit.

### Angiosperms Coevolved with Animal Pollinators

The evolutionary success of angiosperms correlates not only with the adaptations just described, but also with efficient mechanisms of transferring pollen to female reproductive parts. While a conifer depends on air currents to disperse its pollen, angiosperms coevolved with pollinators—insects, bats, birds, and other animals that



**Figure 27.31**

Life cycle of a flowering plant, the monocot *Lilium*. Double fertilization is a notable feature of the cycle. The male gametophyte delivers two sperm to an ovule. One sperm fertilizes the egg, forming the embryo, and the other fertilizes the endosperm-producing cell, which nourishes the embryo.



withdraw pollen from male floral structures (often while obtaining nectar) and inadvertently transfer it to female reproductive parts. **Coevolution** occurs when two or more species interact closely in the same ecological setting. A heritable change in one species affects selection pressure operating between them, and the other species evolves as well. Over time, plants that came to have distinctive flowers, scents, and sugary nectar coevolved with animals that could take advantage of the rich food source.

In general, a flower's reproductive parts are positioned so that visiting pollinators will brush against them. In addition, many floral features correlate with specific pollinators. For example, reproductive parts may be located above nectar-filled floral tubes the same length as the feeding structure of a preferred pollinator. Nectar-sipping bats (**Figure 27.32a**) and moths forage by night. They pollinate intensely sweet-smelling flowers with white or pale petals that are more visible than colored petals in the dark. Long, thin mouthparts of moths and butterflies reach nectar in narrow floral

tubes or floral spurs. The Madagascar hawkmoth uncoils a mouthpart the same length—an astonishing 22 cm—as a narrow floral spur of an orchid it pollinates, *Angraecum sesquipedale* (**Figure 27.32b**). Red and yellow flowers attract birds (**Figure 27.32c**), which have good daytime vision but a poor sense of smell. Hence bird-pollinated plants do not squander metabolic resources to make fragrances. By contrast, flowers of species that are pollinated by beetles or flies may smell like rotten meat, dung, or decaying matter. Daisies and other fragrant flowers with distinctive patterns, shapes, and red or orange components attract butterflies, which forage by day.

Bees see ultraviolet light and visit flowers with sweet odors and parts that appear to humans as yellow, blue, or purple (**Figure 27.32d**). Produced by pigments that absorb ultraviolet light, the colors form patterns called “nectar guides” that attract bees—which may pick up or “drop off” pollen during the visit. Here, as in our other examples, flowers contribute to the reproductive success of plants that bear them.

a. Bat pollinating a giant saguaro



Merlin D. Tuttle, Bat Conservation International

b. Hawk moth pollinating an orchid



Photo by Marcel Lecouffe

c. Hummingbird visiting a hibiscus flower



Robert A. Tyrrell

d. Bee-attracting pattern of a marsh marigold



Visible light

UV light

Thomas Eisner/Cornell University

**Figure 27.32**

**Coevolution of flowering plants and animal pollinators.** The colors and configurations of some flowers, and the production of nectar or odors, have coevolved with specific animal pollinators. **(a)** At night, nectar-feeding bats sip nectar from flowers of the giant saguaro (*Carnegie gigantea*), transferring pollen from flower to flower in the process. **(b)** The hawkmoth *Xanthopan morgani praedicta* has a proboscis long enough to reach nectar at the base of the equally long floral spur of the orchid *Angraecum sesquipedale*. **(c)** A Bahama woodstar hummingbird (*Calliphlox evelynae*) sipping nectar from a hibiscus blossom (*Hibiscus*). The long narrow bill of hummingbirds coevolved with long, narrow floral tubes. **(d)** Under ultraviolet light, the bee-attracting pattern of a gold-petaled marsh marigold becomes visible to human eyes.



## Current Research Focuses on Genes Underlying Transitions in Plant Traits

Improvements in the ability of plant scientists to manipulate, analyze, and compare modern plant genomes, coupled with advances in the analysis of fossil plants, are having a profound impact on our understanding of the evolution of flowering plants. A case in point is research on the gene *LFY*, which encodes the regulatory protein LEAFY (Chapter 16 discusses regu-

latory proteins in detail). The LEAFY protein typically controls expression of several genes by binding to the genes' control sequences. All land plants carry the *LFY* gene, but its effects on phenotype vary markedly in different plant groups. In mosses, which arose almost 400 million years ago, the LEAFY protein regulates growth throughout the plant. In ferns and gymnosperms, which arose later, LEAFY controls growth in a subset of tissues. In angiosperms, LEAFY regulates gene expression only in the particular type of meristem

### UNANSWERED QUESTIONS

#### Where did flowering plants come from?

Flowers are a unique feature of the angiosperms, yet botanists still understand little of their evolutionary origin. When flowering plants appear in the Cretaceous fossil record, they appear suddenly and diversify immediately, a situation Darwin famously referred to as an “abominable mystery.” What did the first angiosperms and the first flower look like? And where did they arise?

As described in this chapter, recent molecular analyses have converged on *Amborella trichopoda* as the living representative of the most ancient lineage in the angiosperm family tree. This research has shed light on many questions. For example, *Amborella* flowers have some features considered evolutionarily primitive, such as petals and sepals that are not distinctly different in form. This observation supports the hypothesis that two other types of flower parts, the calyx and corolla, arose later in angiosperm evolution. But *Amborella* also has some features thought to have evolved much more recently, such as single-sex flowers that have either male or female reproductive parts (but never both). Should we be surprised to find both primitive and advanced traits in this ancient lineage? Not at all. *Amborella* has existed on Earth for millions of years and its flowers may have evolved new features over that time.

The puzzle of where angiosperms came from and what the first flowering plants looked like has not been solved by fossil studies, either. This chapter discusses the fossil species *Archaeofructus*, which dates from the Jurassic and is thought to be the oldest known fossil flower. It consists of an elongated axis with what its discoverers described as stamens (male reproductive structures) toward the base and carpels (female reproductive structures) toward the apex, and no sepals and petals. This elongated flower is unlike the flowers of any modern angiosperm, and its structure suggests that the earliest flowers may have been very different from what we see today. However, some paleobotanists have reinterpreted the *Archaeofructus* “flower” as an inflorescence (a flower cluster), with male flowers at the base and female flowers toward the apex. In addition, radiometric dating places *Archaeofructus* in the early-mid Cretaceous, a period from which other early angiosperm fossils are known. Thus, *Archaeofructus* may not be the oldest flower, and the fossil specimen may represent a cluster of flowers instead of a single flower. This debate continues.

Botanists also disagree about the ancestors of angiosperms. Some gnetophytes—gymnosperms that include *Welwitschia* and *Ephedra* species (refer to Figure 27.23)—have features similar to angiosperms. Botanists long speculated that the two groups were closely related, with a common ancestor that had flowerlike features. However, recent analy-

ses based on DNA sequence data suggest that gnetophytes are not closely related to angiosperms after all. There are also fossil gymnosperm taxa with features that might be forerunners of carpels or other flower parts, but paleobotanists disagree on these interpretations as well. Thus examinations of fossils and extant species have yet to resolve key questions about the evolution of angiosperms.

What, then, can molecular data tell us? Studies of the genetic mechanisms that guide the development of flower parts have provided a framework for understanding how genes control flower formation (a topic of Chapter 34). This research has also given us insight into what kinds of molecular changes may have led to the evolution of flowers. For instance, certain genes that encode transcription factors required for the formation of reproductive organs in flowers are found also in gymnosperms. This finding is not surprising, because gymnosperms also form male and female reproductive structures; the most logical hypothesis is that angiosperms retained the gymnosperm developmental program for these organs. Yet genes for other transcription factors active in flower formation are *not* found in gymnosperms. We know that transcription factors may turn on and off entire developmental pathways, such as those that cause undifferentiated tissue (called meristem tissue) to form a flower. One hypothesis is that in an ancient gymnosperm ancestor, duplications in a particular gene family gave rise to genes that in turn accumulated mutations allowing them to perform new functions that resulted in the formation of the first flowers.

As much insight as these molecular studies give us into events that might have resulted in the evolution of flowers, they have not brought us any closer to understanding the fundamental question of where angiosperms arose. Additional fossil data may help provide the answer, but it is also possible that the earliest angiosperms, or their direct ancestors, lived in habitats where fossils do not readily form. Additional molecular data may deepen our understanding of how changes in genes produced the first flower. But molecular data based on contemporary species will not help decipher what the first angiosperm and the first flower looked like. Thus, it is possible that the abominable mystery will live on.



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tissue that gives rise to flowers (a topic of Chapter 34). Curious about the evolutionary shift from a general to a specific effect, Alexis Maizel and his team at the Max Planck Institute for Developmental Biology in Germany compared *LFY* sequences and their corresponding proteins in fourteen species, including a moss, ferns, gymnosperms, and the angiosperms *Arabidopsis* (thale cress) and snapdragon. Remarkably, they discovered that the evolutionary honing of the effects of the LEAFY protein correlated with only a handful of changes in the base sequence of the *LFY* gene. Each change affected how—or if—the LEAFY protein regulated the expression of a given gene. Over time, LEAFY took on its highly specific, crucial role in angiosperms, helping to direct the developmental events that produce flowers.

Today some of the most exciting research in all of biology involves studies exploring the connections between genetic changes and key evolutionary transitions in plant form and functioning. As the genes of many more plant species are sequenced and correlated

with evidence from comparative morphology and the fossil record, we can expect a steady stream of new insights about the evolutionary journey of all major plant lineages. In Chapter 28 a very different group of organisms, the fungi, takes center stage. Although many fungal species seem superficially plantlike, biologists today are avidly exploring evolutionary links between fungi and animals.

## STUDY BREAK

1. How has the relative lack of fossil early angiosperms affected our understanding of this group?
2. Describe two basic features that distinguish monocots from eudicots, and give some examples of species in each clade.
3. List at least three adaptations that have contributed to the evolutionary success of angiosperms as a group.

## Review

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### 27.1 The Transition to Life on Land

- Plants are thought to have evolved from charophyte green algae between 425 and 490 million years ago (Figure 27.2).
- Adaptations to terrestrial life in early land plants include an outer cuticle that helps prevent desiccation, lignified tissues, spores protected by a wall containing sporopollenin, multicellular chambers that protect developing gametes, and an embryo sheltered inside a parent plant (Figure 27.3).
- Other key evolutionary trends among land plants included the development of vascular tissues, root systems, and shoot systems, including lignified stems and leaves equipped with stomata; a shift from dominance by a long-lived, larger haploid gametophyte to dominance of a long-lived, larger diploid sporophyte, and a shift from homosporous to heterosporous with separate male and female gametophytes (Figures 27.5–27.7).
- Male gametophytes (pollen) became specialized for dispersal without liquid water, and female gametophytes became specialized for enclosing embryo sporophytes in seeds.

**Animation:** Milestones in plant evolution

**Animation:** Haploid to diploid dominance

**Animation:** Evolutionary tree for plants

**Animation:** The importance of alternation of generations

### 27.2 Bryophytes: Nonvascular Land Plants

- Existing nonvascular land plants, or bryophytes, include the liverworts (Hepatophyta), hornworts (Anthoceroophyta), and mosses (Bryophyta). Liverworts may have been the first land plants.

- Bryophytes produce flagellated sperm that swim through free water to reach eggs. They lack a vascular system; true roots, stems, and leaves; and lignified tissue. A larger, dominant gametophyte ( $n$ ) phase alternates with a small, fleeting sporophyte ( $2n$ ) phase. Spores develop inside jacketed sporangia (Figures 27.9 and 27.12).

**Animation:** Moss life cycle

**Animation:** *Marchantia*, a liverwort

### 27.3 Seedless Vascular Plants

- Existing seedless vascular land plants include the lycophytes (club mosses), whisk ferns, horsetails, and ferns. Like bryophytes, they release spores and have swimming sperm. Unlike bryophytes, they have well-developed vascular tissues. The sporophyte is the larger, longer-lived stage of the life cycle and develops independently of the small gametophyte.
- Club mosses (Lycophyta) have sporangia clustered at the bases of specialized leaves called sporophylls. Each sporophylls cluster forms a strobilus (cone). Haploid spores dispersed from the sporangia germinate to form small, free-living gametophytes. Ferns, whisk ferns, and horsetails (Pterophyta) have a similar life cycle. Horsetail sporophytes typically have underground stems (rhizomes) anchored to the soil by roots.
- Ferns are the largest and most diverse group of seedless vascular plants. Most species do not have aboveground stems, only leaves that arise from nodes along an underground rhizome. Fern leaves typically have well-developed stomata, and the vascular system consists of bundles, each with xylem surrounded by phloem. Sporangia on the lower surface of sporophylls (fronds) release spores that develop into gametophytes. Sexual reproduction produces a much larger, long-lived sporophyte (Figure 27.16).

**Animation:** Seedless vascular plants

**Animation:** Fern life cycle

## 27.4 Gymnosperms: The First Seed Plants

- Gymnosperms (conifers and their relatives), together with angiosperms (flowering plants), are the seed-bearing vascular plants. Reproductive innovations include pollination, the ovule, and the seed. An ovule is a sporangium containing a female gametophyte, so the female gametophyte is attached to and protected by the sporophyte. The smaller spore type produces a male gametophyte. Since pollination takes place via air currents or animal pollinators, plants fertilized by pollination do not require liquid water to reproduce. A seed forms when an ovule matures following fertilization; in gymnosperms, its main function is to protect and help disperse the embryonic sporophyte (Figure 27.24).
- During the Mesozoic, gymnosperms were the dominant land plants. Today conifers are the primary vegetation of forests at higher latitudes and elevations and have important economic uses as sources of lumber, resins, and other products.

Animation: *Pinus* cones

Animation: Pine life cycle

## 27.5 Angiosperms: Flowering Plants

- Angiosperms (Anthophyta) have dominated the land for more than 100 million years and currently are the most diverse plant group. There are two main angiosperm clades: monocots and eudicots. Other clades are represented by magnolias and their relatives (magnoliids), water lilies, the star anise group, and *Amborella*, a single species thought to be the most basal living angiosperm (Figures 27.29 and 27.30).
- The angiosperm vascular system moves water from roots to shoots more efficiently than in gymnosperms, and the phloem tissue moves sugars more efficiently through the plant body. Reproductive adaptations include a protective ovary around the ovule, endosperm, fruits that aid seed dispersal, the complex organs called flowers, and the coevolution of flower characteristics with the structural and/or physiological characteristics of animal pollinators (Figures 27.31 and 27.32).

Animation: Flower parts

Animation: Monocot life cycle

## Questions

### Self-Test Questions

1. Which of the following is *not* an evolutionary trend among plants?
  - a. developing vascular tissues
  - b. becoming seedless
  - c. having a dominant diploid generation
  - d. producing nonmotile gametes
  - e. producing two types of spores
2. As plants made the evolutionary transition to a terrestrial existence, they benefited from adaptations that:
  - a. increased the motility of their gametes on dry land.
  - b. flattened the plant body to expose it to the sun.
  - c. reduced the number and distribution of roots to prevent drying.
  - d. provided mechanisms for gaining access to nutrients in soil.
  - e. allowed stems and leaves to absorb water from the atmosphere.
3. Land plants no longer required water as a medium for reproduction with the evolution of:
  - a. fruits and roots.
  - b. flowers and leaves.
  - c. cell walls and rhizoids.
  - d. lignified stems.
  - e. seeds and pollen.
4. Which is the correct matching of phylum and plant group?
  - a. Anthophyta: pines
  - b. Bryophyta: gnetophytes
  - c. Coniferophyta: angiosperms
  - d. Hepatophyta: cycads
  - e. Pterophyta: horsetails
5. A homeowner noticed moss growing between bricks on his patio. Closer examination revealed tiny brown stalks with cuplike tops emerging from green leaflets. These brown structures were:
  - a. the sporophyte generation.
  - b. the gametophyte generation.
  - c. elongated haploid reproductive cells.
  - d. archegonia.
  - e. antheridia.
6. Horsetails are most closely related to:
  - a. mosses and whisk ferns.
  - b. liverworts and hornworts.
  - c. cycads and ginkgos.
  - d. club mosses and ferns.
  - e. gnetophytes and gymnosperms.
7. Which feature(s) do ferns share with all other land plants?
  - a. sporophyte and gametophyte life cycle stages
  - b. gametophytes supported by a thallus
  - c. dispersal of spores from a sorus
  - d. asexual reproduction by way of gemmae
  - e. water uptake by means of rhizoids
8. The evolution of true roots is first seen in:
  - a. liverworts.
  - b. seedless vascular plants.
  - c. mosses.
  - d. flowering plants.
  - e. conifers.
9. Based solely on numbers of species, the most successful plants today are:
  - a. angiosperms.
  - b. ferns.
  - c. gymnosperms.
  - d. mosses.
  - e. the bryophytes as a group.
10. Angiosperms and gymnosperms share the following characteristic(s):
  - a. pollination by means of water.
  - b. seeds protected within an ovary.
  - c. embryonic cotyledons.
  - d. a dominant sporophyte generation.
  - e. a seasonal loss of all leaves.

### Questions for Discussion

1. Suggest adjustments in the angiosperm life cycle that would better suit plants to some future world where environments were generally hotter and more arid. Do the same for a colder and wetter environment.
2. Working in the field, you discover a fossil of a previously undescribed plant species. The specimen is small and may not be complete; the parts you have do not include any floral organs. What sorts of observations would you need in order to classify the fossil as a seedless vascular plant with reasonable accuracy? What evidence would you need in order to distinguish between a fossil lycopod and a fern?



3. Modern humans emerged about 100,000 years ago. How accurate is it to state that our species has lived in the Age of Wood? Explain.
4. Compare the size, anatomical complexity, and degree of independence of a moss gametophyte, a fern gametophyte, a Douglas fir female gametophyte, and a dogwood female gametophyte. Which one is the most protected from the external environment? Which trends in plant evolution does your work on this question bring to mind?

### Experimental Analysis

You are studying mechanisms that control the development of flowers, and your research to date has focused on eudicots, which tend to have showier flowers than monocots. A colleague has suggested that you broaden your analysis to include representative basal angiosperms. Outline the rationale for this expanded approach and indicate which additional species or group(s) you plan

to include. Discuss the type(s) of data you plan to gather and why you feel the information will make your study more complete.

### Evolution Link

Plant evolutionary biologist Spencer C. H. Barrett has written that the reproductive organs of angiosperms are more varied than the equivalent structures of any other group of organisms. Which angiosperm organs was Barrett talking about? Explain why you agree or disagree with his view.

### How Would You Vote?

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