

29

Plant Diversity I: How Plants Colonized Land



▲ Figure 29.1 How did plants change the world?

EVOLUTION

KEY CONCEPTS

- 29.1 Land plants evolved from green algae
- 29.2 Mosses and other nonvascular plants have life cycles dominated by gametophytes
- 29.3 Ferns and other seedless vascular plants were the first plants to grow tall

OVERVIEW

The Greening of Earth

Looking at a lush landscape, such as the forest scene in **Figure 29.1**, it is difficult to imagine the terrestrial environment without any plants or other organisms. Yet for more than 3 billion years of Earth's history, the land surface was largely lifeless. Geochemical evidence suggests that thin coatings of cyanobacteria existed on land about 1.2 billion years ago. But it was only within the last 500 million years that small plants as well as fungi and animals joined them

ashore. Finally, by about 385 million years ago, some plants appeared that could grow much taller, leading to the formation of the first forests (though with a very different set of species than those in Figure 29.1).

Since colonizing land, plants have diversified widely; today, there are more than 290,000 known plant species. Plants inhabit all but the harshest environments, such as some mountaintops, a few desert areas, and the polar regions. A few plant species, such as seagrasses, returned to aquatic habitats during their evolution, but most present-day plants live in terrestrial environments. In this chapter, we'll refer to all plants as *land* plants, even those that are now aquatic, to distinguish them from algae, which are photosynthetic protists.

The presence of land plants has enabled other life-forms—including animals—to survive on land. Plants supply oxygen and ultimately most of the food eaten by terrestrial animals. Also, plant roots create habitats for other organisms by stabilizing the soil in sand dunes and many other environments.

This chapter traces the first 100 million years of plant evolution, including the emergence of seedless plants such as mosses and ferns. Chapter 30 examines the later evolution of seed plants.

CONCEPT 29.1

Land plants evolved from green algae

As you read in Chapter 28, researchers have identified green algae called charophytes as the closest relatives of land plants. What is the evidence for this relationship, and what does it suggest about the algal ancestors of land plants?

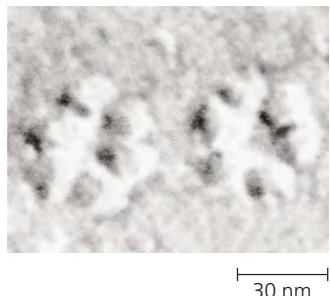
Morphological and Molecular Evidence

Many key traits of land plants also appear in some protists, primarily algae. For example, plants are multicellular, eukaryotic, photosynthetic autotrophs, as are brown, red, and certain green algae. Plants have cell walls made of cellulose, and so do green algae, dinoflagellates, and brown algae. And chloroplasts with chlorophylls *a* and *b* are present in green algae, euglenids, and a few dinoflagellates, as well as in plants.

However, the charophytes are the only algae that share the following four distinctive traits with land plants, strongly suggesting that they are the closest relatives of plants:

- **Rings of cellulose-synthesizing proteins.** The cells of both land plants and charophytes have distinctive circular rings of proteins in the plasma membrane (**Figure 29.2**). These protein rings synthesize the cellulose microfibrils of the cell wall. In contrast, noncharophyte algae have linear sets of proteins that synthesize cellulose.
- **Peroxisome enzymes.** The peroxisomes (see Figure 6.19) of both land plants and charophytes contain enzymes that help minimize the loss of organic products resulting from photorespiration (see Chapter 10).

► Figure 29.2 Rings of cellulose-synthesizing proteins. These circular sets of proteins embedded in the plasma membrane are found only in land plants and charophyte algae (SEM).



- **Structure of flagellated sperm.** In species of land plants that have flagellated sperm, the structure of the sperm closely resembles that of charophyte sperm.

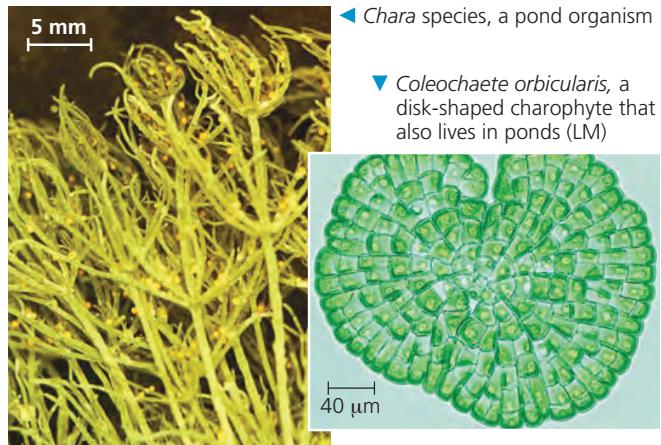
- **Formation of a phragmoplast.** Particular details of cell division occur only in land plants and certain charophytes, including the genera *Chara* and *Coleochaete*. For example, in land plants and certain charophytes, a group of microtubules known as the **phragmoplast** forms between the daughter nuclei of a dividing cell. A cell plate then develops in the middle of the phragmoplast, across the midline of the dividing cell (see Figure 12.10). The cell plate, in turn, gives rise to a new cross wall that separates the daughter cells.

Genetic evidence also supports the conclusion drawn from these four morphological and biochemical traits. Analyses of nuclear and chloroplast genes from a wide range of plants and algae indicate that charophytes—particularly *Chara* and *Coleochaete*—are the closest living relatives of land plants (Figure 29.3). Note that this does not mean that plants are descended from these living algae; however, present-day charophytes may tell us something about what the algal ancestors of plants were like.

Adaptations Enabling the Move to Land

Many species of charophyte algae inhabit shallow waters around the edges of ponds and lakes, where they are subject to occasional drying. In such environments, natural selection favors individual algae that can survive periods when they are not submerged in water. In charophytes, a layer of a durable polymer called **sporopollenin** prevents exposed zygotes from drying out. A similar chemical adaptation is found in the tough sporopollenin walls that encase the spores of plants.

The accumulation of such traits by at least one population of charophyte ancestors probably enabled their descendants—the first land plants—to live permanently above the waterline. These evolutionary novelties opened a new frontier: a terrestrial habitat that offered enormous benefits. The bright sunlight was unfiltered by water and plankton; the atmosphere offered more plentiful carbon dioxide than did water; the soil by the water's edge was rich in some mineral nutrients; and initially there were relatively few herbivores and pathogens. But these benefits were accompanied by challenges: a relative scarcity of water and a lack of structural support against gravity. (To appreciate why such support is important, picture how the soft body of a jellyfish sags when taken out of water.) Land



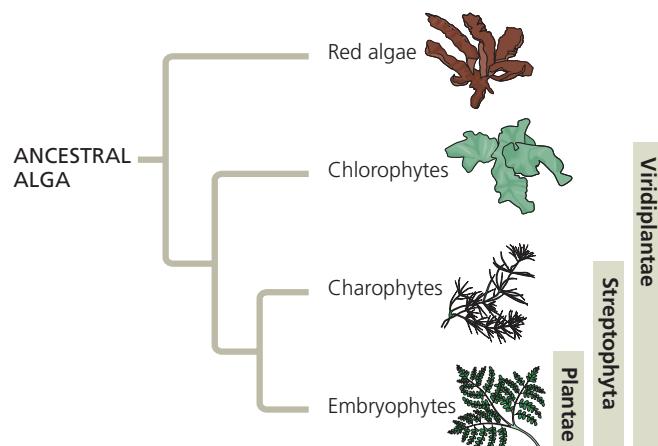
▲ Figure 29.3 Examples of charophytes, the closest algal relatives of land plants.

plants diversified as adaptations evolved that enabled plants to thrive despite these challenges.

Today, what adaptations are unique to plants? The answer to this question depends on where you draw the boundary dividing land plants from algae (Figure 29.4). Many biologists equate the kingdom Plantae with embryophytes (plants with embryos). Others propose that the boundaries of the plant kingdom should be expanded to include some or all of the green algae (kingdoms Streptophyta and Viridiplantae). Since the debate is ongoing, this text retains the embryophyte definition of the plant kingdom and uses Plantae as the formal name for the taxon. In this context, let's now identify the derived traits that separate land plants from their closest algal relatives.

Derived Traits of Plants

Many of the adaptations that appear to have emerged after land plants diverged from their algal relatives facilitated survival and reproduction on dry land. Figure 29.5, on the next two pages, depicts four key traits that appear in land plants but not in the charophyte algae.



▲ Figure 29.4 Three possible “plant” kingdoms.

▼ Figure 29.5

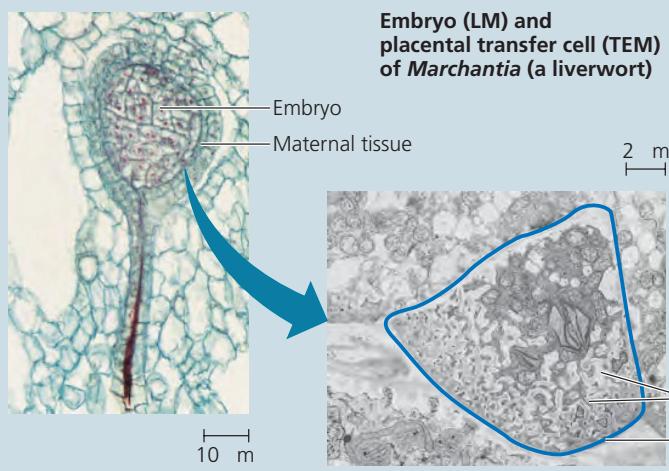
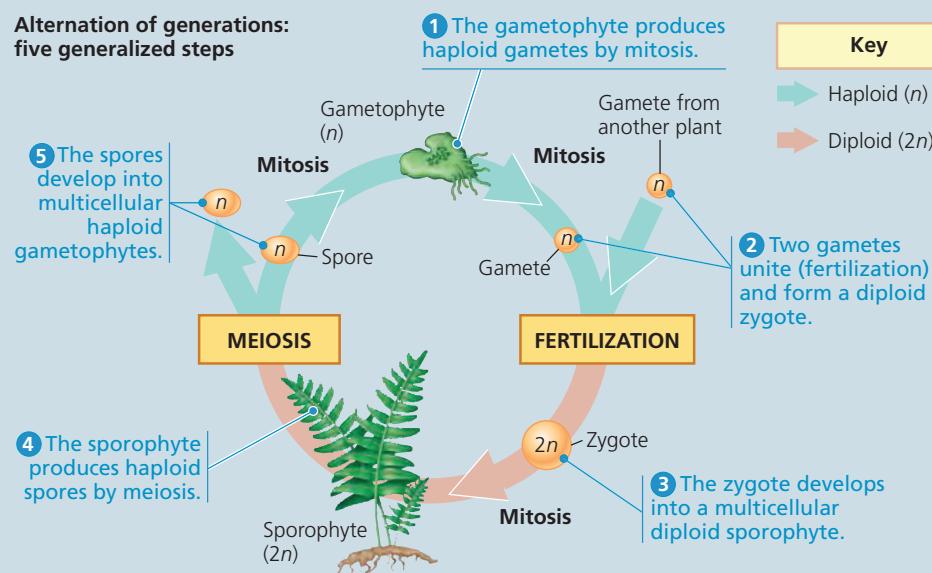
Exploring Derived Traits of Land Plants

Charophyte algae lack the four key traits of land plants described in this figure: alternation of generations (with an associated trait of multicellular, dependent embryos), walled spores produced in sporangia, multicellular gametangia, and apical meristems. This suggests that these four traits were absent in the ancestor common to land plants and charophytes but instead evolved as derived traits of land plants. Note that some of these traits are not unique to plants, having evolved independently in other lineages. And not every land plant exhibits all four of these traits; certain lineages of plants have lost some traits over time.

Alternation of Generations and Multicellular, Dependent Embryos

The life cycles of all land plants alternate between two generations of multicellular organisms: gametophytes and sporophytes. As shown in the diagram (using a fern as an example), each generation gives rise to the other, a process that is called **alternation of generations**. This type of reproductive cycle evolved in various groups of algae but does not occur in the charophytes, the algae most closely related to land plants.

Take care not to confuse the alternation of generations in plants with the haploid and diploid stages in the life cycles of other sexually reproducing organisms (see Figure 13.6). In humans, for example, meiosis produces haploid gametes that unite, forming diploid zygotes that divide and become multicellular. The haploid stage is represented only by single-celled gametes. In contrast, alternation of generations is distinguished by the fact that the life cycle includes both multicellular haploid organisms and multicellular diploid organisms. The multicellular haploid **gametophyte** ("gamete-producing plant") is named for its production by mitosis of haploid gametes—eggs and sperm—that fuse during fertilization, forming diploid zygotes. Mitotic division of the zygote produces a multicellular diploid **sporophyte** ("spore-producing plant"). Meiosis in a mature sporophyte produces haploid **spores**,



reproductive cells that can develop into a new haploid organism without fusing with another cell. Mitotic division of the spore cell produces a new multicellular gametophyte, and the cycle begins again. In many seedless plants, such as the fern in the diagram, the gametophyte and sporophyte look like different types of plants, even though they are forms of the same species. In seed plants, the gametophytes are microscopic; the familiar plants we see are the sporophytes.

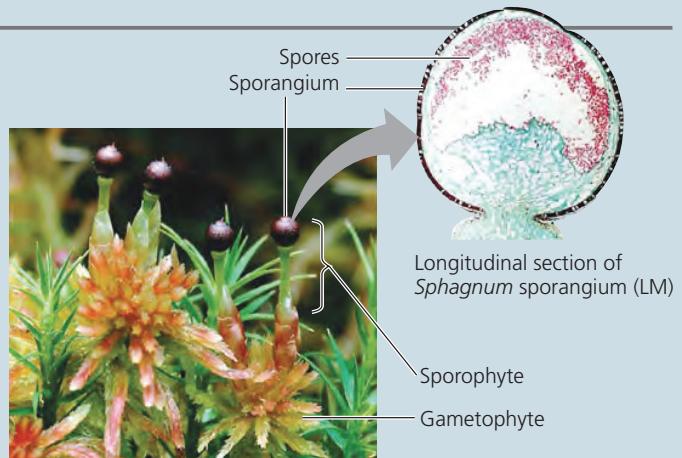
As part of a life cycle with alternation of generations, multicellular plant embryos develop from zygotes that are retained within the tissues of the female parent (a gametophyte). The parental tissues provide the developing embryo with nutrients, such as sugars and amino acids. The embryo has specialized **placental transfer cells**, sometimes present in the adjacent maternal tissue as well, which enhance the transfer of nutrients from parent to embryo through elaborate ingrowths of the wall surface (plasma membrane and cell wall). This interface is analogous to the nutrient-transferring embryo-mother interface of eutherian (placental) mammals. The multicellular, dependent embryo of land plants is such a significant derived trait that land plants are also known as **embryophytes**.

MAKE CONNECTIONS Review sexual life cycles in Figure 13.6 on p. 252. Identify which life cycle has alternation of generations, and summarize how it differs from other life cycles.

Walled Spores Produced in Sporangia

Plant spores are haploid reproductive cells that can grow into multicellular haploid gametophytes by mitosis. The polymer sporopollenin makes the walls of plant spores tough and resistant to harsh environments. This chemical adaptation enables spores to be dispersed through dry air without harm.

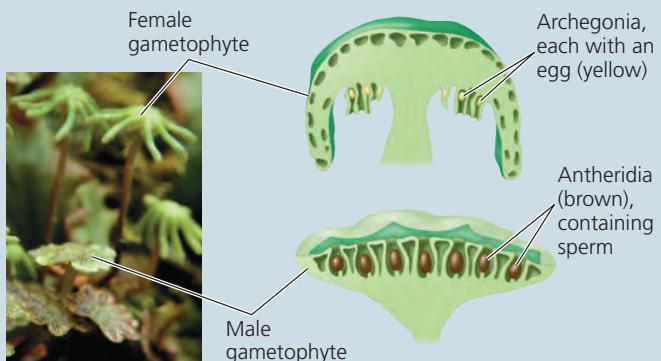
The sporophyte has multicellular organs called **sporangia** (singular, *sporangium*) that produce the spores. Within a sporangium, diploid cells called **sporocytes**, or spore mother cells, undergo meiosis and generate the haploid spores. The outer tissues of the sporangium protect the developing spores until they are released into the air. Multicellular sporangia that produce spores with sporopollenin-enriched walls are key terrestrial adaptations of land plants. Although charophytes also produce spores, these algae lack multicellular sporangia, and their flagellated, water-dispersed spores lack sporopollenin.



Sporophytes and sporangia of *Sphagnum* (a moss)

Multicellular Gametangia

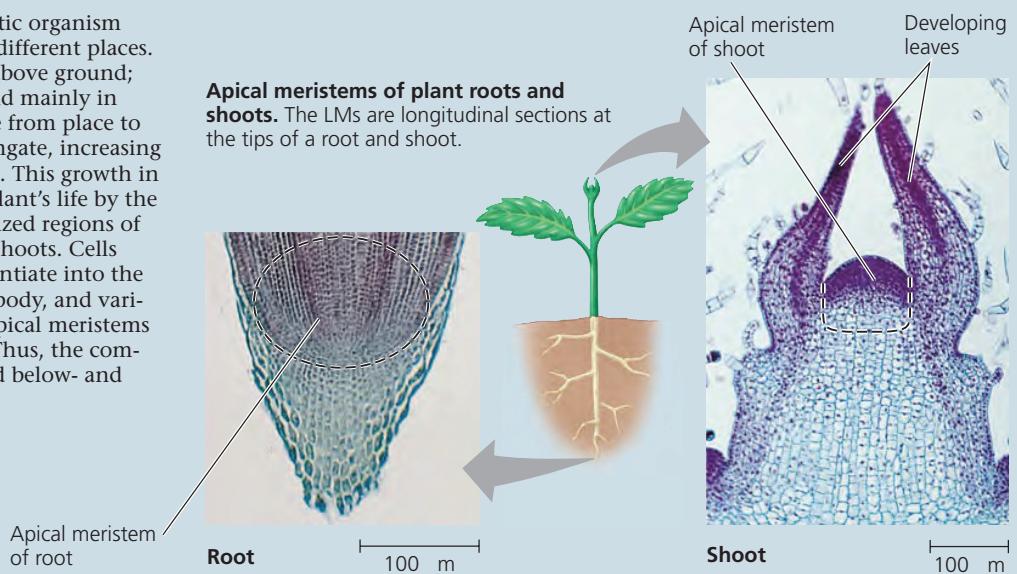
Another feature distinguishing early land plants from their algal ancestors was the production of gametes within multicellular organs called **gametangia**. The female gametangia are called **archegonia** (singular, *archegonium*). Each archegonium is a pear-shaped organ that produces a single nonmotile egg retained within the bulbous part of the organ (the top for the species shown here). The male gametangia, called **antheridia** (singular, *antheridium*), produce sperm and release them into the environment. In many groups of present-day plants, the sperm have flagella and swim to the eggs through water droplets or a film of water. Each egg is fertilized within an archegonium, where the zygote develops into an embryo. As you will see in Chapter 30, the gametophytes of seed plants are so reduced in size that the archegonia and antheridia have been lost in many lineages.



Archegonia and antheridia of *Marchantia* (a liverwort)

Apical Meristems

In terrestrial habitats, a photosynthetic organism finds essential resources in two very different places. Light and CO₂ are mainly available above ground; water and mineral nutrients are found mainly in the soil. Though plants cannot move from place to place, their roots and shoots can elongate, increasing exposure to environmental resources. This growth in length is sustained throughout the plant's life by the activity of **apical meristems**, localized regions of cell division at the tips of roots and shoots. Cells produced by apical meristems differentiate into the outer epidermis, which protects the body, and various types of internal tissues. Shoot apical meristems also generate leaves in most plants. Thus, the complex bodies of plants have specialized below- and aboveground organs.



In addition to the four traits shown in Figure 29.5, other derived traits that relate to terrestrial life have evolved in many plant species. For example, the epidermis in many species has a covering, the **cuticle**, which consists of wax and other polymers. Permanently exposed to the air, land plants run a far greater risk of desiccation (drying out) than their algal ancestors. The cuticle acts as waterproofing, helping prevent excessive water loss from the aboveground plant organs, while also providing some protection from microbial attack.

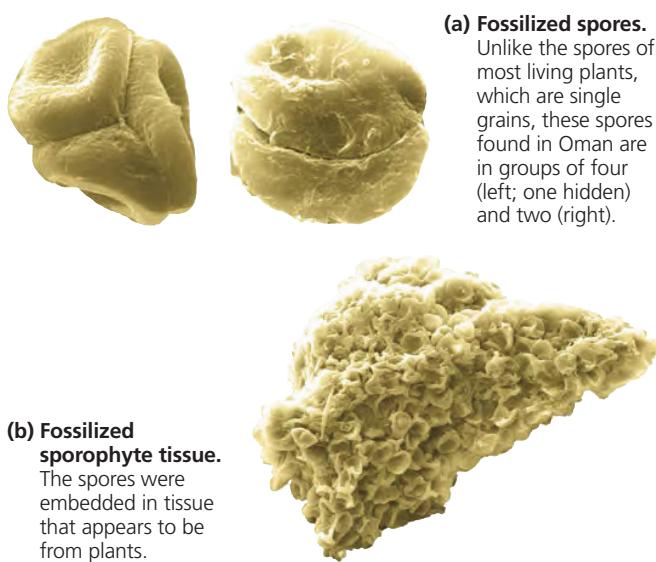
Early land plants lacked true roots and leaves. Without roots, how did these plants absorb nutrients from the soil? Fossils dating from 420 million years ago reveal an adaptation that may have aided early plants in nutrient uptake: They formed symbiotic associations with fungi similar in structure to beneficial associations observed today between plants and fungi. We'll describe these associations, called *mycorrhizae*, and their benefits to both plants and fungi in more detail in Chapter 31. For now, the main point is that mycorrhizal fungi form extensive networks of filaments through the soil, enabling them to absorb nutrients more effectively than a plant can on its own. The fungi transfer nutrients to their symbiotic plant partner, a benefit that may have helped plants without roots to colonize land.

Finally, many land plants produce molecules called *secondary compounds*, so named because they are products of secondary metabolic pathways—side branches off the primary metabolic pathways that produce the lipids, carbohydrates, amino acids, and other compounds common to all organisms. Secondary compounds include compounds called alkaloids, terpenes, tannins, and flavonoids. Various alkaloids, terpenes, and tannins have a bitter taste, strong odor, or toxic effect that helps defend a plant against herbivores and parasites. Flavonoids absorb harmful UV radiation, and some related compounds deter attack by pathogens. Humans also benefit from secondary compounds in plants, many of which are used in spices, medicines, and other products.

The Origin and Diversification of Plants

Paleobotanists seeking the evolutionary origin of plants have long debated what constitutes the oldest fossil evidence of land plants. In the 1970s, researchers found fossil spores dating to the Ordovician period, up to 475 million years old. Although the fossil spores resemble those of living plants, they also have some striking differences. For example, spores of present-day plants are typically dispersed as single grains, but the fossil spores are fused together in groups of two or four. This difference raises the possibility that the fossil spores were not produced by plants, but by some extinct algal relative. Furthermore, the oldest known fragments of plant body tissues are 50 million years younger than the puzzling spores.

In 2003, scientists from Britain and the Middle Eastern country of Oman shed some light on this mystery when they extracted spores from 475-million-year-old rocks from Oman



▲ Figure 29.6 Ancient plant spores and tissue (colorized SEMs).

(Figure 29.6a). Unlike previously discovered spores of this age, these were embedded in plant cuticle material that is similar to spore-bearing tissue in living plants (**Figure 29.6b**). After uncovering other small fragments of tissue that clearly belonged to plants, the scientists concluded that the spores from Oman represent fossil plants rather than algae.

Whatever the precise age of the first land plants, those ancestral species gave rise to the vast diversity of living plants. **Table 29.1** summarizes the ten extant phyla in the taxonomic scheme used in this text. (Extant lineages are those that have surviving members, not only extinct ones.) As you read the rest of this section, look at Table 29.1 together with **Figure 29.7**, which reflects a view of plant phylogeny based on plant morphology, biochemistry, and genetics.

One way to distinguish groups of plants is whether or not they have an extensive system of **vascular tissue**, cells joined into tubes that transport water and nutrients throughout the plant body. Most present-day plants have a complex vascular tissue system and are therefore called **vascular plants**. Plants that do not have an extensive transport system—liverworts, mosses, and hornworts—are described as “nonvascular” plants, even though some mosses do have simple vascular tissue. Non-vascular plants are often informally called **bryophytes** (from the Greek *bryon*, moss, and *phyton*, plant).

Although the term *bryophyte* is commonly used to refer to all nonvascular plants, molecular studies and morphological analyses of sperm structure have concluded that bryophytes do not form a monophyletic group (a clade). Debate continues, however, over the relationships of liverworts, mosses, and hornworts to each other and to vascular plants. Regardless of the outcome of this debate, bryophytes share some derived traits with vascular plants, such as multicellular

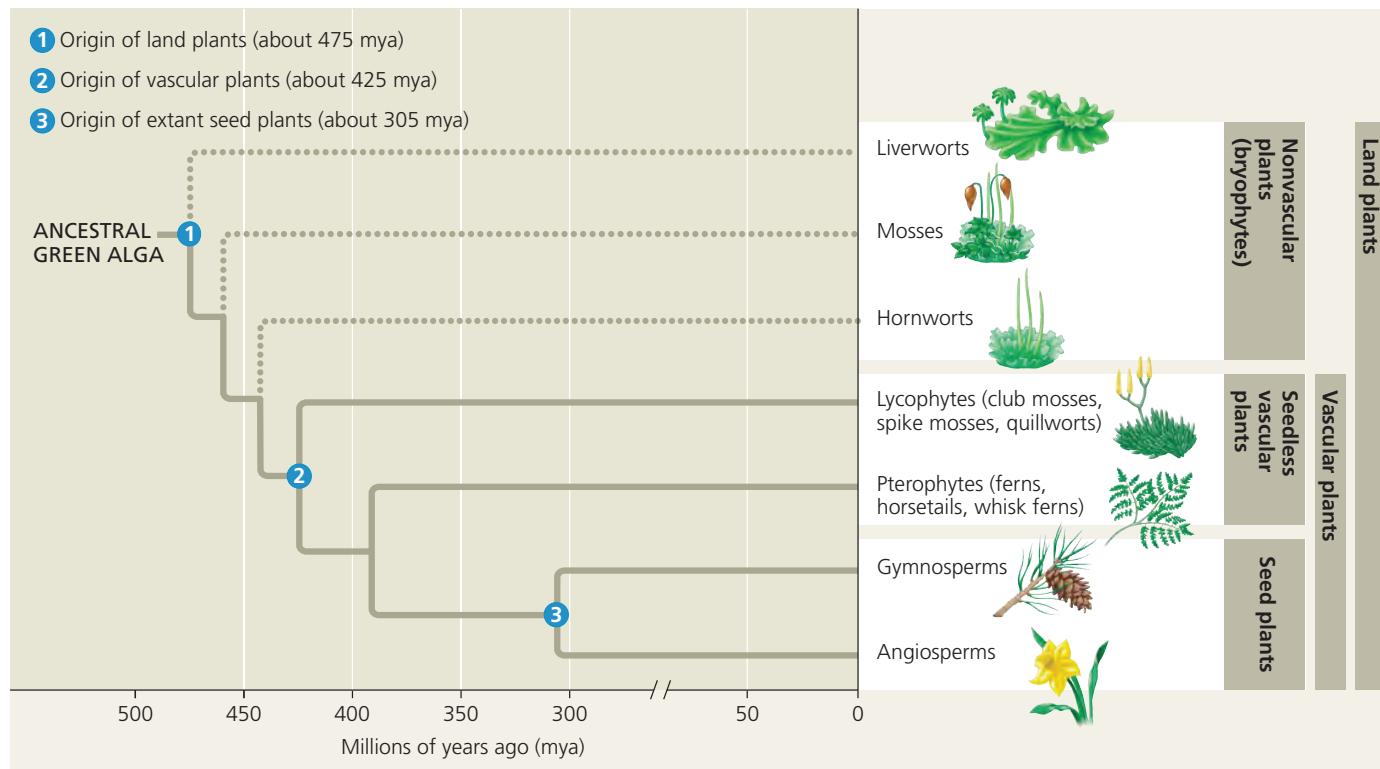
Table 29.1 Ten Phyla of Extant Plants

	Common Name	Number of Known Species
Nonvascular Plants (Bryophytes)		
Phylum Hepatophyta	Liverworts	9,000
Phylum Bryophyta	Mosses	15,000
Phylum Anthocerophyta	Hornworts	100
Vascular Plants		
<i>Seedless Vascular Plants</i>		
Phylum Lycophtya	Lycophtyes	1,200
Phylum Pterophyta	Pterophytes	12,000
Seed Plants		
<i>Gymnosperms</i>		
Phylum Ginkgophyta	Ginkgo	1
Phylum Cycadophyta	Cycads	130
Phylum Gnethophyta	Gnethophytes	75
Phylum Coniferophyta	Conifers	600
<i>Angiosperms</i>		
Phylum Anthophyta	Flowering plants	250,000

embryos and apical meristems, while lacking many innovations of vascular plants, such as roots and true leaves.

Vascular plants, which form a clade that comprises about 93% of all extant plant species, can be categorized further into smaller clades. Two of these clades are the **lycophytes** (club mosses and their relatives) and the **pterophytes** (ferns and their relatives). The plants in each of these clades lack seeds, which is why collectively the two clades are often informally called **seedless vascular plants**. However, notice in Figure 29.7 that seedless vascular plants are paraphyletic, not monophyletic. Groups such as the seedless vascular plants are sometimes referred to as a **grade**, a collection of organisms that share a key biological feature. Grades can be informative by grouping organisms according to features, such as lack of seeds. But members of a grade, unlike members of a clade, do not necessarily share the same ancestry. For example, even though pterophytes and lycophtyes are all seedless plants, pterophytes share a more recent common ancestor with seed plants. As a result, we would expect pterophytes and seed plants to share key traits not found in lycophtyes—and they do, as you'll read.

A third clade of vascular plants consists of seed plants, which represent the vast majority of living plant species. A **seed** is an embryo packaged with a supply of nutrients inside a protective coat. Seed plants can be divided into two groups, gymnosperms and angiosperms, based on the absence or



▲ Figure 29.7 Highlights of plant evolution. The phylogeny shown here illustrates a leading hypothesis about the relationships between plant groups. The dotted lines indicate groups whose evolutionary relationships continue to be debated.

presence of enclosed chambers in which seeds mature. **Gymnosperms** (from the Greek *gymnos*, naked, and *sperm*, seed) are grouped together as “naked seed” plants because their seeds are not enclosed in chambers. Living gymnosperm species, the most familiar of which are the conifers, probably form a clade. **Angiosperms** (from the Greek *angion*, container) are a huge clade consisting of all flowering plants. Angiosperm seeds develop inside chambers called ovaries, which originate within flowers and mature into fruits. Nearly 90% of living plant species are angiosperms.

Note that the phylogeny depicted in Figure 29.7 focuses only on the relationships between extant plant lineages. Paleobotanists have also discovered fossils belonging to extinct plant lineages. As you’ll read later in the chapter, many of these fossils reveal intermediate steps in the emergence of the distinctive plant groups found on Earth today.

CONCEPT CHECK 29.1

1. Why do researchers identify charophytes rather than another group as the closest relatives of land plants?
2. Identify three derived traits that distinguish plants from charophytes *and* facilitate life on land. Explain.
3. **WHAT IF?** What would the human life cycle be like if we had alternation of generations? Assume that the multicellular diploid stage is similar in form to an adult human.
4. **MAKE CONNECTIONS** Figure 29.7 identifies which lineages are land plants, nonvascular plants, vascular plants, seedless vascular plants, and seed plants. Which of these categories are monophyletic, and which are paraphyletic? Explain. See Figure 26.10 on p. 542.

For suggested answers, see Appendix A.

CONCEPT 29.2

Mosses and other nonvascular plants have life cycles dominated by gametophytes



Nonvascular plants (bryophytes)

Seedless vascular plants
Gymnosperms
Angiosperms

The nonvascular plants (bryophytes) are represented today by three phyla of small herbaceous

(nonwoody) plants: **liverworts** (phylum Hepaticophyta), **mosses** (phylum Bryophyta), and **hornworts** (phylum Anthocerophyta). Liverworts and hornworts are named for their shapes, plus the suffix *wort* (from the Anglo-Saxon for “herb”). Mosses are familiar to many people, although some plants commonly called “mosses” are not really mosses at all. These include Irish moss (a red seaweed), reindeer moss (a lichen), club mosses (seedless vascular plants), and Spanish mosses (lichens in some regions and flowering plants in others).

Note that the terms *Bryophyta* and *bryophyte* are not synonymous. *Bryophyta* is the formal taxonomic name for the phylum that consists solely of mosses. As mentioned earlier, the term *bryophyte* is used informally to refer to *all* nonvascular plants—liverworts, mosses, and hornworts.

Liverworts, mosses, and hornworts have acquired many unique adaptations over the long course of their evolution. Nevertheless, living bryophytes likely reflect some traits of the earliest plants. The oldest known fossils of plant fragments, for example, include tissues very similar to those inside liverworts. Researchers hope to discover more parts of these ancient plants to see if this resemblance is reflected more broadly.

Bryophyte Gametophytes

Unlike vascular plants, in all three bryophyte phyla the haploid gametophytes are the dominant stage of the life cycle: That is, they are usually larger and longer-living than the sporophytes, as shown in the moss life cycle in **Figure 29.8**. Sporophytes are typically present only part of the time.

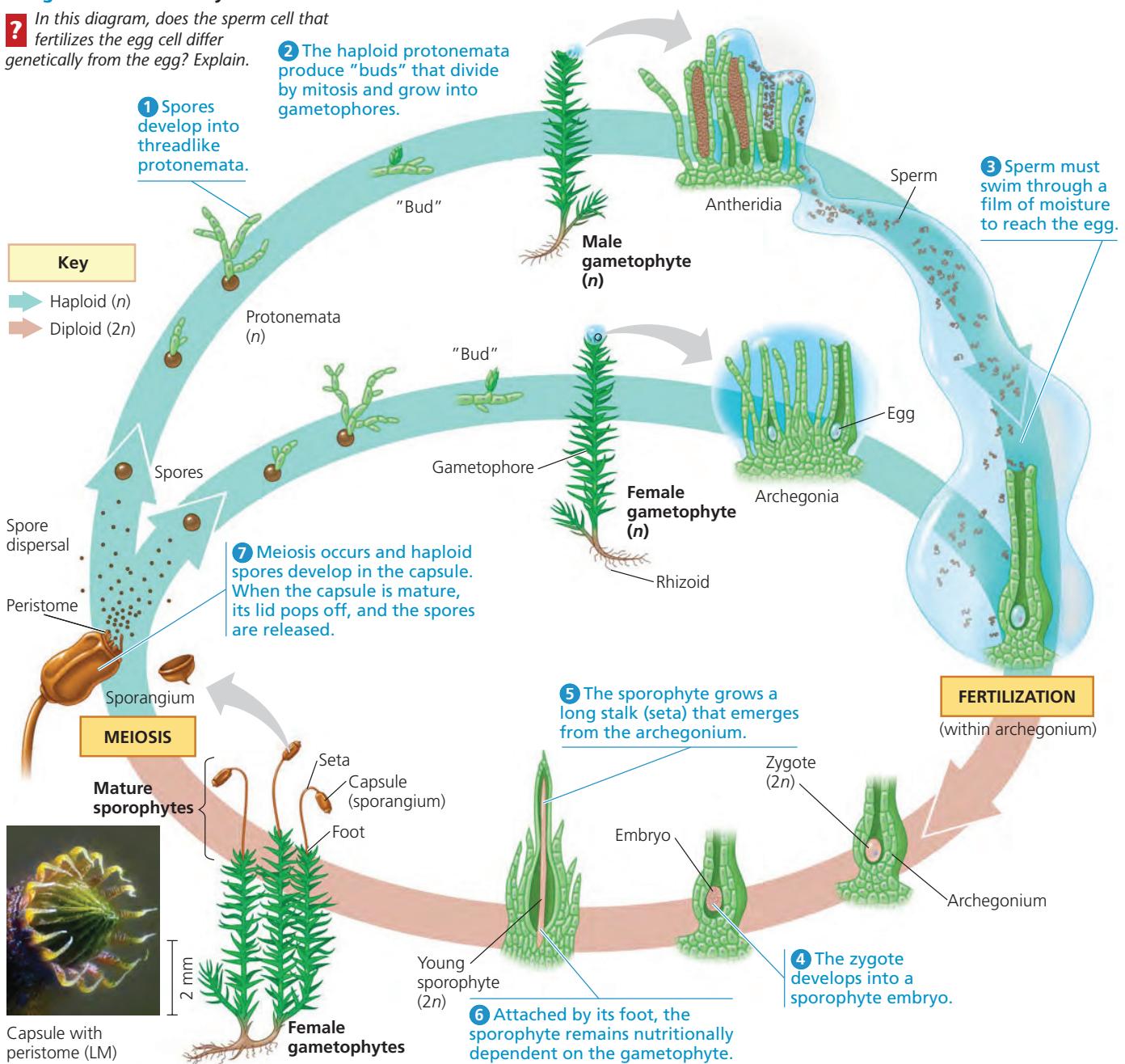
When bryophyte spores are dispersed to a favorable habitat, such as moist soil or tree bark, they may germinate and grow into gametophytes. Germinating moss spores, for example, characteristically produce a mass of green, branched, one-cell-thick filaments known as a **protonema** (plural, *protonemata*; from the Greek *proto*, first, and *nema*, threads). A protonema has a large surface area that enhances absorption of water and minerals. In favorable conditions, a protonema produces one or more “buds.” (Note that when referring to nonvascular plants, we typically use quotation marks for structures similar to the buds, stems, and leaves of vascular plants because the definitions of these terms are based on vascular plant organs.) Each of these bud-like growths has an apical meristem that generates a gamete-producing structure known as a **gametophore** (“gamete bearer”). Together, a protonema and one or more gametophores make up the body of a moss gametophyte.

Bryophyte gametophytes generally form ground-hugging carpets, partly because their body parts are too thin to support a tall plant. A second constraint on the height of many bryophytes is the absence of vascular tissue, which would enable long-distance transport of water and nutrients. (The thin structure of bryophyte organs makes it possible to distribute materials for short distances without specialized vascular tissue.) However, some mosses have conducting tissues in the center of their “stems.” A few of these mosses can grow as tall as 2 m as a result. Phylogenetic analyses suggest that in these and some other bryophytes, conducting tissues similar to those of vascular plants arose independently by convergent evolution.

The gametophytes are anchored by delicate **rhizoids**, which are long, tubular single cells (in liverworts and hornworts) or filaments of cells (in mosses). Unlike roots, which are found in vascular plant sporophytes, rhizoids are not

▼ Figure 29.8 The life cycle of a moss.

? In this diagram, does the sperm cell that fertilizes the egg cell differ genetically from the egg? Explain.



composed of tissues. Bryophyte rhizoids also lack specialized conducting cells and do not play a primary role in water and mineral absorption.

Gametophytes can form multiple gametangia, each of which produces gametes and is covered by protective tissue. Each archegonium produces one egg, whereas each antheridium produces many sperm. Some bryophyte gametophytes are bisexual, but in mosses the archegonia and antheridia are typically carried on separate female and male gametophytes. Flagellated sperm swim through a film of water toward eggs, entering the archegonia in response to chemical attractants.

Eggs are not released but instead remain within the bases of archegonia. After fertilization, embryos are retained within the archegonia. Layers of placental transfer cells help transport nutrients to the embryos as they develop into sporophytes.

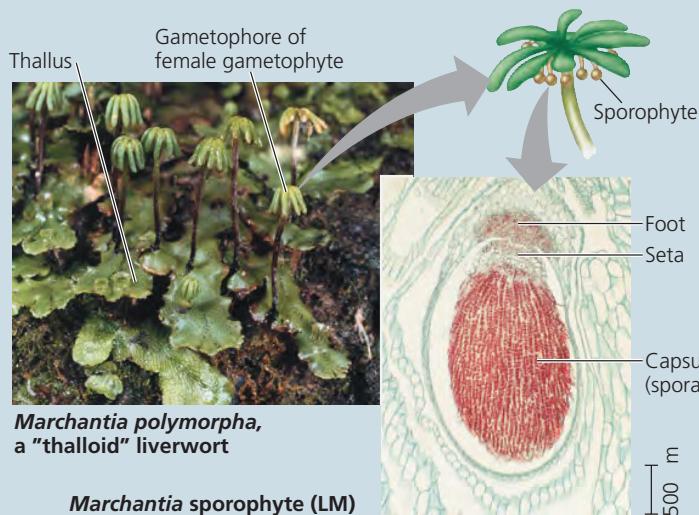
Bryophyte sperm typically require a film of water to reach the eggs. Given this requirement, it is not surprising that many bryophyte species are found in moist habitats. The fact that sperm swim through water to reach the egg also means that in species with separate male and female gametophytes (most mosses), sexual reproduction is likely to be more successful when individuals are located close to one another.

▼ Figure 29.9

Exploring Bryophyte Diversity

Liverworts (Phylum Hepatophyta)

This phylum's common and scientific names (from the Latin *hepaticus*, liver) refer to the liver-shaped gametophytes of its members, such as *Marchantia*, shown below. In medieval times, their shape was thought to be a sign that the plants could help treat



Marchantia polymorpha, a "thalloid" liverwort

Marchantia sporophyte (LM)

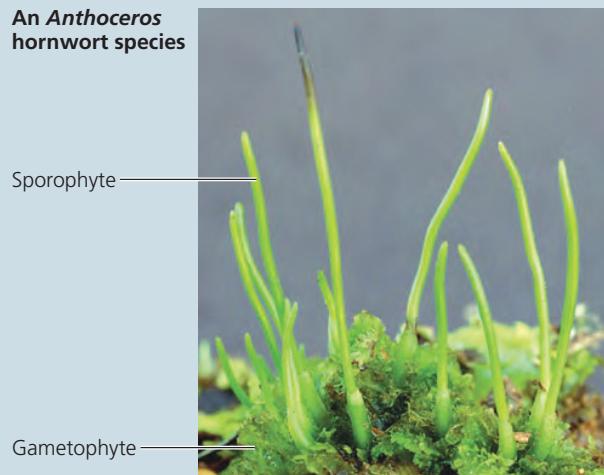
liver diseases. Some liverworts, including *Marchantia*, are described as "thalloid" because of the flattened shape of their gametophytes. (Recall from Chapter 28 that the body of a multicellular alga is called a thallus.) *Marchantia* gametangia are elevated on gametophores that look like miniature trees. You would need a magnifying glass to see the sporophytes, which have a short seta (stalk) with an oval or round capsule. Other liverworts, such as *Plagiochila*, below, are called "leafy" because their stemlike gametophytes have many leaflike appendages. There are many more species of leafy liverworts than thalloid liverworts.



Plagiochila deltoidea, a "leafy" liverwort

Hornworts (Phylum Anthocerophyta)

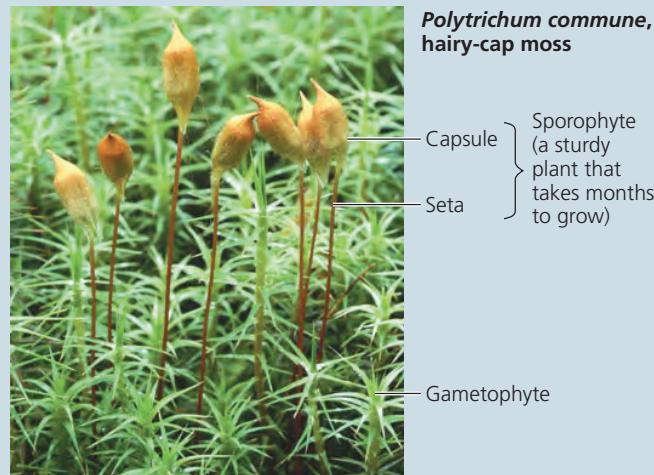
This phylum's common and scientific names (from the Greek *keras*, horn) refer to the long, tapered shape of the sporophyte. A typical sporophyte can grow to about 5 cm high. Unlike a liverwort or moss sporophyte, a hornwort sporophyte lacks a seta and consists only of a sporangium. The sporangium releases mature spores by splitting open, starting at the tip of the horn. The gametophytes, which are usually 1–2 cm in diameter, grow mostly horizontally and often have multiple sporophytes attached. Hornworts are frequently among the first species to colonize open areas with moist soils; a symbiotic relationship with nitrogen-fixing cyanobacteria contributes to their ability to do this (nitrogen is often in short supply in such areas).



An *Anthoceros* hornwort species

Mosses (Phylum Bryophyta)

Moss gametophytes, which range in height from less than 1 mm to up to 2 m, are less than 15 cm tall in most species. The familiar carpet of moss you observe consists mainly of gametophytes. The blades of their "leaves" are usually only one cell thick, but more complex "leaves" that have ridges coated with cuticle can be found on the common hairy-cap moss (*Polytrichum*, below) and its close relatives. Moss sporophytes are typically elongated and visible to the naked eye, with heights ranging up to about 20 cm. Though green and photosynthetic when young, they turn tan or brownish red when ready to release spores.



Polytrichum commune, hairy-cap moss



Many bryophyte species can increase the number of individuals in a local area through various methods of asexual reproduction. For example, some mosses reproduce asexually by forming *brood bodies*, small plantlets (as shown at left) that detach from the parent plant and grow into new, genetically identical copies of their parent.

Bryophyte Sporophytes

Although bryophyte sporophytes are usually green and photosynthetic when young, they cannot live independently. They remain attached to their parental gametophytes, from which they absorb sugars, amino acids, minerals, and water.

Bryophytes have the smallest sporophytes of all extant plant groups, consistent with the hypothesis that larger sporophytes evolved only later, in the vascular plants. A typical bryophyte sporophyte consists of a foot, a seta, and a sporangium. Embedded in the archegonium, the **foot** absorbs nutrients from the gametophyte. The **seta** (plural, *setae*), or stalk, conducts these materials to the sporangium, also called a **capsule**, which uses them to produce spores by meiosis. One capsule can generate up to 50 million spores.

In most mosses, the seta becomes elongated, enhancing spore dispersal by elevating the capsule. Typically, the upper part of the capsule features a ring of interlocking, tooth-like structures known as the **peristome** (see Figure 29.8). These “teeth” open under dry conditions and close again when it is moist. This allows spores to be discharged gradually, via periodic gusts of wind that can carry them long distances.

Moss and hornwort sporophytes are often larger and more complex than those of liverworts. Both moss and hornwort sporophytes also have specialized pores called **stomata** (singular, *stoma*), which are also found in all vascular plants. These pores support photosynthesis by allowing the exchange of CO₂ and O₂ between the outside air and the sporophyte interior (see Figure 10.3). Stomata are also the main avenues by which water evaporates from the sporophyte. In hot, dry conditions, the stomata close, minimizing water loss.

The fact that stomata are present in mosses and hornworts but absent in liverworts suggests three possible hypotheses for their evolution. If liverworts are the deepest-branched lineage of land plants, as in Figure 29.7, then stomata may have evolved once in the ancestor of mosses, hornworts, and vascular plants. If hornworts are the deepest-branched lineage, stomata may have evolved once and then been lost in the liverwort lineage. Finally, if hornworts are the deepest-branched lineage and mosses are the closest relatives of vascular plants, it is also possible that hornworts acquired stomata independently of mosses and vascular plants. This question is important to understanding plant evolution because stomata play a crucial role in the success of vascular plants, as you will learn in Chapter 36.

Figure 29.9, on the facing page, shows some examples of gametophytes and sporophytes in the bryophyte phyla.

The Ecological and Economic Importance of Mosses

Wind dispersal of lightweight spores has distributed mosses throughout the world. These plants are particularly common and diverse in moist forests and wetlands. Some mosses colonize bare, sandy soil, where researchers have found they help retain nitrogen in the soil (**Figure 29.10**). In northern coniferous forests, species such as the feather moss *Pleurozium* harbor nitrogen-fixing cyanobacteria that increase the availability of nitrogen in the ecosystem. Other mosses inhabit such extreme environments as mountaintops, tundra, and deserts. Many mosses are able to live in very cold or dry habitats because they can survive the loss of most of their body water, then rehydrate when moisture is available. Few vascular plants can survive the same degree of desiccation.

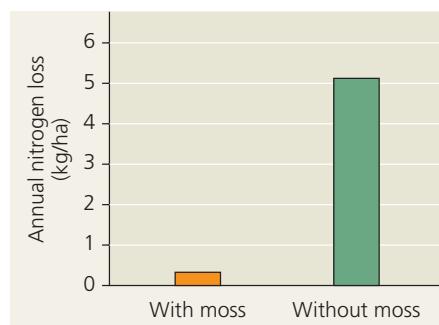
▼ Figure 29.10

INQUIRY

Can bryophytes reduce the rate at which key nutrients are lost from soils?

EXPERIMENT Soils in terrestrial ecosystems are often low in nitrogen, a nutrient required for normal plant growth. Richard Bowden, of Allegheny College, measured annual inputs (gains) and outputs (losses) of nitrogen in a sandy-soil ecosystem dominated by the moss *Polytrichum*. Nitrogen inputs were measured from rainfall (dissolved ions, such as nitrate, NO₃⁻), biological N₂ fixation, and wind deposition. Nitrogen losses were measured in leached water (dissolved ions, such as NO₃⁻) and gaseous emissions (such as NO₂ emitted by bacteria). Bowden measured losses for soils with *Polytrichum* and for soils where the moss was removed two months before the experiment began.

RESULTS A total of 10.5 kg of nitrogen per hectare (kg/ha) entered the ecosystem each year. Little nitrogen was lost by gaseous emissions (0.10 kg/ha · yr). The results of comparing nitrogen losses by leaching are shown below.



CONCLUSION The moss *Polytrichum* greatly reduced the loss of nitrogen by leaching in this ecosystem. Each year, the moss ecosystem retained over 95% of the 10.5 kg/ha of total nitrogen inputs (only 0.1 kg/ha and 0.3 kg/ha were lost to gaseous emissions and leaching, respectively).

SOURCE R. D. Bowden, Inputs, outputs, and accumulation of nitrogen in an early successional moss (*Polytrichum*) ecosystem, *Ecological Monographs* 61:207–223 (1991).

WHAT IF? How might the presence of *Polytrichum* affect plant species that typically colonize the sandy soils after the moss?

One wetland moss genus, *Sphagnum*, or “peat moss,” is often a major component of deposits of partially decayed organic material known as **peat** (Figure 29.11a). Boggy regions with thick layers of peat are called peatlands. *Sphagnum* does not decay readily, in part because of phenolic compounds embedded in its cell walls. The low temperature, pH, and oxygen level of peatlands also inhibit decay of moss and other organisms in these boggy wetlands. As a result, some peatlands have preserved corpses for thousands of years (Figure 29.11b).

Peat has long been a fuel source in Europe and Asia, and it is still harvested for fuel today, notably in Ireland and Canada. Peat moss is also useful as a soil conditioner and for packing plant roots during shipment because it has large dead cells that can absorb roughly 20 times the moss’s weight in water.

Peatlands cover 3% of Earth’s land surface and contain roughly 30% of the world’s soil carbon. Globally, an estimated 450 billion tons of organic carbon is stored as peat. These carbon reservoirs have helped to stabilize atmospheric CO₂.



(a) Peat being harvested from a peatland



(b) “Tollund Man,” a bog mummy dating from 405–100 B.C.E.

The acidic, oxygen-poor conditions produced by *Sphagnum* can preserve human or other animal bodies for thousands of years.

▲ **Figure 29.11** *Sphagnum*, or peat moss: a bryophyte with economic, ecological, and archaeological significance.

concentrations (see Chapter 55). Current overharvesting of *Sphagnum* may reduce peat’s beneficial ecological effects and contribute to global warming by releasing stored CO₂. In addition, if global temperatures continue to rise, the water levels of some peatlands are expected to drop. Such a change would expose peat to air and cause it to decompose, thereby releasing additional stored CO₂ and contributing further to global warming. The historical and expected future effects of *Sphagnum* on the global climate underscore the importance of preserving and managing peatlands.

CONCEPT CHECK 29.2

- How do bryophytes differ from other plants?
- Give three examples of how structure fits function in bryophytes.
- WHAT IF?** For each hypothesis of stomatal evolution, label each gain and loss of stomata on an appropriately modified version of the tree in Figure 29.7.

For suggested answers, see Appendix A.

CONCEPT 29.3

Ferns and other seedless vascular plants were the first plants to grow tall



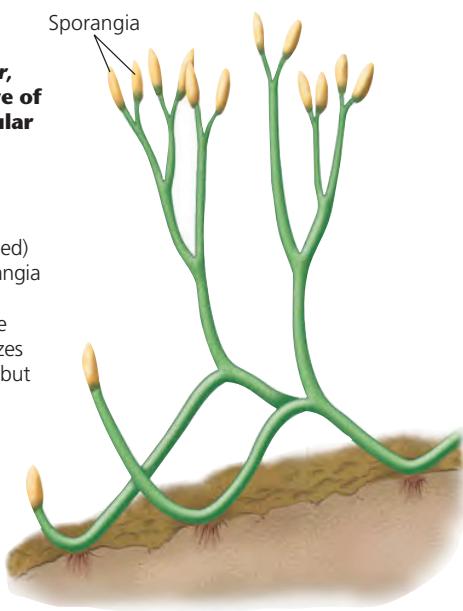
Nonvascular plants (bryophytes)
Seedless vascular plants
Gymnosperms
Angiosperms

During the first 100 million years of plant evolution, nonvascular plants or bryophyte-like plants were the prevalent vegetation. But it is vascular plants that dominate most landscapes today. Fossils and living seedless vascular plants can provide insights into plant evolution during the Devonian and Carboniferous periods, when vascular plants began to diversify but most groups of seed plants had not yet evolved. Fossils show that lycophytes, ferns, and other seedless vascular plants had well-developed vascular systems by the Devonian. As we’ll see, this evolutionary innovation set the stage for vascular plants to grow taller than their bryophyte counterparts. As in nonvascular plants, however, the sperm of ferns and all other seedless vascular plants are flagellated and swim through a film of water to reach eggs. In part because of these swimming sperm, seedless vascular plants today are most common in damp environments.

Origins and Traits of Vascular Plants

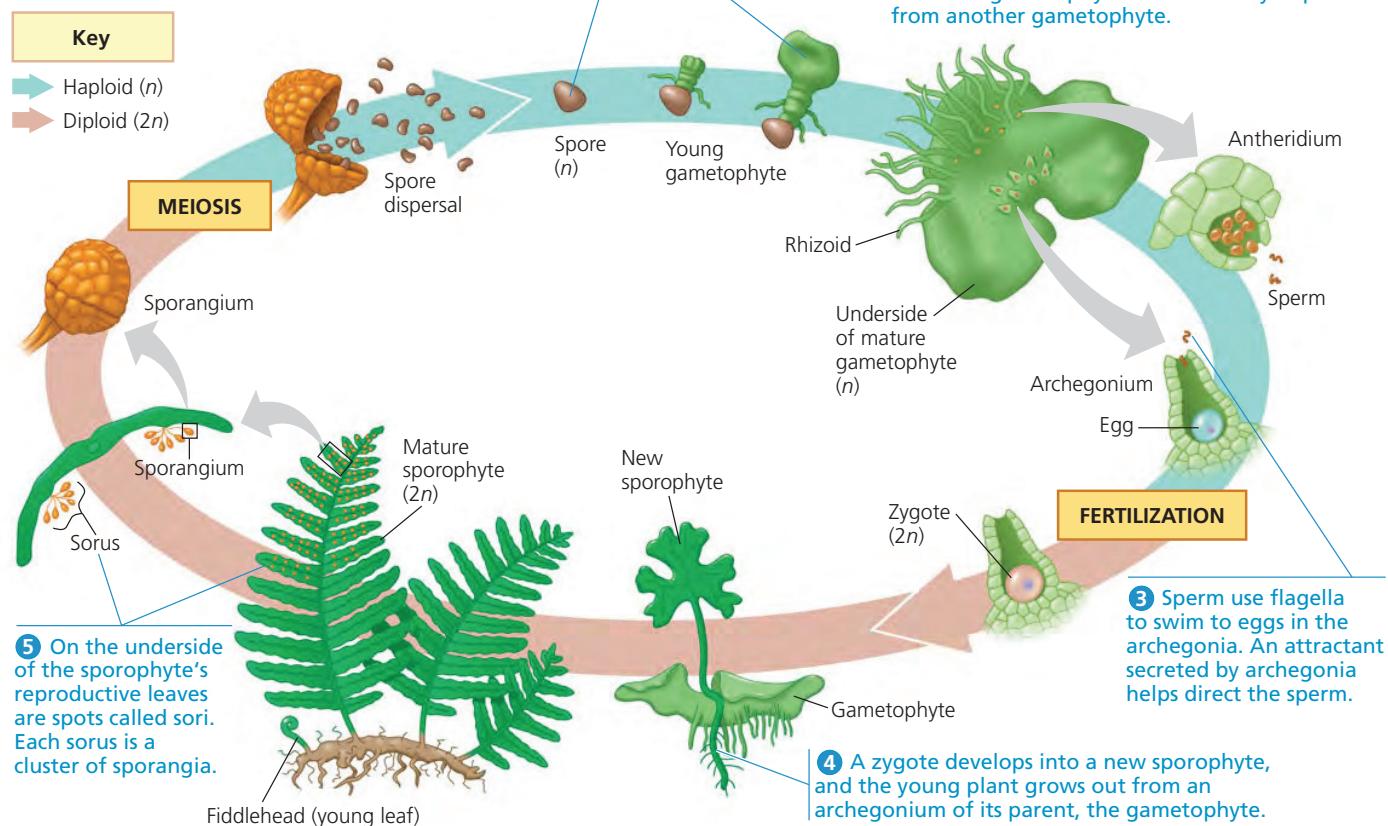
Fossils of the forerunners of present-day vascular plants date back about 425 million years. Unlike the nonvascular plants, these species had branched sporophytes that were not dependent on gametophytes for nutrition (Figure 29.12). Although these ancestors of vascular plants were only about

Figure 29.12
Sporophytes of *Aglaophyton major*, an ancient relative of present-day vascular plants. This reconstruction from 405-million-year-old fossils exhibits dichotomous (Y-shaped) branching with sporangia at the ends of the branches. Sporophyte branching characterizes living vascular plants but is lacking in living nonvascular plants (bryophytes).



▼ Figure 29.13 The life cycle of a fern.

WHAT IF? If the ability to disperse sperm by wind evolved in a fern, how might its life cycle be affected?



15 cm tall, their branching made possible more complex bodies with multiple sporangia. As plant bodies became increasingly complex, competition for space and sunlight probably increased. As we'll see, that competition may have stimulated still more evolution in vascular plants.

The ancestors of vascular plants already had some derived traits of today's vascular plants, but they lacked roots and some other adaptations that evolved later. This section describes the main traits that characterize living vascular plants: life cycles with dominant sporophytes, transport in vascular tissues called xylem and phloem, and well-developed roots and leaves, including spore-bearing leaves called sporophylls.

Life Cycles with Dominant Sporophytes

Fossils suggest that the ancestors of vascular plants had gametophytes and sporophytes that were about equal in size. Among living vascular plants, however, the sporophyte (diploid) generation is the larger and more complex plant in the alternation of generations (Figure 29.13). In ferns, for example, the familiar leafy plants are the sporophytes. You

would have to get down on your hands and knees and search the ground carefully to find fern gametophytes, which are tiny structures that often grow on or just below the soil surface. Until you have a chance to do that, you can study the sporophyte-dominant life cycle of seedless vascular plants in Figure 29.13, which uses a fern as an example. Then, for review, compare this life cycle with Figure 29.8, which represents a gametophyte-dominated life cycle typical of mosses and other nonvascular plants. In Chapter 30, you will see that gametophytes became even more reduced during the evolution of seed plants.

Transport in Xylem and Phloem

Vascular plants have two types of vascular tissue: xylem and phloem. **Xylem** conducts most of the water and minerals. The xylem of most vascular plants includes **tracheids**, tube-shaped cells that carry water and minerals up from roots (see Figure 35.10). (Tracheids have been lost in some highly specialized species, such as *Wolffia*, a tiny aquatic angiosperm.) Because nonvascular plants lack tracheids, vascular plants are sometimes referred to as tracheophytes. The water-conducting cells in vascular plants are *lignified*; that is, their cell walls are strengthened by the polymer **lignin**. The tissue called **phloem** has cells arranged into tubes that distribute sugars, amino acids, and other organic products (see Figure 35.10).

Lignified vascular tissue permitted vascular plants to grow tall. Their stems became strong enough to provide support against gravity, and they could transport water and mineral nutrients high above the ground. Tall plants could also out-compete short plants for access to the sunlight needed for photosynthesis. In addition, the spores of tall plants could disperse farther than those of short plants, enabling tall species to colonize new environments rapidly. Overall, the ability to grow tall was a major evolutionary innovation that gave vascular plants a competitive edge over nonvascular plants, which rarely grow above 20 cm in height. Competition among vascular plants also increased, and taller growth forms were favored by natural selection—such as the trees that formed the first forests about 385 million years ago.

Evolution of Roots

Lignified vascular tissue also provides benefits below ground. Instead of the rhizoids seen in bryophytes, roots evolved in the sporophytes of almost all vascular plants. **Roots** are organs that absorb water and nutrients from the soil. Roots also anchor vascular plants, hence allowing the shoot system to grow taller.

Root tissues of living plants closely resemble stem tissues of early vascular plants preserved in fossils. This suggests that roots may have evolved from the lowest belowground portions of stems in ancient vascular plants. It is unclear whether roots evolved only once in the common ancestor of all vascular plants or independently in different lineages.

Although the roots of living members of these lineages of vascular plants share many similarities, fossil evidence hints at convergent evolution. The oldest lycophyte fossils, for example, already displayed simple roots 400 million years ago, when the ancestors of ferns and seed plants still had none. Studying genes that control root development in different vascular plant species may help resolve this question.

Evolution of Leaves

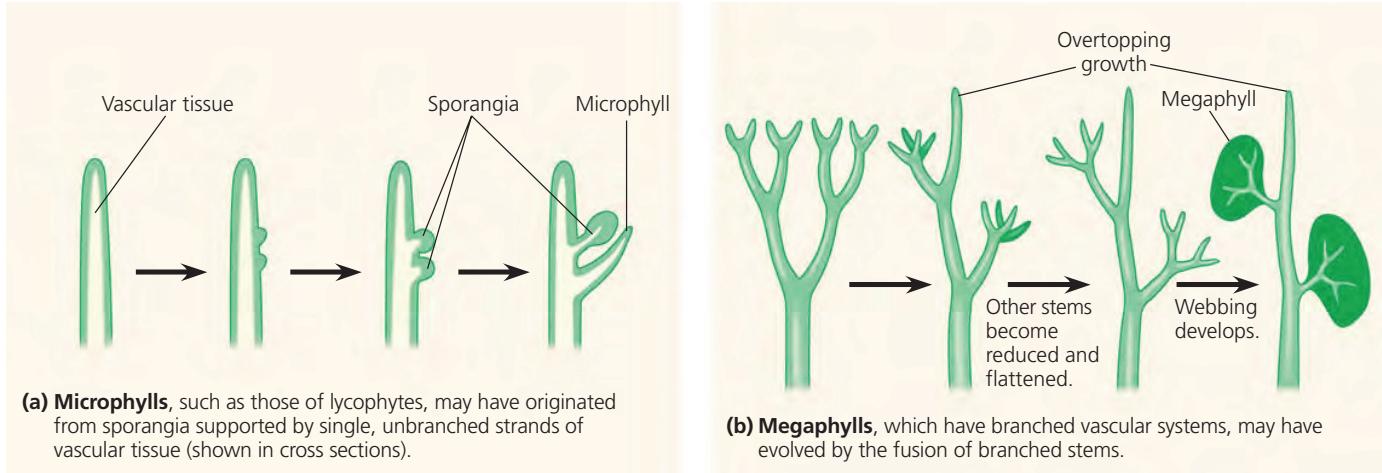
Leaves increase the surface area of the plant body and serve as the primary photosynthetic organ of vascular plants. In terms of size and complexity, leaves can be classified as either microphylls or megaphylls. All of the lycophytes (the oldest lineage of present-day vascular plants)—and only the lycophytes—have **microphylls**, small, usually spine-shaped leaves supported by a single strand of vascular tissue. Almost all other vascular plants have **megaphylls**, leaves with a highly branched vascular system; a few species have reduced leaves that appear to have evolved from megaphylls. So named because they are typically larger than microphylls, megaphylls support greater photosynthetic productivity than microphylls as a result of the greater surface area served by their network of veins. Microphylls first appear in the fossil record 410 million years ago, but megaphylls do not emerge until about 370 million years ago, toward the end of the Devonian period.

According to one model of leaf evolution, microphylls originated from sporangia located on the side of the stem (**Figure 29.14a**). Megaphylls, by contrast, may have evolved from a series of branches lying close together on a stem. As one of these branches came to grow above, or *overtop*, the others, the lower branches became flattened and developed webbing that joined them to one another. These joined branches thus became a leaf attached to the branch that overtopped them (**Figure 29.14b**). To better understand the origin of leaves, scientists are exploring the genetic control of leaf development.

Sporophylls and Spore Variations

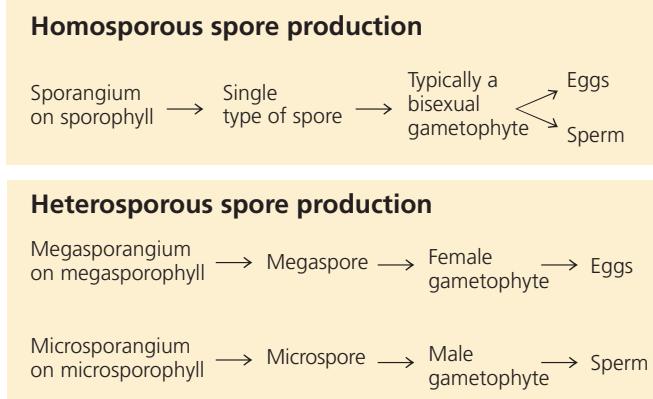
One milestone in the evolution of plants was the emergence of **sporophylls**, modified leaves that bear sporangia. Sporophylls vary greatly in structure. For example, fern sporophylls produce clusters of sporangia known as **sori** (singular, *sorus*), usually on the undersides of the sporophylls (see Figure 29.13). In many lycophytes and in most gymnosperms, groups of sporophylls form cone-like structures called **strobili** (singular, *strobilus*; from the Greek *strobilos*, cone). In Chapter 30, you will see how sporophylls form gymnosperm strobili and parts of angiosperm flowers.

Most seedless vascular plant species are **homosporous**: They have one type of sporangium that produces one type of spore, which typically develops into a bisexual gametophyte, as in most ferns. In contrast, a **heterosporous** species has



▲ Figure 29.14 Hypotheses for the evolution of leaves.

two types of sporangia and produces two kinds of spores: Megasporangia on megasporophylls produce **megaspores**, which develop into female gametophytes; microsporangia on microsporophylls produce the comparatively smaller **microspores**, which develop into male gametophytes. All seed plants and a few seedless vascular plants are heterosporous. The following diagram compares the two conditions:



Classification of Seedless Vascular Plants

As we noted earlier, biologists recognize two clades of living seedless vascular plants: the lycophytes (phylum Lycophyta) and the pterophytes (phylum Pterophyta). The lycophytes include the club mosses, the spike mosses, and the quillworts. The pterophytes include the ferns, the horsetails, and the whisk ferns and their relatives. Because they differ greatly in appearance, the ferns, horsetails, and whisk ferns have long been considered separate phyla: phylum Pterophyta (ferns), phylum Sphenophyta (horsetails), and phylum Psilotophyta (whisk ferns and a related genus). However, recent molecular comparisons provide convincing evidence that all three groups make up a clade. Accordingly, many systematists now classify them together as the phylum Pterophyta, as

we do in this chapter. Others refer to these groups as three separate phyla within a clade.

Figure 29.15, on the next page, describes the two main groups of seedless vascular plants.

Phylum Lycophyta: Club Mosses, Spike Mosses, and Quillworts

Present-day species of lycophytes, the most ancient group of vascular plants, are relicts of a far more impressive past. By the Carboniferous period (359–299 million years ago), the lycophyte evolutionary lineage included small herbaceous plants and giant trees with diameters of more than 2 m and heights of more than 40 m. The giant lycophyte trees thrived for millions of years in moist swamps, but they became extinct when Earth's climate became drier at the end of the Carboniferous period. The small lycophytes survived, represented today by about 1,200 species. Though some are commonly called club mosses and spike mosses, they are not true mosses (which, as discussed earlier, are nonvascular plants).

Phylum Pterophyta: Ferns, Horsetails, and Whisk Ferns and Relatives

Ferns radiated extensively from their Devonian origins and grew alongside lycophyte trees and horsetails in the great Carboniferous swamp forests. Today, ferns are by far the most widespread seedless vascular plants, numbering more than 12,000 species. Though most diverse in the tropics, many ferns thrive in temperate forests, and some species are even adapted to arid habitats.

As mentioned earlier, ferns and other pterophytes are more closely related to seed plants than to lycophytes. As a result, pterophytes and seed plants share traits that are not found in lycophytes, including overtopping growth (see Figure 29.14b), megaphyll leaves, and roots that can branch at various points along the length of an existing root. In lycophytes,

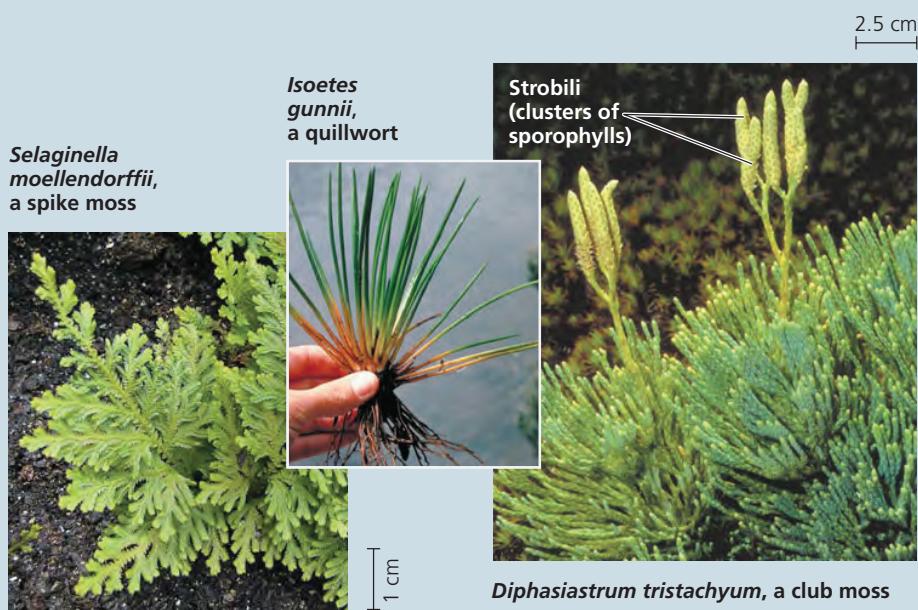
▼ Figure 29.15

Exploring Seedless Vascular Plant Diversity

Lycophytes (Phylum Lycophyta)

Many lycophytes grow on tropical trees as *epiphytes*, plants that use other plants as a substrate but are not parasites. Other species grow on temperate forest floors. In some species, the tiny gametophytes live above ground and are photosynthetic. Others live below ground, nurtured by symbiotic fungi.

Sporophytes have upright stems with many small leaves, as well as ground-hugging stems that produce dichotomously branching roots. Spike mosses are usually relatively small and often grow horizontally. In many club mosses and spike mosses, sporophylls are clustered into club-shaped cones (strobili). Quillworts, named for their leaf shape, form a single genus whose members live in marshy areas or as submerged aquatic plants. Club mosses are all homosporous, whereas spike mosses and quillworts are all heterosporous. The spores of club mosses are released in clouds and are so rich in oil that magicians and photographers once ignited them to create smoke or flashes of light.



Pterophytes (Phylum Pterophyta)



Athyrium filix-femina, lady fern



Equisetum arvense, field horsetail



Psilotum nudum, a whisk fern

Ferns

Unlike the lycophytes, ferns have megaphylls (see Figure 29.14b). The sporophytes typically have horizontal stems that give rise to large leaves called fronds, often divided into leaflets. A frond grows as its coiled tip, the fiddlehead, unfurls.

Almost all species are homosporous. The gametophyte in some species shrivels and dies after the young sporophyte detaches itself. In most species, sporophytes have stalked sporangia with springlike devices that catapult spores several meters. Airborne spores can be carried far from their origin. Some species produce more than a trillion spores in a plant's lifetime.

Horsetails

The group's name refers to the brushy appearance of the stems, which have a gritty texture that made them historically useful as "scouring rushes" for pots and pans. Some species have separate fertile (cone-bearing) and vegetative stems. Horsetails are homosporous, with cones releasing spores that typically give rise to bisexual gametophytes.

Horsetails are also called arthropophytes ("jointed plants") because their stems have joints. Rings of small leaves or branches emerge from each joint, but the stem is the main photosynthetic organ. Large air canals carry oxygen to the roots, which often grow in waterlogged soil.

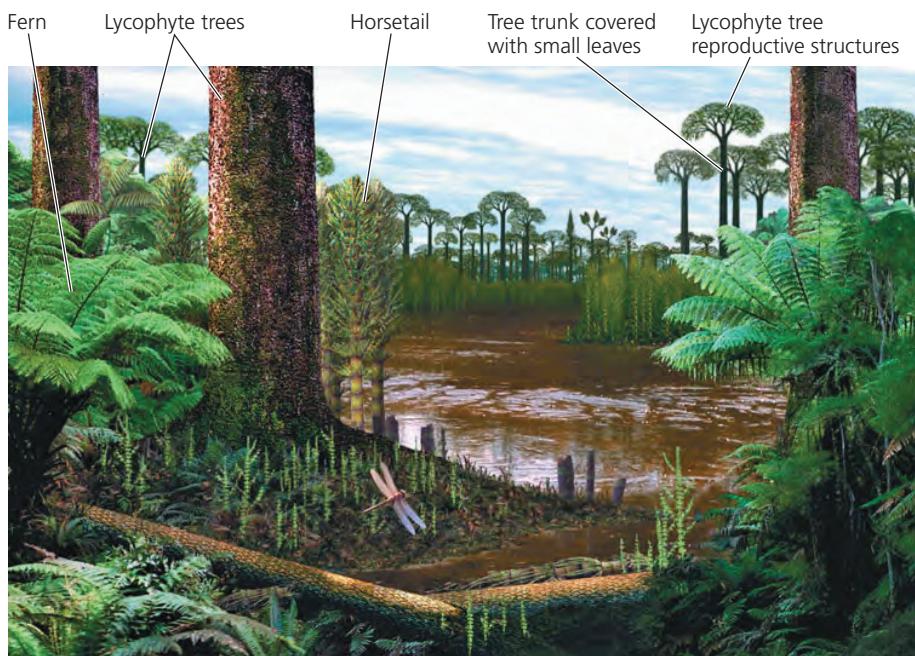
Whisk Ferns and Relatives

Like primitive vascular plant fossils, the sporophytes of whisk ferns (genus *Psilotum*) have dichotomously branching stems but no roots. Stems have scalelike outgrowths that lack vascular tissue and may have resulted from the evolutionary reduction of leaves. Each yellow knob on a stem consists of three fused sporangia. Species of the genus *Tmesipteris*, closely related to whisk ferns and found only in the South Pacific, also lack roots but have small, leaflike outgrowths in their stems, giving them a vine-like appearance. Both genera are homosporous, with spores giving rise to bisexual gametophytes that grow underground and are only about a centimeter long.

by contrast, roots branch only at the growing tip of the root, forming a Y-shaped structure.

The pterophytes called horsetails were very diverse during the Carboniferous period, some growing as tall as 15 m. Today, only 15 species survive as a single, widely distributed genus, *Equisetum*, found in marshy places and along streams.

Psilotum (whisk ferns) and a closely related genus, *Tmesipteris*, form a clade consisting mainly of tropical epiphytes. Plants in these two genera, the only vascular plants lacking true roots, are called “living fossils” because of their resemblance to fossils of ancient relatives of living vascular plants (see Figures 29.12 and 29.15). However, much evidence, including analyses of DNA sequences and sperm structure, indicates that the genera *Psilotum* and *Tmesipteris* are closely related to ferns. This hypothesis suggests that their ancestor’s true roots were lost during evolution. Today, plants in these two genera absorb water and nutrients through numerous absorptive rhizoids.



▲ Figure 29.16 Artist's conception of a Carboniferous forest based on fossil evidence. In addition to plants, animals, including giant dragonflies like the one in the foreground, also thrived in the “coal forests” of the Carboniferous.

WHAT IF? What would this forest look like if few lycophyte trees were reproducing (as would often have been the case)?

The Significance of Seedless Vascular Plants

The ancestors of living lycophytes, horsetails, and ferns, along with their extinct seedless vascular relatives, grew to great heights during the Devonian and early Carboniferous, forming the first forests (Figure 29.16). How did their dramatic growth affect Earth and its other life? With the evolution of vascular tissue, roots, and leaves, these plants accelerated their rate of photosynthesis, dramatically increasing the removal of CO₂ from the atmosphere. Scientists estimate that CO₂ levels dropped by as much as a factor of five during the Carboniferous, causing global cooling that resulted in widespread glacier formation. Ancient CO₂ levels can be estimated in several ways. These include counting the number of stomata in fossil leaves (data from living species show that this number increases as CO₂ levels drop) and measuring carbon isotope levels in fossils of plankton. Different methods yield similar results, suggesting that reconstructions of past climates are accurate.

The seedless vascular plants that formed the first forests eventually became coal. In the stagnant waters of Carboniferous swamps, dead plants did not completely decay. This organic material turned to thick layers of peat, later covered by the sea. Marine sediments piled on top, and over millions of years, heat and pressure converted the peat to coal. In fact, Carboniferous coal deposits are the most extensive ever formed. Coal was crucial to the Industrial Revolution, and people worldwide still burn 6 billion tons a year. It is ironic

that coal, formed from plants that contributed to a global cooling, now contributes to global warming by returning carbon to the atmosphere (see Chapter 55).

Growing along with the seedless plants in Carboniferous swamps were primitive seed plants. Though seed plants were not dominant at that time, they rose to prominence after the swamps began to dry up at the end of the Carboniferous period. The next chapter traces the origin and diversification of seed plants, continuing our story of adaptation to life on land.

CONCEPT CHECK 29.3

1. List the key derived traits found in pterophytes and seed plants, but not in lycophytes.
2. How do the main similarities and differences between seedless vascular plants and nonvascular plants influence function in these plants?
3. **WHAT IF?** If (contrary to the evidence) lycophytes and pterophytes formed a clade, what could you conclude about how members of this clade gained (or lost) traits shared by pterophytes and seed plants?
4. **MAKE CONNECTIONS** In Figure 29.13, if fertilization occurred between gametes from one gametophyte, how would this affect the production of genetic variation from sexual reproduction? See page 258 of Concept 13.4.

For suggested answers, see Appendix A.

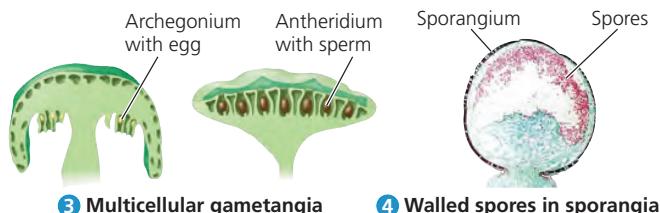
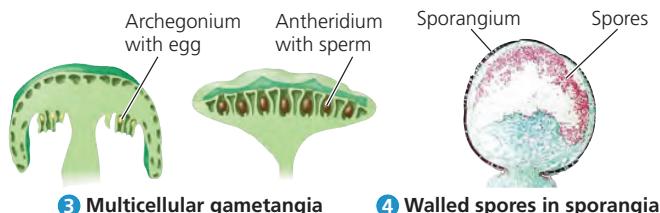
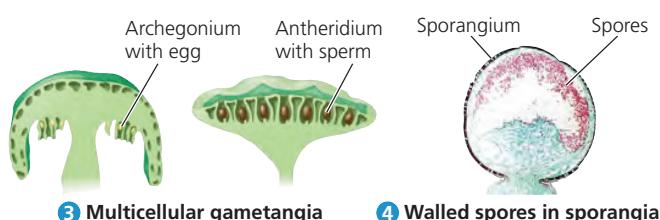
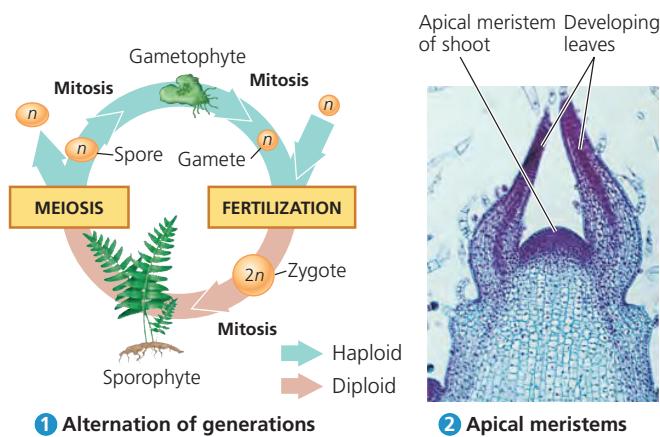
29 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 29.1

Land plants evolved from green algae (pp. 600–606)

- Morphological and biochemical traits, as well as similarities in nuclear and chloroplast genes, suggest that charophytes are the closest living relatives of land plants.
- A protective layer of **sporopollenin** and other traits allow charophytes to tolerate occasional drying along the edges of ponds and lakes. Such traits may have enabled the algal ancestors of plants to survive in terrestrial conditions, opening the way to the colonization of dry land.
- Derived traits that distinguish the clade of land plants from charophytes, their closest algal relatives, include the four shown here:



- Fossil evidence indicates that plants were on land at least 475 million years ago. Subsequently, plants diverged into several major groups, including nonvascular plants (bryophytes); seedless vascular plants, such as lycophytes and ferns; and the two groups of seed plants: gymnosperms and angiosperms.

? Draw a phylogenetic tree illustrating our current understanding of land plant phylogeny; label the common ancestor of land plants and the origins of multicellular gametangia, vascular tissue, and seeds.

CONCEPT 29.2

Mosses and other nonvascular plants have life cycles dominated by gametophytes (pp. 606–610)

- Current evidence indicates that the three phyla of **bryophytes**—liverworts, mosses, and hornworts—do not form a clade.

- In bryophytes, the dominant and typically most visible generation consists of haploid **gametophytes**, such as those that make up a carpet of moss. **Rhizoids** anchor gametophytes to the substrate on which they grow. The flagellated sperm produced by **antheridia** require a film of water to travel to the eggs in the **archegonia**.
- The diploid stage of the bryophyte life cycle—the **sporophytes**—grow out of archegonia and are attached to the gametophytes and dependent on them for nourishment. Smaller and simpler than vascular plant sporophytes, they typically consist of a **foot**, **seta** (stalk), and **sporangium**.
- Sphagnum*, or peat moss, is common in large regions known as peatlands and has many practical uses, including as a fuel.

? Summarize the ecological importance of mosses.

CONCEPT 29.3

Ferns and other seedless vascular plants were the first plants to grow tall (pp. 610–615)

- Fossils of the forerunners of today's vascular plants date back about 425 million years and show that these small plants had independent, branching sporophytes. However, these ancestral species lacked other derived traits of living vascular plants, such as a life cycle with dominant sporophytes; lignified vascular tissue; well-developed roots and leaves; and sporophylls.
- Seedless vascular plants include the **lycophytes** (phylum Lycopodiophyta: club mosses, spike mosses, and quillworts) and the **pterophytes** (phylum Pterophyta: ferns, horsetails, and whisk ferns and relatives). Ancient lycophytes included both small herbaceous plants and large trees. Present-day lycophytes are small herbaceous plants.
- Seedless vascular plants dominated the earliest forests. Their growth may have helped produce the major global cooling that characterized the end of the Carboniferous period. The decaying remnants of the first forests eventually became coal.

? What trait(s) allowed vascular plants to grow tall, and why might increased height have been advantageous?

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

- Which of the following is *not* evidence that charophytes are the closest algal relatives of plants?
 - similar sperm structure
 - the presence of chloroplasts
 - similarities in cell wall formation during cell division
 - genetic similarities in chloroplasts
 - similarities in proteins that synthesize cellulose
- Which of the following characteristics of plants is absent in their closest relatives, the charophyte algae?
 - chlorophyll *b*
 - cellulose in cell walls
 - formation of a cell plate during cytokinesis
 - sexual reproduction
 - alternation of multicellular generations

3. In plants, which of the following are produced by meiosis?
 - a. haploid sporophytes
 - b. haploid gametes
 - c. diploid gametes
 - d. haploid spores
 - e. diploid spores

4. Microphylls are found in which plant group?
 - a. mosses
 - b. liverworts
 - c. lycophytes
 - d. ferns
 - e. hornworts

5. Which of the following is a land plant that has flagellated sperm and a sporophyte-dominated life cycle?
 - a. fern
 - b. moss
 - c. liverwort
 - d. charophyte
 - e. hornwort

6. Identify each of the following structures as haploid or diploid.
 - a. sporophyte
 - b. spore
 - c. gametophyte
 - d. zygote
 - e. sperm

LEVEL 2: APPLICATION/ANALYSIS

7. Suppose an efficient conducting system evolved in a moss that could transport water and other materials as high as a tall tree. Which of the following statements about “trees” of such a species would *not* be true?
 - a. Fertilization would probably be more difficult.
 - b. Spore dispersal distances would probably increase.
 - c. Females could produce only one archegonium.
 - d. Unless its body parts were strengthened, such a “tree” would probably flop over.
 - e. Individuals would probably compete more effectively for access to light.

8. EVOLUTION CONNECTION

DRAW IT Draw a phylogenetic tree that represents our current understanding of evolutionary relationships between a moss, a gymnosperm, a lycophyte, and a fern. Use a charophyte alga as the outgroup. (See Chapter 26 to review phylogenetic trees.) Label each branch point of the phylogeny with at least one derived character unique to the clade descended from the common ancestor represented by the branch point.

LEVEL 3: SYNTHESIS/EVALUATION

9. SCIENTIFIC INQUIRY

DRAW IT The feather moss *Pleurozium schreberi* harbors species of symbiotic nitrogen-fixing bacteria. Scientists studying this moss in northern forests found that the percentage of the ground surface “covered” by the moss increased from about 5% in forests that had burned 35 to 41 years ago to about 70% in forests that had burned 170 or more years ago.

From mosses growing in these forests, they also obtained the following data on nitrogen fixation:

Age (years after fire)	N fixation rate (kg N per ha per yr)
35	0.001
41	0.005
78	0.08
101	0.3
124	0.9
170	2.0
220	1.3
244	2.1
270	1.6
300	3.0
355	2.3

Source: Data from O. Zackrisson et al., Nitrogen fixation increases with successional age in boreal forests, *Ecology* 85: 3327–3334 (2006).

- a. Use the data to draw a line graph, with age on the *x*-axis and the nitrogen fixation rate on the *y*-axis.
- b. Along with the nitrogen added by nitrogen fixation, about 1 kg of nitrogen per hectare per year is deposited into northern forests from the atmosphere as rain and small particles. Evaluate the extent to which *Pleurozium* affects nitrogen availability in northern forests of different ages.

10. WRITE ABOUT A THEME

ENVIRONMENTAL INTERACTIONS Giant lycophyte trees had microphylls, whereas ferns and seed plants have megaphylls. Write a short essay (100–150 words) describing how a forest of lycophyte trees may have differed from a forest of large ferns or seed plants. In your answer, consider how the type of forest in which they grew may have affected interactions among small plants growing beneath the tall ones.

For selected answers, see Appendix A.

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