37

Evolutionary History of Plants

Concept Outline

37.1 Plants have multicellular haploid and diploid stages in their life cycles.

The Evolutionary Origins of Plants. Plants evolved from freshwater green algae and eventually developed cuticles, stomata, conducting systems, and reproductive strategies that adapt them well for life on land.

Plant Life Cycles. Plants have haplodiplontic life cycles. Diploid sporophytes produce haploid spores which develop into haploid gametophytes that produce haploid gametes.

37.2 Nonvascular plants are relatively unspecialized, but successful in many terrestrial environments.

Mosses, Liverworts, and Hornworts. The most conspicuous part of a nonvascular plant is the green photosynthetic gametophyte, which supports the smaller sporophyte nutritionally.

37.3 Seedless vascular plants have well-developed conducting tissues in their sporophytes.

Features of Vascular Plants. In vascular plants, specialized tissue called xylem conducts water and dissolved minerals within the plant, and tissue called phloem conducts sucrose and plant growth regulators within the plant.

Seedless Vascular Plants. Seedless vascular plants have a much more conspicuous sporophyte than nonvascular plants do, and many have well-developed conducting systems in stem, roots, and leaves.

37.4 Seeds protect and aid in the dispersal of plant embryos.

Seed Plants. In seed plants, the sporophyte is dominant. Male and female gametophytes develop within the sporophyte and depend on it for food. Seeds allow embryos to germinate when conditions are favorable.

Gymnosperms. In gymnosperms, the female gametophyte (ovule) is not completely enclosed by sporophyte tissue at the time of pollination by male gametophytes (pollen).

Angiosperms. In angiosperms, the ovule is completely enclosed by sporophyte tissue at the time of pollination. Angiosperms, by far the most successful plant group, produce flowers.
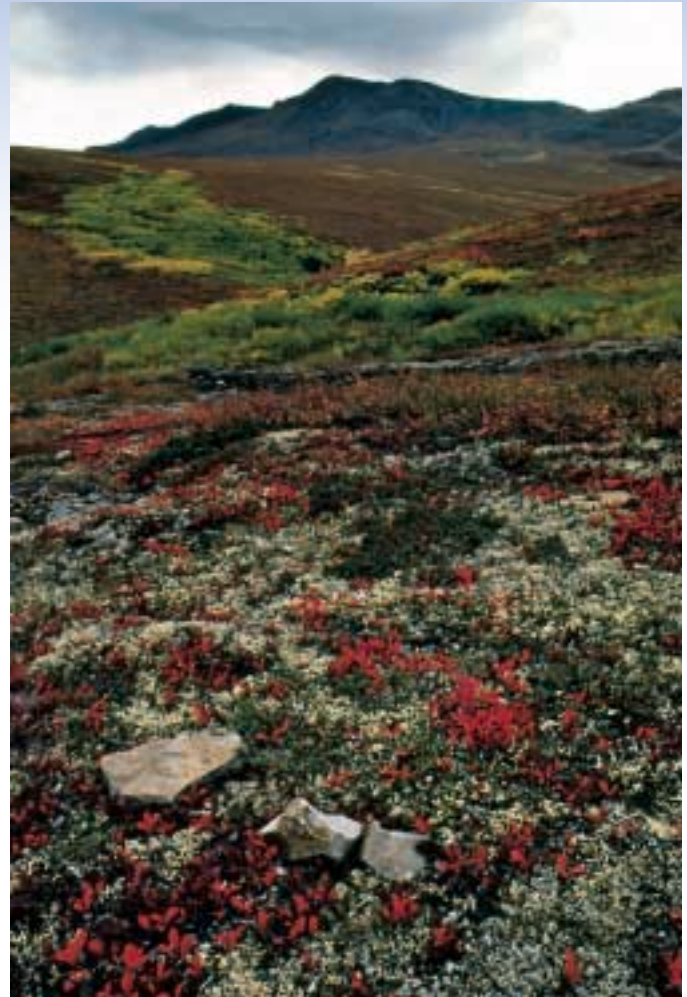

FIGURE 37.1
An arctic tundra. This is one of the harshest environments on earth, yet a diversity of plants have made this home. These ecosystems are fragile and particularly susceptible to global change.

Plant evolution is the story of the conquest of land by green algal ancestors. For about 500 million years, algae were confined to a watery domain, limited by the need for water to reproduce, provide structural support, prevent water loss, and provide some protection from the sun's ultraviolet irradiation. Numerous evolutionary solutions to these challenges have resulted in over 300,000 species of plants dominating all terrestrial communities today, from forests to alpine tundra, from agricultural fields to deserts (figure 37.1). Most plants are photosynthetic, converting light energy into chemical-bond energy and providing oxygen for all aerobic organisms. We rely on plants for food, clothing, wood for shelter and fuel, chemicals, and many medicines. This chapter explores the evolutionary history and strategies that have allowed plants to inhabit most terrestrial environments over millions of years.

The Evolutionary Origins of Plants

Biologists have long suspected that plants are the evolutionary descendants of green algae. Now we are sure. The evolutionary history of plants was laid bare at the 1999 International Botanical Congress held in St. Louis, Missouri, by a team of 200 biologists from 12 countries that had been working together for five years with U.S. federal funding. Their project, Deep Green (more formally known as The Green Plant Phylogeny Research Coordination Group), coordinated the efforts of laboratories using molecular, morphological, and anatomical traits to create a new "Tree of Life." Deep Green confirmed the long-standing claim that green algae were ancestral to plants. More surprising was the finding that just a single species of green algae gave rise to the entire terrestrial plant lineage from moss through the flowering plants (angiosperms). Exactly what this ancestral alga was is still a mystery, but close relatives are believed to exist in freshwater lakes today. DNA sequence data is consistent with the claim that a single "Eve" gave rise to the entire kingdom Plantae 450 million years ago. At each subsequent step in evolution, the evidence suggests that only a single family of plants made the transition. The fungi appear to have branched later than the plants and are more closely related to us.

There are 12 plant phyla, all of which afford some protection to their embryos. All plants also have a haploid and a diploid stage that is multicellular. The trend over time has been toward increasing embryo protection and a smaller haploid stage in the life cycle. The plants are divided into two groups based on the presence or absence of vascular tissues which facilitate the transport of water and nutrients in plants. Three phyla (mosses, liverworts, and hornworts) lack vascular tissue and are referred to as the **nonvascular plants**. Members of 9 of the 12 plant phyla are collectively called **vascular plants,** and include, among others, the ferns, conifers, and flowering plants. Vascular plants have water-conducting xylem and food-conducting phloem strands of tissues in their stems, roots, and leaves. Vascular plants can be further grouped based on how much protection embryos have. The seedless vascular plants (ferns) provide less protection than the seeds of the gymnosperms (conifers) and angiosperms (flowering plants) (figure 37.2). About 150 million years ago the angiosperms arose with further innovations—flowers to attract pollinators and fruit surrounding the seed to protect the embryo and aid in seed dispersal. Many of these lineages have persisted. If you could travel back 65 million years to the dinosaur era, you would encounter oak, walnut, and sycamore trees!
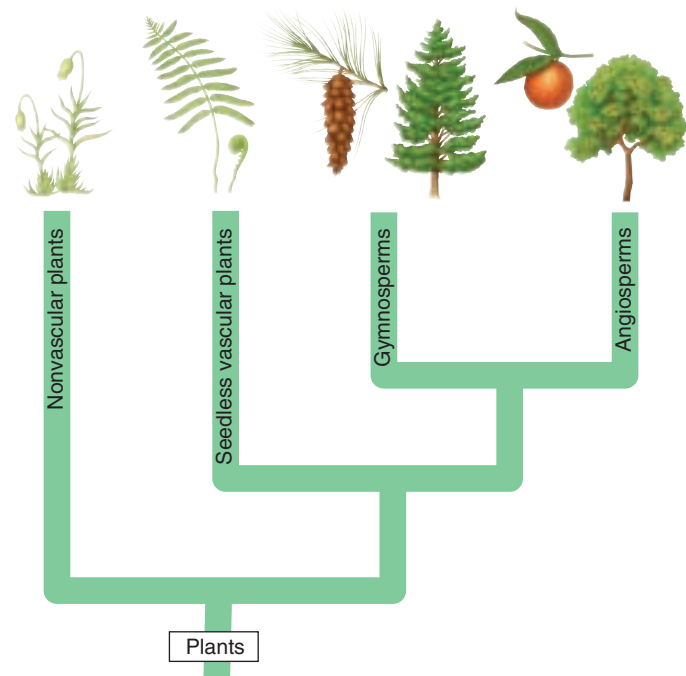

FIGURE 37.2
The four major groups of plants. In this chapter we will discuss four major groups of plants. The green algae, discussed in chapter 35, are the protists from which plants are thought to have evolved.

Adaptations to Land

Plants and fungi are the only major groups of organisms that are primarily terrestrial. Most plants are protected from **desiccation**—the tendency of organisms to lose water to the air—by a waxy **cuticle** that is secreted onto their exposed surfaces. The cuticle is relatively impermeable and provides an effective barrier to water loss.

This solution creates another problem by limiting gas exchange essential for respiration and photosynthesis. Water and gas diffusion into and out of a plant occurs through tiny mouth-shaped openings called **stomata** (singular, **stoma**).

The evolution of leaves resulted in increased photosynthetic surface area. The shift to a dominant diploid generation, accompanied by the structural support of vascular tissue, allowed plants to take advantage of the vertical dimension of the terrestrial environment, resulting in trees.

Plants evolved from freshwater green algae and eventually developed cuticles, stomata, conducting systems, and reproductive strategies that adapt them well for life on land.

Plant Life Cycles

All plants undergo mitosis after both gamete fusion *and* meiosis. The result is a multicellular haploid and a multicellular diploid individual, unlike us where gamete fusion directly follows meiosis. We have a **diplontic** life cycle (only the diploid stage is multicellular), but the plant life cycle is **haplodiplontic** (with multicellular haploid and diploid stages). The basic haplodiplontic cycle is summarized in figure 37.3. Brown, red, and green algae are also haplodiplontic (see chapter 35). While we produce gametes via meiosis, plants actually produce gametes by mitosis in a multicellular, haploid individual. The diploid generation, or **sporophyte,** alternates with the haploid generation, or **gametophyte.** Sporophyte means "spore plant," and gametophyte means "gamete plant." These terms indicate the kinds of reproductive cells the respective generations produce.

The diploid sporophyte undergoes meiosis to produce haploid spores (*not* gametes). Meiosis takes place in structures called **sporangia,** where diploid **spore mother cells (sporocytes)** undergo meiosis, each producing four haploid **spores.** Spores divide by mitosis, producing a multicellular, haploid gametophyte. Spores are the first cells of the gametophyte generation.

In turn, the haploid gametophyte produces haploid gametes by mitosis. When the gametes fuse, the zygote they form is diploid and is the first cell of the next sporophyte generation. The zygote grows into a diploid sporophyte that produces sporangia in which meiosis ultimately occurs.

While all plants are haplodiplontic, the haploid generation consumes a much larger chunk of the life cycle in mosses than in gymnosperms and angiosperms. In mosses, liverworts, and ferns, the gametophyte is photosynthetic and free-living; in other plants it is either nutritionally dependent on the sporophyte, or **saprobic** (deriving its energy directly from nonliving organic matter). When you look at moss, what you see is largely gametophyte tissue; their sporophytes are usually smaller, brownish or yellowish structures attached to or enclosed within tissues of the gametophyte. In most vascular plants the gametophytes are much smaller than the sporophytes. In seed plants, the gametophytes are nutritionally dependent on the sporophytes and are enclosed within their tissues. When you look at a gymnosperm or angiosperm, what you see, with rare exceptions, is a sporophyte.

The difference between dominant gametophytes and sporophytes is key to understanding why there are no moss trees. What we identify as a moss plant is a gameto-
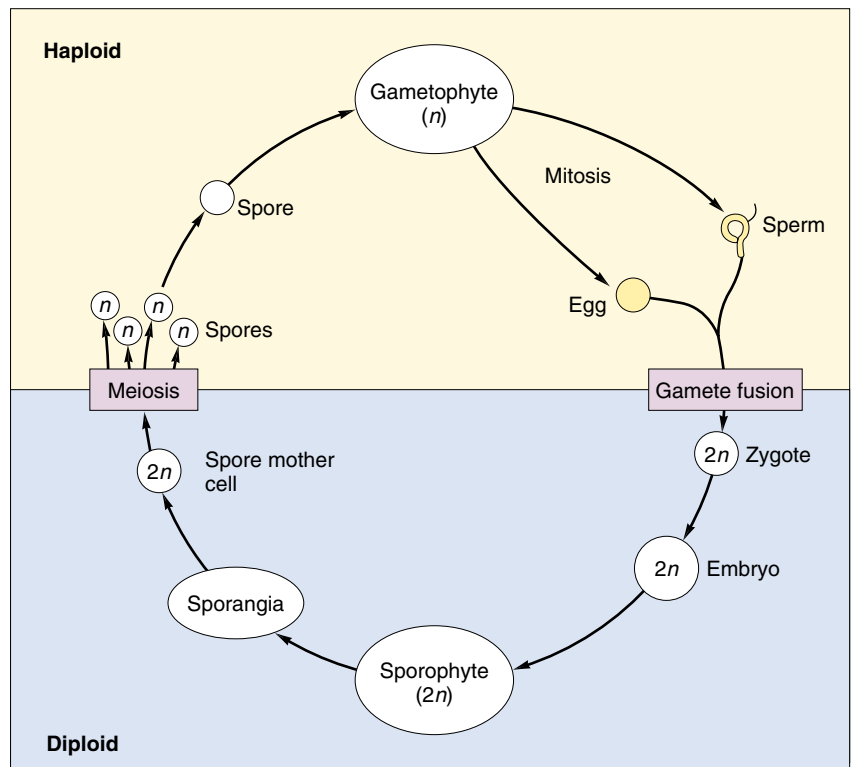

FIGURE 37.3
A generalized plant life cycle. Anything yellow is haploid and anything blue is diploid. Note that both haploid and diploid individuals can be multicellular. Also, spores are produced by meiosis while gametes are produced by mitosis.

phyte and it produces gametes at its tip. The egg is stationery and sperm lands near the egg in a droplet of water. If the moss were the height of a sequoia, not only would it need vascular tissue for conduction and support, the sperm would have to swim up the tree! In contrast, the fern gametophyte develops on the forest floor where gametes can meet. Fern trees abound in Australia and the haploid spores fall to the ground and develop into gametophytes.

Having completed our overview of plant life cycles, we will consider the major plant groups. As we do, we will see a progressive reduction of the gametophyte from group to group, a loss of multicellular **gametangia** (structures in which gametes are produced), and increasing specialization for life on the land, culminating with the remarkable structural adaptations of the flowering plants, the dominant plants today. Similar trends must have characterized the progression to seed plants over the hundreds of millions of years since a freshwater alga made the move onto land.

Plants have haplodiplontic life cycles. Diploid sporophytes produce haploid spores which develop into haploid gametophytes that produce haploid gametes.

Mosses, Liverworts, and Hornworts

There are about 24,700 **bryophytes**—mosses, liverworts, and hornworts—that are simply but highly adapted to a diversity of terrestrial environments (even deserts!). Scientists now agree that bryophytes consist of three quite distinct phyla of relatively unspecialized plants. Their gametophytes are photosynthetic. Sporophytes are attached to the gametophytes and depend on them nutritionally to varying degrees. Bryophytes, like ferns and certain other vascular plants, require water (for example, rainwater) to reproduce sexually. It is not surprising that they are especially common in moist places, both in the tropics and temperate regions.

Most bryophytes are small; few exceed 7 centimeters in height. The gametophytes are more conspicuous than the sporophytes. Some of the sporophytes are completely enclosed within gametophyte tissue; others are not and usually turn brownish or straw-colored at maturity.

Mosses (Bryophyta)

The gametophytes of mosses typically consist of small leaflike structures arranged spirally or alternately around a stemlike axis (figure 37.4); the axis is anchored to its substrate by means of **rhizoids.** Each rhizoid consists of several cells that absorb water, but nothing like the volume of water absorbed by a vascular plant root. Moss "leaves" have little in common with true leaves, except for the superficial appearance of the green, flattened blade and slightly thickened midrib that runs lengthwise down the middle. They are only one cell thick (except at the midrib), lack vascular strands and stomata, and all the cells are haploid.

Water may rise up a strand of specialized cells in the center of a moss gametophyte axis, but most water used by the plant travels up the outside of the plant. Some mosses
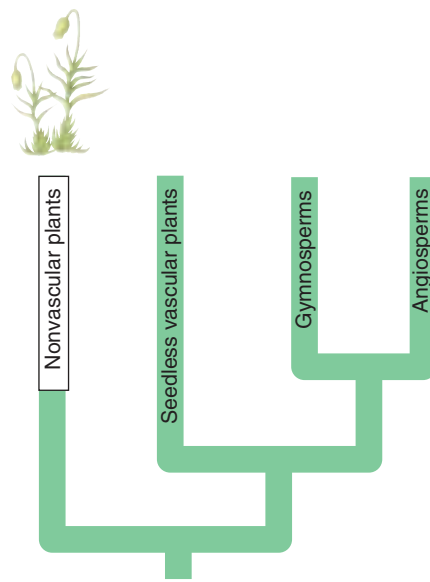

FIGURE 37.4
A hair-cup moss, *Polytrichum* (phylum Bryophyta). The "leaves" belong to the gametophyte. Each of the yellowish-brown stalks, with the capsule, or sporangium, at its summit, is a sporophyte.

also have specialized food-conducting cells surrounding those that conduct water.

Multicellular gametangia are formed at the tips of the leafy gametophytes (figure 37.5). Female gametangia (**archegonia**) may develop either on the same gametophyte as the male gametangia (**antheridia**) or on separate plants. A single egg is produced in the swollen lower part of an archegonium while numerous sperm are produced in an antheridium. When sperm are released from an antheridium, they swim with the aid of flagella through a film of dew or rainwater to the archegonia. One sperm (which is haploid) unites with an egg (also haploid), forming a diploid zygote. The zygote divides by mitosis and develops into the sporophyte, a slender, basal stalk with a swollen capsule, the *sporangium,* at its tip. As the sporophyte develops, its base becomes embedded in gametophyte tissue, its nutritional source. The sporangium is often cylindrical or club-shaped. Spore mother cells within the sporangium undergo meiosis, each becoming four haploid spores. At maturity, the top of the sporangium pops off, and the spores are released. A spore that lands in a suitable damp location may germinate and grow into a threadlike structure that branches to form rhizoids and "buds" that grow upright. Each bud develops into a new gametophyte plant consisting of a leafy axis.

In the Arctic and the Antarctic, mosses are the most abundant plants, boasting not only the largest number of individuals in these harsh regions, but also the largest number of species. Many mosses are able to withstand prolonged periods of drought, although they are not common in deserts. Most are remarkably sensitive to air pollution and are rarely found in abundance in or near cities or other areas with high levels of air pollution. Some mosses, such as the peat mosses (*Sphagnum*), can absorb up to 25 times their weight in water and are valuable commercially as a soil conditioner, or as a fuel when dry.

Liverworts (Hepaticophyta)

The old English word *wyrt* means "plant" or "herb." Some common liverworts have flattened gametophytes with lobes resembling those of liver—hence the combination "liverwort." Although the lobed liverworts are the best-known representatives of this phylum, they constitute only about 20% of the species (figure 37.6). The other 80% are leafy and superficially resemble mosses. Liverworts are less complex than mosses. Gametophytes are prostrate instead of erect, and the rhizoids are one-celled.

Some liverworts have air chambers containing upright, branching rows of photosynthetic cells, each chamber having a pore at the top to facilitate gas exchange. Unlike stomata, the pores are fixed open and cannot close.

Sexual reproduction in liverworts is similar to that in mosses. Lobed liverworts form gametangia in umbrella-like structures. Asexual reproduction occurs when lens-shaped pieces of tissue that are released from the gametophyte grow to form new gametophytes.

Hornworts (Anthocerotophyta)

The origins of hornworts are a puzzle. They are most likely among the earliest land plants, yet the earliest fossil spores date from the Cretaceous period, 65 to 145 million years ago, when angiosperms were emerging.

The small hornwort sporophytes resemble tiny green broom handles rising from filmy gametophytes usually less than 2 centimeters in diameter (figure 37.7). The sporophyte base is embedded in gametophyte tissue, from which it derives some of its nutrition. However, the sporophyte has stomata, is photosynthetic, and provides much of the energy needed for growth and reproduction. Hornwort cells usually have a single chloroplast.

> The three major phyla of nonvascular plants are all relatively unspecialized, but well suited for diverse terrestrial environments.
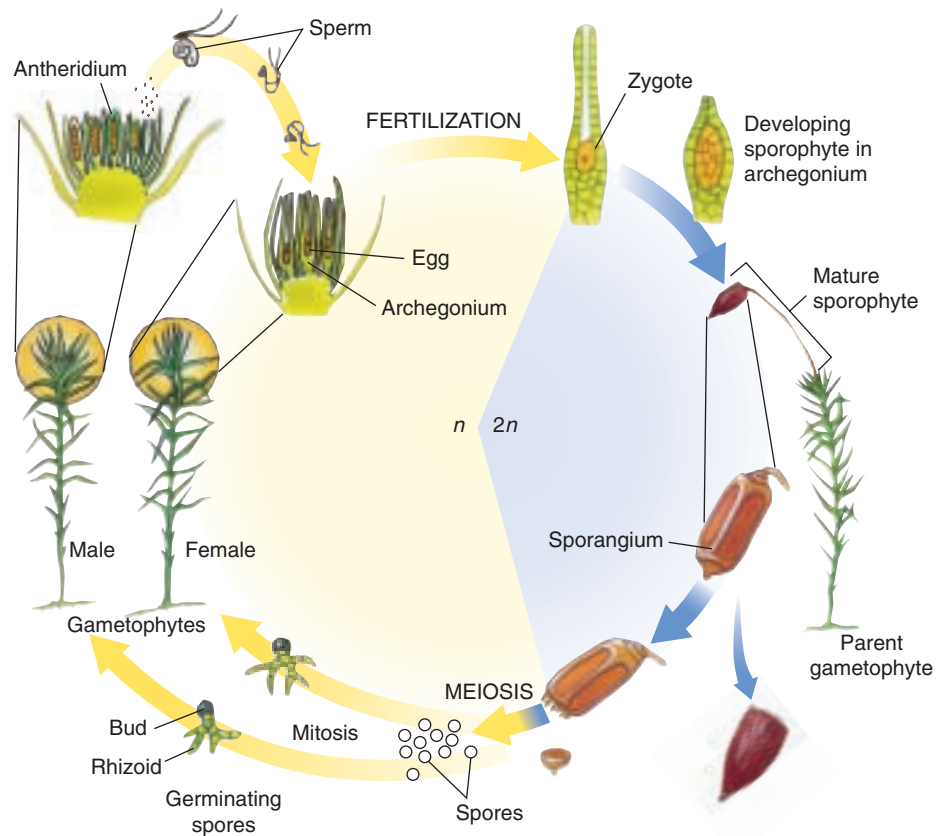

FERTILIZATION

n   2*n*

MEIOSIS

FIGURE 37.5
Life cycle of a typical moss. The majority of the life cycle of a moss is in the haploid state. The leafy gametophyte is photosynthetic, while the smaller sporophyte is not, and is nutritionally dependent on the gametophyte. Water is required to carry sperm to the egg.

FIGURE 37.6
A common liverwort, *Marchantia* (phylum Marchantiophyta). The sporophytes are borne within the tissues of the umbrella-shaped structures that arise from the surface of the flat, green, creeping gametophyte.

FIGURE 37.7
Hornworts (phylum Anthocerotophyta). Hornwort sporophytes are seen in this photo. Unlike the sporophytes of other bryophytes, these are photosynthetic, but they also depend on the gametophyte for nutrition.

Features of Vascular Plants

The first vascular plants for which we have a relatively complete record belonged to the phylum Rhyniophyta; they flourished some 410 million years ago but are now extinct. We are not certain what the very earliest of these vascular plants looked like, but fossils of *Cooksonia* provide some insight into their characteristics (figure 37.8). *Cooksonia,* the first known vascular land plant, appeared in the late Silurian period about 420 million years ago. It was successful partly because it encountered little competition as it spread out over vast tracts of land. The plants were only a few centimeters tall and had no roots or leaves. They consisted of little more than a branching axis, the branches forking evenly and expanding slightly toward the tips. They were **homosporous** (producing only one type of spore). Sporangia formed at branch tips. Other ancient vascular plants that followed evolved more complex arrangements of sporangia. Leaves began to appear as protuberances from stems.

Cooksonia and the other early plants that followed it became successful colonizers of the land through the development of efficient water- and food-conducting systems known as **vascular tissues.** The word *vascular* comes from the Latin *vasculum,* meaning a "vessel or duct." These tissues consist of strands of specialized cylindrical or elongated cells that form a network throughout a plant, extending from near the tips of the roots, through the stems, and into true leaves. One type of vascular tissue, the *xylem,* conducts water and dissolved minerals upward from the roots; another type of tissue, *phloem,* conducts sucrose and hormonal signals throughout the plant. It is important to note that vascular tissue developed in the sporophyte, but (with few exceptions) not the gametophyte. (See the discussion of vascular tissue structure in chapter 38.) The presence of a cuticle and stomata are also characteristic of vascular plants.

The nine phyla of vascular plants (table 37.1) dominate terrestrial habitats everywhere, except for the highest mountains and the tundra. The haplodiplontic life cycle persists, but the gametophyte has been reduced during evolution of vascular plants. A similar reduction in multicellular gametangia has occurred.

Accompanying this reduction in size and complexity of the gametophytes has been the appearance of the seed. Seeds are highly resistant structures well suited to protect a plant embryo from drought and to some extent from predators. In addition, most seeds contain a supply of food for the young plant. Seeds occur only in **heterosporous** plants (plants that produce two types of spores). H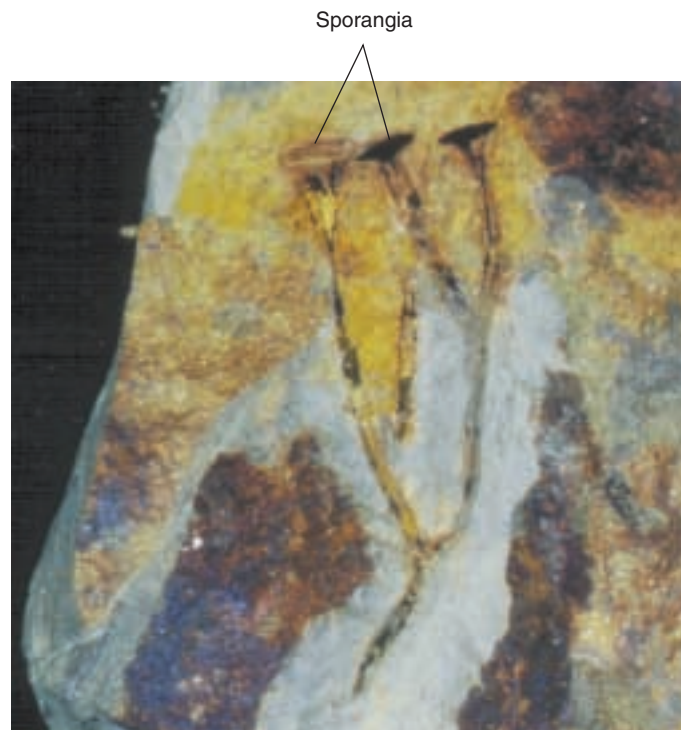eterospory is believed to have arisen multiple times in the plants. Fruits in the flowering plants add a layer of protection to seeds and attract animals that assist in seed dispersal, expanding the potential range of the species. Flowers, which evolved among the angiosperms, attract pollinators. Flowers allow plants to overcome limitations of their rooted, immobile nature and secure the benefits of wide outcrossing in promoting genetic diversity.

Sporangia

FIGURE 37.8
Cooksonia, **the first known vascular land plant.** Its upright, branched stems, which were no more than a few centimeters tall, terminated in sporangia, as seen here. It probably lived in moist environments such as mudflats, had a resistant cuticle, and produced spores typical of vascular plants. This fossil represents a plant that lived some 410 million years ago. *Cooksonia* belongs to phylum Rhyniophyta, consisting entirely of extinct plants.

> Most vascular plants have well-developed conducting tissues, specialized stems, leaves, roots, cuticles, and stomata. Many have seeds which protect embryos until conditions are suitable for further development.

		Table 37.1 The Nine Phyla of Extant Vascular Plants	

Phylum	Examples	Key Characteristics	Approximate Number of Living Species
Anthophyta	Flowering plants (angiosperms)	Heterosporous seed plants. Sperm not motile; conducted to egg by a pollen tube. Seeds enclosed within a fruit. Leaves greatly varied in size and form. Herbs, vines, shrubs, trees. About 14,000 genera.	250,000
Pterophyta	Ferns	Primarily homosporous (a few heterosporous) vascular plants. Sperm motile. External water necessary for fertilization. Leaves are megaphylls that uncoil as they mature. Sporophytes and virtually all gametophytes photosynthetic. About 365 genera.	11,000
Lycophyta	Club mosses	Homosporous or heterosporous vascular plants. Sperm motile. External water necessary for fertilization. Leaves are microphylls. About 12–13 genera.	1,150
Coniferophyta	Conifers (including pines, spruces, firs, yews, redwoods, and others)	Heterosporous seed plants. Sperm not motile; conducted to egg by a pollen tube. Leaves mostly needlelike or scalelike. Trees, shrubs. About 50 genera.	601
Cycadophyta	Cycads	Heterosporous vascular seed plants. Sperm flagellated and motile but confined within a pollen tube that grows to the vicinity of the egg. Palmlike plants with pinnate leaves. Secondary growth slow compared with that of the conifers. Ten genera.	206
Gnetophyta	Gnetophytes	Heterosporous vascular seed plants. Sperm not motile; conducted to egg by a pollen tube. The only gymnosperms with vessels. Trees, shrubs, vines. Three very diverse genera (*Ephedra, Gnetum, Welwitschia*).	65
Arthrophyta	Horsetails	Homosporous vascular plants. Sperm motile. External water necessary for fertilization. Stems ribbed, jointed, either photosynthetic or nonphotosynthetic. Leaves scalelike, in whorls, nonphotosynthetic at maturity. One genus.	15
Psilophyta	Whisk ferns	Homosporous vascular plants. Sperm motile. External water necessary for fertilization. No differentiation between root and shoot. No leaves; one of the two genera has scalelike enations and the other leaflike appendages.	6
Ginkgophyta	*Ginkgo*	Heterosporous vascular seed plants. Sperm flagellated and motile but conducted to the vicinity of the egg by a pollen tube. Deciduous tree with fan-shaped leaves that have evenly forking veins. Seeds resemble a small plum with fleshy, ill-scented outer covering.	1

Seedless Vascular Plants

The earliest vascular plants lacked seeds. Members of four phyla of living vascular plants lack seeds, as do at least three other phyla known only from fossils. As we explore the adaptations of the vascular plants, we focus on both reproductive strategies and the advantages of increasingly complex transport systems. We will begin with the most familiar phylum of seedless vascular plants, the ferns.
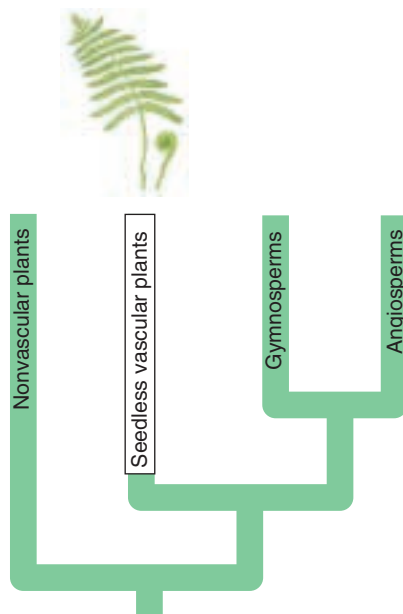
Ferns (Pterophyta)

Ferns are the most abundant group of seedless vascular plants, with about 12,000 living species. The fossil record indicates that they originated during the Devonian period about 350 million years ago and became abundant and varied in form during the next 50 million years. Their apparent ancestors had no broad leaves and were established on land as much as 375 million years ago.

Today, ferns flourish in a wide range of habitats throughout the world; about 75% of the species, however, occur in the tropics. The conspicuous sporophytes may be less than a centimeter in diameter—as seen in small aquatic ferns such as *Azolla*—or more than 24 meters tall and with leaves up to 5 meters or more long in the tree ferns (figure 37.9). The sporophytes and the smaller gametophytes, which rarely reach 6 millimeters in diameter, are both photosynthetic. The fern life cycle differs from that of a moss primarily in the much greater development, independence, and dominance of the fern's sporophyte. The fern's sporophyte is much more complex than that of the moss's; the fern sporophyte has vascular tissue and well-differentiated roots, stems, and leaves. The gametophyte, however, lacks vascular tissue.

Fern sporophytes typically have a horizontal underground stem called a *rhizome,* with roots emerging from the sides. The leaves, referred to as *fronds,* usually develop at the tip of the rhizome as tightly rolled-up coils ("fiddleheads") that unroll and expand. Many fronds are highly dissected and feathery, making the ferns that produce them prized as ornamentals. Some ferns, such as *Marsilea,* have fronds that resemble a four-leaf clover, but *Marsilea* fronds still begin as coiled fiddleheads. Other ferns produce a mixture of photosynthetic fronds and nonphotosynthetic reproductive fronds that tend to be brownish in color.

Most ferns are homosporous, producing distinctive, *sporangia,* usually in clusters called *sori,* typically on the backs of the fronds. Sori are often protected during their development by a transparent, umbrella-like covering. At first glance, one might mistake the sori for an infection on the plant. Diploid *spore mother cells* in each sporangium undergo meiosis, producing haploid spores. At maturity, the spores are catapulted from the sporangium by a snapping action, and those that land in suitable damp locations may germinate, producing gametophytes which are often heart-shaped, are only one cell thick (except in the center) and have rhizoids that anchor them to their substrate. These rhizoids are not true roots as they lack vascular tissue, but as with many of the nonvascular plants they do aid in transporting water and nutrients from the soil. Flask-shaped *archegonia* and globular *antheridia* are produced on either the same or different gametophyte.

FIGURE 37.9
A tree fern (phylum Pterophyta) in the forests of Malaysia.
The ferns are by far the largest group of seedless vascular plants. Trees in other phyla are now extinct.
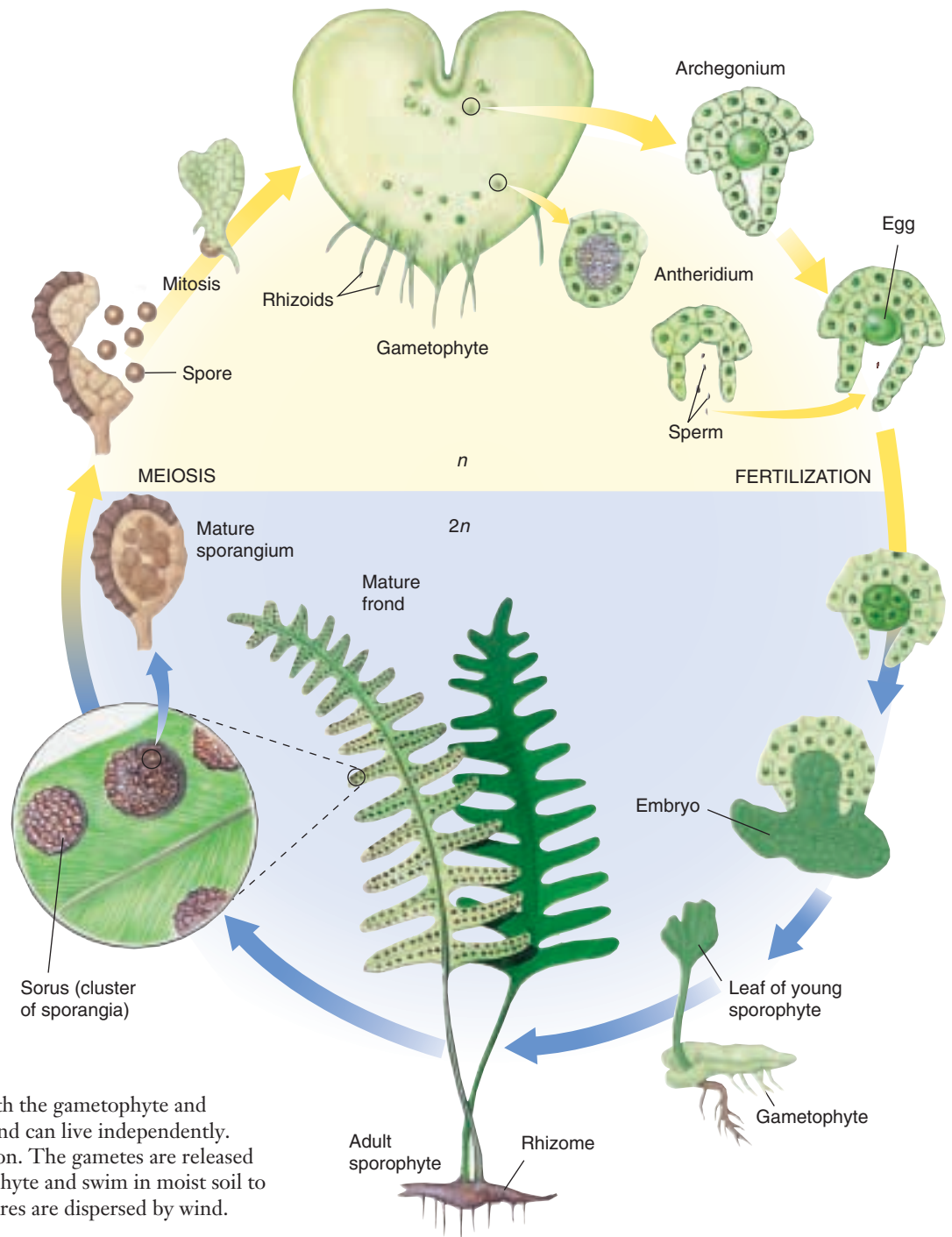
FIGURE 37.10
Life cycle of a typical fern. Both the gametophyte and sporophyte are photosynthetic and can live independently. Water is necessary for fertilization. The gametes are released on the underside of the gametophyte and swim in moist soil to neighboring gametophytes. Spores are dispersed by wind.

The sperm formed in the antheridia have flagella, with which they swim toward the archegonia when water is present, often in response to a chemical signal secreted by the archegonia. One sperm unites with the single egg toward the base of an archegonium, forming a *zygote*. The zygote then develops into a new sporophyte, completing the life cycle (figure 37.10). There are still multicellular gametangia. As discussed earlier, the shift to a dominant sporophyte generation allows ferns to achieve significant height without interfering with sperm swimming efficiently to the egg. The multicellular archegonia provide some protection for the developing embryo.

Whisk Ferns (Psilophyta)

The three other phyla of seedless vascular plants, the Psilophyta, (whisk ferns), Lycophyta (club mosses), and Arthrophyta (horsetails), have many features in common with ferns. For example, they all form antheridia and archegonia. Free water is required for the process of fertilization, during which the sperm, which have flagella, swim to and unite with the eggs. In contrast, most seed plants have non-flagellated sperm; none form antheridia, although a few form archegonia.

The origins of the two genera of whisk ferns, which occur in the tropics and subtropics, are not clear, but they are considered to be living remnants of the very earliest vascular plants. Certainly they are the simplest of all extant vascular plants, consisting merely of evenly forking green stems without roots or leaves. The two or three species of the genus *Psilotum* do, however, have tiny, green, spirally arranged, flaps of tissue lacking veins and stomata. Another genus, *Tmespiteris*, has leaflike appendages.

The gametophytes of whisk ferns were unknown for many years until their discovery in the soil beneath the sporophytes. They are essentially colorless and are less than 2 millimeters in diameter, but they can be up to 18 millimeters long. They form saprobic or parasitic associations with fungi, which furnish their nutrients. Some develop elements of vascular tissue and have the distinction of being the only gametophytes known to do so.

Club Mosses (Lycophyta)

The club mosses are worldwide in distribution but are most abundant in the tropics and moist temperate regions. Several genera of club mosses, some of them treelike, became extinct about 270 million years ago. Members of the four genera and nearly 1000 living species of club mosses superficially resemble true mosses, but once their internal structure and reproductive processes became known it was clear that these vascular plants are quite unrelated to mosses. Modern club mosses are either homosporous or heterosporous. The sporophytes have leafy stems that are seldom more than 30 centimeters long.

Horsetails (Arthrophyta)

The 15 living species of horsetails, also called scouring rushes, are all heterosporous and herbaceous. They constitute a single genus, *Equisetum*. Fossil forms of *Equisetum* extend back 300 million years to an era when some of their relatives were treelike. Today, they are widely scattered around the world, mostly in damp places. Some that grow among the coastal redwoods of California may reach a height of 3 meters, but most are less than a meter tall (figure 37.11).

FIGURE 37.11
A horsetail, *Equisetum telmateia,* **a representative of the only living genus of the phylum Arthrophyta.** This species forms two kinds of erect stems; one is green and photosynthetic, and the other, which terminates in a spore-producing "cone," is mostly light brown.

Horsetail sporophytes consist of ribbed, jointed, photosynthetic stems that arise from branching underground rhizomes with roots at their nodes. A whorl of nonphotosynthetic, scalelike leaves emerges at each node. The stems, which are hollow in the center, have silica deposits in the epidermal cells of the ribs, and the interior parts of the stems have two sets of vertical, somewhat tubular canals. The larger outer canals, which alternate with the ribs, contain air, while the smaller inner canals opposite the ribs contain water.

Ferns and other seedless vascular plants have a much larger and more conspicuous sporophyte, with vascular tissue. Many have well-differentiated roots, stem, and leaves. The shift to a dominant sporophyte lead to the evolution of trees.

37.4   Seeds protect and aid in the dispersal of plant embryos.

Seed Plants

Seed plants first appeared about 425 million years ago. Their ancestors appear to have been spore-bearing plants known as progymnosperms. Progymnosperms shared several features with modern gymnosperms, including secondary xylem and phloem (which allows for an increase in girth later in development). Some progymnosperms had leaves. Their reproduction was very simple, and it is not certain which particular group of progymnosperms gave rise to seed plants.

From an evolutionary and ecological perspective, the seed represents an important advance. The embryo is protected by an extra layer of sporophyte tissue creating the ovule. During development this tissue hardens to produce the seed coat. In addition to protection from drought, dispersal is enhanced. Perhaps even more significantly, a dormant phase is introduced into the life cycle that allows the embryo to survive until environmental conditions are favorable for further growth.

Seed plants produce two kinds of gametophytes—male and female, each of which consists of just a few cells. Pollen grains, multicellular male gametophytes, are conveyed to the egg in the female gametophyte by wind or a pollinator. The sperm move toward the egg through a growing pollen tube. This eliminates the need for water. In contrast to the seedless plants, the whole male gametophyte rather than just the sperm moves to the female gametophyte. A female gametophyte develops within an ovule. In flowering plants (angiosperms), the ovules are completely enclosed within diploid sporophyte tissue (ovaries which develop into the fruit). In gymnosperms (mostly cone-bearing seed plants), the ovules are not completely enclosed by sporophyte tissue at the time of pollination.

A common ancestor with seeds gave rise to the gymnosperms and the angiosperms. Seeds can allow for a pause in the life cycle until environmental conditions are more optimal.

A Vocabulary of Plant Terms

androecium   The stamens of a flower.

anther   The pollen-producing portion of a stamen. This is a sporophyte structure where male gametophytes are produced by meiosis.

antheridium   The male sperm-producing structure found in the gametophytes of seedless plants and certain fungi.

archegonium   The multicellular egg-producing structure in the gametophytes of seedless plants and gymnosperms.

carpel   A leaflike organ in angiosperms that encloses one or more ovules; a unit of a gynoecium.

double fertilization   The process, unique to angiosperms, in which one sperm fuses with the egg, forming a zygote, and the other sperm fuses with the two polar nuclei, forming the primary endosperm nucleus.

endosperm   The usually triploid (although it can have a much higher ploidy level) food supply of some angiosperm seeds.

filament   The stalklike structure that supports the anther of a stamen.

gametophyte   The multicellular, haploid phase of a plant life cycle in which gametes are produced by mitosis.

gynoecium   The carpel(s) of a flower.

heterosporous   Refers to a plant that produces two types of spores: microspores and megaspores.

homosporous   Refers to a plant that produces only one type of spore.

integument   The outer layer(s) of an ovule; integuments become the seed coat of a seed.

micropyle   The opening in the ovule integument through which the pollen tube grows.

nucellus   The tissue of an ovule in which an embryo sac develops.

ovary   The basal, swollen portion of a carpel (gynoecium); it contains the ovules and develops into the fruit.

ovule   A seed plant structure within an ovary; it contains a female gametophyte surrounded by the nucellus and one or two integuments. At maturity, an ovule becomes a seed.

pollen grain   A binucleate or trinucleate seed plant structure produced from a microspore in a microsporangium.

pollination   The transfer of a pollen grain from an anther to a stigma in angiosperms, or to the vicinity of the ovule in gymnosperms.

primary endosperm nucleus   The triploid nucleus resulting from the fusion of a single sperm with the two polar nuclei.

seed   A reproductive structure that develops from an ovule in seed plants. It consists of an embryo and a food supply surrounded by a seed coat.

seed coat   The protective layer of a seed; it develops from the integument or integuments.

spore   A haploid reproductive cell, produced when a diploid spore mother cell undergoes meiosis; it gives rise by mitosis to a gametophyte.

sporophyte   The multicellular, diploid phase of a plant life cycle; it is the generation that ultimately produces spores.

stamen   A unit of an androecium; it consists of a pollen-bearing anther and usually a stalklike filament.

**stigma**   The uppermost pollen-receptive portion of a gynoecium.

Gymnosperms

There are several groups of living gymnosperms (conifers, cycads, gnetophytes, and *Ginkgo*), none of which are directly related to one another, but all of which lack the flowers and fruits of angiosperms. In all of them the **ovule,** which becomes a seed, rests exposed on a scale (modified leaf) and is not completely enclosed by sporophyte tissues at the time of pollination. The name gymnosperm combines the Greek root *gymnos,* or "naked," with *sperma,* or "seed." In other words, gymnosperms are naked-seeded plants. However, although the ovules are naked at the time of pollination, the seeds of gymnosperms are sometimes enclosed by other sporophyte tissues by the time they are mature.

Details of reproduction vary somewhat in gymnosperms, and their forms vary greatly. For example, cycads and *Ginkgo* have motile sperm, even though the sperm are borne within a pollen tube, while many others have sperm with no flagella. The female cones range from tiny woody structures weighing less than 25 grams with a diameter of a few millimeters, to massive structures weighing more than 45 kilograms growing to lengths more than a meter.

Conifers (Coniferophyta)

The most familiar gymnosperms are conifers (phylum Coniferophyta), which include pines (figure 37.12), spruces, firs, cedars, hemlocks, yews, larches, cypresses, and others. The coastal redwood (*Sequoia sempervirens*), a conifer native to northwestern California and southwestern Oregon, is the tallest living vascular plant; it may attain nearly 100 meters (300 feet) in height. Another conifer, the bristlecone pine (*Pinus longaeva*) of the White Mountains of California is the oldest living tree; one is 4900 years of age. Conifers are found in the colder temperate and sometimes drier regions of the world, especially in the northern hemisphere. They are sources of timber, paper, resin, turpentine, taxol (used to treat cancer) and other economically important products.

Pines. More than 100 species of pines exist today, all native to the northern hemisphere, although the range of one species does extend a little south of the equator. Pines and spruces are members of the vast coniferous forests that lie between the arctic tundra and the temperate deciduous forests and prairies to their south. During the past century, pines have been extensively planted in the southern hemisphere.
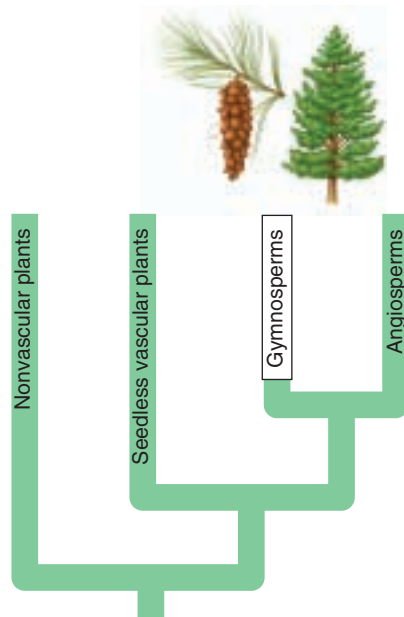
Pines have tough, needlelike leaves produced mostly in clusters of two to five. The leaves, which have a thick cuticle and recessed stomata, represent an evolutionary adaptation for retarding water loss. This is important because many of the trees grow in areas where the topsoil is frozen for part of the year, making it difficult for the roots to obtain water. The leaves and other parts of the sporophyte have canals into which surrounding cells secrete resin. The resin, apparently secreted in response to wounding, deters insect and fungal attacks. The resin of certain pines is harvested commercially for its volatile liquid portion, called *turpentine,* and for the solid *rosin,* which is used on stringed instruments. The wood of pines consists primarily of xylem tissue that lacks some of the more rigid cell types found in other trees. Thus it is considered a "soft" rather than a "hard" wood. The thick bark of pines represents another adaptation for surviving fires and subzero temperatures. Some cones actually depend on fire to open, releasing seed to reforest burnt areas.

FIGURE 37.12
Conifers. Slash pines, *Pinus palustris*, in Florida, are representative of the Coniferophyta, the largest phylum of gymnosperms.

As mentioned earlier, all seed plants are heterosporous, so the spores give rise to two types of gametophytes (figure 37.13). The male gametophytes of pines develop from pollen grains, which are produced in male cones that develop in clusters of 30 to 70, typically at the tips of the lower branches; there may be hundreds of such clusters on any single tree. The male cones generally are 1 to 4 centimeters long and consist of small, papery scales arranged in a spiral or in whorls. A pair of microsporangia form as sacs within each scale. Numerous microspore mother cells in the microsporangia undergo meiosis, each becoming four microspores. The microspores develop into four-celled pollen grains with a pair of air sacs that give them added buoyancy when released into the air. A single cluster of male pine cones may produce more than 1 million pollen grains.

Female cones typically are produced on the upper branches of the same tree that produces male cones. Female cones are larger than male cones, and their scales become woody. Two ovules develop toward the base of each scale. Each ovule contains a megasporangium called the **nucellus.** The nucellus itself is completely surrounded by a thick layer of cells called the integument that has a small opening (the **micropyle**) toward one end. One of the layers of the integument later becomes the seed coat. A single megaspore mother cell within each megasporangium undergoes meiosis, becoming a row of four megaspores. Three of the megaspores break down, but the remaining one, over the better part of a year, slowly develops into a female gametophyte. The female gametophyte at maturity may consist of thousands of cells, with two to six archegonia formed at the micropylar end. Each archegonium contains an egg so large it can be seen without a microscope.

Female cones usually take two or more seasons to mature. At first they may be reddish or purplish in color, but they soon turn green, and during the first spring, the scales spread apart. While the scales are open, pollen grains carried by the wind drift down between them, some catching in sticky fluid oozing out of the micropyle. As the sticky fluid evaporates, the pollen grains are slowly drawn down through the micropyle to the top of the nucellus, and the scales close shortly thereafter. The archegonia and the rest of the female gametophyte
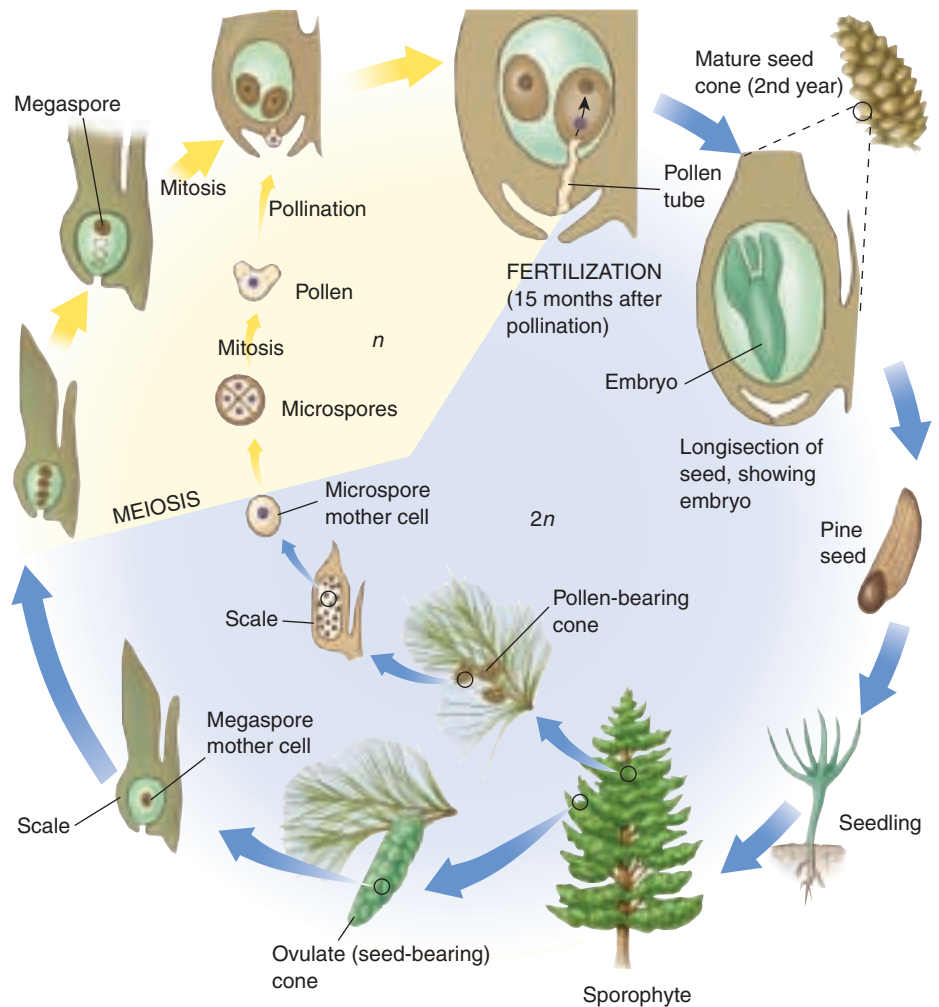

FIGURE 37.13
Life cycle of a typical pine. The male and female gametophytes have been dramatically reduced in size. Wind generally disperses sperm that is within the male gametophyte (pollen). Pollen tube growth delivers the sperm to the egg on the female cone. Additional protection for the embryo is provided by the ovule which develops into the seed coat.

are not mature until about a year later. While the female gametophyte is developing, a pollen tube emerges from a pollen grain at the bottom of the micropyle and slowly digests its way through the nucellus to the archegonia. While the pollen tube is growing, one of the pollen grain's four cells, the generative cell, divides by mitosis, with one of the resulting two cells dividing once more. These last two cells function as sperm. The germinated pollen grain with its two sperm is the mature male gametophyte.

About 15 months after pollination, the pollen tube reaches an archegonium, and discharges its contents into it. One sperm unites with the egg, forming a zygote. The other sperm and cells of the pollen grain degenerate. The zygote develops into an embryo within a seed. After dispersal and germination of the seed, the young sporophyte of the next generation grows into a tree.

(a)   (b)   (c)

FIGURE 37.14
Three phyla of gymnosperms.
(*a*) An African cycad, *Encephalartos transvenosus.*
(*b*) *Welwitschia mirabilis*, one of the three genera of gnetophytes.
(*c*) Maidenhair tree, *Ginkgo biloba*, the only living representative of the phylum Ginkgophyta.

Cycads (Cycadophyta)

Cycads are slow-growing gymnosperms of tropical and subtropical regions. The sporophytes of most of the 100 known species resemble palm trees (figure 37.14*a*) with trunks that can attain heights of 15 meters or more. Unlike palm trees—which are flowering plants—cycads produce cones and have a life cycle similar to that of pines. The female cones, which develop upright among the leaf bases, are huge in some species and can weigh up to 45 kilograms. The sperm of cycads, although conveyed to an archegonium by a pollen tube, have thousands of spirally arranged flagella. Several species are facing extinction in the wild and soon may exist only in botanical gardens.

Gnetophytes (Gnetophyta)

There are three genera and about 70 living species of Gnetophyta. Gnetophytes are the closest living relatives of angiosperms and probably share a common ancestor with that group. They are the only gymnosperms with vessels (a particularly efficient conducting cell type) in their xylem—a common feature in angiosperms. The members of the three genera differ greatly from one another in form. One of the most bizarre of all plants is *Welwitschia*, which occurs in the Namib and Mossamedes deserts of southwestern Africa (figure 37.14*b*). The stem is shaped like a large, shallow cup that tapers into a taproot below the surface. It has two strap-shaped, leathery leaves that grow continuously from their base, splitting as they flap in the wind. The reproductive structures of *Welwitschia* are conelike, appear toward the bases of the leaves around the rims of the stems, and are produced on separate male and female plants.

More than half of the gnetophyte species are in the genus *Ephedra*, which is common in arid regions of the western United States and Mexico. The plants are shrubby, with stems that superficially resemble those of horsetails as they are jointed and have tiny, scalelike leaves at each node. Male and female reproductive structures may be produced on the same or different plants. The drug ephedrine, widely used in the treatment of respiratory problems, was in the past extracted from Chinese species of *Ephedra*, but it has now been largely replaced with synthetic preparations. Mormon tea is brewed from *Ephedra* stems in the southwestern United States.

The best known species of *Gnetum* is a tropical tree, but most species are vinelike. All species have broad leaves similar to those of angiosperms. One *Gnetum* species is cultivated in Java for its tender shoots, which are cooked as a vegetable.

Ginkgo (Ginkgophyta)

The fossil record indicates that members of the Ginkgo family were once widely distributed, particularly in the northern hemisphere; today only one living species, the maidenhair tree (*Ginkgo biloba*), remains. The tree, which sheds its leaves in the fall, was first encountered by Europeans in cultivation in Japan and China; it apparently no longer exists in the wild (figure 37.14*c*). The common name comes from the resemblance of its fan-shaped leaves to the leaflets of maidenhair ferns. Like the sperm of cycads, those of *Ginkgo* have flagella. The *Ginkgo* is diecious, that is, the male and female reproductive structures of *Ginkgo* are produced on separate trees. The fleshy outer coverings of the seeds of female *Ginkgo* plants exude the foul smell of rancid butter caused by butyric and isobutyric acids. In the Orient, however, the seeds are considered a delicacy. In Western countries, because of the seed odor, male plants vegetatively propagated from shoots are preferred for cultivation. Because it is resistant to air pollution, *Ginkgo* is commonly planted along city streets.

Gymnosperms are mostly cone-bearing seed plants. In gymnosperms, the ovules are not completely enclosed by sporophyte tissue at pollination.

Angiosperms

The 250,000 known species of flowering plants are called angiosperms because their ovules, unlike those of gymnosperms, are enclosed within diploid tissues at the time of pollination. The name *angiosperm* derives from the Greek words *angeion*, "vessel," and *sperma*, "seed." The "vessel" in this instance refers to the carpel, which is a modified leaf that encapsulates seeds. The carpel develops into the fruit, a unique angiosperm feature. While some gymnosperms, including yew, have fleshlike tissue around their seeds, it is of a different origin and not a true fruit.

The origins of the angiosperms puzzled even Darwin (his "abominable mystery"). Recently, consensus has been reached on the most basal, living angiosperm—*Amborella trichopoda* (figure 37.15). This has ended the debate between the supporters of magnolias and those of water lilies as the closest relatives of the original angiosperm. *Amborella*, with small, cream-colored flowers, is even more primitive than either the magnolias or water lilies. This small shrub found only on the island of New Caledonia in the South Pacific is the last remaining species of the earliest extant lineage of the angiosperms. About 135 million years ago a close relative of *Amborella* developed floral parts and branched off from the gymnosperms. While *Amborella* is not the original angiosperm, it is sufficiently close that much will be learned from studying its reproductive biology that will help us understand the early radiation of the angiosperms.

Flowering plants (phylum Anthophyta) exhibit an almost infinite variety of shapes, sizes, and textures. They vary, for example, from the huge Tasmanian *Eucalyptus* trees, which have nearly as much mass as the giant redwoods, to the tiniest duckweeds, which are less than 1 millimeter long. In addition to the typical flattened green leaves with which everyone is familiar, flowering plant leaves may be succulent, floating, submerged, cup-shaped, spinelike, scalelike, feathery, papery, hairy, or insect-trapping, and of almost any color. Some are so tiny one needs a microscope to examine them, while others, such as those of the Seychelles Island palm, can be up to 6 meters long. Their flowers vary from the simple blossoms of buttercups to the extraordinarily complex flowers of some orchids, which may lure their pollinators with drugs, forcibly attach bags of pollen to their bodies, or dunk them in fluid they secrete. The flowers may weigh less than 1 gram and remain functional for only a few minutes, or they can weigh up to 9 kilograms and be functional for months. Plants of several families are parasitic or partially parasitic (for example, dodder, or
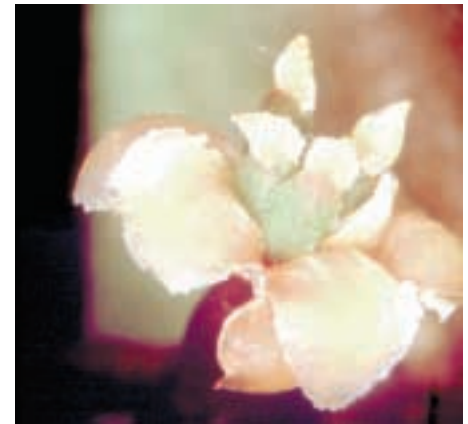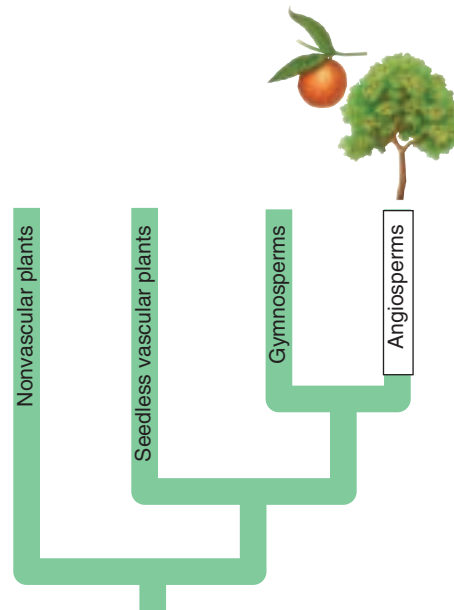

FIGURE 37.15
A flowering plant. *Amborella trichopoda.* This plant is believed to be the closest living relative to the original angiosperm.

mistletoe) on other plants, or *mycotrophic* (deriving their nutrients from fungi that form a mutualism with plant roots). Others, such as many orchids, are *epiphytic* (attached to other plants, with no roots in the ground, and not in any way parasitic).

The Structure of Flowers

Flowers are considered to be modified stems bearing modified leaves. Regardless of their size and shape, they all share certain features (see figure 37.16). Each flower originates as a **primordium** that develops into a bud at the end of a stalk called a **pedicel.** The pedicel expands slightly at the tip into a base, the **receptacle,** to which the remaining flower parts are attached. The other flower parts typically are attached in circles called *whorls*. The outermost whorl is composed of **sepals.** In most flowers there are three to five sepals, which are green and somewhat leaflike; they often function in protecting the immature flower and in some species may drop off as the flower opens. The next whorl consists of **petals** that are often colored and attract pollinators such as insects and birds. The petals, which commonly number three to five, may be separate, fused together, or missing altogether *in wind-pollinated flowers.*

The third whorl consists of **stamens,** collectively called the **androecium,** a term derived from the Greek words *andros*, "male," and *oikos*, "house." Each stamen consists of a pollen-bearing **anther** and a stalk called a **filament,** which may be missing in some flowers. The **gynoecium,** consisting of one or more **carpels,** is at the center of the flower. The term *gynoecium* derives from the Greek words *gynos*, which means "female," and *oikos*, or "house." The first carpel is believed to have been formed from a leaflike structure with ovules along its margins. The edges of the blade then rolled inward and fused together, forming a carpel.

FIGURE 37.16
Diagram of an angiosperm flower.
(*a*) The main structures of the flower are labeled. (*b*) Details of an ovule. The ovary as it matures will become a fruit; as the ovule's outer layers (integuments) mature, they will become a seed coat.
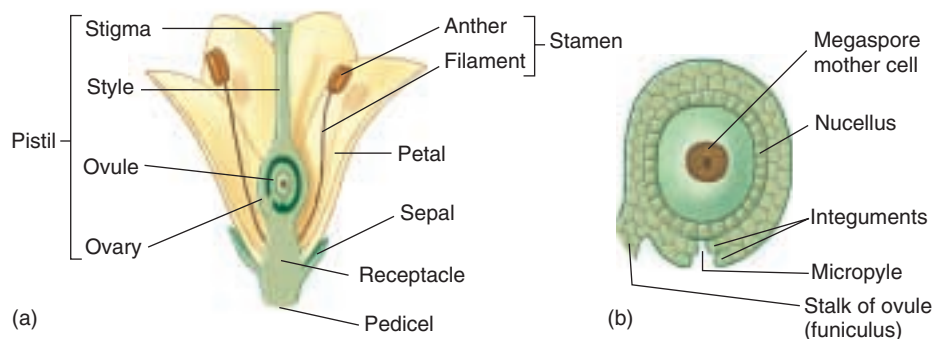
Primitive flowers can have several to many separate carpels, but in most flowers, two to several carpels are fused together. Such fusion can be seen in an orange sliced in half; each segment represents one carpel. A carpel has three major regions (figure 37.16). The **ovary** is the swollen base, which contains from one to hundreds of **ovules;** the ovary later develops into a **fruit.** The tip of the pistil is called a **stigma.** Most stigmas are sticky or feathery, causing pollen grains that land on them to adhere. Typically there is a neck or stalk called a **style** connecting the stigma and the ovary; in some flowers, the style may be very short or even missing. Many flowers have nectar-secreting glands called *nectaries*, often located toward the base of the ovary. Nectar is a fluid containing sugars, amino acids, and other molecules used to attract insects, birds, and other animals to flowers.

The Angiosperm Life Cycle

While a flower bud is developing, a single megaspore mother cell in the ovule undergoes meiosis, producing four megaspores (figure 37.17). In most flowering plants, three of the megaspores soon disappear while the nucleus of the remaining one divides mitotically, and the cell slowly expands until it becomes many times its original size. While this expansion is occurring, each of the daughter nuclei divide twice, resulting in eight haploid nuclei arranged in two groups of four. At the same time, two layers of the ovule, the **integuments,** differentiate and become the *seed coat* of a seed. The integuments, as they develop, leave a small gap or pore at one end—the *micropyle* (see figure 37.16). One nucleus from each group of four migrates toward the center, where they function as **polar nuclei.** Polar nuclei may fuse together, forming a single diploid nucleus, or they may form a single cell with two haploid nuclei. Cell walls also form around the remaining nuclei. In the group closest to the micropyle, one cell functions as the **egg;** the other two nuclei are called **synergids.** At the other end, the three cells are now called **antipodals;** they have no apparent function and eventually break down and disappear. The large sac with eight nuclei in seven cells is called an **embryo sac;** it constitutes the female gametophyte. Although it is completely dependent on the sporophyte for nutrition, it is a multicellular, haploid individual.

While the female gametophyte is developing, a similar but less complex process takes place in the anthers. Most anthers have patches of tissue (usually four) that eventually become chambers lined with nutritive cells. The tissue in each patch is composed of many diploid microspore mother cells that undergo meiosis more or less simultaneously, each producing four microspores. The four microspores at first remain together as a quartet or tetrad, and the nucleus of each microspore divides once; in most species the microspores of each quartet then separate. At the same time, a two-layered wall develops around each microspore. As the anther matures, the wall between adjacent pairs of chambers breaks down, leaving two larger sacs. At this point, the binucleate microspores have become **pollen grains.** The outer pollen grain wall layer often becomes beautifully sculptured, and it contains chemicals that may react with others in a stigma to signal whether or not development of the male gametophyte should proceed to completion. The pollen grain has areas called *apertures*, through which a pollen tube may later emerge.

Pollination is simply the mechanical transfer of pollen from its source (an anther) to a receptive area (the stigma of a flowering plant). Most pollination takes place between flowers of different plants and is brought about by insects, wind, water, gravity, bats, and other animals. In as many as a quarter of all angiosperms, however, a pollen grain may be deposited directly on the stigma of its own flower, and self-pollination occurs. Pollination may or may not be followed by *fertilization*, depending on the genetic compatibility of the pollen grain and the flower on whose stigma it has landed. (In some species, complex, genetically controlled mechanisms prevent self-fertilization to enhance genetic diversity in the progeny.) If the stigma is receptive, the pollen grain's dense cytoplasm absorbs substances from the stigma and bulges through an aperture. The bulge develops into a *pollen tube* that responds to chemicals released by the embryo sac. It follows a diffusion gradient of the chemicals and grows down through the style and into the micropyle. The pollen tube usually takes several hours to two days to reach the micropyle, but in a few instances, it may take up to a year. One of the pollen grain's two nuclei, the *generative nucleus*, lags behind. This nucleus divides, ei-
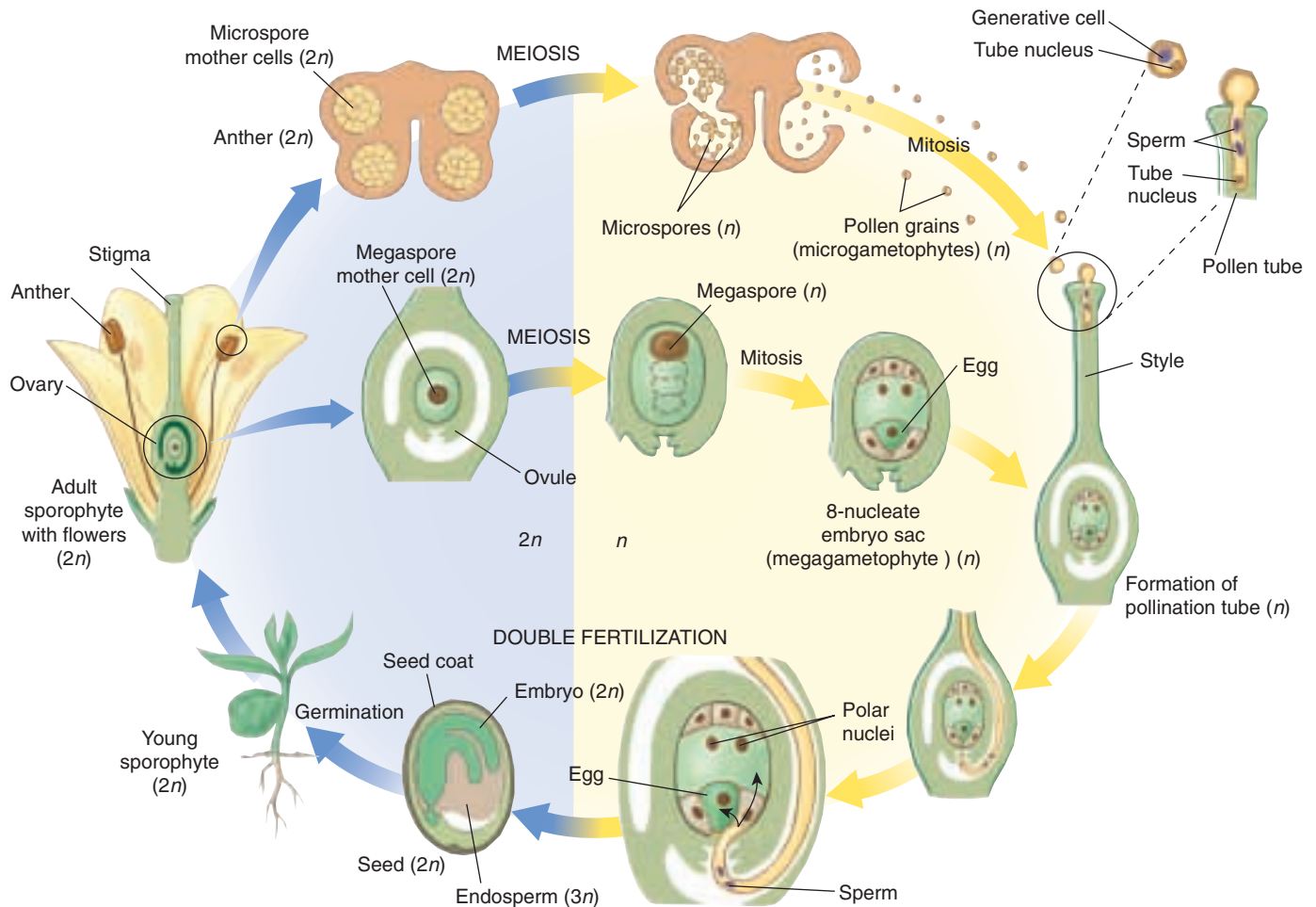
FIGURE 37.17
Life cycle of a typical angiosperm. As in pines, water is no longer required for fertilization. In most species of angiosperms, animals carry pollen to the carpel. The outer wall of the carpel forms the fruit that entices animals to disperse seed.

ther in the pollen grain or in the pollen tube, producing two sperm nuclei. Unlike sperm in mosses, ferns, and some gymnosperms, the sperm of flowering plants have no flagella. At this point, the pollen grain with its tube and sperm has become a mature male gametophyte.

As the pollen tube enters the embryo sac, it destroys a synergid in the process and then discharges its contents. Both sperm are functional, and an event called **double fertilization,** unique to angiosperms, follows. One sperm unites with the egg and forms a zygote, which develops into an embryo sporophyte plant. The other sperm and the two polar nuclei unite, forming a triploid primary endosperm nucleus. The primary endosperm nucleus begins dividing rapidly and repeatedly, becoming triploid **endosperm** tissue that may soon consist of thousands of cells. Endosperm tissue can become an extensive part of the seed in grasses such as corn (see figure 41.7). But in most flowering plants, it provides nutrients for the embryo that develops from the zygote; in many species, such as

peas and beans, it disappears completely by the time the seed is mature. Following double fertilization, the integuments harden and become the seed coat of a seed. The haploid cells remaining in the embryo sac (antipodals, synergid, tube nucleus) degenerate. There is some evidence for a type of double fertilization in gymnosperms believed to be closely related to the angiosperms. Further studies of this and of fertilization in *Amborella*, the most basal, extant angiosperm, may provide clues to the evolution of this double fertilization event.

Angiosperms are characterized by ovules that at pollination are enclosed within an ovary at the base of a carpel—a structure unique to the phylum; a fruit develops from the ovary. Evolutionary innovations including flowers to attract pollinators, fruits to protect and aid in embryo dispersal, and double fertilization providing additional nutrients for the embryo all have contributed to the widespread success of this phylum.

Chapter 37   Evolutionary History of Plants   **751**

Summary	Questions	Media Resources

37.1 Plants have multicellular haploid and diploid stages in their life cycles.

- Plants evolved from a multicellular, freshwater green algae 450 million years ago. The evolution of their conducting tissues, cuticle, stomata, and seeds has made them progressively less dependent on external water for reproduction.
- All plants have a haplodiplontic life cycle in which haploid gametophytes alternate with diploid sporophytes.

1. Where did the most recent ancestors of land plants live? What were they like? What adaptations were necessary for the "move" onto land?

2. What does it mean for a plant to alternate generations? Distinguish between sporophyte and gametophyte.

- Life Cycles of Plants

- Student Research: Plant Biodiversity in New Hampshire
- Book Review: *A Rum Affair* by Sabbagh
- Book Review: The Orchid Thief by Orlean

37.2 Nonvascular plants are relatively unspecialized, but successful in many terrestrial environments.

- Three phyla of plants lack well-developed vascular tissue, are the simplest in structure, and have been grouped as bryophytes. This grouping does not reflect a common ancestry or close relationship.
- Sporophytes of mosses, liverworts, and hornworts are usually nutritionally dependent on the gametophytes, which are more conspicuous and photosynthetic.

3. Distinguish between male gametophytes and female gametophytes. Which specific haploid spores give rise to each of these?

4. What reproductive limitations would a moss tree (if one existed) face?

- Non-Vascular Plants

37.3 Seedless vascular plants have well-developed conducting tissues in their sporophytes.

- Nine of the 12 plant phyla contain vascular plants, which have two kinds of well-defined conducting tissues: xylem, which is specialized to conduct water and dissolved minerals; and phloem, which is specialized to conduct the sugars produced by photosynthesis and plant growth regulators.
- In ferns and other seedless vascular plants, the sporophyte generation is dominant. The fern sporophyte has vascular tissue and well-differentiated roots, stems, and leaves.

5. In what ways are the gametophytes of seedless plants different from the gametophytes of seed plants?

6. Which generation(s) of the fern are nutritionally independent?

- Seedless Vascular Plants

37.4 Seeds protect and aid in the dispersal of plant embryos.

- Seeds were an important evolutionary advance providing for a dormant stage in development.
- In gymnosperms, ovules are exposed directly to pollen at the time of pollination; in angiosperms, ovules are enclosed within an ovary, and a pollen tube grows from the stigma to the ovule.
- The pollen of gymnosperms is usually disseminated by wind. In most angiosperms the pollen is transported by insects and other animals. Both flowers and fruits are found only in angiosperms and may account for the extensive colonization of terrestrial environments by the flowering plants.

7. What is a seed? Why is the seed a crucial adaptation to terrestrial life?

8. What is the principal difference between gymnosperms and angiosperms?

9. If all the offspring of a plant were to develop in a small area, they would suffer from limited resources. Compare dispersal strategies in moss, pine, and angiosperms.

- Gymnosperms
- Angiosperms