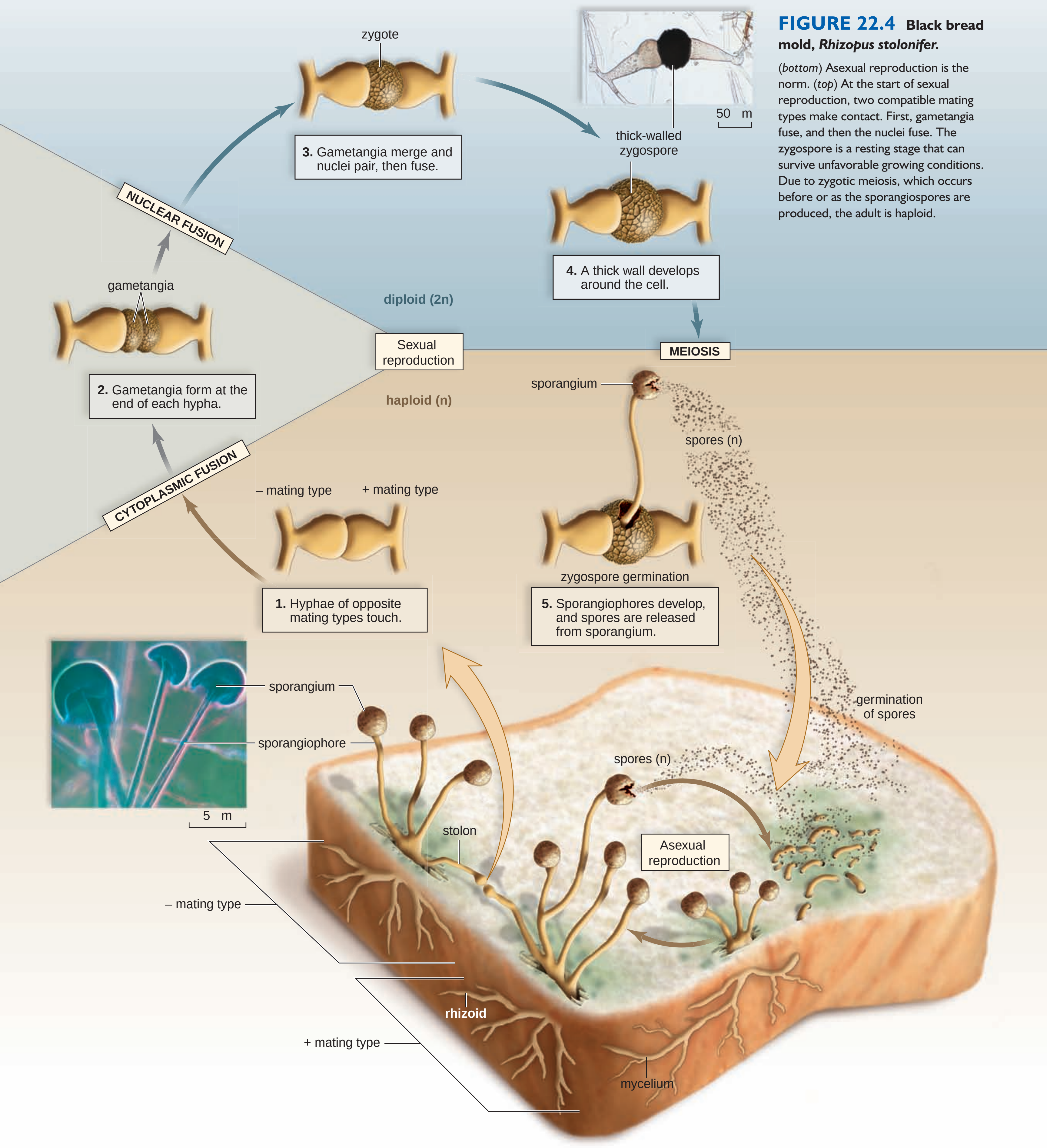


FIGURE 22.4 **Black bread mold, *Rhizopus stolonifer*.**

(*bottom*) Asexual reproduction is the norm. (*top*) At the start of sexual reproduction, two compatible mating types make contact. First, gametangia fuse, and then the nuclei fuse. The zygospore is a resting stage that can survive unfavorable growing conditions. Due to zygotic meiosis, which occurs before or as the sporangiospores are produced, the adult is haploid.

Sac Fungi

The **sac fungi** (ascomycota) consist of about 50,000 species of fungi. The sac fungi can be thought of as having two main groups: the sexual sac fungi, in which sexual reproduction has long been known, and the asexual sac fungi, in which sexual reproduction has not yet been observed. The sexual sac fungi include such organisms as the **yeast** *Saccharomyces,* the unicellular fungi important in the baking and brewing industries and also in various molecular biological studies. *Neurospora,* the experimental material for the one-gene–one-enzyme studies, and the other **red bread molds** are sexual sac fungi. So are the **morels** and **truffles,** which are famous gourmet delicacies revered throughout the world. The asexual sac fungi used to be in the phylum Deuteromycota, sometimes called the imperfect fungi because their means of sexual reproduction was unknown. However, on the basis of molecular data and structural characteristics, these fungi have now been identified as sac fungi. The asexual sac fungi include the yeast *Candida* and the **molds** *Aspergillus* and *Penicillium.* The asci of *Penicillium* were discovered and, therefore, it was renamed *Talaromyces*.

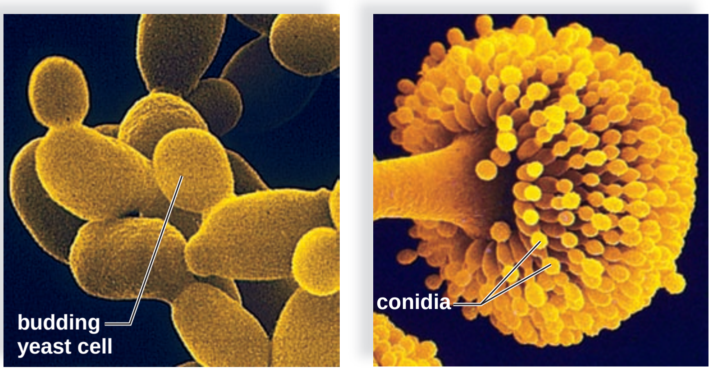
Biology of the Sac Fungi

The body of the sac fungus can be a single cell, as in yeasts, but more often it is a mycelium composed of septate hyphae. The sac fungi are distinguished by the structures they form when they reproduce asexually and sexually.

Asexual Reproduction. Asexual reproduction is the norm among sac fungi. The yeasts usually reproduce by budding. A small cell forms and pinches off as it grows to full size (Fig. 22.5*a*). The other sac fungi produce spores called conidia or **conidiospores** that vary in size and shape and may be multicellular. The conidia usually develop at the tips of specialized aerial hyphae called conidiophores (Fig. 22.5*b*). Conidiophores differ in appearance and this helps mycologists identify the particular sac fungi. When released, the spores are windblown. The conidia of the allergy-causing mold *Cladosporium* are carried easily through the air and transported even over oceans. One researcher found a concentration of more than 35,000 *Cladosporium* conidia/m^3 over Leiden (Germany).

Sexual Reproduction. Their formal name, ascomycota, refers to the **ascus** [Gk. *askos,* bag, sac], a fingerlike sac that develops during sexual reproduction. On occasion, the asci are surrounded and protected by sterile hyphae within a fruiting body called an *ascocarp* (Fig. 22.6*a*, *b*). A **fruiting body** is a reproductive structure where spores are produced and released. Ascocarps can have different shapes; in cup fungi they are cup shaped and in morels they are stalked and crowned by a pitted bell-shaped ascocarp.

Ascus-producing hyphae remain dikaryotic except in the walled-off portion that becomes the ascus, where nuclear fusion



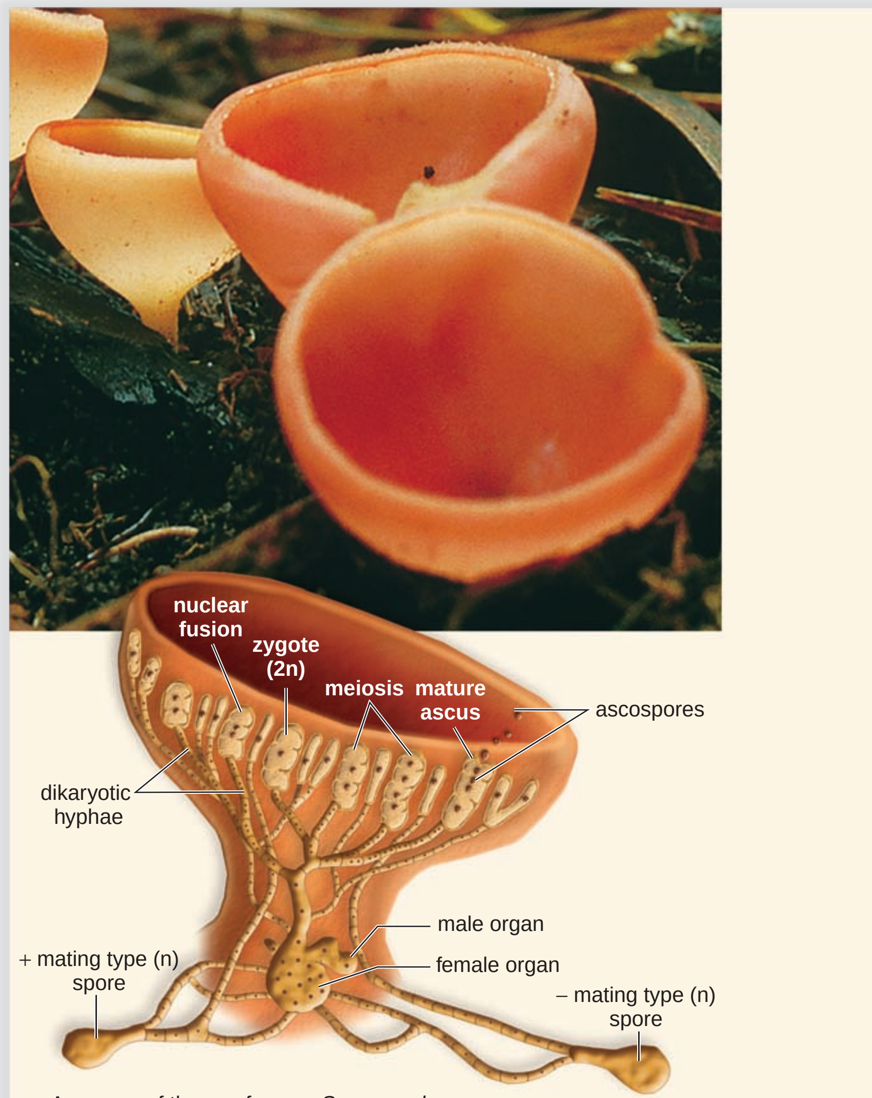
a. b.

FIGURE 22.5 Asexual reproduction in sac fungi.

a. Yeasts, unique among fungi, reproduce by budding. **b.** The sac fungi usually reproduce asexually by producing spores called conidia or conidiospores.

FIGURE 22.6 Sexual reproduction in sac fungi.

The sac fungi reproduce sexually by producing asci, in fruiting bodies called ascocarps. **a.** In the ascocarp of cup fungi, dikaryotic hyphae terminate forming the asci, where meiosis follows nuclear fusion and spore formation takes place. **b.** In morels, the asci are borne on the ridges of pits. **c.** Peach leaf curl, a parasite of leaves, forms asci as shown.



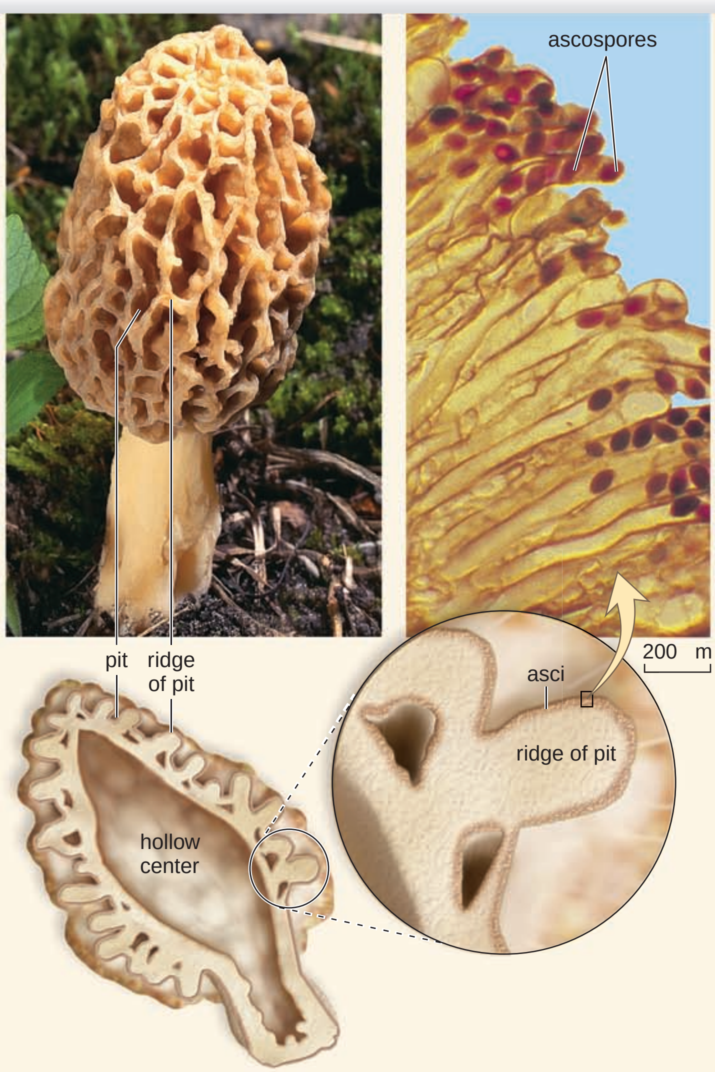
a. Ascocarp of the cup fungus, *Sarcoscypha* and meiosis take place. Because mitosis follows meiosis, each ascus contains eight haploid nuclei and produces eight spores. In most ascomycetes, the asci become swollen as they mature, and then they burst, expelling the ascospores. If released into the air, the spores are then windblown.

The Benefits and Drawbacks of Sac Fungi

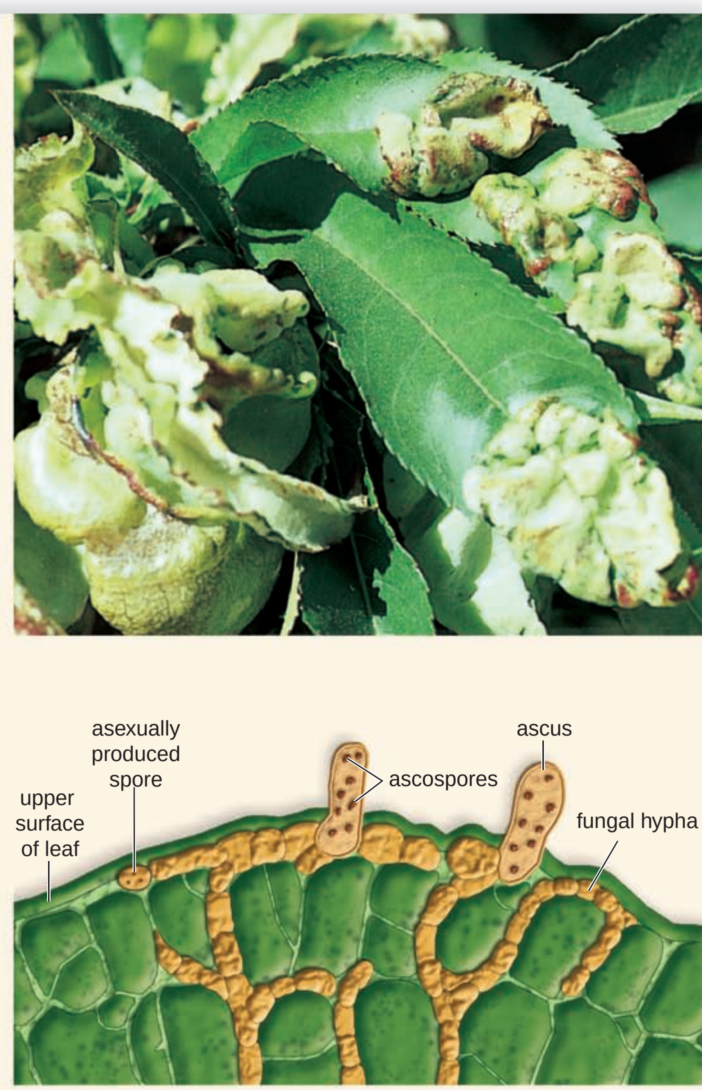
The sac fungi play an essential role in recycling by digesting resistant (not easily decomposed) materials containing cellulose, lignin, or collagen. Species are also known that can even consume jet fuel and wall paint. Some are symbiotic with algae, forming lichens, and plant roots, forming mycorrhizae. They also account for most of the known fungal pathogens causing various plant diseases. Powdery mildews grow on leaves, as do leaf curl fungi (Fig. 22.6*c*); chestnut blight and Dutch elm disease destroy the trees named. Ergot, a parasitic sac fungus that infects rye and (less commonly) other grains, is discussed in the Health Focus on page 401.

A sac fungus produces the drug penicillin, which cures bacterial infections; cyclosporine, which suppresses the immune system leading to the success of transplantation operations; and the steroids, which are present in the birth control pill. They are also used during the production of various foods such as blue cheese and Coke. Many human diseases caused by sac fungi are acquired from the environment. Ringworm comes from soil fungi, rose gardener's disease from thorns, Chicago disease from old buildings, and basketweaver's disease from grass cuttings.

Yeasts. Yeasts can be both beneficial and harmful to humans. In the wild, yeasts grow on fruits, and historically the yeasts already present on grapes were used to produce wine. Today, selected yeasts, such as *Saccharomyces cerevisiae*, are added to relatively sterile grape juice to make wine. Also, this yeast is added to prepared grains to make beer. When *Saccharomyces* ferments, it produces ethanol and also carbon dioxide. Both the ethanol and the carbon dioxide are retained for beers and sparkling wines; carbon dioxide is released for still wines. In baking, the carbon dioxide given off is the leavening agent that causes bread to rise. *Saccharomyces* is serviceable to humans in another way. It is sometimes used in genetic engineering experiments requiring a eukaryote.



b. Ascocarp of the morel, *Morchella*



c. Peach leaf curl, *Taphrina*

Yeasts can be harmful to humans. *Candida albicans* is a yeast that causes the widest variety of fungal infections. Disease occurs when the normal balance of microbes in an organ, such as the vagina, is disturbed, particularly by antibiotic therapy. Then *Candida* proliferates and symptoms result. A vaginal infection results in inflammation, itching, and discharge. Oral thrush is a *Candida* infection of the mouth, common in newborns and AIDS patients. In immunocompromised individuals, *Candida* can move through the body, causing a systemic infection that can damage the heart, brain, and other organs.

Molds. Molds can be helpful to humans. *Aspergillus* is a group of green molds recognized by the bottle-shaped structure that bears their conidiospores. It is used to produce soy sauce by fermentation of soybeans. A Japanese food called miso is made by fermenting soybeans and rice with *Aspergillus*. In the United States, *Aspergillus* is used to produce citric and gallic acids, which serve as additives during the manufacture of a wide variety of products, including foods, inks, medicines, dyes, plastics, toothpaste, soap, and even chewing gum.

A species of *Penicillium* (blue molds now classified as *Talaromyces*) is the source of the familiar antibiotic called penicillin, which was first manufactured during World War II and still has many applications today. Since the discovery of penicillin by Sir Alexander Fleming, it has saved countless lives. Other *Penicillium* species give the characteristic flavor and aroma to cheeses such as Roquefort and Camembert. The bluish streaks in blue cheese are patches of conidiospores.

Molds can also be harmful to humans. Commonly isolated from soil, plant debris, and house dust, *Aspergillus* is sometimes pathogenic to humans. *Aspergillus flavus*, which grows on moist seeds, secretes a toxin that is the most potent natural carcinogen known. Therefore, in humid climates such as that in the southeastern United States, care must be taken to store grains properly. *Aspergillus* also causes a potentially deadly disease of the respiratory tract that arises after spores have been inhaled.

The mold *Stachybotrys chartarum* (Fig. 22.7) grows well on building materials. It is known as black mold and is responsible for the "sick-building" syndrome. Individuals with chronic exposure to toxins produced by this fungus have reported cold and flulike symptoms, fatigue, and dermatitis. The toxins may suppress and could destroy the immune system, affecting the lymphoid tissue and the bone marrow.

Moldlike fungi cause infections of the skin called tineas. Athlete's foot, caused by a species of *Trichophyton*, is a tinea characterized by itching and peeling of the skin between the toes (Fig. 22.8*a*). In ringworm, which can be caused by several different fungi, the fungus releases enzymes that degrade keratin and collagen in skin. The area of infection becomes red and inflamed. The fungal colony grows outward, forming a ring of inflammation. The center of the lesion begins to heal, thereby giving ringworm its characteristic appearance, a red ring surrounding an area of healed skin (Fig. 22.8*b*). Tinea infections of the scalp are rampant among school-age children, affecting as much as 30% of the population, with the possibility of permanent hair loss.

The vast majority of people living in the eastern and central United States have been infected with *Histoplasma capsulatum*, a thermally dimorphic fungus that grows in mold form at 25°C and in yeast form at 37°C. This common soil fungus, often associated with bird droppings, leads in most cases to a mild "fungal flu." Less than half of those infected notice any symptoms, with 3,000 showing severe disease and about 50 dying each year from histoplasmosis. The fungal pathogen lives and grows within cells of the immune system and causes systemic illness. Lesions are formed in the lungs that leave calcifications, visible in X-ray images, that resemble those of tuberculosis.

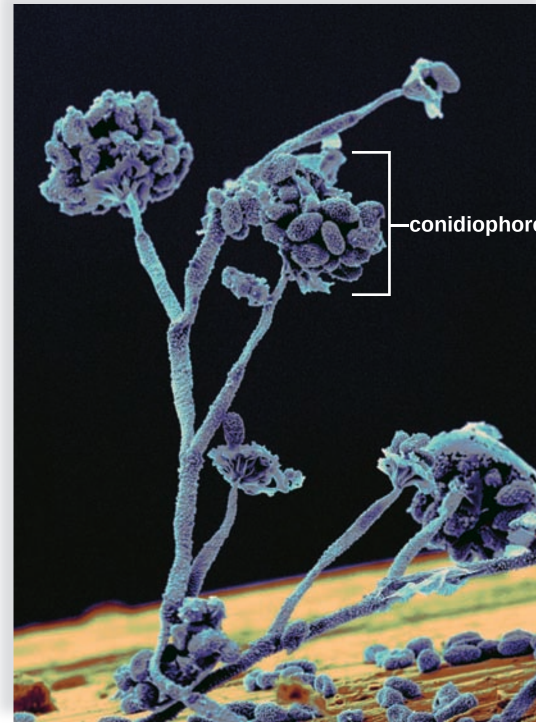


FIGURE 22.7 Black mold.

Stachybotrys chartarum, or black mold, grows well in moist areas, including the walls of homes. It represents a potential health risk.

Control of Fungal Infections. The strong similarities between fungal and human cells make it difficult to design fungal medications that do not also harm humans. Researchers exploit any biochemical differences they can discover. The biosynthesis of steroids in fungi differs somewhat from the same pathways in humans. A variety of fungicides are directed against steroid biosynthesis, including some that are applied to fields of grain. Fungicides based on heavy metals are applied to seeds of sorghum and other crops. Topical agents are available for the treatment of yeast infections and tineas, and systemic medications are available for systemic sac fungi infections.

a.

b.

FIGURE 22.8 Tineas.

a. Athlete's foot and (**b**) ringworm are termed tineas.

health focus

Deadly Fungi

It is unwise for amateurs to collect mushrooms in the wild because certain mushroom species are poisonous. The red and yellow *Amanitas* are especially dangerous. These species are also known as fly agaric because they were once thought to kill flies (the mushrooms were gathered and then sprinkled with sugar to attract flies). Its toxins include muscarine and muscaridine, which produce symptoms similar to those of acute alcoholic intoxication. In one to six hours, the victim staggers, loses consciousness, and becomes delirious, sometimes suffering from hallucinations, manic conditions, and stupor. Luckily, it also causes vomiting, which rids the system of the poison, so death occurs in less than 1% of cases. The death angel mushroom (*Amanita phalloides,* Fig. 22A) causes 90% of the fatalities attributed to mushroom poisoning. When this mushroom is eaten, symptoms don't begin until 10–12 hours later. Abdominal pain, vomiting, delirium, and hallucinations are not the real problem; rather, a poison interferes with RNA (ribonucleic acid) transcription by inhibiting RNA polymerase, and the victim dies from liver and kidney damage.

Some hallucinogenic mushrooms are used in religious ceremonies, particularly among Mexican Indians. *Psilocybe mexicana* contains a chemical called psilocybin that is a structural analogue of LSD and mescaline. It produces a dreamlike state in which visions of colorful patterns and objects seem to fill up space and dance past in endless succession. Other senses are also sharpened to produce a feeling of intense reality.

The only reliable way to tell a nonpoisonous mushroom from a poisonous one is to be able to correctly identify the species. Poisonous mushrooms cannot be identified with simple tests, such as whether they peel easily, have a bad odor, or blacken a silver coin during cooking. Only consume mushrooms identified by an expert!

Like club fungi, some sac fungi also contain chemicals that can be dangerous to people. *Claviceps purpurea,* the ergot fungus, infects rye and replaces the grain with ergot—hard, purple-black bodies consisting of tightly cemented hyphae (Fig. 22B). When ground with the rye and made into bread, the fungus releases toxic alkaloids that cause the disease ergotism. In humans, vomiting, feelings of intense heat or cold, muscle pain, a yellow face, and lesions on the hands and feet are accompanied by hysteria and hallucinations. Ergotism was common in Europe during the Middle Ages. During this period, it was known as St. Anthony's Fire and was responsible for 40,000 deaths in an epidemic in AD 994. We now know that ergot contains lysergic acid, from which LSD is easily synthesized. Based on recorded symptoms, historians believe that those individuals who were accused of practicing witchcraft in Salem, Massachusetts, during the seventeenth century were actually suffering from ergotism. It is also speculated that ergotism is to blame for supposed demonic possessions throughout the centuries. As recently as 1951, an epidemic of ergotism occurred in Pont-Saint-Esprit, France. Over 150 persons became hysterical, and four died.

Because the alkaloids that cause ergotism stimulate smooth muscle and selectively block the sympathetic nervous system, they can be used in medicine to cause uterine contractions and to treat certain circulatory disorders, including migraine headaches. Although the ergot fungus can be cultured in petri dishes, no one has succeeded in inducing it to form ergot in the laboratory. So far, the only way to obtain ergot, even for medical purposes, is to collect it in an infected field of rye.

FIGURE 22A **Poisonous mushroom, *Amanita phalloides.***

FIGURE 22B **Ergot infection of rye, caused by *Claviceps purpurea.***

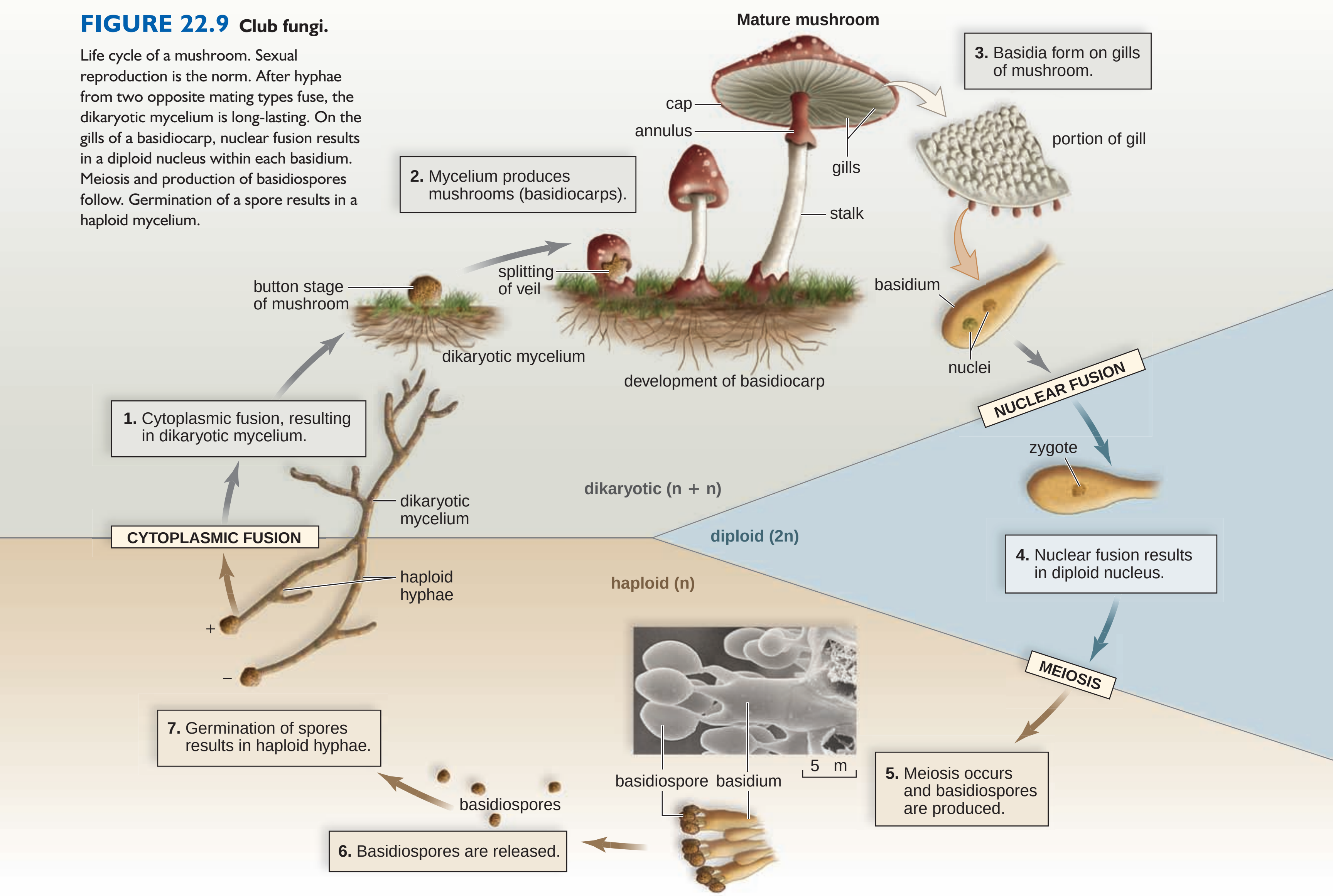


FIGURE 22.9 **Club fungi.**

Life cycle of a mushroom. Sexual reproduction is the norm. After hyphae from two opposite mating types fuse, the dikaryotic mycelium is long-lasting. On the gills of a basidiocarp, nuclear fusion results in a diploid nucleus within each basidium. Meiosis and production of basidiospores follow. Germination of a spore results in a haploid mycelium.

Club Fungi

Club fungi (basidiomycota) consist of over 22,000 species. Mushrooms, toadstools, puffballs, shelf fungi, jelly fungi, bird's-nest fungi, and stinkhorns are basidiomycetes. In addition, fungi that cause plant diseases such as the smuts and rusts are placed in this phylum. Several mushrooms such as the portabella and shiitake mushrooms are savored as foods by humans. Approximately 75 species of basidiomycetes are considered poisonous. The poisonous death angel mushroom is discussed in the Health Focus on page 401.

Biology of Club Fungi

The body of a basidomycota is a mycelium composed of septate hyphae. Most members of this phylum are saprotrophs, although several parasitic species exist.

Reproduction. Although club fungi occasionally do produce conidia asexually, they usually reproduce sexually. Their formal name, basidiomycota, refers to the **basidium** [L. *basidi,* small pedestal], a club-shaped structure in which spores called basidiospores develop. Basidia are located within a fruiting body called a basidiocarp (Fig. 22.9). Prior to formation of a basidiocarp, haploid hyphae of opposite mating types meet and fuse, producing a dikaryotic (n + n) mycelium. The dikaryotic mycelium continues its existence year after year, even for hundreds of years on occasion. In many species of mushrooms, the dikaryotic mycelium often radiates out and produces mushrooms in an ever larger, so-called fairy ring (Fig. 22.10*a*).

Mushrooms are composed of nothing but tightly packed hyphae whose walled-off ends become basidia. In gilled mushrooms, the basidia are located on radiating lamellae, the gills. In shelf fungi and pore mushrooms (Fig. 22.10*b, c*), the basidia terminate in tubes. In any case, the extensive surface area of a basidiocarp is lined by basidia, where nuclear fusion, meiosis, and spore production occur. A basidium has four projections in which cytoplasm and a haploid nucleus enter as the basidiospore forms. Basidiospores are windblown; when they germinate, a new haploid mycelium forms. It is estimated that some large mushrooms can produce up to 40 million spores per hour.

In puffballs, spores are produced inside parchmentlike membranes, and the spores are released through a pore or

a. Fairy ring

b. Shelf fungus

c. Pore mushroom, *Boletus*

d. Puffball, *Calvatiga gigantea*

FIGURE 22.10 Club fungi.

a. Fairy ring. Mushrooms develop in a ring on the outer living fringes of a dikaryotic mycelium. The center has used up its nutrients and is no longer living. **b.** A shelf fungus. **c.** Fruiting bodies of *Boletus*. This mushroom is not gilled; instead, it has basidia-lined tubes that open on the undersurface of the cap. **d.** In puffballs, the spores develop inside an enclosed fruiting body. Giant puffballs are estimated to contain 7 trillion spores.

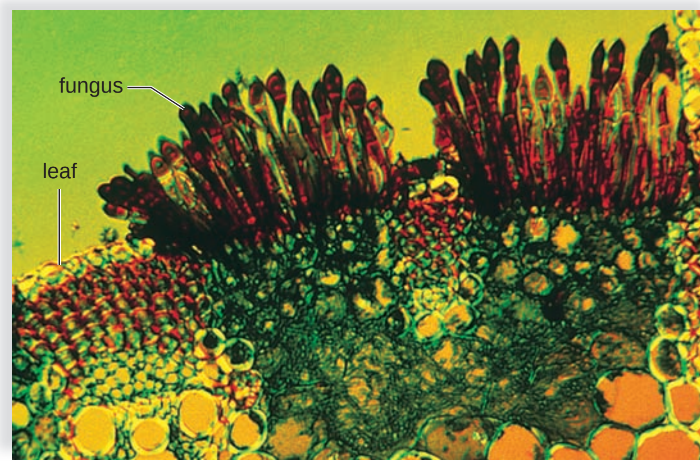
when the membrane breaks down (Fig. 22.10*d*). In bird's-nest fungi, falling raindrops provide the force that causes the nest's basidiospore-containing "eggs" to fly through the air and land on vegetation. Stinkhorns resemble a mushroom with a spongy stalk and a compact, slimy cap. The long stalk bears the elongated basidiocarp. Stinkhorns emit an incredibly disagreeable odor; flies are attracted by the odor, and when they linger to feed on the sweet jelly, the flies pick up spores that they later distribute.

Smuts and Rusts

Smuts and rusts are club fungi that parasitize cereal crops such as corn, wheat, oats, and rye. They are of great economic importance because of the crop losses they cause every year. Smuts and rusts don't form basidiocarps, and their spores are small and numerous, resembling soot. Some smuts enter seeds and exist inside the plant, becoming visible only near maturity. Other smuts externally infect plants. In corn smut, the mycelium grows between the corn kernels and secretes substances that cause the development of tumors on the ears of corn (Fig. 22.11*a*).

The life cycle of rusts requires alternate hosts, and one way to keep them in check is to eradicate the alternate host. Wheat rust (Fig. 22.11*b*) is also controlled by producing new and resistant strains of wheat. The process is continuous, because rust can mutate to cause infection once again.

a. Corn smut, *Ustilago*



b. Wheat rust, *Puccinia*

FIGURE 22.11 Smuts and rusts.

a. Corn smut. **b.** Micrograph of wheat rust.

Check Your Progress 22.2

1. What makes members of the chytrids different from all other fungi?
2. What are fungal infections called? Which type of fungus produces most of the known fungal pathogens?
3. Name the type of fungi for each of these: puffballs, ergots, athlete's foot, and black bread mold.

22.3 Symbiotic Relationships of Fungi

Several instances in which fungi are parasites of plants and animals have been mentioned. Two other symbiotic associations are of interest.

Lichens

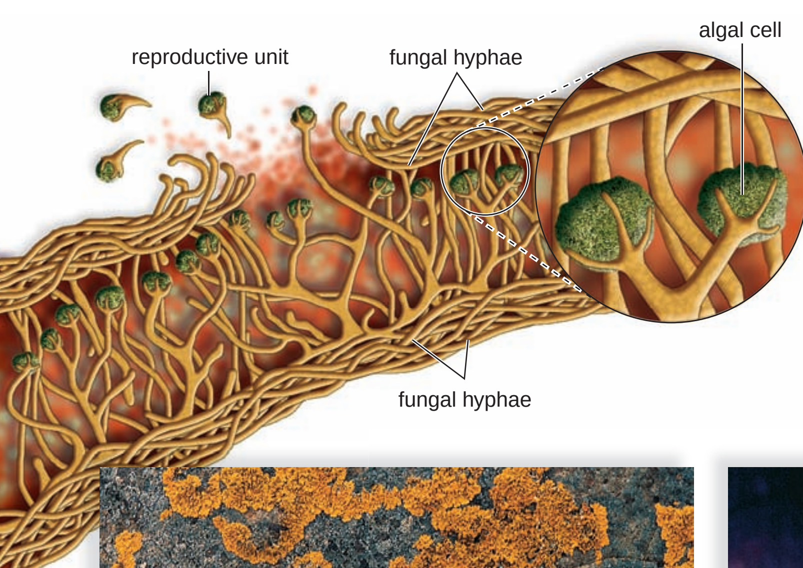
Lichens are an association between a fungus, usually a sac fungus, and a cyanobacterium or a green alga. The body of a crustose lichen has three layers: The fungus forms a thin, tough upper layer and a loosely packed lower layer that shield the photosynthetic cells in the middle layer (Fig. 22.12*a*). Specialized fungal hyphae, which penetrate or envelop the photosynthetic cells, transfer nutrients directly to the rest of the fungus. Lichens can reproduce asexually by releasing fragments that contain hyphae and an algal cell. In fruticose lichens, the sac fungus reproduces sexually (Fig. 22.12*b*).

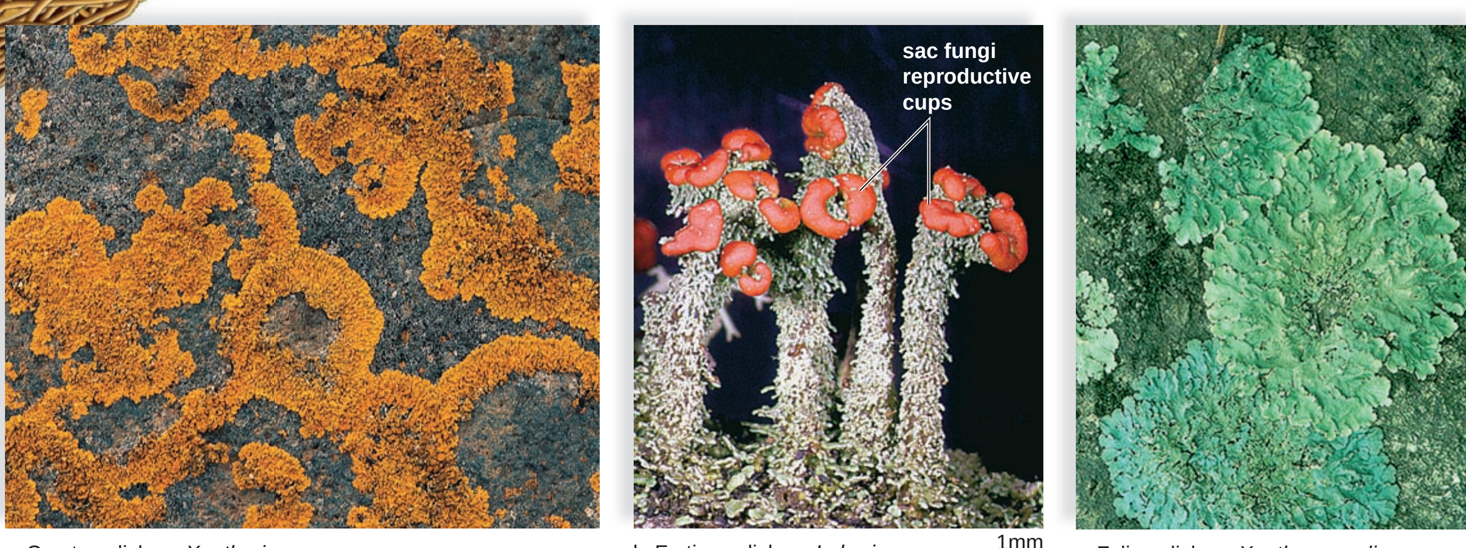
In the past, lichens were assumed to be mutualistic relationships in which the fungus received nutrients from the algal cells, and the algal cells were protected from desiccation by the fungus. Actually, lichens may involve a controlled form of parasitism of the algal cells by the fungus, with the algae not benefiting at all from the association. This is supported by experiments in which the fungal and algal components are removed and grown separately. The algae grow faster when they are alone than when they are part of a lichen. On the other hand, it is difficult to cultivate the fungus, which does not naturally grow alone. The different lichen species are identified according to the fungal partner.

Three types of lichens are recognized. Compact crustose lichens are often seen on bare rocks or on tree bark; fruticose lichens are shrublike; and foliose lichens are leaflike (Fig. 22.12*c*). Lichens are efficient at acquiring nutrients and moisture, and therefore they can survive in areas of low moisture and low temperature as well as in areas with poor or no soil. They produce and improve the soil, thus making it suitable for plants to invade the area. Unfortunately, lichens also take up pollutants and cannot survive where the air is polluted. Therefore, lichens can serve as air pollution sensors.

Mycorrhizae

Mycorrhizae [Gk. *mykes,* fungus, and *rhizion,* dim. for root] are mutualistic relationships between soil fungi and the roots of most plants. Plants whose roots are invaded by mycorrhizae grow more successfully in poor soils—particularly soils deficient in phosphates—than do plants without mycorrhizae (Fig. 22.13). The fungal partner, either a glomerulomycete or a sac fungus, may enter the cortex of roots but does not enter the cytoplasm of plant cells. Ectomycorrhizae form a mantle that is exterior to the root, and they grow between cell walls. Endomycorrhizae, such as the AM fungi, penetrate only the cell walls. In any case, the presence of the fungus gives the plant a greater absorptive surface for the intake of minerals. The fungus also benefits from the association by receiving carbohydrates from the plant. As mentioned, even the earli-





a. Crustose lichen, *Xanthoria*   b. Fruticose lichen, *Lobaria*   c. Foliose lichen, *Xanthoparmelia*

FIGURE 22.12 Lichen morphology.

a. A section of a compact crustose lichen shows the placement of the algal cells and the fungal hyphae, which encircle and penetrate the algal cells. **b.** Fruticose lichens are shrublike. **c.** Foliose lichens are leaflike.

FIGURE 22.13 Plant growth experiment.

A soybean plant (*left*) without mycorrhizae grows poorly compared to two other (*right*) plants infected with different strains of mycorrhizae.

est fossil plants have mycorrhizae associated with them. It would appear, then, that mycorrhizae helped plants adapt to and flourish on land.

It is of interest to know that the truffle, a gourmet delight whose ascocarp is somewhat prunelike in appearance, is a mycorrhizal sac fungus living in association with oak and beech tree roots. In the past, the French used pigs (truffle-hounds) to sniff out and dig up truffles, but now they have succeeded in cultivating truffles by inoculating the roots of seedlings with the proper mycelium.

Check Your Progress 22.3

1. What type of symbiotic relationship exists in mycorrhizae?
2. How does a lichen reproduce?
3. What is the relationship between air pollution and the presence of lichens?

Connecting the Concepts

At one time, fungi were considered a part of the plant kingdom, and then later, they were considered a protist. Whittaker argued that, because of their multicellular nature and mode of nutrition, fungi should be in their own kingdom. Like animals, they are heterotrophic, but they do not ingest food—they absorb nutrients. Like plants, they have cell walls, but their cell walls contain chitin instead of cellulose. Fungal cells store energy in the form of glycogen, as do animal cells.

Fungi have been around for at least 570 million years and may be descendants of flagellated protists. The chytrids are fungi that produce spores and gametes with flagella. Flagella have been lost by other fungal phyla over the course of evolution.

Today, the range of species within the kingdom Fungi is broad. Some fungi are unicellular (such as yeasts), some are multicellular parasites (such as those that cause athlete's foot), and some form mutualistic relationships with other species (such as those found in lichens). Most, however, are saprotrophic decomposers that play a vital role in all ecosystems. The decomposers work with bacteria to break down the waste products and dead remains of plants and animals so that organic materials are recycled.

In addition to their various ways of life, fungi have been successful because they have diverse reproductive strategies. During sexual reproduction, the filaments of different mating types typically fuse. Asexual reproduction via spores, fragmentation, and budding is common.

summary

22.1 Evolution and Characteristics of Fungi

Fungi are multicellular eukaryotes that are heterotrophic by absorption. After external digestion, they absorb the resulting nutrient molecules. Most fungi act as saprotrophic decomposers that aid the cycling of chemicals in ecosystems by decomposing dead remains. Some fungi are parasitic, especially on plants, and others are mutualistic with plant roots and algae.

The body of a fungus is composed of thin filaments called hyphae, which collectively are termed a mycelium. The cell wall contains chitin, and the energy reserve is glycogen. With the notable exception of the chytrids, which have flagellated spores and gametes, fungi do not have flagella at any stage in their life cycle. Nonseptate hyphae have no cross walls; septate hyphae have cross walls, but there are pores that allow the cytoplasm and even organelles to pass through.

Fungi produce spores during both asexual and sexual reproduction. During sexual reproduction, hyphae tips fuse so that dikaryotic (n + n) hyphae usually result, depending on the type of fungus. Following nuclear fusion, zygotic meiosis occurs during the production of the sexual spores.

22.2 Diversity of Fungi

Five significant groups of fungi are the chytrids (chytridiomycota), zygospore fungi (zygomycota), AM fungi (glomeromycota), sac fungi (ascomycota), and club fungi (basidiomycota).

The chytrids are unique because they produce motile zoospores and gametes. Some chytrids have an alternation of generations life cycle similar to that of plants and certain algae. There are unicellular as well as hyphae-forming chytrids. When hyphae form, they are nonseptate. *Chytriomyces* is an example of a chytrid.

The zygospore fungi are nonseptate, and during sexual reproduction they have a dormant stage consisting of a thick-walled zygospore. When the zygospore germinates, sporangia produce windblown spores. Asexual reproduction occurs when nutrients are plentiful and sporangia again produce spores. An example of a zygomycete is black bread mold.

The AM (arbuscular mycorrhizal) fungi were once classified with the zygospore fungi but are now viewed as a distinct group. AM fungi exist in mutualistic associations with the roots of land plants.

The sac fungi are septate, and during sexual reproduction saclike cells called asci produce spores. Asci are sometimes located in fruiting bodies called ascocarps. Asexual reproduction, which is dependent on the production of conidiospores, is more common. Sexual reproduction is unknown in some sac fungi. Sac fungi include *Talaromyces*, *Aspergillus*, *Candida*, morels and truffles, and various yeasts and molds, some of which cause disease in plants and animals, including humans.

The club fungi are septate, and during sexual reproduction club-shaped structures called basidia produce spores. Basidia are located in fruiting bodies called basidiocarps. Club fungi have a prolonged dikaryotic stage, and asexual reproduction by conidiospores is rare. A dikaryotic mycelium periodically produces fruiting bodies. Mushrooms and puffballs are examples of club fungi.

22.3 Symbiotic Relationships of Fungi

Lichens are an association between a fungus, usually a sac fungus, and a cyanobacterium or a green alga. Traditionally, this association was considered mutualistic, but experimentation suggests a controlled parasitism by the fungus on the alga. Lichens may live in extreme environments and on bare rocks; they allow other organisms that will eventually form soil to establish.

The term *mycorrhizae* refers to an association between a fungus and the roots of a plant. The fungus helps the plant absorb minerals, and the plant supplies the fungus with carbohydrates.

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sporangium 396
spore 395
truffle 398
yeast 398
zoospore 396
zygospore 396
zygospore fungi 396

Match the terms to these definitions:

a. ______________ Clublike structure in which nuclear fusion and meiosis occur during sexual reproduction of club fungi.
b. ______________ Tangled mass of hyphal filaments composing the vegetative body of a fungus.
c. ______________ Spore produced by sac and club fungi during asexual reproduction.
d. ______________ Spore-producing and spore-disseminating structure found in sac and club fungi.
e. ______________ Symbiotic relationship between fungal hyphae and roots of vascular plants. The fungus allows the plant to absorb more mineral ions and obtain carbohydrates from the plant.
f. ______________ Fungi with motile spores and gametes.

reviewing this chapter

1. Which characteristics best define fungi? Describe the body of a fungus and how fungi reproduce. 394–95
2. Discuss the evolution and classification of fungi. 394
3. Explain how chytrids are different from the other phyla of fungi. 396
4. Explain the term *zygospore fungi*. How does black bread mold reproduce asexually? Sexually? 396–97
5. Explain the terms *sexual sac fungi* and *asexual sac fungi*. 398–99
6. Explain the term *sac fungi*. How do sac fungi reproduce asexually? Describe the structure of an ascocarp. 398–99
7. Describe the structure of yeasts, and explain how they reproduce. How are yeasts and molds useful/harmful to humans? 399–400
8. Explain the term *club fungi*. Draw and explain a diagram of the life cycle of a typical mushroom. 402
9. What is the economic importance of smuts and rusts? How can their numbers be controlled? 403
10. Describe the structure of a lichen, and name the three different types. What is the nature of this fungal association? 404
11. Describe the association known as mycorrhizae, and explain how each partner benefits. 404–5

testing yourself

Choose the best answer for each question.
For questions 1–3, match the fungi to the phyla in the key.

KEY:

a. chytridiomycota
b. zygomycota
c. ascomycota
d. basidiomycota

1. club fungi
2. zygospore fungi
3. sac fungi
4. During sexual reproduction, the zygospore fungi produce
   a. an ascus.
   b. a basidium.
   c. a sporangium.
   d. a conidiophore.
5. An organism that decomposes remains is most likely to use which mode of nutrition?
   a. parasitic
   b. saprotrophic
   c. ingestion
   d. chemosynthesis
   e. Both a and b are correct.
6. Hyphae are generally characterized by
   a. strong, impermeable walls.
   b. rapid growth.
   c. large surface area.
   d. pigmented cells.
   e. Both b and c are correct.
7. A fungal spore
   a. contains an embryonic organism.
   b. germinates directly into an organism.
   c. is always windblown, because none are motile.
   d. is most often diploid.
   e. Both b and c are correct.
8. Fungal groups have different
   a. sexual reproductive structures.
   b. sporocarp shapes.
   c. modes of nutrition.
   d. types of cell wall.
   e. levels of organization.
9. In the life cycle of black bread mold, the zygospore
   a. undergoes meiosis and produces zoospores.
   b. produces spores as a part of asexual reproduction.
   c. is a thick-walled dormant stage.
   d. is equivalent to asci and basidia.
   e. All of these are correct.
10. In an ascocarp,
    a. there are fertile and sterile hyphae.
    b. hyphae fuse, forming the dikaryotic stage.
    c. a sperm fertilizes an egg.

d. hyphae do not have chitinous walls.
e. conidiospores form.

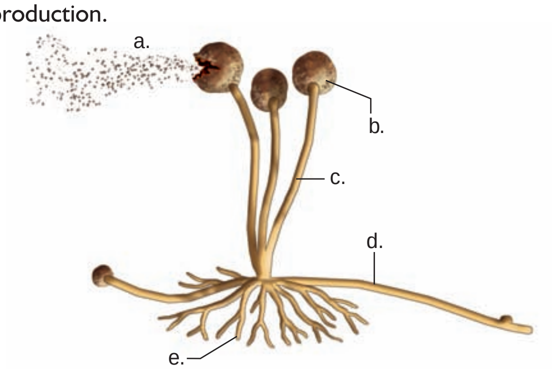
11. In which fungus is the dikaryotic stage longer lasting?
a. zygospore fungus
b. sac fungus
c. club fungus
d. chytrids

12. Conidiospores are formed
a. asexually at the tips of special hyphae.
b. during sexual reproduction.
c. by all types of fungi except water molds.
d. when it is windy and dry.
e. as a way to survive a harsh environment.

13. The asexual sac fungi are so called because
a. they have no zygospore.
b. they cause diseases.
c. they form conidiospores.
d. sexual reproduction has not been observed.
e. All of these are correct.

14. Lichens
a. cannot reproduce.
b. need a nitrogen source to live.
c. are parasitic on trees.
d. are able to live in extreme environments.

15. Label this diagram of black bread mold structure and asexual reproduction.



16. Why is it challenging to treat fungal infections of the human body?
a. Human and fungal cells share common characteristics.
b. Fungal cells share no features in common with human cells.
c. All fungal cells are highly resistant to drug treatments.
d. Both b and c are correct.

17. Mycorrhizae
a. are a type of lichen.
b. are mutualistic relationships.
c. help plants gather solar energy.
d. help plants gather inorganic nutrients.
e. Both b and d are correct.

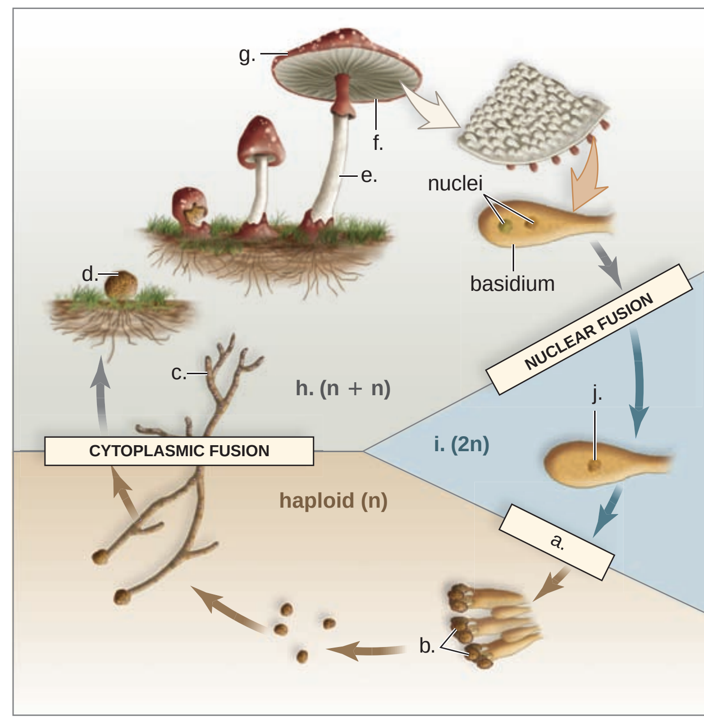
18. Which stage(s) in the chytrid life cycle is/are motile?
a. diploid zoospores
b. haploid zoospores
c. male gametes
d. female gametes
e. All of these are correct.

19. Yeasts are what type of fungi?
a. zygospores
b. single cell
c. sac fungi
d. Both b and c are correct.
e. All of these are correct.

20. Which statement is incorrect?
a. Some fungi are parasitic on plants, and others are mutualistic with plant roots and algae.
b. There are no fungi with motile cells.
c. The cell walls of fungi contain chitin.
d. Following nuclear fusion, zygotic meiosis occurs during the production of spores.
e. Lichens are an association between a fungus and a bacterium or a green alga.

21. Symbiotic relationships of fungi include
a. athlete's foot.
b. lichens.
c. mycorrhizae.
d. Only b and c are correct.
e. All three examples are correct.

22. Label this diagram of the life cycle of a mushroom.



thinking scientifically

1. The very earliest bakers observed that dough left in the air would rise. Unknown to them, yeast from the air "contaminated" the bread, began to grow, and produced carbon dioxide. Carbon dioxide caused the bread to rise. Later, cooks began to save some soft dough (before much flour was added) from the previous loaf to use in the next loaf. The saved portion was called the mother. What is in the mother, and why was it important to save it in a cool place?
2. There seems to be a fine line between symbiosis and parasitism when you examine the relationships between fungi and plants. What hypotheses could explain how different selective pressures may have caused particular fungal species to adopt one or the other relationship? Under what circumstances might a mutualistic relationship evolve between fungi and plants? Under what circumstances might a parasitic relationship evolve?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

part V

Plant Evolution and Biology

Life would be impossible without plants. Plants provide all living things with food and the oxygen needed to break down nutrient molecules and produce ATP. They are a source of fuel to keep us warm, and we use their fibers to make our clothes. The frame of our houses and the furniture therein is often made of wood and other plant products. We even use plants to make the paper for our newspapers and textbooks.

Altogether, it would be a good idea to know the principles of plant biology—plant structure and function. Plants have the same characteristics of life as animals do and most reproduce sexually, as we do. Life began in the sea and plants invaded the terrestrial environment before animals, as you would expect since animals are so dependent on plants. When our ancestors evolved, they lived in trees and fed on fruit and only later did they come down from the trees and begin to walk erect. These chapters introduce you to the biology of plants, those incredible organisms that keep the biosphere functioning as it should.

23

Plant Evolution and Diversity

Most likely, when you think of plants, you envision a scene much like that shown below. But plants have a very long evolutionary history, and many other types of plants preceded the evolution of flowering plants. Representatives of each of these groups are alive today and functioning well within their own particular environment. The closest relatives to land plants still live today in an aquatic environment, as do most animals.

This chapter attempts to trace the evolutionary history of plants by presenting and discussing many other types of plants, both living and extinct, aside from the flowering plants. In other words, you will be studying the diversity of plants within an evolutionary context. We will also give reasons why the most successful and abundant members of the plant kingdom are the flowering plants. Much of their success is due to coevolution between flowering plants and their pollinators, various terrestrial animals with which they share the land environment.

Grape hyacinth, *Muscaris,* and tulips, *Tulipa,* bloom in spring.

concepts

23.1 THE GREEN ALGAL ANCESTOR OF PLANTS

- Plants evolved from freshwater green algae and, over a long evolutionary history, became fully adapted to living on land. 410–11
- Plants have a life cycle in which two multicellular forms alternate. During the evolution of plants, the gametophyte (produces gametes) became reduced and dependent on the sporophyte (produces spores). 412–13

23.2 EVOLUTION OF BRYOPHYTES: COLONIZATION OF LAND

- Nonvascular plants lack well-developed conducting tissues. 413
- The life cycle of a moss demonstrates reproductive strategies, such as flagellated sperm and a dependent sporophyte. 413–15

23.3 EVOLUTION OF LYCOPHYTES: VASCULAR TISSUE

- In vascular plants, the sporophyte has vascular tissue for conducting materials in a body that has roots, stems, and leaves. 416

23.4 EVOLUTION OF PTERIDOPHYTES: MEGAPHYLLS

- Like other seedless vascular plants, a fern has a multibranched sporophyte that produces many windblown spores. The gametophyte is smaller and produces flagellated sperm. 417–19

23.5 EVOLUTION OF SEED PLANTS: FULL ADAPTATION TO LAND

- Seeds, which protect, nourish, and disperse the sporophyte, have great survival value. 420
- Seed plants produce heterospores. Megaspores become the dependent egg-bearing female gametophyte. The microspore becomes the sperm-bearing male gametophyte, the mature pollen grain. 420
- Many gymnosperms have pollen-producing cones and seed-producing cones. 420–22
- The flower is the reproductive structure of angiosperms that produces seeds covered by fruit. 424–27
- Much of the diversity among flowers comes from specialization for certain pollinators. 427

23.1 The Green Algal Ancestor of Plants

Plants are multicellular, photosynthetic eukaryotes, whose evolution is marked by adaptations to a land existence. A land environment does offer certain advantages to plants. For example, there is plentiful light for photosynthesis—water, even if clear, filters light. Also, carbon dioxide is present in higher concentrations and diffuses more readily in air than in water.

The land environment, however, requires adaptations, in particular, to deal with the constant threat of desiccation (drying out). The most successful land plants are those that protect all phases of reproduction (sperm, egg, embryo) from drying out and have an efficient means of dispersing offspring on land. Seed plants disperse their embryos within the seed, which provides the embryo with food within a protective seed coat.

The water environment not only provides plentiful water, it also offers support for the body of a plant. To conserve water, the land plant body, at the very least, is covered by a waxy cuticle that prevents loss of water while still allowing carbon dioxide to enter so that photosynthesis can continue. In many land plants, the roots absorb water from the soil, and a vascular system transports water in the body of the land plant. The vascular system that evolved in land plants allows them to stand tall and support expansive broad leaves that efficiently collect sunlight. The flowering plants, the last type to evolve, employ animals to assist with reproduction and dispersal of seed. The evolutionary history of plants given in Figure 23.1 shows the sequence in which land plants evolved adaptive features for an existence on land.

The Ancestry of Plants

The plants (listed in Table 23.1) evolved from a freshwater green algal species some 450 million years ago. As evidence for a green algal ancestry, scientists have known for some time that all green algae and plants contain chlorophylls *a* and *b* and various accessory pigments; store excess carbohydrates as starch; and have cellulose in their cell walls.

In recent years, molecular systematists have compared the sequence of ribosomal RNA bases between organisms. The results suggest that among the green algae, land plants are most closely related to freshwater green algae, known as **charophytes.** Fresh water, of course, exists in bodies of water on land, and natural selection would have favored those specimens best able to make the transition to the land itself. The land environment, at the time, was barren and represented a vast opportunity for any photosynthetic plants that were able to leave the water and take advantage of the new environment.

There are several types of charophytes—*Spirogyra*, for example, is a charophyte. But botantists tell us that

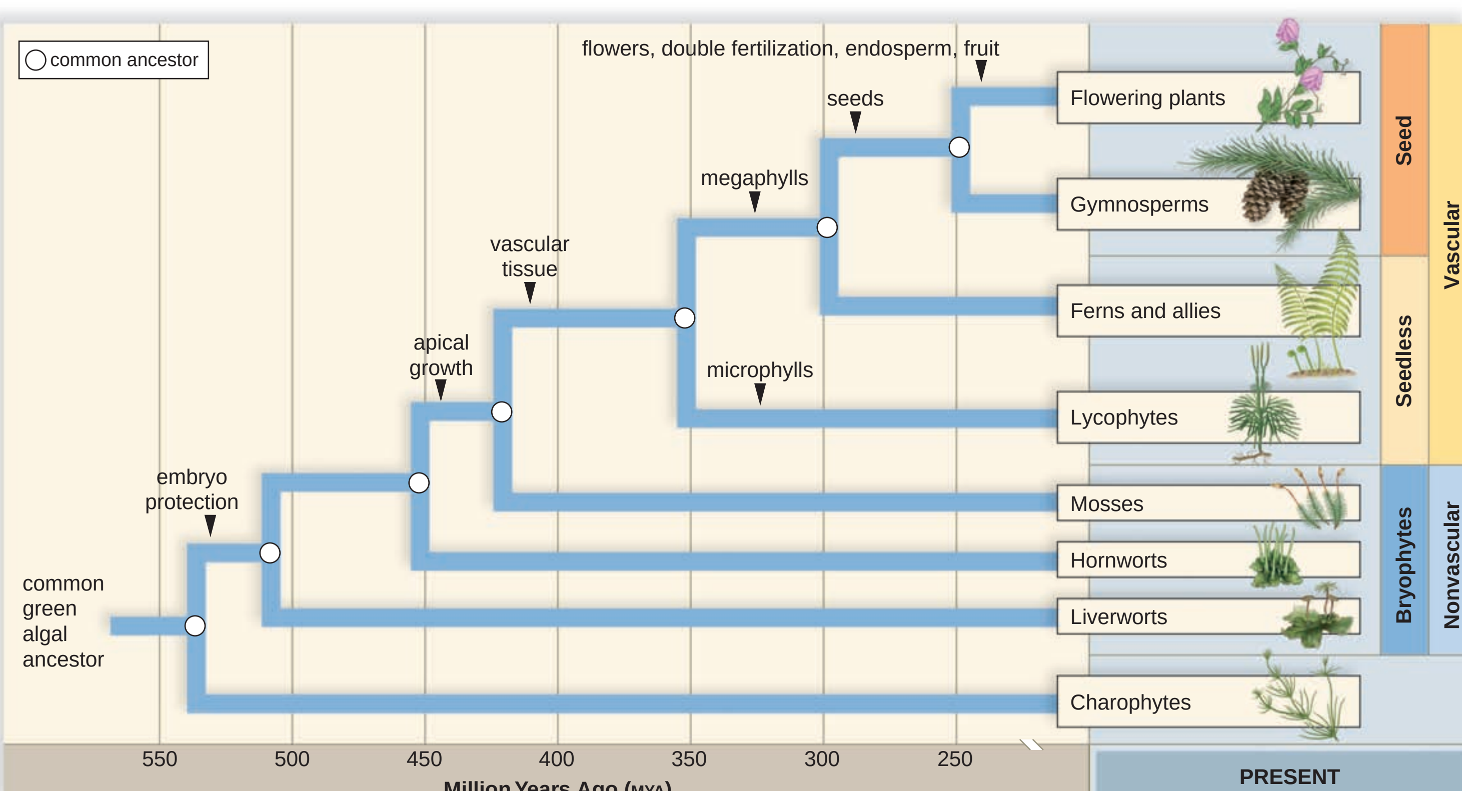


FIGURE 23.1 **Evolutionary history of plants.**

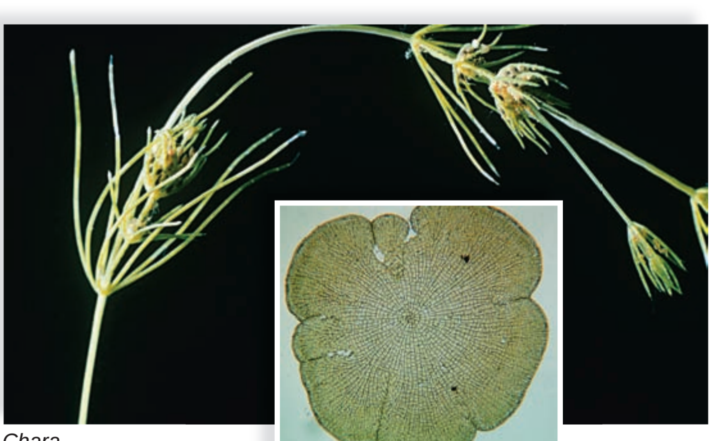
The evolution of plants involves these significant innovations. In particular, protection of a multicellular embryo was seen in the first plants to live on land. Vascular tissue permits the transport of water and nutrients. The evolution of the seed increased the chance of survival for the next generation.

among living charophytes, Charales (an order with 300 macroscopic species) and the *Coleochaete* (a genus with 30 microscopic species), featured in Figure 23.2, are most like land plants. Charophytes and land plants are in the same clade and form a monophyletic group (see Fig. 23.1). Their common ancestor no longer exists, but if it did, it would have features that resemble those of the Charales and *Coleochaete*.

First, let's take a look at these filamentous green algae (Fig. 23.2). The Charales (e.g., *Chara*) are commonly known as stoneworts because some species are encrusted with calcium carbonate deposits. The body consists of a single file of very long cells anchored in mud by thin filaments. Whorls of branches occur at multicellular nodes, regions between the giant cells of the main axis. Male and female reproductive structures grow at the nodes. The zygote is retained until it is enclosed by tough walls. A *Coleochaete* looks like a flat pancake, but the body is actually composed of elongated branched filaments of cells that spread flat across the substrate or form a three-dimensional cushion. The zygote is also retained in *Coleochaete*.

These two groups of charophytes have several features that would have promoted the evolution of multicellular land plants listed in Table 23.1, which have complex tissues and organs. And these features are present in charophytes and/or improved upon in land plants today:

1. *The cellulose cell walls of charophytes* and the land plant lineage are laid down by the same unique type of cellulose synthesizing complexes. Charophytes also have a mechanism of cell-wall formation during cytokinesis that is nearly identical to that of land plants. In land plants, a strong cell wall assists staying erect.
2. *The apical cells of charophytes* produce cells that allow their filaments to increase in length. At the nodes, other cells can divide asymmetrically to produce reproductive structures. Land plants are noted for their apical tissue that produces specialized tissues that add to or develop into new organs, such as new branches and leaves.
3. *The plasmodesmata of charophytes* provide a means of communication between neighboring cells, otherwise separated by cell walls. Perhaps plasmodesmata play a role in the evolution of specialized tissues in land plants, but this is not known for certain.
4. *The placenta* (designated cells) *of charophytes* transfers nutrients from haploid cells of the previous generation to the diploid zygote. Both charophytes and land plants retain and care for the zygote.



Chara

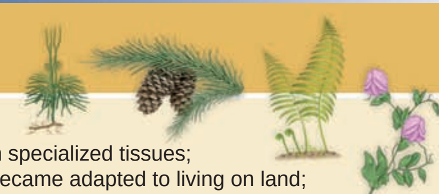
Coleochaete

FIGURE 23.2 Charophytes.

The charophytes (represented here by *Chara* and *Coleochaete*) are the green algae most closely related to the land pants.

TABLE 23.1

DOMAIN: Eukarya
KINGDOM: Plants



CHARACTERISTICS
Multicellular, usually with specialized tissues; photosynthesizers that became adapted to living on land; most have alternation of generations life cycle.

Charophytes
Live in water; haploid life cycle; share certain traits with the land plants

LAND PLANTS (embryophytes)
Alternation of generation life cycle; protect a multicellular sporophyte embryo; gametangia produce gametes; apical tissue produces complex tissues; waxy cuticle prevents water loss.

Bryophytes (liverworts, hornworts, mosses)
Low-lying, nonvascular plants that prefer moist locations: Dominant gametophyte produces flagellated sperm; unbranched, dependent sporophyte produces windblown spores.

VASCULAR PLANTS (lycophytes, ferns and their allies, seed plants)
Dominant, branched sporophyte has vascular tissue: Lignified xylem transports water, and phloem transports organic nutrients; typically has roots, stems, and leaves; and gametophyte is eventually dependent on sporophyte.

Lycophytes (club mosses)
Leaves are microphylls with a single, unbranched vein; sporangia borne on sides of leaves produce windblown spores; independent and separate gametophyte produces flagellated sperm.

Ferns and Allies (pteridophytes)
Leaves are megaphylls with branched veins; dominant sporophyte produces windblown spores in sporangia borne on leaves; and independent and separate gametophyte produces flagellated sperm.

SEED PLANTS (gymnosperms and angiosperms)
Leaves are megaphylls; dominant sporophyte produces heterospores that become dependent male and female gametophytes. Male gametophyte is pollen grain and female gametophyte occurs within ovule, which becomes a seed.

Gymnosperms (cycads, ginkgoes, conifers, gnetophytes)
Usually large; cone-bearing; existing as trees in forests. Sporophyte bears pollen cones, which produce windblown pollen (male gametophyte), and seed cones, which produce seeds.

Angiosperms (flowering plants)
Diverse; live in all habitats. Sporophyte bears flowers, which produce pollen grains, and bear ovules within ovary. Following double fertilization, ovules become seeds that enclose a sporophyte embryo and endosperm (nutrient tissue). Fruit develops from ovary.

Alternation of Generations Life Cycle

All land plants have an **alternation of generations life cycle.** Study the alternation of generation life cycle in Figure 23.3 to realize that the sporophyte (2n) is so named for its production of spores by meiosis. A **spore** is a haploid reproductive cell that develops into a new organism without the need to fuse with another reproductive cell. In the plant life cycle, a spore undergoes mitosis and becomes a gametophyte.

The gametophyte (n) is so named for its production of gametes. In plants, eggs and sperm are produced by mitotic cell division. A sperm and egg fuse, forming a diploid zygote that undergoes mitosis—becoming the sporophyte embryo, and then the 2n generation.

Two observations are in order. First, meiosis produces haploid spores. This is consistent with the realization that the sporophyte is the diploid generation and spores are haploid reproductive cells. Second, mitosis occurs as a spore becomes a gametophyte, and mitosis occurs as a zygote becomes a sporophyte. Indeed, it is the occurrence of mitosis at these times that results in two generations.

As a contrast to the alternation of generation life cycle, consider the haploid life cycle of charophytes. In the haploid life cycle (see page 380), the zygote undergoes meiosis, and therefore only four zoospores are produced per zygote. In the plant life cycle, the zygote becomes a multicellular sporophyte with one or more sporangia that produces many windblown spores. The production of so many spores would most likely have assisted land plants in colonizing the land environment.

Dominant Generation

Land plants differ as to which generation is dominant—that is, more conspicuous. In a moss, the gametophyte is dominant, but in ferns, pine trees, and peach trees, the sporophyte is dominant (Fig. 23.4). In the history of land plants, only the sporophyte evolves vascular tissue; therefore, the shift to sporophyte dominance is an adaptation to life on land. Notice that as the sporophyte gains in dominance, the gametophyte becomes microscopic. It also becomes dependent on the sporophyte.

Other Derived Traits of Land Plants

Also, in land plants,

1. Not just the zygote but also the multicellular 2n embryo are retained and protected from drying out. Because they protect the embryo, an alternate name for the land plant clade is **embryophyta.**
2. This 2n generation, called a **sporophyte,** produces at least one, and perhaps several, multicellular, sporangia.
3. **Sporangia** (sing., sporangium) produce spores by meiosis. Spores (and pollen grains, if present) have a wall that contains **sporopollenin,** a molecule that prevents drying out.

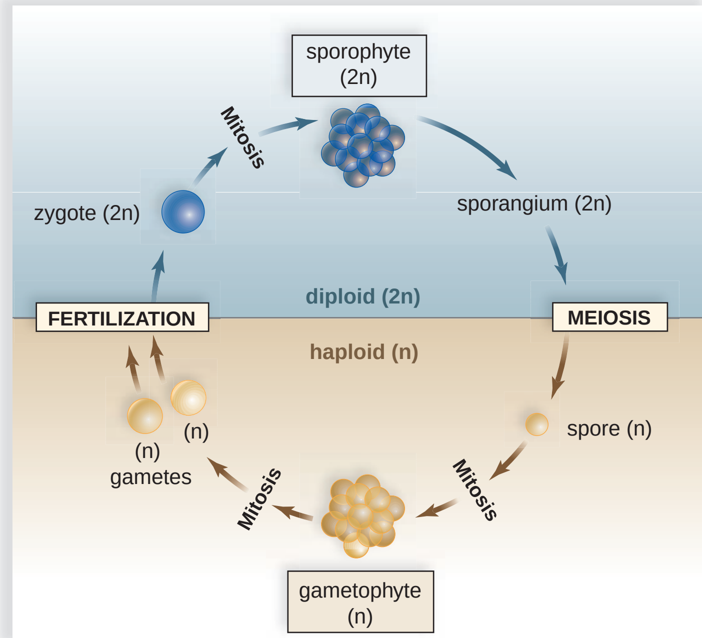
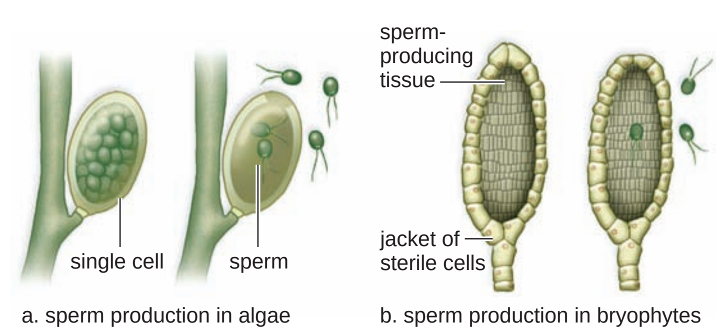


FIGURE 23.3 **Alternation of generations in land plants.**

The zygote develops into a multicellular 2n generation, and meiosis produces spores in multicellular sporangia. The gametophyte generation produces gametes within multicellular gametangia.

4. Spores become an n generation, called a **gametophyte,** that bears multicellular gametangia, which have an outer layer of sterile cells and an inner mass of cells that become the gametes:



A male gametangium is called an **antheridium,** and a female gametangium is called an **archegonium.**

Aside from innovations associated with the life cycle, the exposed parts of land plants are covered by an impervious waxy **cuticle,** which prevents loss of water. Most land plants also have **stomata** (sing., **stoma**), little openings, that allow gas exchange, despite the plant being covered by a cuticle (Fig. 23.5).

Another trait we see in most land plants is the presence of apical tissue, which has the ability to produce complex tissues and organs.

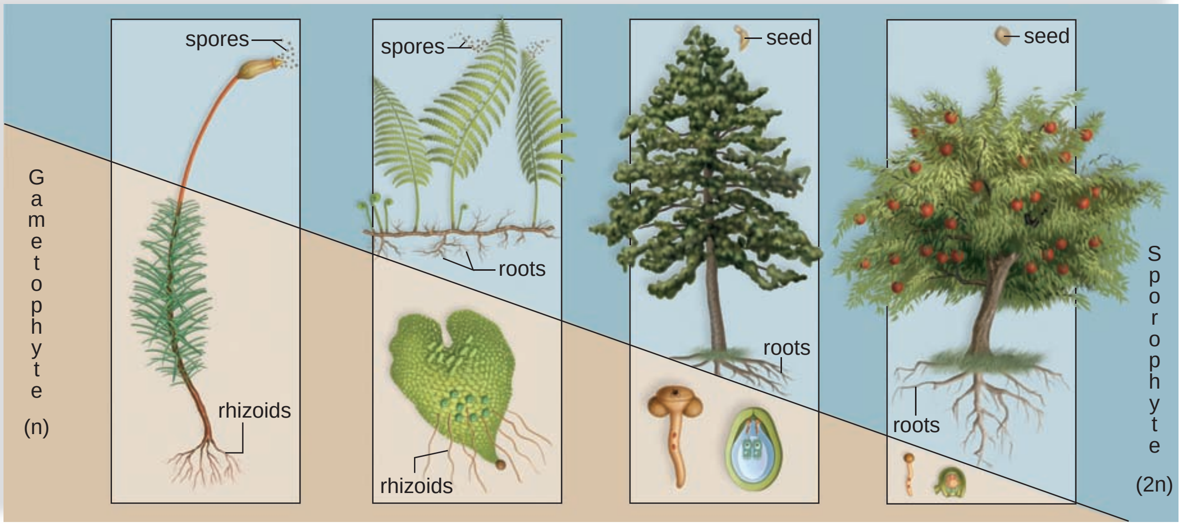


FIGURE 23.4 Reduction in the size of the gametophyte.

Notice the reduction in the size of the gametophyte and the increase in the size of the sporophyte among these representatives of today's land plants. This trend occurred as these plants became adapted for life on land. In the moss and fern, spores disperse the gametophyte. In gymnosperms and angiosperms, seeds disperse the sporophyte.

Check Your Progress 23.1

1. What are the benefits of a land existence for plants?
2. What traits are shared by both charophytes and land plants?
3. What is the role of each generation in the alternation of generations life cycle?

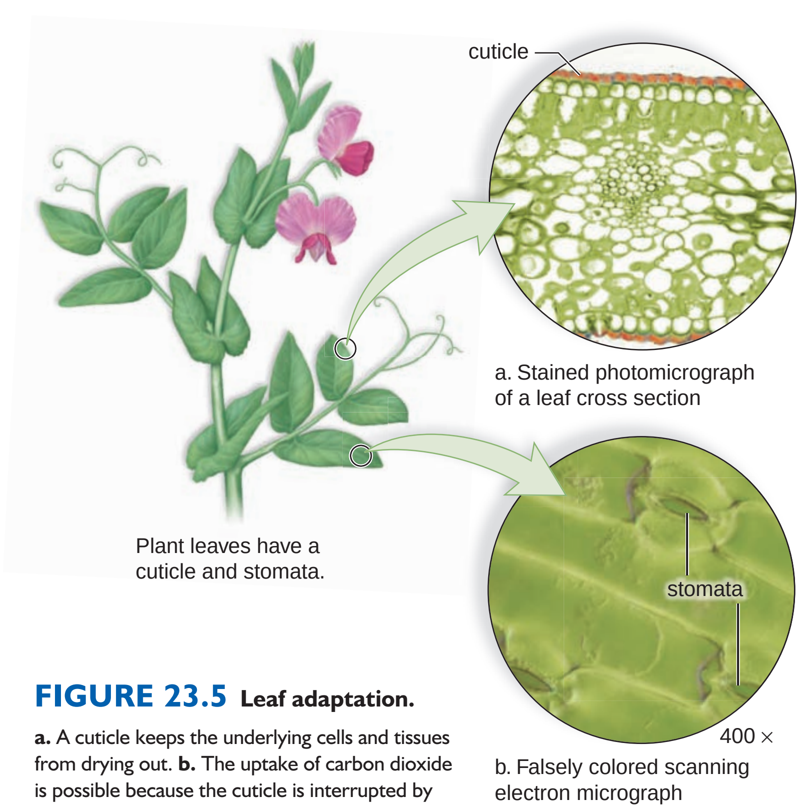


FIGURE 23.5 Leaf adaptation.

a. A cuticle keeps the underlying cells and tissues from drying out. **b.** The uptake of carbon dioxide is possible because the cuticle is interrupted by stomata.

23.2 Evolution of Bryophytes: Colonization of Land

The **bryophytes**—the liverworts, hornworts, and mosses—are the first plants to colonize land. The suffix wort is an Anglo-Saxon term meaning herb. They only superficially appear to have the roots, stems, and leaves because, by definition, true roots, stems, and leaves must contain vascular tissue, which the bryophytes lack. Therefore, bryophytes are often called the **nonvascular plants.** Lacking **vascular tissue,** which is specialized for the transport of water and organic nutrients throughout the body of a plant, bryophytes remain low-lying, and even mosses, which do stand erect, only reach a maximum height of about 20 cm.

The fossil record contains some evidence that the various bryophytes evolved during the Ordovician period. An incomplete fossil record makes it difficult to tell how closely related the various bryophytes are. Molecular data, in particular, suggest that these plants have individual lines of descent, as shown in Figure 23.1, and that they do not form a monophyletic group. The observation that today's mosses have a rudimentary form of vascular tissue suggests that they are more closely related to vascular plants than the hornworts and liverworts.

Bryophytes do share other traits with the vascular plants. For example, they have an alternation of generations life cycle and they have the numbered traits listed on page 412. Their bodies are covered by a cuticle that is interrupted in hornworts and mosses by stomata and they have apical tissue that produces complex tissues. However, bryophytes are the only land plants in which the gametophyte is dominant (see Fig. 23.4). Their gametangia are called antheridia and archegonia. Antheridia produce flagellated sperm, which means they need a film of moisture in order for sperm to swim to eggs located inside archegonia. The lack of vascular tissue and the presence of flagellated sperm means that you are apt to find bryophytes in moist locations. Some bryophytes compete well in harsh environments because they reproduce asexually.

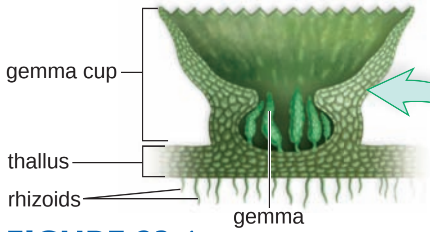
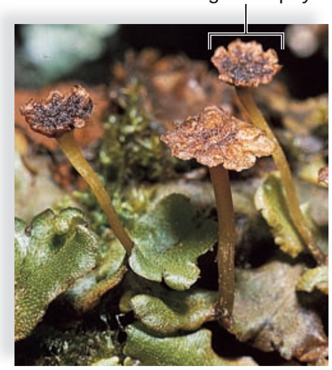


FIGURE 23.6

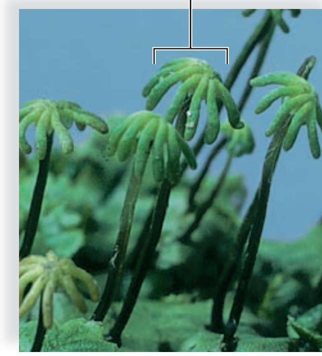
Liverwort, *Marchantia*.

a. Gemmae can detach and start a new plant. **b.** Antheridia are present in disk-shaped structures, and archegonia are present in umbrella-shaped structures.

a. Thallus with gemmae cups



b. Male gametophytes bear antheridia



c. Female gametophytes bear archegonia

Liverworts

Liverworts are divided into two groups—the thallose liverworts with flattened bodies, known as a thallus; and the leafy liverworts, which superficially resemble mosses. The name liverwort refers to the lobes of a thallus, which to some resemble those of the liver. The majority of liverwort species are the leafy types.

The liverworts in the genus *Marchantia* have a thin thallus, about 30 cells thick in the center. Each branched lobe of the thallus is approximately a centimeter in length; the upper surface is divided into diamond-shaped segments with a small pore, and the lower surface bears numerous hairlike extensions called **rhizoids** [Gk., *rhizion,* dim. of root] that project into the soil (Fig. 23.6). Rhizoids serve in anchorage and limited absorption. *Marchantia* reproduces both asexually and sexually. Gemma cups on the upper surface of the thallus contain gemmae, groups of cells that detach from the thallus and can start a new plant. Sexual reproduction depends on disk-headed stalks that bear antheridia and on umbrella-headed stalks that bear archegonia. Following fertilization, tiny sporophytes composed of a foot, a short stalk, and a capsule begin growing within archegonia. Windblown spores are produced within the capsule.

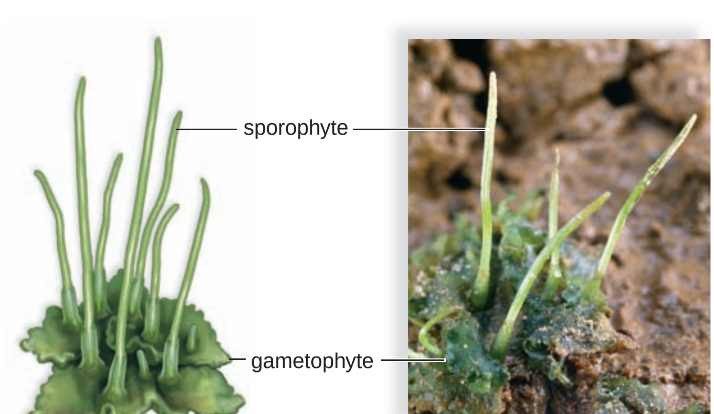


FIGURE 23.7 **Hornwort, *Anthoceros* sp.**

The "horns" of a hornwort are sporophytes that grow continuously from a base anchored in gametophyte tissue.

Hornworts

The **hornwort** gametophyte usually grows as a thin rosette or ribbonlike thallus between 1 and 5 cm in diameter. Although some species of hornworts live on trees, the majority of species live in moist, well-shaded areas. They photosynthesize, but they also have a symbiotic relationship with cyanobacteria, which, unlike plants, can fix nitrogen from the air.

The small sporophytes of a hornwort resemble tiny, green broom handles rising from a thin gametophyte, usually less than 2 cm in diameter (Fig. 23.7). Like the gametophyte, a sporophyte can photosynthesize, although it has only one chloroplast per cell. A hornwort can bypass the alternation of generations life cycle by producing asexually through fragmentation.

Mosses

Mosses are the largest phyla of nonvascular plants, with over 15,000 species. The term bryophytes is sometime used to refer only to mosses. There are three distinct groups of mosses: peat mosses, granite mosses, and true mosses. Although most prefer damp, shaded locations in the temperate zone, some survive in deserts, and others inhabit bogs and streams. In forests, they frequently form a mat that covers the ground and rotting logs. In dry environments, they may become shriveled, turn brown, and look completely dead. As soon as it rains, however, the plant becomes green and resumes metabolic activity.

Figure 23.8 describes the life cycle of a typical temperate-zone moss. The gametophyte of mosses begins as an algalike branching filament of cells, the protonema, which precedes and produces upright leafy shoots that sprout rhizoids. The shoots bear either antheridia or archegonia. The dependent sporophyte consists of a foot, which is enclosed in female gametophyte tissue; a stalk; and an upper capsule, the sporangium, where spores are produced. A moss sporophyte can be likened to a child that never leaves home—it is always attached to the gametophyte. At first, the sporophyte is green and photosynthetic; at maturity, it is brown and nonphotosynthetic. In some species, the sporangium can produce as many as 50 million spores. The spores disperse the gametophyte generation.

Check Your Progress 23.2

1. Name an advantage and disadvantage to the manner in which bryophytes reproduce on land.

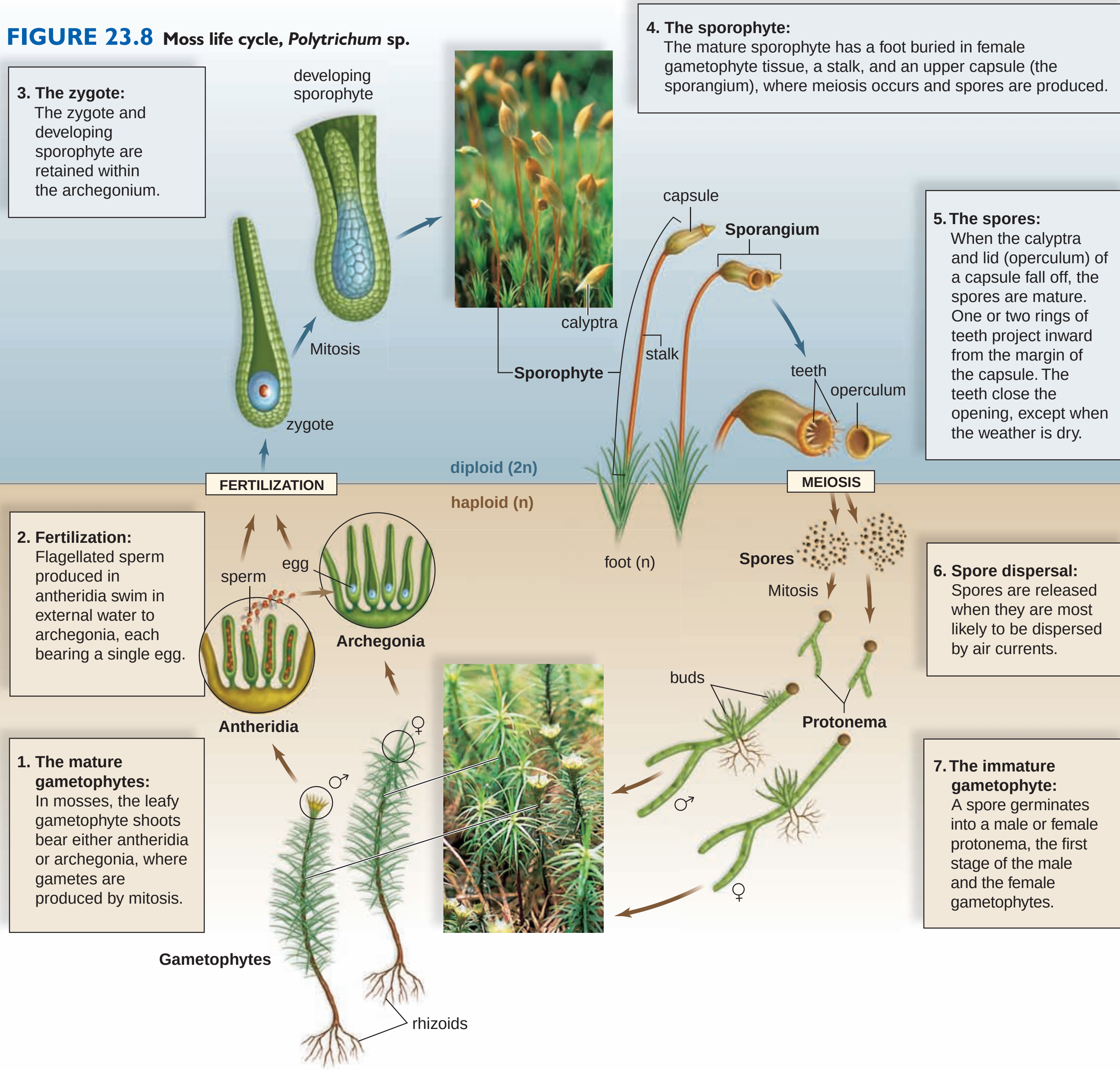


FIGURE 23.8 Moss life cycle, *Polytrichum* sp.

The Uses of Bryophytes

Mosses, and also liverworts and hornworts, are of great ecological significance. They contribute to the lush beauty of rain forests, the stability of dunes, and conversion of mountain rocks to soil because of their ability to trap and hold moisture, retain metals in the soil, and tolerate desiccation. An effort to conserve bryophytes will most likely center on *Sphagnum* (peat moss) because of its commercial and ecological importance. The cell walls of peat moss have a tremendous ability to absorb water, which is why peat moss is often used in gardening to improve the water-holding capacity of the soil. One percent of the Earth's surface is peatlands, where dead *Sphagnum*, in particular, accumulates and does not decay. This material called peat can be extracted and used for various purposes, such as fuel and building materials. Peat holds much CO_2, and there is concern that when peat is extracted, we are losing this depository for CO_2, the gas that contributes most to global warming.

Bryophytes are expected to become valuable to genetic research and applications. Once scientists know which genes give bryophytes the ability to resist chemical reagents and decay, as well as animal attacks, these qualities could be transferred to other plants through genetic engineering.

23.3 Evolution of Lycophytes: Vascular Tissue

Today, **vascular plants** dominate the natural landscape in nearly all terrestrial habitats. Trees are vascular plants that achieve great height because they have roots that absorb water from the soil and a vascular tissue called **xylem,** which transports water through the stem to the leaves. (Another conducting tissue called **phloem** transports nutrients in a plant.) Further, the cell walls of the conducting cells in xylem contain **lignin,** a material that strengthens plant cell walls; therefore, the evolution of xylem was essential to the evolution of trees.

However, we are getting ahead of our story because the fossil record tells us that the first vascular plants, such as *Cooksonia,* were more likely a bush than a tree. *Cooksonia* is a rhyniophyte, a group of vascular plants that flourished during the Silurian period, but then became extinct by the mid-Devonian period. The rhyniophytes were only about 6.5 cm tall and had no roots or leaves. They consisted simply of a stem that forked evenly to produce branches ending in sporangia (Fig. 23.9). The branching of *Cooksonia* was significant because instead of the single sporangium produced by a bryophyte, the plant produced many sporangia, and therefore many more spores. For branching to occur, meristem has to be positioned at the apex (tip) of stems and its branches, as it is in vascular plants today.

The sporangia of *Cooksonia* produced windblown spores, and since it was not a seed plant, it was a **seedless vascular plant,** as are lycophytes.

Lycophytes

In addition to the stem of early vascular plants, the first **lycophytes** also had leaves and roots. The leaves are called **microphylls** because they had only one strand of vascular tissue. Microphylls most likely evolved as simple side extensions of the stem (see Fig 23.11*a*). Roots evolved simply as lower extensions of the stem; the organization of vascular tissue in the roots of lycophytes today is much like it was in the stems of fossil vascular plants—the vascular tissue is centrally placed.

Today's lycophytes, also called club mosses, include three groups of 1,150 species: the ground pines (*Lycopodium*), spike mosses (*Selaginella*), and quillworts (*Isoetes*). Figure 23.10 shows the structure of *Lycopodium;* note the structure of the roots and leaves and the location of sporangia. The roots come off a branching, underground stem called a **rhizome.** The microphylls that bear sporangia are called **sporophylls,** and they are grouped into club-shaped **strobili,** accounting for their common name club mosses.

The sporophyte is dominant in lycophytes, as it is in all vascular plants. (This is the generation that has vascular tissue!) Ground pines are homosporous; the spores germinate into inconspicuous and independent gametophytes, as they do in a fern (see Fig. 23.15). The sperm are flagellated in bryophytes, lycophytes, and ferns. (The spike mosses and quillworts are heterosporous, as are seed plants; microspores develop into male gametophytes, and megaspores develop into female gametophytes.)

Check Your Progress 23.3

1. Name two features of lycophytes significant to the evolution of land plants.
2. How does the structure of xylem contribute to helping a plant stay erect?

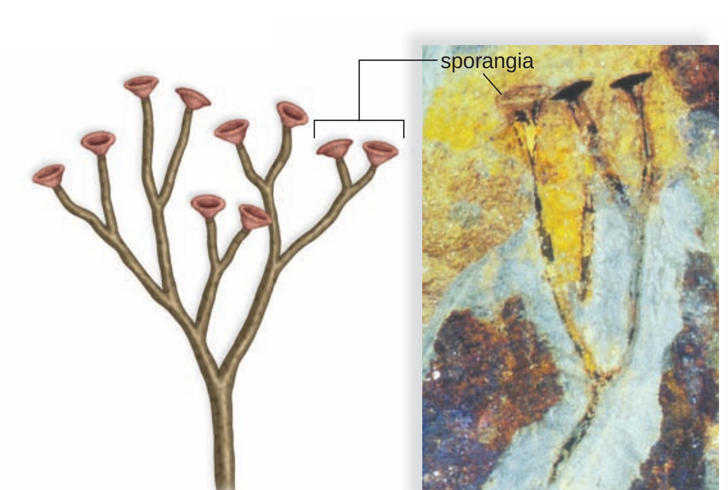


FIGURE 23.9 A *Cooksonia* fossil.

The upright branches of a *Cooksonia* fossil, no more than a few centimeters tall, terminated in sporangia as seen here in the drawing and photo.

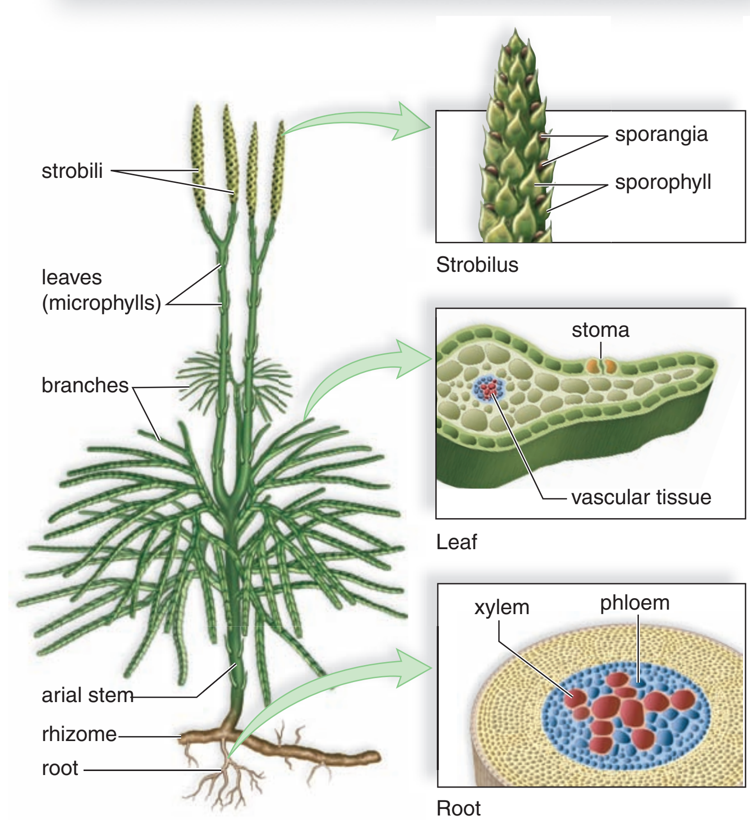


FIGURE 23.10 Ground pine, *Lycopodium*.

The *Lycopodium* sporophyte develops an underground rhizome system. A rhizome is an underground stem. This rhizome produces true roots along its length.

23.4 Evolution of Pteridophytes: Megaphylls

Pteridophytes, consisting of ferns and their allies—horsetails, and whisk ferns—are seedless vascular plants. However, both pteridophytes and seed plants, which are studied in Section 23.5, have megaphylls. **Megaphylls** are broad leaves with several strands of vascular tissue. Figure 23.11*a* shows the difference between microphylls and megaphylls, and Figure 23.11*b* shows how megaphylls could have evolved.

Megaphylls, which evolved about 370 MYA (million years ago), allow plants to efficiently collect solar energy, leading to the production of more food and the possibility of producing more offspring than plants without megaphylls. Therefore, the evolution of megaphylls made plants more fit. Recall that fitness, in an evolutionary sense, is judged by the number of living offspring an organism produces in relationship to others of its own kind.

The pteridophytes, like the lycophytes, were dominant from the late Devonian period through the Carboniferous period. Today, the lycophytes are quite small, but some of the extinct relatives of today's club mosses were 35 m tall and dominated by the Carboniferous swamps. The horsetails, at 18 m, and ancient tree ferns, at 8 m, also contributed significantly to the great swamp forests of the time (see the Ecology Focus on page 423).

Horsetails

Today, **horsetails** consist of one genus, *Equisetum,* and approximately 25 species of distinct seedless vascular plants. Most horsetails inhabit wet, marshy environments around the globe. About 300 MYA, horsetails were dominant plants and grew as large as modern trees. Today, horsetails have a rhizome that produces hollow, ribbed aerial stems and reaches a height of 1.3 m (Fig. 23.12). The whorls of slender, green side branches at the joints (nodes) of the stem make the plant bear a resemblance to a horse's tail. The leaves may have been megaphylls at one time but now they are reduced and form whorls at the nodes. Many horsetails have strobili at the tips of all stems; others send up special buff-colored stems that bear the strobili. The spores germinate into inconspicuous and independent gametophytes.

The stems are tough and rigid because of silica deposited in cell walls. Early Americans, in particular, used horsetails for scouring pots and called them "scouring rushes." Today, they are still used as ingredients in a few abrasive powders.

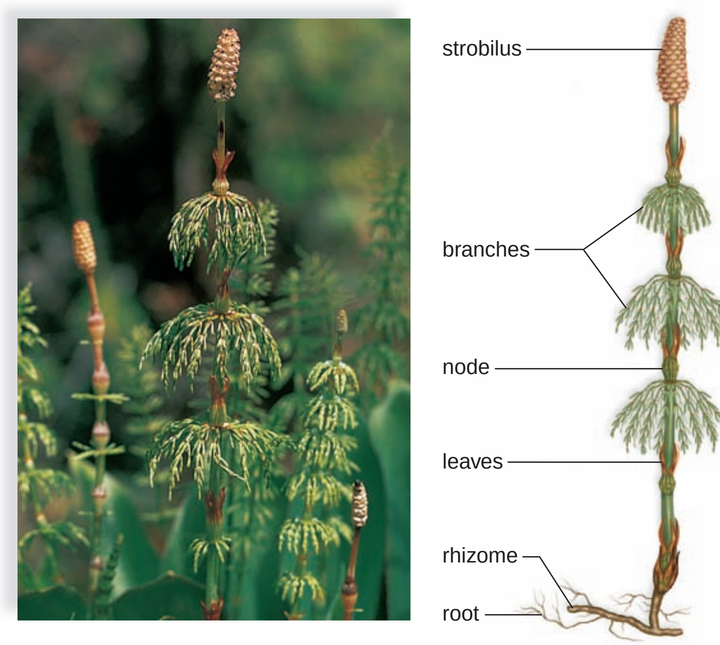
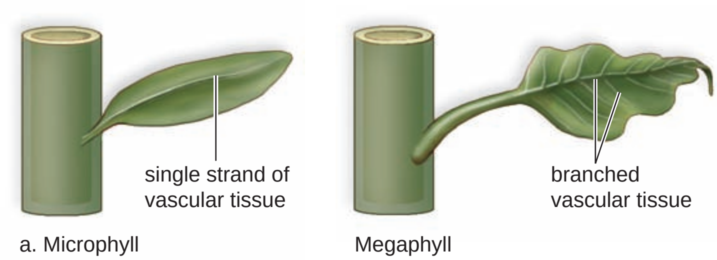


FIGURE 23.12 Horsetail, *Equisetum*.

Whorls of branches and tiny leaves are at the nodes of the stem. Spore-producing sporangia are borne in strobili.



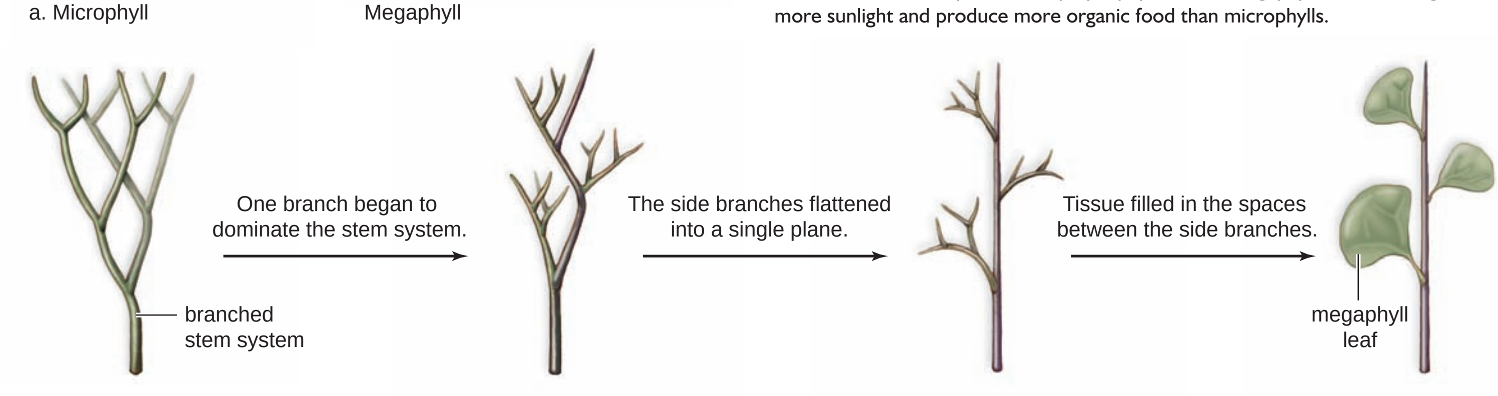


FIGURE 23.11 Microphylls and megaphylls.

a. Microphylls have a single strand of vascular tissue, which explains why they are quite narrow. In contrast, megaphylls have several branches of vascular tissue and are more broad. **b.** These steps show the manner in which megaphylls may have evolved. All vascular plants, except lycophytes, bear megaphylls, which can gather more sunlight and produce more organic food than microphylls.

Whisk Ferns

Whisk ferns are represented by the genera *Psilotum* and *Tmesipteris*. Both genera live in southern climates as epiphytes (plants that live in/on trees), or they can also be found on the ground. The two *Psilotum* species resemble a whisk broom (Fig. 23.13) because they have no leaves. A horizontal rhizome gives rise to an aerial stem that repeatedly forks. The sporangia are borne on short side branches. The two to three species of *Tmesipteris* have appendages that some maintain are reduced megaphylls.

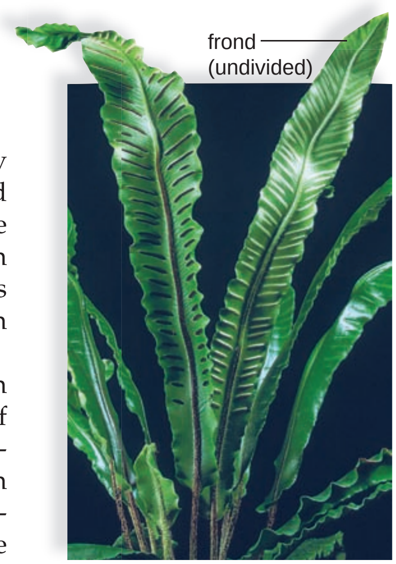
Ferns

Ferns include approximately 11,000 species. Ferns are most abundant in warm, moist, tropical regions, but they can also be found in temperate regions and as far north as the Arctic Circle. Several species live in dry, rocky places and others have adapted to an aquatic life. Ferns range in size from minute aquatic species less than 1 cm in diameter to modern giant tropical tree ferns that exceed 20 m in height.

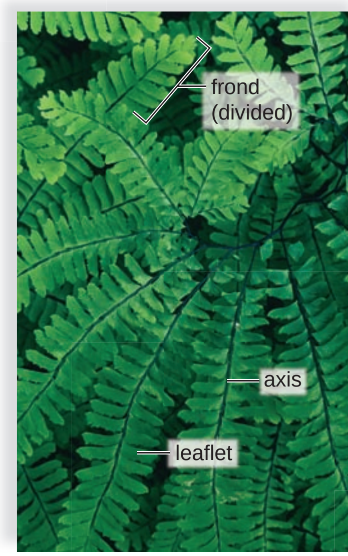
The megaphylls of ferns, called **fronds,** are commonly divided into leaflets. The royal fern has fronds that stand about 1.8 m tall; those of the hart's tongue fern are straplike and leathery; and those of the maidenhair fern are broad, with subdivided leaflets (Fig. 23.14). In nearly all ferns, the leaves first appear in a curled-up form called a fiddlehead, which unrolls as it grows.

The life cycle of a typical temperate zone fern, shown in Figure 23.15, applies in general to the other types of vascular seedless plants. The dominant sporophyte produces windblown spores by meiosis within sporangia. In a fern, the sporangia can be located within sori on the underside of the leaflets. The windblown spores disperse the gametophyte, the generation that lacks vascular tissue.

Cinnamon fern, *Osmunda cinnamomea*



Hart's tongue fern,
Campyloneurum scolopendrium



Maidenhair fern,
Adiantum pedatum

FIGURE 23.14 **Diversity of ferns.**

The separate heart-shaped gametophyte produces flagellated sperm that swim in a film of water from the antheridium to the egg within the archegonium, where fertilization occurs. Eventually, the gametophyte disappears and the sporophyte is independent. This can be likened to a child that grows up in its parents' house, and then goes out on its own. The two generations of a fern are considered to be separate and independent of one another. Many ferns can reproduce asexually by fragmentation of the fern rhizome.

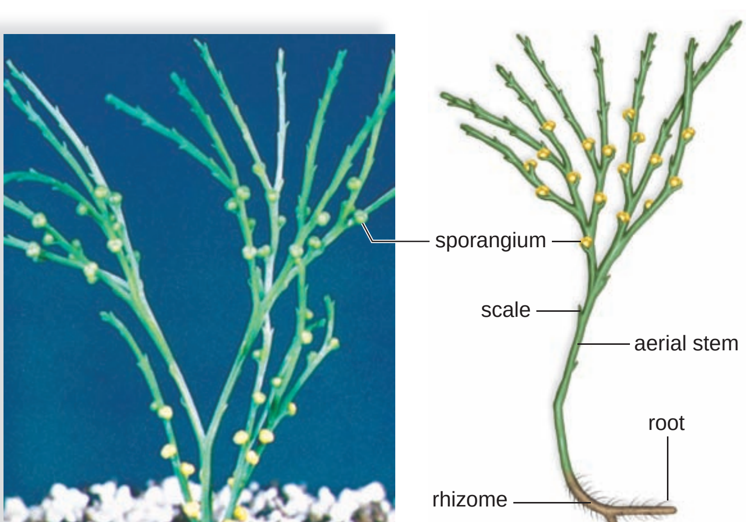


FIGURE 23.13 **Whisk fern, *Psilotum*.**

Psilotum has no leaves—the branches carry on photosynthesis. The sporangia are yellow.

Check Your Progress 23.4

1. In what two ways is the fern life cycle dependent on external water?
2. How is the life cycle of a fern different from the life cycle of a moss?

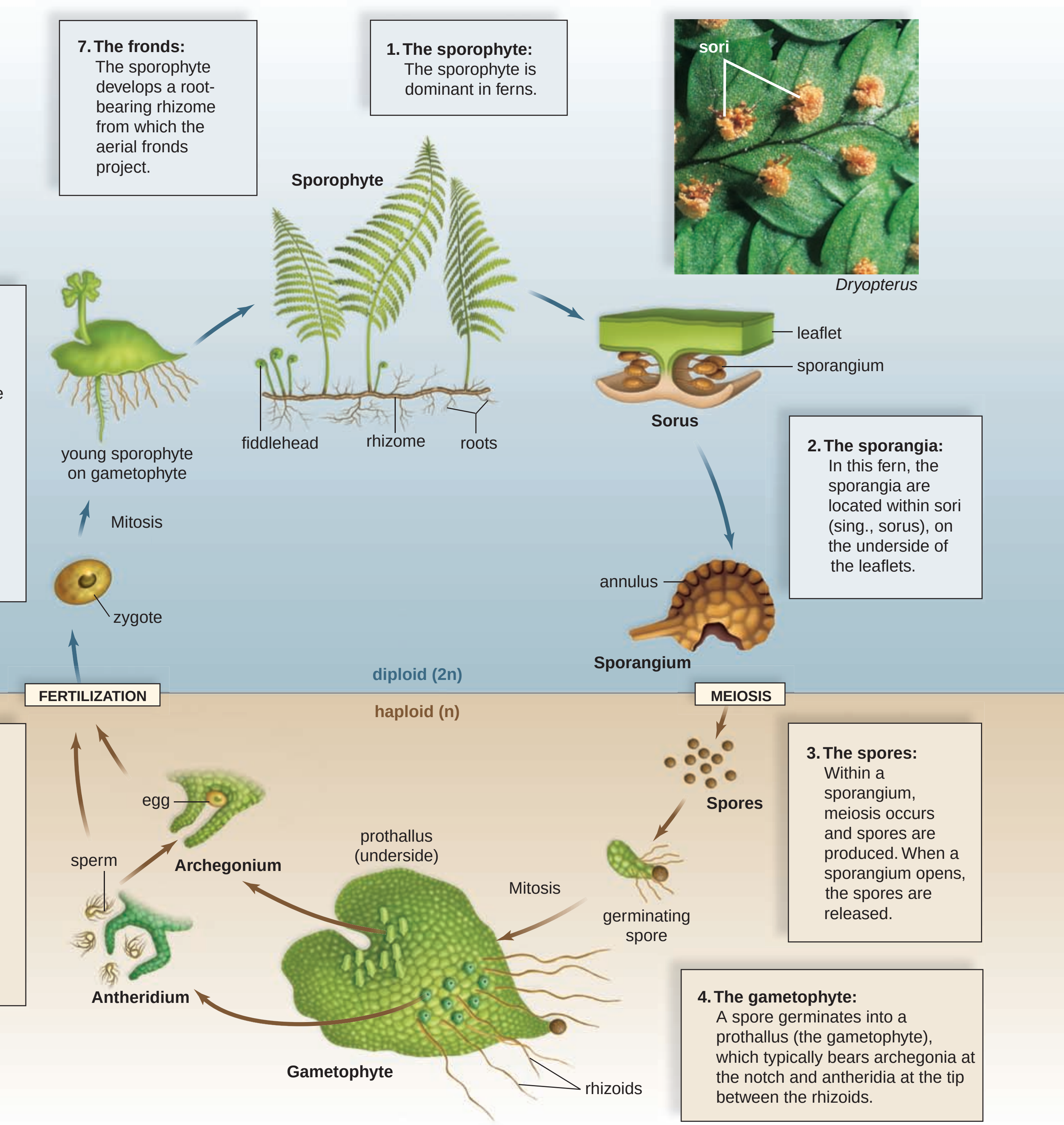


FIGURE 23.15
Fern life cycle.

The Uses of Ferns

Ostrich fern (*Matteuccia truthiopteris*) is the only edible fern to be traded as a food, and it comes to the table in North America as "fiddleheads." In tropical regions of Asia, Africa, and the western Pacific, dozens of types of ferns are taken from the wild and used as food. The fern *Azolla* harbors *Anabaena*, a nitrogen-fixing cyanobacteria, and *Azolla* is grown in rice paddies, where it fertilizes rice plants. It is estimated that each year, *Azolla* converts more atmospheric nitrogen into a form available for plant growth than all the legumes. And like legumes, its use avoids the problems associated with artificial fertilizer applications.

Several authorities have noted that ferns and their allies are used as medicines in China. Among the conditions being treated are boils and ulcers, whooping cough, and dysentery. Extracts from ferns have also been used to kill insects because they inhibit insect molting.

Ferns beautify gardens and horticulturists may use them in floral arrangements. Vases, small boxes and baskets, and also jewelry are made from the trunk of tree ferns. Their black and very hard vascular tissue provides many interesting patterns.

23.5 Evolution of Seed Plants: Full Adaptation to Land

Seed plants are vascular plants that use seeds as the dispersal stage. **Seeds** contain a sporophyte embryo and stored food within a protective seed coat. The seed coat and stored food allow an embryo to survive harsh conditions during long periods of dormancy (arrested state) until environmental conditions become favorable for growth. When a seed germinates, the stored food is a source of nutrients for the growing seedling. The survival value of seeds largely accounts for the dominance of seed plants today.

Like a few of the seedless vascular plants, seed plants are **heterosporous** (have microspores and megaspores) but their innovation was to retain the spores. (Seed plants do not release their spores! See Fig. 23.17.) The **microspores** become male gametophytes, called **pollen grains. Pollination** occurs when a pollen grain is brought to the vicinity of the female gametophyte by wind or a pollinator. Then, sperm move toward the female gametophyte through a growing **pollen tube.** A **megaspore** develops into a female gametophyte within an **ovule,** which becomes a seed following fertilization. Note that because the whole male gametophyte, rather than just the sperm as in seedless plants, moves to the female gametophyte, no external water is needed to accomplish fertilization.

The two types of seed plants alive today are called gymnosperms and angiosperms. In **gymnosperms** (mostly cone-bearing seed plants), the ovules are not completely enclosed by sporophyte tissue at the time of pollination. In **angiosperms** (flowering plants), the ovules are completely enclosed within diploid sporophyte tissue (ovaries), which becomes a fruit.

The first type of seed plant was a woody plant that appeared during the Devonian period and is miscalled a seed fern. The seed ferns of the Devonian were not ferns at all, they were progymnosperms. It's possible that these were the type of progymnosperm that gave rise to today's gymnosperms and angiosperms. All gymnosperms are still woody plants, but whereas the first angiosperms were woody, many today are nonwoody. Progymnosperms, including seed ferns, were part of the Carboniferous swamp forests (see the Ecology Focus on page 423).

Gymnosperms

The four groups of living gymnosperms [Gk. *gymnos,* naked, and *sperma,* seed] are conifers, cycads, ginkgoes, and gnetophytes. Since their seeds are not enclosed by fruit, gymnosperms have "naked seeds." Today, living gymnosperms are classified into 780 species. Still, the conifers are more plentiful today than other types of gymnosperms.

Conifers

Conifers consist of about 575 species of trees, many evergreen, including pines, spruces, firs, cedars, hemlocks, redwoods, cypresses, yews, and junipers. The name *conifers* signifies plants that bear **cones,** but other gymnosperm phyla are also cone-bearing. The coastal redwood (*Sequoia sempervirens*), a conifer native to northwestern California and southwestern Oregon, is the tallest living vascular plant and may attain nearly 100 m in height. Another conifer, the bristlecone pine (*Pinus longaeva*) of the White Mountains of California, is the oldest living tree; one is 4,900 years of age.

Vast areas of northern temperate regions are covered in evergreen coniferous forests (Fig. 23.16). The tough, needlelike leaves of pines conserve water because they have a thick cuticle and recessed stomata. Note in the life cycle of the pine (Fig. 23.17) that the sporophyte is dominant, pollen grains are windblown, and the seed is the dispersal stage. Conifers are **monoecious,** since they produce both pollen and seed cones.

Cycads

Cycads include 10 genera and 140 species of distinctive gymnosperms. The cycads are native to tropical and subtropical forests. *Zamia pumila* found in Florida is the only species of cycad native to North America. Cycads are commonly used in landscaping. One species, *Cycas revoluta,* referred to as the sago palm, is a common landscaping plant. Their large, finely divided leaves grow in clusters at the top of the stem, and therefore they resemble palms or ferns, depending on their height. The trunk of a cycad is unbranched, even if it reaches a height of 15–18 m, as is possible in some species.

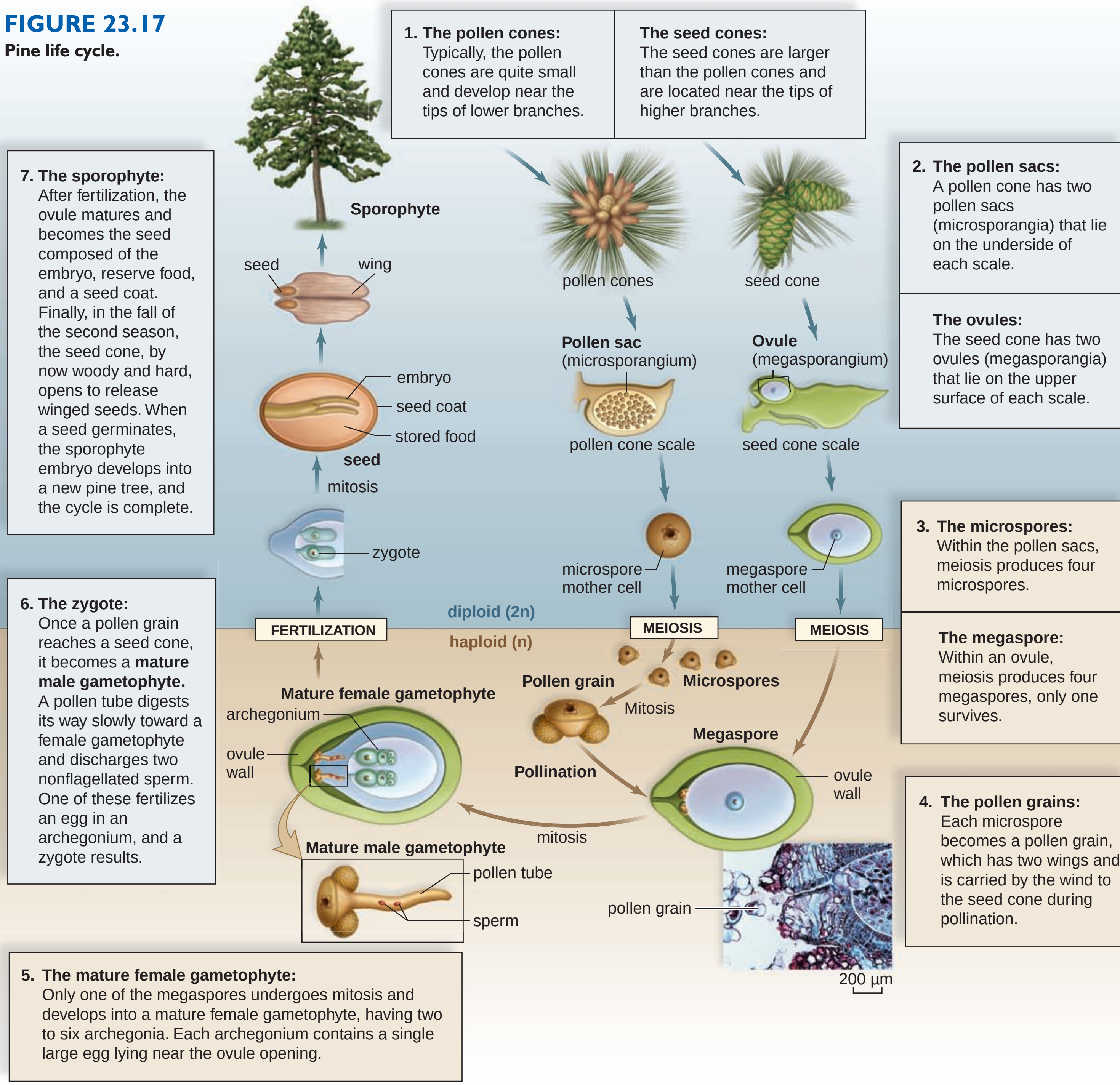
a. A northern coniferous forest of evergreen trees

b. Cones of lodgepole pine, *Pinus contorta*

c. Fleshy seed cones of juniper, *Juniperus*

FIGURE 23.16 **Conifers.**

FIGURE 23.17
Pine life cycle.



The Uses of Pines

Today, pines are grown in dense plantations for the purpose of providing wood for construction of all sorts. Although technically a softwood, some pinewoods are actually harder than so-called hardwoods. The foundations of the 125-year-old Brooklyn Bridge are made of Southern yellow pine.

Pines are well known for their beauty and pleasant smell; they make attractive additions to parks and gardens, and a number of dwarf varieties are now available for smaller gardens. Some pines are used as Christmas trees or for Christmas decorations.

Pine needles and the inner bark are rich in vitamins A and C. Pine needles can be boiled to make a tea to ease the symptoms of a cold, and the inner bark of white pines can be used in wound dressings or to provide a medicine for colds and coughs. Today, large pine seeds, called pine nuts, are sometimes harvested for use in cooking and baking.

Pine oil is distilled from the twigs and needles of Scotch pines and used to scent a number of household and personal care products, such as room sprays and masculine perfumes. Resin, made by pines as an insect and fungal deterrent, is harvested commercially for a derived product called turpentine.

Cycads have pollen and seed cones on separate plants. The cones, which grow at the top of the stem surrounded by the leaves, can be huge—even more than a meter long with a weight of 40 kg (Fig. 23.18*a*). Cycads have a life cycle of a gymnosperm, except they are pollinated by insects rather than by wind. Also, the pollen tube bursts in the vicinity of the archegonium, and multiflagellated sperm swim to reach an egg.

Cycads were plentiful in the Mesozoic era at the time of the dinosaurs, and it's likely that dinosaurs fed on cycad seeds. Now, cycads are in danger of extinction because they grow very slowly, a distinct disadvantage.

Ginkgoes

Although **ginkgoes** are plentiful in the fossil record, they are represented today by only one surviving species, *Ginkgo biloba*, the ginkgo or maidenhair tree. It is called the maiden hair tree because its leaves resemble those of a maiden hair fern. Ginkgoes are **dioecious**—some trees produce seeds (Fig. 23.18*b*), and others produce pollen. The fleshy seeds, which ripen in the fall, give off such a foul odor that male trees are usually preferred for planting. Ginkgo trees are resistant to pollution and do well along city streets and in city parks. Ginkgo is native to China, and in Asia, ginkgo seeds are considered a delicacy. Extracts from ginkgo trees have been used to improve blood circulation.

Like cycads, the pollen tube of gingko bursts to release multiflagellated sperm that swim to the egg produced by the female gametophyte located within an ovule.

Gnetophytes

Gnetophytes are represented by three living genera and 70 species of plants that are very diverse in appearance. In all gnetophytes, xylem is structured similarly, none have archegonia, and their strobili (cones) have a similar construction. The reproductive structures of some gnetophyte species produce nectar, and insects play a role in the pollination of these species. *Gnetum*, which occurs in the tropics, consists of trees or climbing vines with broad, leathery leaves arranged in pairs. *Ephedra*, occurring only in southwestern North America and southeast Asia, is a shrub with small, scalelike leaves (Fig. 23.18*c*). Ephedrine, a medicine with serious side effects, is extracted from *Ephedra*. *Welwitschia*, living in the deserts of southwestern Africa, has only two enormous, straplike leaves (Fig. 23.18*d*).

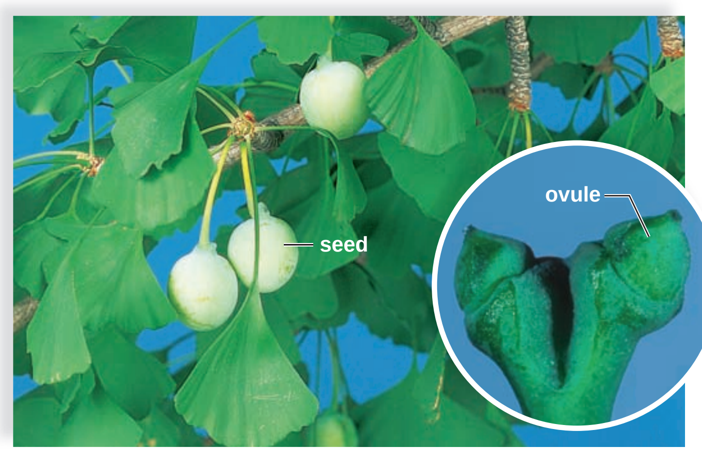
Check Your Progress 23.5A

1. Cite life cycle changes that represent seed plant adaptations, as exemplified by a pine tree, for reproducing on land.
2. What are the four types of gymnosperms?

FIGURE 23.18 Three groups of gymnosperms.

a. Cycads may resemble ferns or palms but they are cone-producing gymnosperms. **b.** A ginkgo tree has broad leaves and fleshy seeds borne at the end of stalklike megasporophylls. **c.** *Ephedra*, a type of gnetophyte, is a branched shrub. This specimen produces pollen in microsporangia. **d.** *Welwitschia miribilis*, another type of gnetophyte, produces two straplike leaves that split one to several times.

a. *Encephalartos transvenosus*, an African cycad



b. *Ginkgo biloba*, a native of China

c. *Ephedra*, a type of gnetophyte

d. *Welwitschia mirabilis*, a type of gnetophyte ecology focus

Carboniferous Forests

Our industrial society runs on fossil fuels such as coal. The term *fossil fuel* might seem odd at first until one realizes that it refers to the remains of organic material from ancient times. During the Carboniferous period more than 300 million years ago, a great swamp forest (Fig. 23A) encompassed what is now northern Europe, the Ukraine, and the Appalachian Mountains in the United States. The weather was warm and humid, and the trees grew very tall. These are not the trees we know today; instead, they are related to today's seedless vascular plants: the lycophytes, horsetails, and ferns! Lycophytes today may stand as high as 30 cm, but their ancient relatives were 35 m tall and 1 m wide. The stroboli were up to 30 cm long, and some had leaves more than 1 m long. Horsetails too—at 18 m tall—were giants compared to today's specimens. Tree ferns were also taller than tree ferns found in the tropics today. The progymnosperms, including "seed ferns," were significant plants of a Carboniferous swamp. Seed ferns are misnamed because they were actually progymnosperms.

The amount of biomass in a Carboniferous swamp forest was enormous, and occasionally the swampy water rose and the trees fell. Trees under water do not decompose well, and their partially decayed remains became covered by sediment that sometimes changed to sedimentary rock. Exposed to pressure from sedimentary rock, the organic material then became coal, a fossil fuel. This process continued for millions of years, resulting in immense deposits of coal. Geological upheavals raised the deposits to the level where they can be mined today.

With a change of climate, the trees of the Carboniferous period became extinct, and only their herbaceous relatives survived to our time. Without these ancient forests, our life today would be far different because they helped bring about our industrialized society.

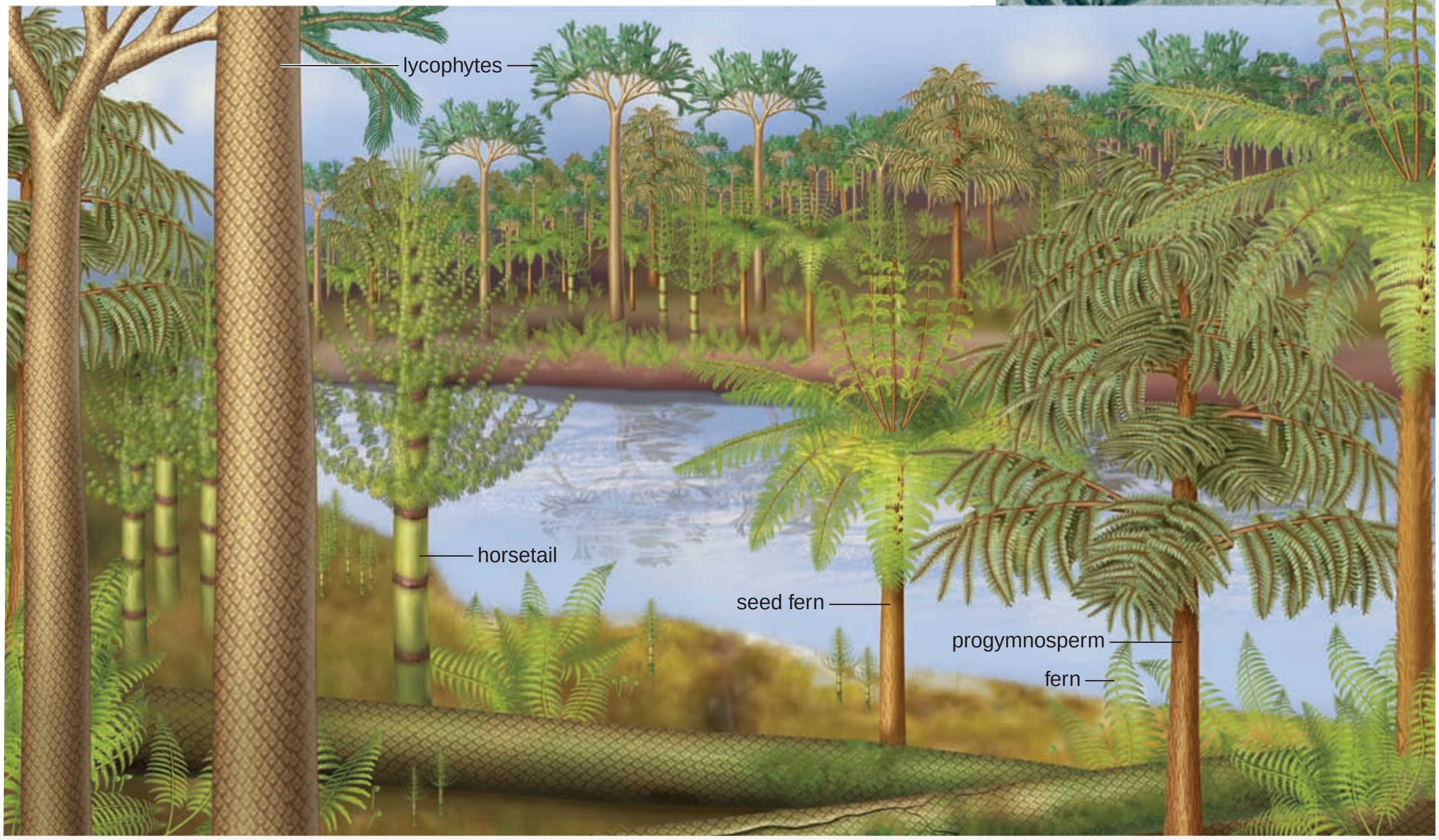


FIGURE 23A Swamp forest of the Carboniferous period.
Nonvascular plants and early gymnosperms dominated the swamp forests of the Carboniferous period. Among the early gymnosperms were the seed ferns, so named because their leaves looked like fronds, as shown in a micrograph of fossil remains in the upper right.

Angiosperms

Angiosperms [Gk. *angion,* dim. of *angos,* vessel, and *sperma,* seed] are the flowering plants. They are an exceptionally large and successful group of plants, with 240,000 known species—six times the number of all other plant groups combined. Angiosperms live in all sorts of habitats, from fresh water to desert, and from the frigid north to the torrid tropics. They range in size from the tiny, almost microscopic duckweed to *Eucalyptus* trees over 100 m tall. It would be impossible to exaggerate the importance of angiosperms in our everyday lives. Angiosperms include all the hardwood trees of temperate deciduous forests and all the broadleaved evergreen trees of tropical forests. Also, all herbaceous (nonwoody plants, such as grasses), and most garden plants are flowering plants. This means that all fruits, vegetables, nuts, herbs, and grains that are the staples of the human diet are angiosperms. As discussed in the Ecology Focus on pages 428–29, they provide us with clothing, food, medicines, and other commercially valuable products.

The flowering plants are called angiosperms because their ovules, unlike those of gymnosperms, are always enclosed within diploid tissues. In the Greek derivation of their name, *angio* ("vessel") refers to the ovary, which develops into a fruit, a unique angiosperm feature.

Origin and Radiation of Angiosperms

Although the first fossils of angiosperms are no older than about 135 million years (see Fig. 19.8), the angiosperms probably arose much earlier. Indirect evidence suggests the possible ancestors of angiosperms may have originated as long ago as 200 MYA. But their exact ancestral past has remained a mystery since Charles Darwin pondered it.

To find the angiosperm of today that might be most closely related to the first angiosperms, botanists have turned to DNA comparisons. Gene-sequencing data singled out *Amborella trichopoda* (Fig. 23.19) as having ancestral traits. This small woody shrub, with small cream-colored flowers, lives only on the island of New Caledonia in the South Pacific. Its flowers are only about 4–8 mm and the petals and sepals look the same; therefore, they are called tepals. Plants bear either male or female flowers, with a variable number of stamens or carpels.

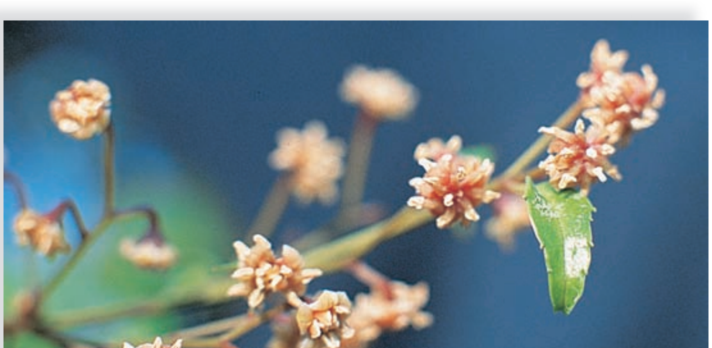


FIGURE 23.19 ***Amborella trichopoda.***
Molecular data suggest this plant is most closely related to the first flowering plants.

Although *A. trichopoda* may not be the original angiosperm species, it is sufficiently close that much may be learned from studying its reproductive biology. Botanists hope that this knowledge will help them understand the early adaptive radiation of angiosperms during the Tertiary period. The gymnosperms were abundant during the Mesozoic era but declined during the mass extinction that occurred at the end of the Cretaceous. Angiosperms survived and went on to become the dominant plants during modern times.

Monocots and Eudicots

Most flowering plants belong to one of two classes. These classes are the **Monocotyledones,** often shortened to simply the **monocots** (about 65,000 species), and the **Eudicotyledones,** shortened to **eudicots** (about 175,000 species). The term *eudicot* (meaning true dicot) is more specific than the term *dicot.* It was discovered that some of the plants formerly classified as dicots diverged before the evolutionary split that gave rise to the two major classes of angiosperms. These earlier-evolving plants are not included in the designation eudicots.

Monocots are so called because they have only one cotyledon (seed leaf) in their seeds. Several common monocots include corn, tulips, pineapples, bamboos, and sugarcane. Eudicots are so called because they possess two cotyledons in their seeds. Several common eudicots include cactuses, strawberries, dandelions, poplars, and beans. **Cotyledons** are the seed leaves that contain nutrients that nourish the plant embryo. Table 23.2 lists several fundamental differences between monocots and eudicots.

The Flower

Although **flowers** vary widely in appearance (Fig. 23.20), most have certain structures in common. The **peduncle,** a flower stalk, expands slightly at the tip into a **receptacle,** which bears the other flower parts. These parts, called sepals, petals, stamens, and carpels, are attached to the receptacle in whorls (circles) (Fig. 23.21).

1. The **sepals,** collectively called the calyx, protect the flower bud before it opens. The sepals may

TABLE 23.2

Monocots and Eudicots

Monocots	*Eudicots*
One cotyledon	Two cotyledons
Flower parts in threes or multiples of three	Flower parts in fours or fives or multiples of four or five
Pollen grain with one pore	Pollen grain with three pores
Usually herbaceous	Woody or herbaceous
Usually parallel venation	Usually net venation
Scattered bundles in stem	Vascular bundles in a ring
Fibrous root system	Taproot system