24 FUNGI

Food, Forests, and Fungi

Somewhere between 6 million and 2 million years ago, the first caribou (*Rangifer tarandus caribou*) appeared. In time, this hoofed mammal nibbled its way across North America, Europe, and Asia. Spring through summer, it fattens up on plants and lichens of the arctic tundra. In the fall, regional herds of 50,000 to 500,000 migrate to the more protected boreal forests inland and to the south. You can hear them coming. As they walk, a tendon slips over a bone in their foot and makes a clicking sound, and all those running feet sound like a cacophony of castanets. Once caribou reach winter foraging grounds, their keen sense of smell helps them snuffle out lichens buried in snow on the forest floor.

Humans started herding caribou about 3,000 years ago; we call the domesticated kinds reindeer. From Russia down through Scandinavia, people have accompanied the herds during the migrations. But now the northern Scandinavian forests have been cleared to make way for industrialization. Reindeer are herded into big trailers that can move them past cities to the remaining wintering grounds.

Whether natural or human-assisted, these migrations are testimony to the connections among diverse organisms. Lichens feed reindeer, the nitrogen-rich urine and feces of which enrich the soil for lichens. A connection exists *within* the lichens that help feed reindeer, which help feed their herders. Symbiosis, remember, refers to one species that is partnered for all or part of its life cycle with another. In cases of **mutualism**, the partnership benefits both or does one of them no harm. A **lichen** is a vegetative body in which a fungus and one or more photosynthetic organisms, such as cyanobacteria, live together in mutual dependency. Figure 24.1 shows the type that helps sustain reindeer.

Many lichens colonize substrates that most organisms bypass, such as rocks, fence posts, and tree trunks. Some even take hold on bedrock that became exposed after an ancient glacier melted away. Lichens can absorb minerals from substrates. They make antibiotics against bacteria that might otherwise decompose them. They make toxins against invertebrate larvae that graze on them.

Coincidentally, their metabolic products and remains enrich nutrient-poor soil or help convert bedrock to soil. Their cyanobacterial component helps cycle nitrogen by converting gaseous nitrogen in the air to forms that plants can take up and use during growth. After lichens improve the soil, other species move in and typically replace the pioneers. That might be what happened when plants first invaded the land.

Collectively, lichens also are vital components of forest ecosystems. For instance, lichens of the genus *Lobaria* secure 20 percent of the nitrogen that trees of old-growth forests in the Pacific Northwest require for their growth.

Figure 24.1 Luscious lichens (*Cladonia rangiferina*), at least to reindeer that have migrated long distances to their wintering grounds.

IMPACTS, ISSUES

Yet lichens are on the decline. For one thing, they are sensitive to air pollution. They all sponge up fine airborne particles but cannot neutralize or eliminate some harmful ones. That is why lichens are considered useful indicators of deteriorating environmental conditions. They are absent from dense, urbanized areas where air is heavily polluted with sulfur dioxide, nitrous oxides, and other emissions from gas-powered vehicles and coal-burning power plants. Lichens also do not fare well in agricultural regions where fields are seasonally sprayed with herbicides and pesticides. Deforestation, too, is destroying many of their habitats.

With this example, we turn to the fungi, a diverse group of organisms that many of us tend to overlook unless we happen to shop for edible kinds or fight a fungal infection. Yet uncountable unseen fungi connect with us in global ways, as when their activities secure and cycle the nutrients that help keep ecosystems functioning.

How Would You Vote?

The disappearance of lichens and soil fungi may be an early indication that coal-fired power plants are emitting pollutants that also can endanger human health. Controlling emissions raises the cost of energy for consumers. Should pollution standards for these power plants be tightened? See BiologyNow for details, then vote online.

Key Concepts

MAJOR GROUPS AND THEIR SHARED TRAITS

Fungi share amoeboid ancestors with animals. Chytrids and microsporidians are basal groups. The zygomycetes, basidiomycetes, and ascomycetes are three major groups.

Fungal cells secrete enzymes that digest food in their surroundings, they absorb breakdown products, and they release carbon dioxide and nutrients that producers take up. The body of multicelled species is a mesh of hyphae, or absorptive filaments, some of which intertwine as spore-producing structures during the life cycle. Section 24.1

REPRESENTATIVE LIFE CYCLES

The rapid formation of a large number of asexual spores dominates fungal life cycles, which also include sexual phases. In zygomycetes, a spore capsule simply forms at the tip of a tall hypha. In basidiomycetes, or club fungi, spores form in club-shaped structures, often along gill margins of mushrooms. Ascomycetes, or sac fungi, form sexual spores in sac-shaped cells. Sections 24.2–24.4

ABOUT THE NOTORIOUS ONES

Together with some bacteria, fungi are decomposers of the biosphere. Vexing or dangerous species sometimes overshadow their greater role in nature. Section 24.5

THE SYMBIONTS

Many fungi are mutualistic symbionts. Lichens are fungi partnered with one or more photoautotrophs. Mycorrhizae are fungi partnered with young plant roots. The fungus withdraws some food from the plant, which gets mineral ions from the fungus. Section 24.6

Links to Earlier Concepts

Before starting, review the tree of life in Section 19.7 to get a sense of the relationship of fungi relative to other groups. Apply your understanding of the one-way flow of energy and cycling of nutrients in the biosphere to gain perspective on the perhaps surprising impact of fungal decomposers and symbionts (6.1). You may wish to review the fermentation pathways (8.5).

24.1 Characteristics of Fungi

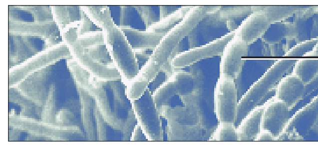
LINK TO SECTION 19.7

Fungi evolved from single-celled eukaryotes more than 900 million years ago. Remember the tree of life in Section 19.7? This monophyletic group is closest to animals, with which they share an amoeboid ancestor. Figure 24.2 shows the fungal branchings of that tree.

DEFINING FEATURES

Fungi are heterotrophs, which cannot make their own food; they must obtain organic compounds that other organisms have already synthesized. Most species are **saprobes**, which feed on and thus decompose organic wastes and remains. Some are **parasites** that withdraw nutrients from the tissues of a living host. As fungal cells grow in or on top of organic matter, they secrete digestive enzymes and absorb breakdown products. This nutritional mode is called *extracellular digestion and absorption*. It benefits plants, which readily absorb some of the released nutrients and the carbon dioxide products. Without fungal and bacterial decomposers, nutrients would no longer be cycled in communities, and life as we know it would be over.

Some species of fungi are single celled. Multicelled kinds develop as a mesh of branched filaments called a **mycelium** (plural, mycelia). Collectively, the filaments grow quickly on or into organic material and have a good surface-to-volume ratio for absorbing nutrients. Each filament is one **hypha** (plural, hyphae). Its cells often have chitin-reinforced walls. The cytoplasm of abutting cells interconnects at gaps in the crosswalls, so nutrients flow unimpeded through the mycelium.



In many species, hyphae also form complex spore-producing bodies, as in Figure 24.3. Among the fungi, **spores** are reproductive cells or multicelled structures,

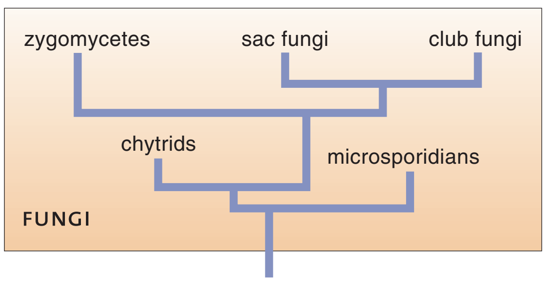


Figure 24.2 Fungal family tree

a PURPLE CORAL FUNGUS *Clavaria* **b** RUBBER CUP FUNGUS *Sarcosoma*

c TRUMPET CHANTERELLE *Craterellus* **d** SCARLET HOOD *Hygrophorus* **e** BIG LAUGHING MUSHROOM *Gymnophilus*

Figure 24.3 A sampling of fungal spore-producing structures on the floor of a Virginia forest.

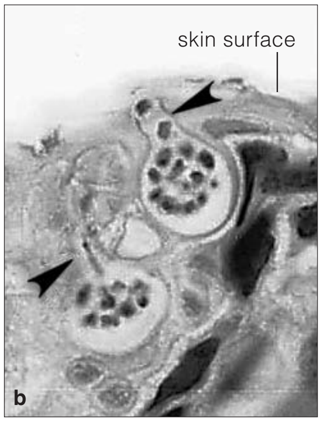



Figure 24.4 (**a**) Harlequin frog (*Atelopus varius*) from Central America. (**b**) Section through skin of a frog with *chytridomycosis*, a fungal infection. The two arrows point to two flask-shaped cells of the parasitic chytrid *Batrachochytrium dendrobatidis*. Each contains fungal spores that are discharged to the skin surface, through the neck of the flask.

Chytridomycosis is one cause of the recent mass deaths of rain forest amphibians, even in regions that are still untouched by agriculture, pollution, and deforestation. Researchers report long-term, catastrophic declines in many amphibian species from a large part of their habitats. Because losses are occurring on such a wide scale, they cannot all be attributed to isolated disturbances.

often walled, that germinate after dispersal from the parent. Most are small, dry, and profuse, and currents of air can disperse them. Each germinating spore may start a new mycelium.

Fungi form sexual spores, asexual spores, or both, depending on food availability, on how cool or damp conditions are, and on whether a hypha grows on its own or contacts a hypha of a compatible mating strain.

SURVEY OF FUNGAL GROUPS

For many of us, "fungi" are the mushrooms sold in grocery stores. However, commercial mushrooms are simply the reproductive structures of a few species of a far more diverse group. About 56,000 fungal species have been named, and there may be at least a million more we do not even know about. We have fossilized forms that date to 900 million years ago.

Chytrids and **microsporidians** belong to the most ancient lineages (Figure 24.2). They produce flagellated spores, a trait that is derived from fungal ancestors in aquatic habitats. All chytrids and microsporidians are intracellular parasites.

Figure 24.4 focuses on a chytrid that is contributing to a drastic decline of amphibians in rain forests. Some of the microsporidians, such as *Enterocytozoon bieneusi*, cause chronic diarrhea in AIDS patients who already have been weakened by an HIV infection. Others in this group infect skeletal muscle cells.

Besides these two basal groups, three major fungal lineages became established by 300 million years ago. They are classified as **zygomycetes** (Zygomycota), **sac fungi** (Ascomycota), and **club fungi** (Basidiomycota). These groups are the focus of the rest of the chapter.

Some species are known informally as "imperfect fungi." They are set aside in this taxonomic holding station not because they are somehow defective, but rather because no one has yet discovered what kind of sexual spores they produce (if any). Figure 24.5 shows one of the as-yet unclassified trapping fungi. Certain other previously puzzling species have been grouped with other sac fungi. Species of *Aspergillus*, *Candida*, and *Penicillium* are among them.

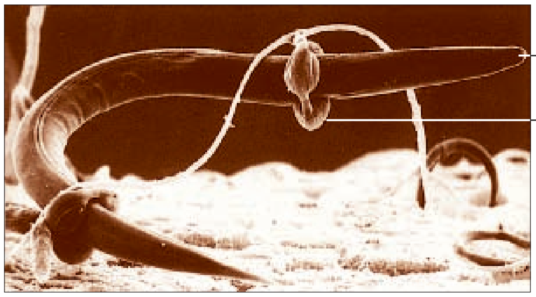


Figure 24.5 *Animated!* *Arthrobotrys dactyloides*, a trapping fungus grouped with other imperfect fungi. The presence of certain proteins on roundworms (nematodes) stimulates its hyphae to form a sticky trap. Nooselike rings swell rapidly and shrink around the worm body, into which hyphae grow.

Fungi are single-celled or multicelled heterotrophs. They digest organic material in their environment, and their individual cells absorb breakdown products. Plants, too, absorb some of the released nutrients.

Most fungal species are saprobes; they absorb organic wastes and remains. Other species parasitize living hosts.

Multicelled fungi form mycelia and spore-producing structures. They rapidly make asexual and sexual spores on organic matter. Their penchant for making a profusion of spores is central to their reproductive success.

Chytrids and microsporidians are basal groups. The three major groups are zygomycetes, sac fungi, and club fungi.

24.2 Zygomycetes

The zygomycete spore-producing structure is a tall, stout hypha that balloons under a spore sac at its tip.

Zygomycetes represent about 1 percent of the known fungi, but some saprobic types rapidly form immense colonies on just about anything that is a rich carbon source, such as sugar and starch. Others are parasites of mushrooms and other organisms. *Rhizopus* species live in soil, in compost and other decaying matter, and in food being stored, shipped, or marketed. They are all successful, rapid reproducers. Wounds in fruits and vegetables are swiftly colonized by *R. nigricans* spores in orchards and packing houses. *R. stolonifer*, a black bread mold, is a pest in labs and bakeries. People who are malnourished, diabetic, or badly burned, and those with a weakened immune system, are vulnerable to *R. oryzae*, the main cause of the disease zygomycosis.

Focus on the life cycle of *R. stolonifer*, starting with the formation of a diploid zygote in the sexual phase. This becomes a **zygospore**, a thick-walled sexual spore enclosed in a thin, clear covering (Figure 24.6). Under favorable conditions, the zygospore finishes meiosis, and a tall, sturdy hypha grows from it. A sporangium (plural, sporangia) forms around the ballooned-out tip of the hypha. Inside this spore sac, hundreds of tiny haploid spores form. Each spore may give rise to a new mycelium. Additional spore sacs form on top of more stalked hyphae that grow from each mycelium.

Zygomycetes produce thick-walled sexual spores. They rapidly colonize substrates by producing and dispersing hundreds of nonmotile, asexual spores, which form in sacs at the tip of a specialized hypha.

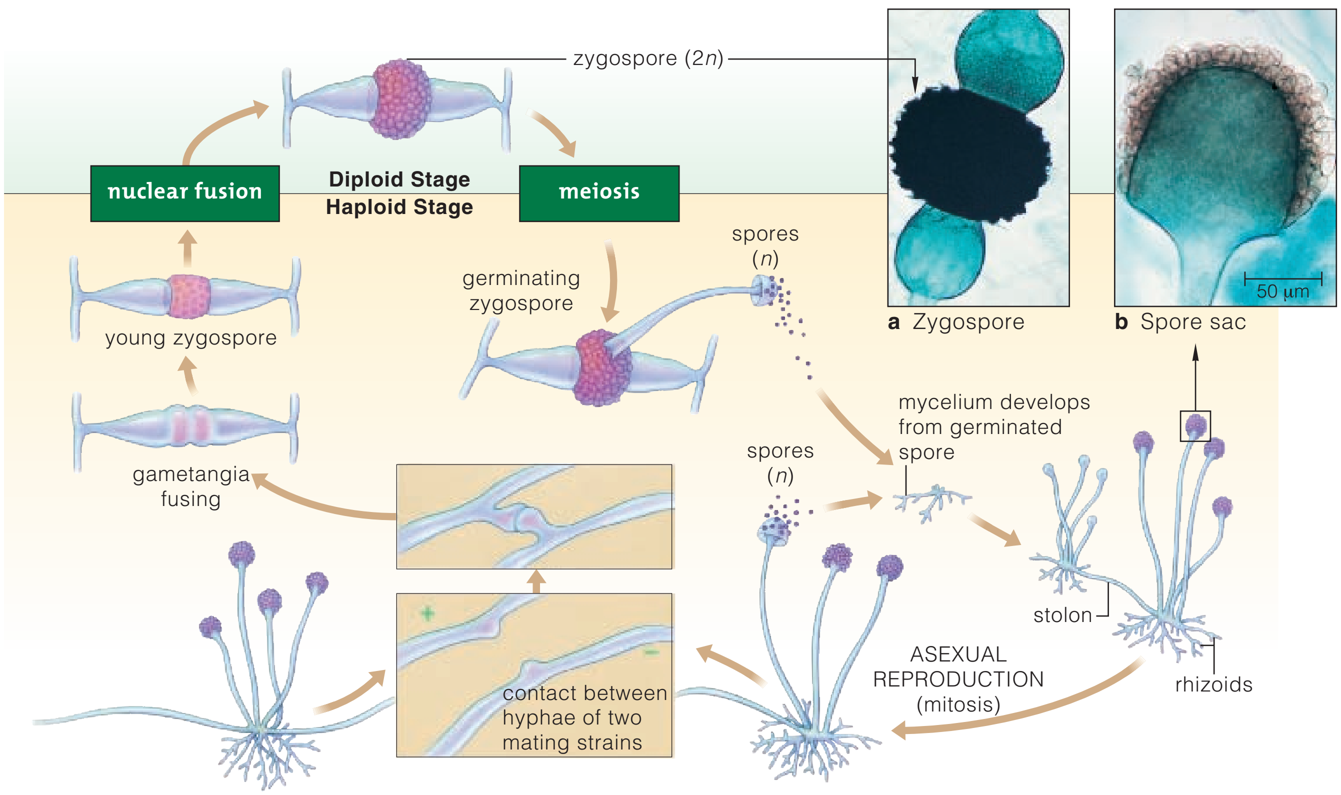


Figure 24.6 ***Animated!*** Life cycle of *Rhizopus stolonifer*, a black bread mold.

Asexual phases are frequent. Different mating strains (+ and −) reproduce sexually as well. Either way, haploid spores form and give rise to mycelia. Chemical attraction between a + hypha and a − hypha causes them to fuse. Two gamete-producing structures (gametangia) form, each with several haploid nuclei. The nuclei pair up. Each pair fuses, forming a zygote. Some zygotes disintegrate; others become thick-walled zygospores and may be dormant for several months. Meiosis occurs when the zygospore germinates. The photograph at right shows what the resulting proliferation of spore sacs and asexual spores can look like on a slice of stale bread.

24.3 Basidiomycetes—The Club Fungi

In many club fungi, club-shaped sexual spores form on gills of mushrooms, which are spore-producing structures.

You may know *Agaricus brunnescens*. It is the common mushroom in grocery stores, and it is a good example of a basidiomycete's life cycle. As for many other club fungi, its reproductive structures protrude out from a mycelium that grows through soil or decaying matter. These short-lived, stalked structures are mushrooms. Each has a cap with leaflike gills suspended from its inner surface (Figure 24.7). Sexual spores form along the gill margins, on club-shaped structures (basidia, singular basidium). Air currents disperse the haploid spores, which are of a type called **basidiospores**. When the spores land on a suitable site, they may germinate and give rise to a haploid mycelium.

Hyphal cells of two compatible mating strains may undergo cytoplasmic fusion. Their nuclei will not fuse right away. The fused portion may start growing into an extensive *dikaryotic* mycelium in which hyphal cells have one nucleus of each mating type (Figure 24.7*f*). If nutrient availability and moisture favor reproduction, mushrooms form. Initially, each club-shaped basidium is dikaryotic, but its two nuclei fuse and form a zygote, which undergoes meiosis. Haploid sexual spores form and migrate into cytoplasmic extensions at the cell's tip. When they are released, the cycle turns again.

Club fungi make sexual spores in club-shaped structures.

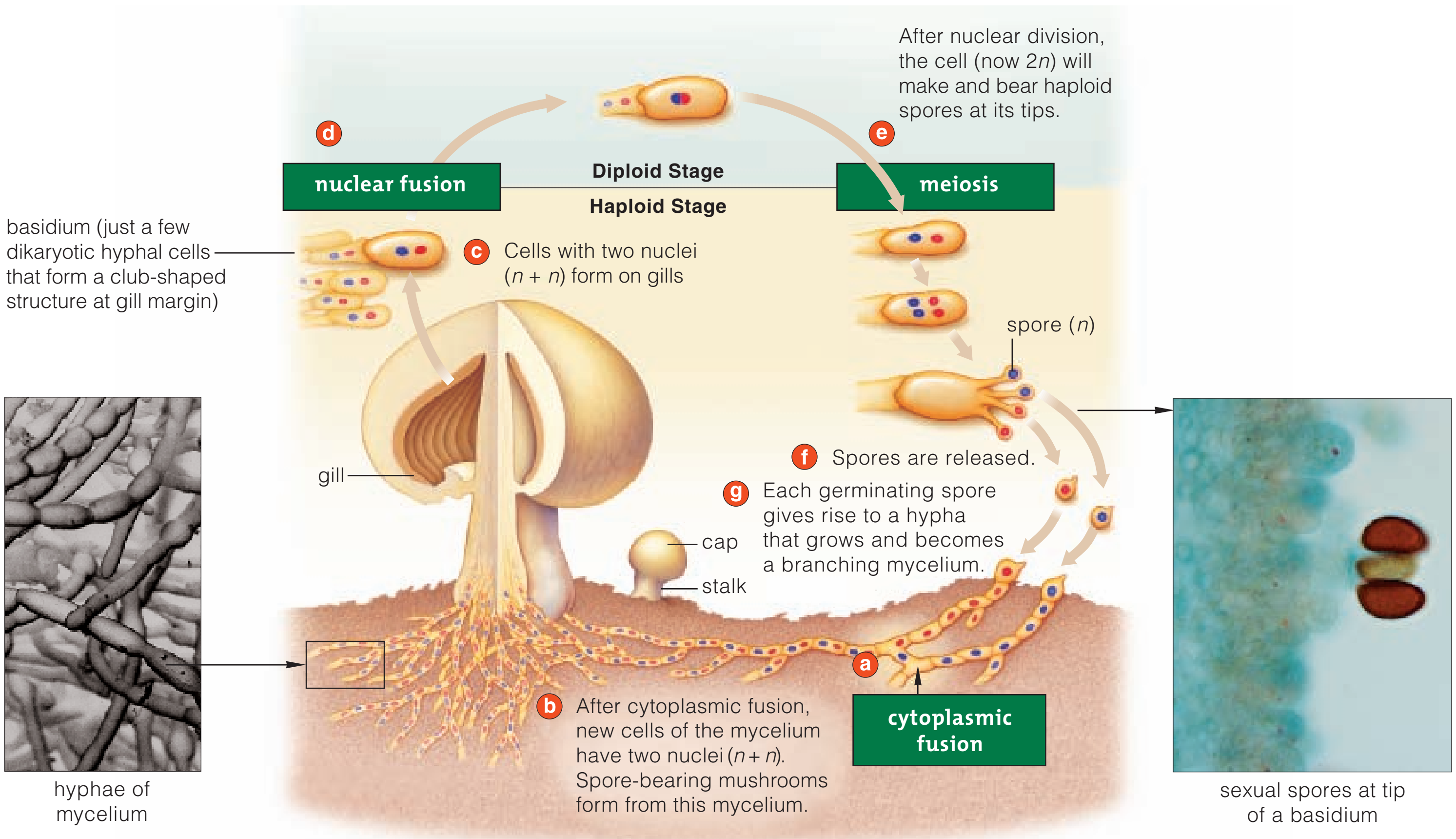


Figure 24.7 ***Animated!*** Generalized life cycle of many club fungi. Hyphae of different mating strains often grow through the same patch of soil. (**a**) When hyphal cells of two compatible strains contact each other, their cytoplasm fuses but their nuclei do not. (**b**) Mitotic cell divisions yield a mycelium in which each cell contains two nuclei. When conditions are favorable, many hyphae of this mycelium start intertwining into the type of fruiting body called a mushroom. (**c**) Club-shaped structures form on its gills. (**d**) Inside the terminal cell of each structure, two nuclei fuse and form a diploid zygote. (**e**) Four haploid spores form by meiosis. They migrate into the cytoplasmic extensions at the tip of the club-shaped structure. After spores are released (**f**), each may germinate and give rise to a new mycelium (**g**).

24.4 Ascomycetes—The Sac Fungi

LINKS TO SECTIONS 8.5, 16.6

In sac fungi, spore-producing structures are sac-shaped cells that form in cup-shaped, flask-shaped, or globular reproductive structures.

The vast majority of more than 30,000 known species of sac fungi are multicelled. Most produce **ascospores**, a type of sexual spore, in the life cycle (Figure 24.8). Spores form in sac-shaped cells called asci (singular, ascus). Asci are enclosed in reproductive structures of tightly interwoven hyphae, as shown in Figure 24.9.

Most food-spoiling molds are multicelled sac fungi. So are some of the single-celled yeasts (others are club fungi). A packet of baking yeast holds thousands of *Saccharomyces cerevisiae* spores. In a warm, moist spot, such as bread dough, the spores give rise to cells that may reproduce asexually by budding. Carbon dioxide released by these fermenting cells makes the dough rise. Other fermenting yeasts help make wine (Section 8.5). Genetically engineered yeasts are grown in large vats, as drug-producing factories (Section 16.6). One relative, *Candida albicans*, can cause vexing infections in humans (Figure 24.9*d*).

Among the sac fungi are symbionts with tree roots: the truffles. Their fruiting bodies form undergound, and when spores are mature, they produce a complex mixture of aromatic compounds. The smell and taste of those "truffles" are so prized that even an ounce of several kinds can sell for hundreds of dollars. Trained dogs or pigs are often used to snuffle out truffles.

Aspergillus makes the citric acid used in candies and soft drinks, and ferments soybeans for soy sauce. *Penicillium* species flavor Camembert and Roquefort cheeses; others make penicillin antibiotics. Most food-spoiling red, bluish-green, and brown fungal molds are a conidial stage of multicelled sac fungi (Figure 24.9*c*). *Neurospora sitophila* is tough to eradicate from bakeries and research laboratories. Yet geneticists use *N. crassa* for research. Nuclei of different mating strains line up in predictable order in ascospores (Figure 24.8).

Most sac fungi produce sexual spores that divide in a predictable, linear order inside sac-shaped cells.

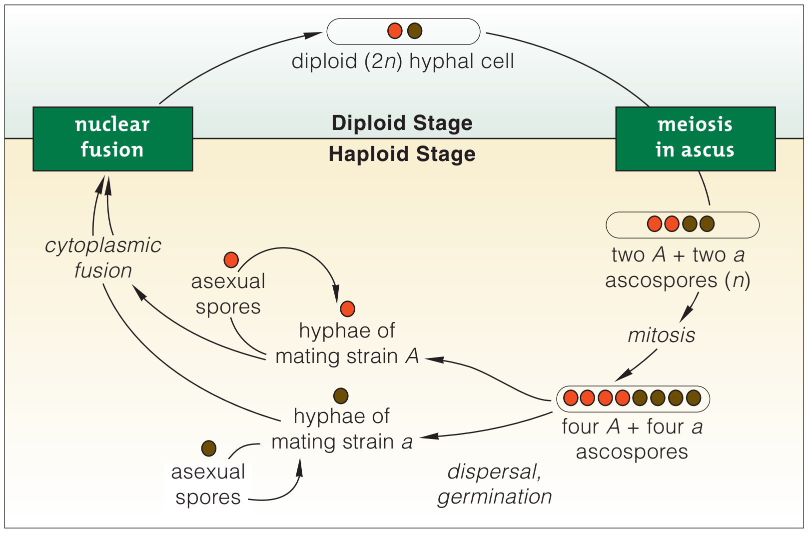
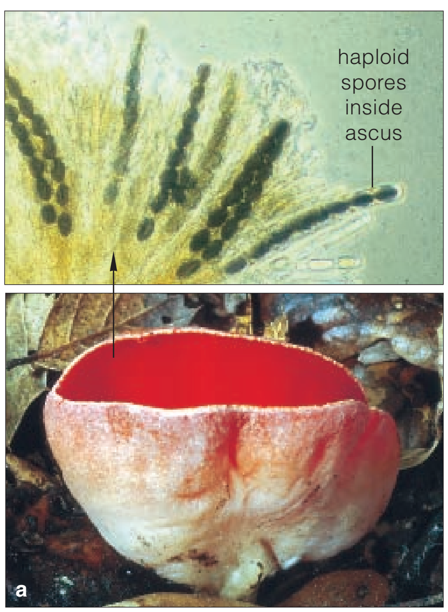


Figure 24.8 Life cycle of *Neurospora crassa*.



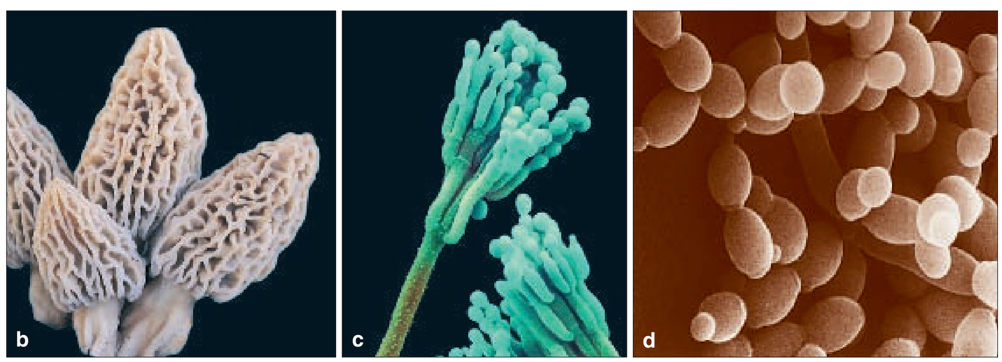


Figure 24.9 Sac fungi. (**a**) *Sarcoscypha coccinia*, the scarlet cup fungus. Inside each saclike structure on the cup's inner surface, eight sexual spores (ascospores) form predictably in a row. (**b**) One of the morels (*Morchella esculenta*). This edible species has a poisonous relative. (**c**) From *Eupenicillium*, chains of asexual spores of a type called conidiospores, which drift away, like dust, after even the slightest jiggling. "Conidia" means dust. (**d**) Cells of *Candida albicans*, the agent that causes "yeast" infections of the vagina, mouth, intestines, and skin. The cell at the lower left was caught in the act of reproducing asexually by budding.

ABOUT THE NOTORIOUS ONES

24.5 A Look at the Unloved Few

FOCUS ON HEALTH

You know you are a serious student of biology when you can view organisms objectively in terms of their place in nature. As a student you salute saprobic fungi as vital decomposers and praise parasitic fungi that help keep populations of harmful insects and weeds in check. The true test is when you cross paths with a fungus that goes to work on your tissues or resources (Table 24.1).

What thoughts run through your head when you open the fridge to get a bowl of fruit and discover a fungus beat you to it? How much perspective would you have if a fungus started feeding on warm, damp tissues between your toes and made them scaly, reddened, and cracked (Figure 24.10*a*)?

Which home gardeners wax poetic about black spot or powdery mildew on roses? Which farmers happily hand over millions of dollars a year to sac fungi that attack corn, wheat, peaches, and apples (Figure 24.10*b*)? Who rejoices that a certain sac fungus, *Cryphonectria parasitica*, blitzed the chestnut trees in eastern North America?

Who willingly inhales airborne spores of *Ajellomyces capsulatus*? After landing on soil, spores give rise to mycelia. When they land in moist lung tissues, they form yeastlike cells that cause *histoplasmosis*, a respiratory disease. The body's macrophages normally engulf the cells, but debris from the battle results in calcified lung tissue. Extensive spore proliferation invites fungal pneumonia.

And what about *Pneumocystis carinii*? This sac fungus lives in the lungs of humans and many domestic and wild animals. Malnutrition or a weak immune system gives it the opportunity to threaten its host. It causes a deadly form of pneumonia in about three-fourths of all AIDS patients. *P. carinii* forms resistant cysts. When the cysts germinate, the fungus starts reproducing in interstitial fluid in the lungs. An infected lung's tiny air sacs fill with foamy material teeming with the fungus. Fever, coughing, shallow rapid breathing, and bluish skin around the eyes and mouth follow. Untreated patients die from asphyxia; they stop breathing. Treatment can help, but death rates are still high.

And household molds! Thank them for sinus, ear, and lung infections, hearing losses, memory losses, and asthma attacks, boosted 300 percent in the past twenty years. The worst culprits are *Stachybotrys*, *Memnoliella*, *Cladosporium*, and certain *Aspergillus* and *Penicillium* species.

Certain fungi have even tweaked human history. One notorious species, *Claviceps purpurea*, parasitizes rye and other cereal grains (Figure 24.10*c*). Give it credit; we use some of its alkaloid products to treat migraine headaches and to stop hemorrhaging after childbirth by shrinking the uterus. However, the alkaloids can be toxic. Eat a lot of bread made with tainted rye flour and you end up with *ergotism*. The symptoms include vomiting, diarrhea, hallucinations, hysteria, and convulsions. Untreated, the disease results in gangrenous limbs and brings on death.

Ergotism epidemics were common in Europe during the Middle Ages, when rye was a major crop. They thwarted Peter the Great, the Russian czar who became obsessed with conquering ports along the Black Sea for his nearly land-locked empire. Soldiers laying siege to the ports ate mostly rye bread and fed rye to their horses. The soldiers went into convulsions and the horses into "blind staggers." Ergotism outbreaks also may have been used as an excuse to launch witch hunts in the early American colonies.

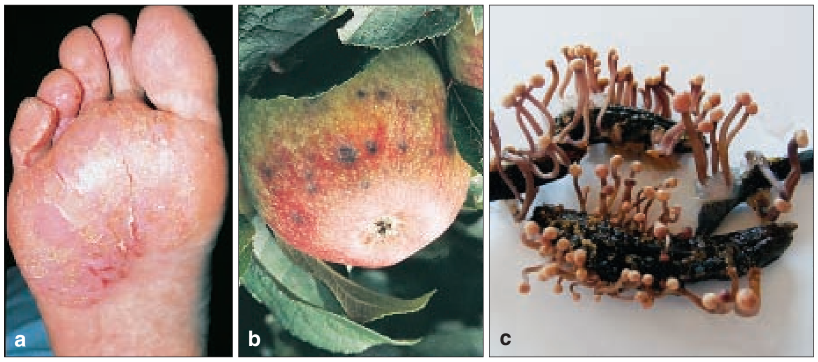


Figure 24.10 Love those fungi! Examples: (**a**) Athlete's foot, courtesy of *Epidermophyton floccosum*. (**b**) Apple scab, the trademark of *Venturia inaequalis*. (**c**) Emerging from infected parts of rye plants, hyphae bearing the spore sacs of *Claviceps purpurea*, a historically notable fungus.

Table 24.1 A Sampling of the Notorious Fungi

Chytrids	
Batrachochytrium dendrobatidis	Deadly skin disease among amphibians
Microsporidians	
Enterocytozoon bieneusi	Chronic diarrhea, especially in AIDS patients
Zygomycetes	
Rhizopus	Fruit, vegetable rot; some human diseases
Club Fungi	
Amanita (some species)	Dangerous mushroom poisoning
Puccinia graminis	Black stem wheat rust
Tilletia indica	Smut of cereal grains
Ustilago maydis	Smut of corn
Sac Fungi	
Ajellomyces capsulatus	Histoplasmosis
Aspergillus (some)	Aspergilloses (allergic reactions; sinus, ear, lung infections; *A. flavus* toxin linked to cancers)
Candida albicans	Infection of mucous membranes
Claviceps purpurea	Ergot of rye, ergotism
Coccidioides immitis	Valley fever
Cryphonectria parasitica	Chestnut blight
Microsporum, Trichophyton, Epidermophyton	Various species cause ringworms of scalp, body, nails, beard; cause athlete's foot
Monilinia fructicola	Brown rot of peaches, other stone fruits
Ophiostoma ulmi	Dutch elm disease
Pneumocystis carinii	Fungal pneumonia
Venturia inaequalis	Apple scab
Verticillium	Plant wilt

24.6 Fungal Symbionts

LINK TO SECTION 19.7

Return now to the fungal symbionts introduced at the start of the chapter. In cases of mutualism, one or both partners benefit from the interaction, and neither is harmed. Most fungal endophytes, lichens, and mycorrhizae are like this.

FUNGAL ENDOPHYTES

Endophytic fungi are symbionts that live inside the leaves and stems of most plants. Different kinds have beneficial or neutral effects; some are quite harmful. Tall fescue (*Festuca arundinacea*) provides an example. Lush clumps of this grass are tasty to herbivores, but fungi living in tissues of most *F. arundinacea* strains make alkaloids that are toxic to grazers, which quickly learn to avoid the plants. Certain fungal endophytes also help protect host plants from pathogens, such as other fungi and the oomycote *Phytophthora*.

LICHENS REVISITED

In the single vegetative body called a lichen, recall, one or more photosynthetic species are intertwined with fungal hyphae. The fungal part is the *myco*biont. The photosynthetic portion is the *photo*biont. Of about 20,000 known types of lichens, nearly half incorporate sac fungi. Only 100 or so species are photobionts, and most often these are green algae and cyanobacteria.

A lichen forms after the tip of a fungal hypha binds with a suitable host cell. Both of the bound cells lose their wall. Either their cytoplasm fuses or the hypha induces the host cell to cup around it. The mycobiont and photobiont then grow and multiply together.

A lichen typically forms distinct layers. Its overall growth pattern may be leaflike, flattened, pendulous, or erect, as shown in Figures 24.1 and 24.11.

Again, lichens can colonize places too hostile for most organisms, including sunbaked or frozen rocks, fence posts, gravestones, and plants, even the tops of giant Douglas firs. Almost always, the fungus is the largest component. Cyanobacteria typically reside in a separate structure inside or outside the main body. The fungus receives a long-term source of nutrients, which it absorbs from the photobiont cells. Nutrient

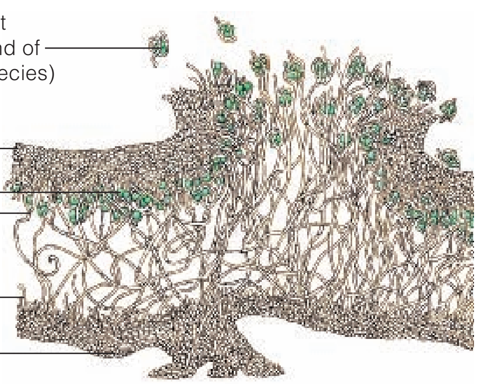


Figure 24.11 (**a**) Foliose (leaflike) lichen on a birch tree. (**b**) *Usnea*, a pendant lichen known as old man's beard. (**c**) Encrusting lichens on a rock. (**d**) Organization of one stratified lichen, as it would look in cross-section.

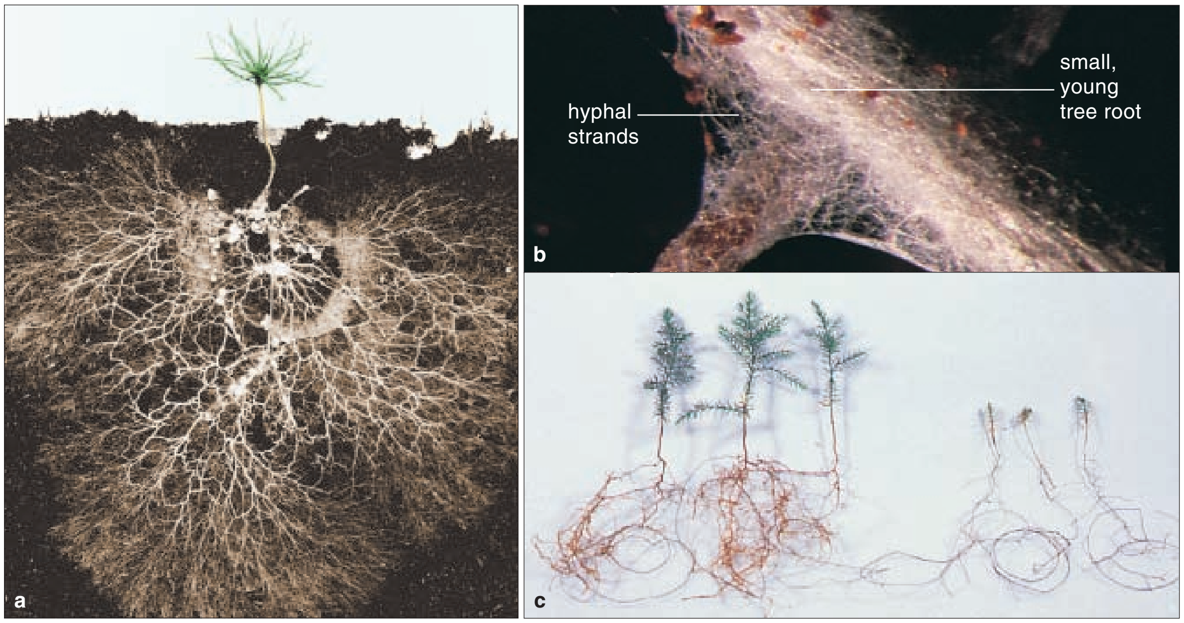


Figure 24.12 (**a**) Cutaway view of the root system of a lodgepole pine (*Pinus contorta*) seedling. Compare the extent of the mycorrhiza with the shoot system, which is about four centimeters tall. (**b**) Ectomycorrhiza from a hemlock tree.

(**c**) Results of an experiment to determine the effect of the presence or absence of mycorrhizae on plant growth. The juniper seedlings shown at left were photographed when they were six months old. They were grown in sterilized, phosphorus-poor soil with a mycorrhizal fungus. The seedlings at right, a control group, were grown in the same soil but with no fungal partner.

withdrawals affect the photobiont's growth a bit, but the lichen helps shelter it. If more than one fungus is present in a lichen, it may be a mycobiont, a parasite, or even an opportunist that simply is using the lichen as a substrate.

THE FUNGUS-ROOTS

Many soil fungi, including truffles, are mutualists with young tree roots. This type of partnering is known as a **mycorrhiza** (plural, mycorrhizae). The name means "fungus-root." Underground parts of the fungus grow throughout the soil and functionally increase the tree's absorptive surface area. Its young roots start out with hairlike absorptive structures, but fungal hyphae are thinner and far better at growing around soil particles. Where fungal mutualists are present, young roots do not waste time making root hairs. The fungus swiftly absorbs nitrogen, phosphorus, and other mineral ions when they are abundant and releases them to the plant when they are scarce. The plant gives up some sugars, but the loss is a necessary trade-off. Many plants cannot grow well without mycorrhizae (Figure 24.12).

Ectomycorrhizae In *ecto*mycorrhizae, some of the hyphae form a dense net around living cells inside roots but do not penetrate them (Figure 24.12*b*). Other hyphae form a velvety wrapping around the roots as the mycelium grows through soil. Ectomycorrhizae are common in temperate forests, where the trees face seasonal changes in temperature and rainfall. About 5,000 species enter into this type of association. Most of them are club fungi.

Endomycorrhizae Far more common are the kinds of interactions called *endo*mycorrhizae, which form in about 80 percent of all vascular plants. In this case, fungal hyphae do penetrate living plant cells. Fewer than 200 species of zygomycetes are fungal partners. The hyphae branch extensively and form tree-shaped absorptive structures in the cells. Hyphae also extend for several centimeters into the soil. Chapter 30 offers a closer look at these beneficial species.

When something kills a mycorrhizal fungus, a plant that was its partner does not do as well during severe frosts or droughts, exposure to acid rain, and similar environmental challenges. We return to this topic when we look at the world's forests (Chapter 48). Something *is* killing their fungi, with dramatic consequences.

Endophytes are fungal symbionts living in leaves or stems. Their toxins often protect plants from grazing animals.

In lichens, a fungus shelters one or more photoautotrophs and shares carbon dioxide and mineral ions with them, while receiving some carbohydrates in return. Often the photosymbionts are nitrogen fixers, such as cyanobacteria.

In mycorrhizae, a fungus living in or on a plant's young roots increases the plant's uptake of water and dissolved mineral ions and helps protect it from pathogens. The fungus withdraws some nutrients from its partner.

Summary

Section 24.1 Fungi are heterotrophs and major decomposers. Saprobic types feed on nonliving organic matter; parasitic types occur in or on living hosts and feed on their tissues. Some fungal species are symbiotic partners with other organisms.

Cells of all fungal species secrete digestive enzymes that digest outside sources of food, then the cells absorb breakdown products.

Nearly all fungi are multicelled. The food-absorbing part of their body, the mycelium, is a mesh of filaments (hyphae). Aboveground spore-producing reproductive structures form from large numbers of tightly interwoven hyphae. A mushroom is such a structure.

Fungi share an amoeboid ancestor with animals. Chytrids and microsporidia are basal groups of fungi. Three major groups are zygomycetes, basidiomycetes, and ascomycetes. Each species forms distinctive sexual and asexual spores. If a sexual phase cannot be detected or is absent from the life cycle, a fungus is assigned to an informal holding station known as the imperfect fungi.

Fungi are notable for their reproductive success. When nutrients are available and other conditions favor growth, asexual spores especially proliferate.

BiologyNow

See a nematode-trapping fungus in action with the video on BiologyNow.

Section 24.2 The zygomycetes make thick-walled sexual spores called zygospores. A single, stout hypha grows from each zygospore and balloons at its tip, under a spore capsule. In the capsule, spores undergo meiosis and are released. Germinating spores may give rise to mycelia. The life cycle includes phases of asexual spore formation from the mycelia. New zygospores may form after fusion of two hyphae of different mating strains. *Rhizopus stolonifer* is a representative species.

BiologyNow

Observe the life cycle of a zygomycete with the animation on BiologyNow.

Section 24.3 Basidiomycetes, or club fungi, make spores by way of meiosis inside club-shaped structures that often occur on gill margins of mushrooms. Mature spores migrate into cytoplasmic extensions at the tip of the "club" and are released.

Two hyphal cells of different mating strains may fuse and form a dikaryotic cell, which retains the nuclei from both. A mycelium forms and gives rise to reproductive structures, in which dikaryotic spores are produced. The life cycle also has phases of asexual spore production. The field mushroom is a typical club fungus.

BiologyNow

Learn about the life cycle of a club fungus with the animation on BiologyNow.

Section 24.4 Ascomycetes, or sac fungi, produce orderly rows of spores in unique sac-shaped cells (asci). The cells have two nuclei, one from each of two different mating strains. They undergo meiosis, then mitosis, and each sac ends up with eight spores. Life cycles of sac fungi also include phases of mycelium formation and proliferation of asexual spores. Truffles, morels, some yeasts, and *Penicillium* species are in this group.

Section 24.5 We view most fungi as beneficial. Others destroy crops, spoil food, and cause diseases.

Section 24.6 Endophytes, lichens, and mycorrhizae are forms of symbiosis called mutualism. One or both of the interacting species benefits; neither is harmed.

Endophytic fungi live in most stems and leaves, with helpful, neutral, or sometimes harmful effects. The type that releases herbivore-repelling toxins in tall fescue is an example.

Lichens are vegetative bodies consisting of a fungus and one or more photosynthetic partners, such as green algae and cyanobacteria. The fungus provides shelter, mineral ions, and carbon dioxide. Its symbiont gives up some carbohydrates in return.

In a mycorrhiza (a fungus-root), a fungus grows around or inside young roots. Fungal hyphae take up mineral ions and release some to the plant; the plant gives up some carbohydrates in return.

BiologyNow

Read the InfoTrac article "The Fungus Among Us: Tiny But Ubiquitous, Fungi Form Vital Connections Underground," Janet Wallace, Alternatives Journal, *December 2004.*

Self-Quiz

Answers in Appendix II

1. A mycorrhiza is a ______ .
   a. fungal disease of the foot
   b. fungus–plant relationship
   c. parasitic water mold
   d. fungus of barnyards

2. Parasitic fungi obtain nutrients from ______ .
   a. tissues of living hosts
   b. nonliving organic matter
   c. only living animals
   d. none of the above

3. Saprobic fungi derive nutrients from ______ .
   a. nonliving organic matter
   b. living plants
   c. living animals
   d. both b and c

4. New mycelia form after ______ germinate.
   a. hyphae b. mycelia c. spores d. mushrooms

5. A mushroom is ______ .
   a. the food-absorbing part of a fungal body
   b. part of the fungal body not constructed of hyphae
   c. a reproductive structure
   d. a nonessential part of the fungus

6. Match the terms appropriately.

____ zygomycete	a. intracellular parasite
____ lichen	b. type of sexual spore
____ hypha	c. partnership between fungus, one or more photoautotrophs
____ club fungi	d. each filament in a mycelium
____ ascospore	e. black bread mold
____ sac fungi	f. truffles, morels, some yeasts
____ chytrid	g. form dikaryotic structures

Additional questions are available on **BiologyNow™**

Critical Thinking

1. *Pilobolus* is a type of fungus that commonly dines on horse dung. Each morning, stalked reproductive hyphae emerge from irregularly spaced piles of dung. By early afternoon, they have dispersed spores to sunlit grasses where horses feed. The spores pass through the horse gut unharmed and exit with their own pile of dung.

Right at the tip of each stalked hypha is a dark-walled, spore-containing sac (Figure 24.13). Below the sac, the stalk balloons outward; it is swollen with a fluid-filled central vacuole. Below this is a ring of light-sensitive, pigmented cytoplasm. The stalk bends as it grows until its wall is parallel with the sun's rays and light strikes all of the ring. When that happens, turgor pressure builds up inside the central vacuole until the vesicle ruptures.

The forceful blast can propel the spore sacs as far away as 2 meters (about 6.5 feet)—which is amazing, when you consider that the stalk is less than ten millimeters tall.

Reflect on the examples of fungi discussed in this chapter. Would you say *Pilobolus* is a zygomycete, a club fungus, or a sac fungus?

2. Figure 24.14 shows a sulfur shelf fungus (*Polyporus*) on a forest tree. Is it a symbiont or parasitic? Research its life cycle and describe how it interacts with the tree.

3. One kind of zygomycete, *Trichoderma*, is being tested as a natural pest control agent. Laboratory experiments demonstrated that some strains of this fungus combat other fungi that cause plant diseases. Some even promote seed germination and plant growth. In one set of twenty trials, workers increased lettuce yields by 54 percent. Which concerns should be addressed before *Trichoderma* is used for commercial agriculture?

4. The fungus *Fusarium oxysporum* is a plant pathogen. Some view it as a potential weapon in the war on drugs. Why? Strains of the fungus attack and kill only specific plants—including coca plants used to produce cocaine. Proposals to spray *F. oxysporum* to kill marijuana plants in Florida were abandoned after public outcries.

What concerns might you have about allowing the use of such natural *mycoherbicides* to kill off plants that are sources of the drugs favored by substance abusers?

5. When you notice mushrooms or any other fungus growing outdoors, think twice before nibbling on them. Some are distinctive enough to be recognized as toxic, but others might fool you (Figure 24.15). As the saying goes, there are old mushroom hunters and bold mushroom hunters—but no old, bold mushroom hunters.

So how do commercial mushroom farms identify and keep out the poisonous kinds? Do some research and write a brief report on what you discover.

Figure 24.13 Reproductive structures of *Pilobolus*, a name from a Greek word for "hat-thrower." The "hats" actually are spore sacs.

Figure 24.14 Sulfur shelf fungus on a forest tree.

Figure 24.15 (**a**) Fly agaric mushroom (*Amanita muscaria*), a hallucinogenic species. In Central America, India, and Russia, it was used in ancient rituals to induce trances. (**b**) *A. phalloides*, the death cap mushroom. Nausea and diarrhea start within five to forty-eight hours after eating it. These initial symptoms pass, but without treatment, a person's liver and kidneys become badly damaged. Coma and death may follow.